BRITISH UPPER
JURASSIC PLESIOSAURS

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by

D. S. Brown

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SECTION 1 INTRODUCTORY SECTION

(i) Introduction

The suborder Plesiosauria is a group of extinct marine reptiles of the order Sauropterygia which dominated the seas throughout the Jurassic and Cretaceous periods. The first specimens, from the Lower Lias of Dorset, were described by Conybeare in 1821. Since that date there has been remarkably little confusion of remains of this group with its contemporaries, a fact which reflects upon the degree of morphological distinctness of the plesiosaur skeleton.

Specimens range from 2 to 12 metres in length. The skull was equipped with numerous teeth which were long, curved and sharply pointed, and which interlocked when the jaws were closed. They were replaced by teeth which developed in a primary alveolus lingual and posterior to the secondary tooth sockets, a condition not found outside the order Sauropterygia. The vertebrae usually had amphicoelous centra, as had the contemporary ichthyosaurs, but are distinguished by the fusion of the neural arches to the centra in adults, and by the presence of a transverse process in the dorsal vertebrae. The coracoids, pubes and ischia were expanded into large ventral plates, and the scapulae met in the midline. The gastralia were retained and developed into a substantial ventral plastron. The limbs were highly modified for swimming, all four limbs being retained and developed into flattened paddles by a progressive shortening of the epipodials and by hyperphalangy.

Plesiosaurs first appear on the fossil record in the Triassic Upper Muschelkalk deposits of Germany, from which two skulls of the problematical genus Pistosaurus are known. Isolated vertebrae and teeth have been collected from the Keuper of Germany, and more especially from the Rhaetic deposits of Aust Cliff, Gloucestershire. It is, however, from the lowest beds of the Jurassic Lias of Dorset that the first entire skeletons are known. Material is plentiful from most stages of the Jurassic in Europe, and in particular from Britain. European plesiosaurs become scarce in the Cretaceous, and the principle 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, became extinct by the close of the Mesozoic era.

On the basis of features which include the form of the skull and the comparative length of the neck, the Plesiosauria have been divided into three superfamilies, these being the Plesiosauroidea, the Pliosauroidea and the Pistosauroidea. This latter superfamily has been erected (Romer, 1966) for the reception of Pistosaurus and allied forms, and is of doubtful validity.

In the present work the vernacular name "plesiosaur" ~~will be~~ is used in a limited sense to refer only to members of the Plesiosauroidea. Where necessary, the term "plesiosaurid" ~~will be~~ is used to refer exclusively to members of the type family (the Plesiosauridae), and "plesiosaurian" to members of the suborder. The word "plesiosauroid" ~~will be~~ is used in taxonomic sections to refer to members of the superfamily Plesiosauroidea only where the use of the word "plesiosaur" might be misunderstood to mean "belonging to the genus Plesiosaurus".

Most plesiosaur and pliosaur material was found and described in the nineteenth century. Early collectors depleated the coastal exposures, and by about 1910 most quarries became mechanised, preventing collection of 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 much of the original description was for its time, it proved to be inadequate for subsequent workers. This, unfortunately, led to considerable confusion in the literature, and the need arose for a complete review of the whole suborder Plesiosauria. In more recent years, Welles (1943; 1952; 1962; 1971 with Gregg) has reviewed the Cretaceous plesiosaurs and pliosaurs, and Tarlo (1960) reviewed the Upper Jurassic pliosaurs. All Lower and Middle Jurassic forms still remain to be reviewed in this way.

Most of the material of Upper Jurassic plesiosaurs has been found in British deposits, and their taxonomy is based on British type specimens. In the present work all available British Upper Jurassic material is reviewed, and a classification proposed. Species held to be valid are described, and an account of rejected names is included. In addition, an attempt is made to explain aspects of plesiosaurian structure in functional terms.

(ii) Synopsis of British Jurassic stratigraphy

This brief account is drawn from Wills (1951) and Rayner (1967), whose work was based upon the standard text by Arkell (1933).

Throughout most of the Triassic period the British Isles was non-marine. High ground existed in Devon; the Mendip Hills; Wales; in most of East Anglia, the London Basin and South-East England; and in Central Scotland and Northern England. The remaining area (Central England and Western Scotland) was a broad, low-lying plain on which salt-pans and salt lakes were to be found. The climate was probably semi-arid.

The close of the Triassic period is marked by the transgression over this central plain of a shallow epicontinental sea, continuous with the Tethys Sea of Southern Europe. The Rhaetic deposits were laid down at the time of this transgression, and it is from these that the earliest British plesiosaur material has been recovered.

The distribution of land and sea remained much the same throughout the major part of the Jurassic, the principal changes being variation in the depth of the sea, with associated changes in the sediments which were laid down. Throughout the Lower Jurassic the sea was shallow and relatively clear. The Lias deposits laid down at this time consist of shales, thin limestones and ironstones, with sandy beds near the coastlines. This pattern of deposition continued into the Middle Jurassic, the principal change being the development of deltaic conditions in Western Scotland and Yorkshire.

The Upper Jurassic was marked by a general deepening of the epicontinental sea, and an increase in sedimentation. Thick deposits of clay (the Oxford Clay, followed by the Kimmeridge Clay) were laid down over a period of 16 million years, briefly interrupted midway by deposits formed when the sea was shallower and in places clear enough to permit corals to grow (Corallian Beds).

At the end of Kimmeridgian times there was a widespread uplifting of the epicontinental sea floor and a regression of the sea from all the British Isles except for a gulf in the southern counties which reached as far north as Oxfordshire. In this area the Kimmeridge Clay was followed by the Portland Sand and Portland Stone beds. By the end of the Portlandian stage and the beginning of the Purbeckian, this gulf had become a drainage area of large rivers. During Purbeckian times it was a deltaic area, often fresh-water or dry land, with occasional marine transgressions, one of the most widespread being represented by the "cinder bed", from which the latest British Jurassic plesiosaur remains were extracted. Deltaic conditions continued into the Lower Cretaceous period.

Rayner (1967) correlated a generalised British lithology with the internationally recognised stages of the Upper Jurassic system. The following is a summary of this work.

SYSTEM	STAGE	TIME-SCALE (m. years)	BRITISH LITHOLOGY
		136	
UPPER JURASSIC	PURBECKIAN		Purbeck beds
		141	
	PORTLANDIAN		Portland Stone Portland Sand
		146	
	KIMMERIDGIAN		Kimmeridge Clay
		151	
	OXFORDIAN		Corallian beds
		157	Oxford Clay
	CALLOVIAN		Kellaways beds Upper Cornbrash
		162	

Upper Jurassic rocks now outcrop in a continuous north-south belt from the Yorkshire coast through Lincolnshire, Northamptonshire, Rutland, Cambridgeshire, Huntingdonshire, Bedfordshire, North Buckinghamshire, Oxfordshire, Northern Berkshire, Gloucestershire, West Wiltshire and East Somerset, to reach the South Coast in Dorset.

(iii) Occurrence of British Upper Jurassic plesiosaur remains

Plesiosaur remains have been collected from the Oxford Clay of most counties from Northamptonshire to Dorset. There are no records known to me from the Corallian beds, but a few finds of plesiosaur remains have been made from the Kimmeridge Clay of most counties from Cambridgeshire to the South Coast. Fragmentary remains have been recorded from the Portland Rock of Dorset and from Quainton, Buckinghamshire. Only two vertebral centra are known from the Purbeck beds, these being from Portland Island, Dorset.

(iv) Historical review of plesiosaurian taxonomy

Conybeare (1821) proposed the generic name *Plesiosaurus* for an animal whose structure he considered to be intermediate between *Ichthyosaurus* and crocodiles. He realised that both ichthyosaurs and plesiosaurs were marine, and proposed to group them together under the ordinal name "Enalio-Sauri". His original material, recovered by numerous associates from the Lias deposits of the Bristol area, was fragmentary, but further collecting enabled him in 1822 to describe the general features of the genus. Various remains were figured, including a skull from the Lias of Street, Somerset, and the lower jaw of a pliosaur. He refrained from proposing any specific names until 1824, when he described and figured a virtually complete specimen from the Lias of Lyme Regis, Dorset, calling it *Plesiosaurus dolichodeirus*, a reference to its long neck. Originally the property of the Duke of Buckingham, this specimen is now in the British Museum (Natural History), and is the holotype of the type-species.

In 1835, de Blainville named and defined the order Plesiosauria to include only the plesiosaurians. However, Owen (e.g. 1840a; 1841; 1854), Mantell (1851) and others continued to use Conybeare's term Enaliosauria. In 1860, Owen published the ordinal names Ichthyopterygia and Sauropterygia for the ichthyosaurs and plesiosaurians (of de Blainville). The Sauropterygia were defined as "long-necked marine reptiles with fin-like limbs and not more than five digits", and the type genus was named as *Plesiosaurus*.

Boulenger (1917) argued that the historically correct name for the order should be Plesiosauria, and that the name Sauropterygia should only be applied to the suborder including the family Plesiosauridae. Despite his publication, the term Sauropterygia continued to be used as an ordinal name (e.g. in Williston, 1925; Romer, 1933; Kuhn, 1935), and in 1943, Welles reviewed the situation. He decided to accept Sauropterygia as the original name because of its well-established usage, whilst at the same time admitting the correctness of Boulenger's argument. All subsequent authors have followed Welles, the order Sauropterygia Owen, 1860, and suborder Plesiosauria de Blainville, 1835, being maintained in the interests of taxonomic stability.

Owen made the first major division of the suborder by introducing the name Pliosaurus (in 1841 as a subgenus; in 1861 as a genus) to include all plesiosaurians with large "canine" teeth, a short neck and a long head. The genera Plesiosaurus and Pliosaurus are now the types of the two major superfamilies, but the significance of Owen's division has not always been appreciated. The century from 1841 to 1943 saw a host of attempts to provide a satisfactory classification. Many of these were based on features of isolated skeletal parts rather than upon a synthesis of features from whole specimens.

As vertebrae are the most frequent remains to be found, their features were the basis of many of these classifications. Owen (1865) recognised three groups of plesiosaurs characterised by long, intermediate and short centra. Kipriianov (1882), Bogolubov (1912) and Nopcsa (1928) emphasised the length of the neck, and Pravoslavlev (1916) relied entirely upon vertebral indices. The number of cervical rib heads (one or two) was used by Woodward (1933) and Kuhn (1935), and also by Williston (1925), who included relative skull length as a secondary consideration.

Other skeletal parts have been similarly used. Cope (1887) relied upon the proportions of epipodials; Seeley (1874b) and Sauvage (1879a) emphasised the presence or absence of an interclavicle, and Mehl (1912), though not actually introducing a scheme of classification, stressed the importance of the relative length of the pelvis. The most extreme case, however, is the classification presented by T. White (1940). On the basis of features of the pectoral girdle he divided the suborder into nine families, and added that there was sufficient variation in this one structure to distinguish the total of 29 genera. He used such negative features as the absence of an interclavicle (which may, perhaps, not have been collected), and he had little understanding of the growth of the pectoral girdle with the age of the individual. Nevertheless, his paper contained a useful discussion dismissing all previously used features as of doubtful taxonomic value.

Lydekker (1889b) was one of the first people to attempt a classification based on a synthesis of several characters. His genera were distinguished on the basis of relative skull length; relative length of neck; character of cervical rib head; structure of the pectoral girdle and the form of the limbs. However, all his genera were included within the single family Plesiosauridae. All British Upper Jurassic plesiosaurs were assigned to the genus _Cimoliasaurus_ Leidy 1852, which has subsequently been shown by Welles (1962) to be a _nomen vanum_, _sensu_ Simpson (1945).

Seeley (1892) divided the Plesiosauria into Dicranopleura and Cercidopleura on the basis of double-headed or single-headed cervical ribs. The Dicranopleura he divided into Brachydeira and Dolichodeira on the basis of a relatively short or long neck, with a few intermediate forms being termed "mesodeiran". He overlooked the fact that his Cercidopleura also contained brachydeiran and dolichodeiran forms. Though his classification is not now used, his names are still employed as descriptive terms.

Of greater ultimate importance were attempts to correlate taxonomically usable features one with another. In 1865, Owen correlated large teeth with a short neck and a large head (as in _Pliosaurus_), and also smaller teeth with a relatively long neck and small head (as in _Plesiosaurus_).

Pravoslavlev (1919) suggested that laterally ridged centra were found only in long-necked forms, and Mehl (1912) showed that short ischia were correlated with long necks, and long ischia with short necks.

It was not, however, until Watson's paper of 1924 that an evolutionary interpretation of the differences between the genera Plesiosaurus and Pliosaurus was put forward. Watson considered the nothosaurs to be ancestral to both, then distinguished divergent lines of long-necked and short-necked forms ranging from the Lower Jurassic to the Upper Cretaceous.

In 1943, Welles discussed previous attempts to classify the Plesiosauria, and concluded that it was "useless to set up facile schemes based upon single characters or even several characters". He listed twenty two features available for observation, and stressed the importance of considering all of these together. Several characters including general increase in size, reduction of cervical rib-heads from two to one, shortening and broadening of epipodials and progressive hyperphalangy were recognised as evolutionary trends applying throughout the group with the passage of time. For this reason they were deemed to be of only secondary importance in taxonomic subdivision. Of greater importance were the characters of opposing nature, occurring simultaneously throughout the group. Included in this category were the tendencies to shorten or lengthen the neck and the individual vertebrae; to lengthen or shorten the head; and to lengthen or shorten the pelvis in the midline. These were the distinguishing features of Watson's phyletic lines, and it was between these that Welles made his primary and vertical division of the suborder into the two superfamilies Plesiosauroidea and Pliosauroidea. Each superfamily he then divided horizontally using his first group of characters, those of a general, evolutionary nature. The earlier (primitive) families Plesiosauridae and Pliosauridae included plesiosaurians which were dicranopleurous with elongate epipodials. The later (more advanced) families Elasmosauridae and Polycotylidae contained the cercidopleurous forms with short epipodials.

All subsequent taxonomists have followed Welles (1943) in distinguishing the superfamilies Plesiosauroidea and Pliosauroidea, though at first Romer (1945) preferred to rank them as infraorders. Opinions differ regarding the status of the pistosaurs. Only Welles (1962) has limited them to a single family within the Plesiosauroidea. In 1945, Romer elevated them as a distinct infraorder, the Pistosauroidea, which contained the single family Pistosauridae. In 1956 he agreed with Welles (1943) in calling the major groupings superfamilies, and pointed to the similarity between the Pistosauridae and nothosaurs of the family Cymatosauridae. This classification of the pistosaurs was followed by Persson (1963). In 1966 Romer included the Cymatosauridae with the Pistosauroidea.

Welles' division of the Plesiosauroidea and Pliosauroidea into two families each, largely on the basis of double or single-headed cervical ribs, has the advantage of easy practical application. However, the "mesodeiran" forms of Seeley (1892) have proved difficult to assign to a superfamily. Attractive as are Watson's (1924) diverging phyletic lines as a basis for classification, it nevertheless appears true that there were "mesodeiran" forms present until the close of the Cretaceous. Both Romer (1956; 1966) and Persson (1960; 1963) have recognised this, and have produced schemes of classification which include additional families containing "mesodeiran" forms. They differ from each other and from Welles (1943; 1962) in their diagnoses and nomenclature of these families, such that there are now three independent schemes of classification available for use, using differing and in some cases erroneous family names. In order to clarify, compare and assess these alternatives, I will now briefly review the taxonomy of the confused families, and then list the three schemes with appropriate emendations.

In 1923, Nopcsa proposed and defined the subfamily Rhomaleosaurinae for the inclusion of the genus *Rhomaleosaurus* with another species of mesodeiran plesiosaur, *"Plesiosaurus" megacephalus*. This latter species was referred by Andrews (1922) to the genus *Eurycleidus*. In 1940, White included the three genera *Rhomaleosaurus*, *Eurycleidus* and *Leptocleidus* in a family for which he proposed the new family name Leptocleididae. His name was published in synonymy with Rhomaleosauridae Nopcsa, 1923, and therefore should be regarded only as a reference of *Leptocleidus* to the family Rhomaleosauridae.

In 1956, Romer grouped together, with a new family diagnosis, the genera *Brancasaurus*, *Eurycleidus*, *Seeleyosaurus*, *Simolestes*, *Sthenarosaurus* and *Thaumatosaurus*. Listed as a junior synonym of *Thaumatosaurus* Meyer, 1841 was *Rhomaleosaurus* Seeley, 1874. The names Simolestidae Nopcsa, 1923 and Rhomaleosauridae Nopcsa, 1923 (published simultaneously) were both available to Romer, but he used the new family name Thaumatosauridae. However, Tarlo (1960) reviewed the genus *Thaumatosaurus*, showed that the original type material was indeterminate, and that the valid name for subsequently referred diagnostic material was *Rhomaleosaurus*. In the same paper, *Simolestes* was included by Tarlo in the family Pliosauridae. In consequence, the family name Thaumatosauridae was replaced by Kuhn (1961) with Rhomaleosauridae. In 1966, Romer continued to use his invalid name, and placed the family in the Plesiosauroidea.

In 1956, Romer formed a second mesodeiran family from the genera *Leptocleidus* and *Peyerus*, calling the family Leptocleididae. This name, as has been shown above, was originally published in synonymy by White (1940), who included different genera and a completely different diagnosis. Romer did not cite the original date and authorship and so, in the terms of Article 11(d) of the "International Code of Zoological Nomenclature", 2nd edition (Stoll *et al*, 1964) the name Leptocleididae is not available from 1940.

The family must therefore now be cited as Leptocleididae Romer, 1956. Romer (1966) includes this family in the Pliosauroidea.

In 1963, Persson discussed the two mesodeiran families of Romer's classification (Rhomaleosauridae and Leptocleididae), and believed them to be so similar that he combined them into one family. He correctly retained the name Rhomaleosauridae for this family, which he placed in the Pliosauroidea.

Delair (1959) introduced the family name "Cimoliosauridae" for a "very provisional" family, with the intention of using it to embrace "many inadequately known forms of problematical affinities". The name was incorrectly spelt, and was based on the genus Cimoliasaurus Leidy, 1852. In this family Delair included the British Upper Jurassic genera Cryptoclidus, Muraenosaurus and Colymbosaurus. His name was published in synonymy with Cryptoclididae Williston, 1925 and Muraenosauridae White, 1940, and so is invalid and not available from his publication. In 1960, Persson independently named and defined a family Cimoliasauridae, which contained only the genera Cimoliasaurus and Scanisaurus, and does not involve synonymy. The correct citation of the family name is therefore Cimoliasauridae Persson, 1960.

In 1962, Welles reviewed the Cretaceous plesiosaurians, and showed that many genera were founded upon indeterminate and non-diagnostic fragments. These he reduced to the nomen vanum category defined by Simpson (1945). It is important both for the clarification of literature and for the stability of nomenclature that these generic names, and the names of higher categories based upon them, should cease to be used. Included as nomina vana were the generic names Cimoliasaurus Leidy, 1852, and Polycotylus Cope, 1869a. In Welles' classification of 1943, his cercidopleurous pliosaurian family was Polycotylidae Williston, 1908, and in his review of 1962, Welles had to replace this name with one founded on a valid genus. The family contained the three valid genera Leptocleidus, Peyerus and Dolichorhynchops, and the only available family-group name was Leptocleididae Romer, 1956. However, he proposed and used the new name Dolichorhynchopidae which, being first published in synonymy, is invalid and not available (Stoll et al, 1964, Article 11,d). Welles' publication is a reference of the genus Dolichorhynchops to the family Leptocleididae Romer, 1956.

When the nomina vana are erased from the list of genera assigned by Romer (1966) to the family Polycotylidae, only two names remain. These are Scarrisaurus and Dolichorhynchus, neither of which are described names of plesiosaurians. The latter name is apparently a lapsus for Dolichorhynchops Williston, 1902, as it was twice cited with this author and date by Romer in 1956. Scarrisaurus is probably a lapsus for Scanisaurus Persson, 1959. However, Romer (1966) placed the genus Scanisaurus (with correct spelling) in the Elasmosauridae, and Dolichorhynchops in the Leptocleididae. Scarrisaurus and Dolichorhynchus are nomina nuda, and in addition, the latter is a junior homonym of Dolichorhynchus Willey, 1901, which is a cephalochordate. There are no valid genera assigned by Romer to the Polycotylidae, and this family should be omitted from his classification.

Persson (1963) diagnosed the family Polycotylidae using different criteria from Welles and Romer. After the erasure of nomina vana, two valid genera remain assigned to it, these being Dolichorhynchops and Brachauchenius. Only one family-group name is available for replacement of Polycotylidae, that being Brachaucheniidae Williston, 1925. However, there are several reasons why this should not be proposed as a replacement at this time. The genus Brachauchenius is monotypic, and the species (B. lucasi Williston, 1903) is known from a single specimen of which only the skull and vertebrae are preserved. Welles (1962) retained it as a valid name, but was unable to place it in his classification as it was insufficiently characterised and showed several oddities. On the other hand, Dolichorhynchops is known from several almost complete skeletons, and Welles was able to distinguish three species. Recommendation 64A of Stoll _et al_, 1964 advises that so far as possible, the type-genus should be both well known and representative of the family. _Dolichorhynchops_ is to be preferred on this account, and could now be made the type-genus since Brachaucheniidae Williston, 1925, has become a _nomen oblitum_ (Stoll _et al_, 1964, Article 23b). As I do not intend to follow Persson's classification, I will continue to refer to the family in question as "Polycotylidae", the apostrophes indicating that this name is now invalid.

A similar situation exists when considering Persson's family Cimoliasauridae. After erasure of the type-genus (which Welles, 1962, has made a _nomen vanum_), two valid genera remain assigned to the family in his 1963 classification, these being _Aristonectes_ Cabrera and _Scanisaurus_ Persson. There are no available family-group names; both genera are imperfectly known; and _Aristonectes_ exhibits some unusual features which are discussed later. I will continue to refer to this family, in apostrophes, by its now invalid name "Cimoliasauridae".

The three schemes for classification of the suborder Plesiosauria may now be listed to facilitate a comparison.

(a) Classification of Welles (1962), emended as above, now reads:-

- Suborder Plesiosauria de Blainville, 1835
  - Superfamily Plesiosauroidea (Gray, 1825) Welles, 1943
    - Family Pistosauridae Baur, 1889
    - Family Plesiosauridae Gray, 1825
    - Family Elasmosauridae Cope, 1869
      - Subfamily Elasmosaurinae (Cope, 1869) Nopcsa, 1923
      - Subfamily Alzadasaurinae Welles, 1962
  - Superfamily Pliosauroidea (Seeley, 1874) Welles, 1943
    - Family Pliosauridae Seeley, 1874(b)
    - Family Leptocleididae Romer, 1956.

(b) Classification of Persson (1963), emended as above, now reads:-

Suborder Plesiosauria de Blainville, 1835
    Superfamily Pistosauroidea (Baur, 1889) Romer, 1956
        Family Pistosauridae Baur, 1889
    Superfamily Plesiosauroidea (Gray, 1825) Welles, 1943
        Family Plesiosauridae Gray, 1825
        Family "Cimoliasauridae" Persson, 1960
        Family Elasmosauridae Cope, 1869
    Superfamily Pliosauroidea (Seeley, 1874) Welles, 1943
        Family Pliosauridae Seeley, 1874
        Family Rhomaleosauridae (Nopcsa, 1923) Kuhn, 1961
        Family "Polycotylidae" Williston, 1908

(c) Classification of Romer (1966), emended as above, now reads:-

Suborder Plesiosauria de Blainville, 1835
    Superfamily Pistosauroidea (Baur, 1889) Romer, 1956
        Family Pistosauridae Baur, 1889
        Family Cymatosauridae
    Superfamily Plesiosauroidea (Gray, 1825) Welles, 1943
        Family Plesiosauridae Gray, 1825
        Family Rhomaleosauridae (Nopcsa, 1923) Kuhn, 1961
        Family Elasmosauridae Cope, 1869
    Superfamily Pliosauroidea (Seeley, 1874) Welles, 1943
        Family Pliosauridae Seeley, 1874
        Family Leptocleididae Romer, 1956

(v) Comparison of current classifications

It is generally agreed (Welles, 1943, 1962; Romer, 1956, 1966; Persson, 1963) that the pistosaurs form a phyletic link between the Triassic nothosaurs and the plesiosaurians of the Jurassic and Cretaceous. Their precise taxonomic position is therefore questionable, Welles and Persson including only one family with the Plesiosauria, while Romer includes two.

Leaving aside this problematical subject, the remaining major groups of plesiosaurians have been variously classified, as listed above. Welles (1962) has presented the simplest classification, dividing them vertically down the timescale into two superfamilies which are regarded as distinct lines of evolution. His diagnoses were as follows:-

Superfamily Plesiosauroidea

"Plesiosauria with relatively small heads and long necks; teeth conical, no diastema; occipital condyle projecting, hemispherical, marked off by constricting groove; retroarticular process depressed, curving dorsally; cervical centra elongate, especially the median cervicals; vertebral pedicles flat; ventral plates of scapulae becoming very broad; ischia relatively short anteroposteriorly; anterior paddles longer than posterior; propodials massive; fibular facet of femur about equal to tibial facet".

Superfamily Pliosauroidea

"Plesiosauria with relatively long heads and short necks; teeth often keeled; diastema between premaxillary and maxillary teeth; occipital condyle short and close to the skull; retroarticular process compressed; cervical centra short; pedicles thick; ventral plates of scapulae narrow; ischia elongate anteroposteriorly; anterior paddles smaller than posterior; propodials slender and pendulous; fibular facet of femur larger than tibial facet".

Welles then divided each of these into grades at the point where the (primitive) dichocephalous cervical ribs become reduced to the monocephalous condition. It may be mentioned here that this feature is conveniently correlated with the timescale. In the Pliosauroidea the appearance of monocephalous cervical ribs coincides with the Jurassic-Cretaceous boundary, and in the Plesiosauroidea with the Middle-Upper Jurassic boundary in all known forms. There are several supporting features, such as progressive lengthening or shortening of the neck or the head, and progressive hyperphalangy; but, being of a continuous nature, these do not provide a readily identifiable taxonomic distinction.

Romer (1956, 1966) and Persson (1963) have accepted Welles' major division, but have used different criteria both from him and from each other in order to distinguish the families. Both have divided the Plesiosauroidea into three families, listing several features purporting to be characteristic of these families, and at the same time reducing the emphasis which was placed by Welles upon the nature of cervical rib-heads. Unfortunately neither of these authors have consistently listed their various features for each family diagnosis. The differences between families within each classification are not always clear; nor can the two classifications be compared by comparing the diagnoses of homonymous families. In practical application, genera must be allocated to families because of a comparative similarity of the generic and family diagnoses, and not through an absolute conformity to the diagnosis of one family.

The diagnoses given by Romer (1956) for his three plesiosaur families were as follows:-

Family Plesiosauridae

"Neck moderately long, with 22-44 vertebrae, usually toward the upper figure. Cervical ribs generally two-headed. Humerus usually longer than femur. Epipodials not greatly reduced, longer than broad; no accessory epipodials".

(Romer's attributed genera have a range from the Upper Triassic to Upper Jurassic in his 1966 listing.)

Family Rhomaleosauridae ("Thaumatosauridae" in Romer)

"Head short but broad; neck relatively short with about 27 segments; cervical ribs usually with two heads. 'Odontoid' small".

(Attributed genera are entirely Jurassic.)

Family Elasmosauridae

"Neck greatly elongated, with 42-76 cervical vertebrae. Cervical ribs single-headed. Humerus and femur subequal in length. Epipodials short and broad; no accessory epipodials".

(Attributed genera are confined to the Cretaceous.)

Romer appears to have found difficulty in applying his diagnoses to British Upper Jurassic forms. The genera <u>Cryptoclidus</u>, <u>Muraenosaurus</u>, <u>Tricleidus</u> and <u>Tremamesacleis</u> were included in the Plesiosauridae, yet they have epipodials which are broader than long, sometimes accessory epipodials, and cervical ribs which have one head, all of which he listed as diagnostic features of the Elasmosauridae.

The diagnoses given by Persson (1963) for his three plesiosaur families were:-

Family Plesiosauridae

"Dolichodeiran forms. Number of cervical vertebrae 26-44. Cervical centra usually not longer than high. Coracoids not separated posteriorly".

(Attributed genera range from the Upper Triassic to Lower Cretaceous.)

Family "Cimoliasauridae"

"Mesodeiran forms. Head comparatively large. The height of the cervical centra approximately equal to the length, but the breadth of these centra considerably greater than the length. The end faces of the centra almost flat. Cercidopleurous. Pubes sub-rounded. Propodial bones short and stout."

(Attributed genera are Cretaceous.)

Family Elasmosauridae

"Extremely long-necked forms. Number of cervical vertebrae (47 estimated by Welles, 1952, in Morenosaurus) 57-76. At least the anterior and middle cervical centra much longer than high. A sharp lateral longitudinal ridge present on the anterior cervical centra. Cercidopleurous. Anterior cervical ribs 'hatchet-shaped', fused with the centra. Clavicular arch large and fused. Scapulae with large flat ventral plates. Coracoids separated posteriorly. Pubes expanded into sub-rounded plates. Propodial bones short and stout. Epipodial bones broader than long".

(Attributed genera are Cretaceous.)

In Persson's classification, considerable emphasis is placed on the comparative proportions of cervical vertebrae. The extent of variation of these proportions is discussed below, and it is concluded that these variations are unsatisfactory as taxonomic distinctions. The additional features which Persson lists are insufficient to form distinctive diagnoses, and several of these (such as hatchet-shaped cervical ribs or sub-rounded pubes) are characteristics of the superfamily.

Persson considered the Jurassic Plesiosauridae to have been ancestral to both of his Cretaceous families. Romer made no suggestion regarding the interrelationship of his families, two of which were Jurassic, with only the Elasmosauridae containing Cretaceous forms.

With regard to the Pliosauroidea, it would seem that Romer and Welles are in agreement, since, with the removal of the Polycotylidae from Romer's classification (1956, 1966), this is now identical with that of Welles (1962). Persson (1963) diagnosed his three pliosaur families as below:-

Family Rhomaleosauridae

"Mesodeiran forms. Pre-orbital part of skull slightly elongate, with a more or less distinct constriction at the maxillo-premaxillary suture. 20-27 cervical vertebrae."

(Attributed genera range from the Upper Triassic to Upper Cretaceous.)

Family Pliosauridae

"Brachydeiran forms. Skull large, pre-orbital part strongly elongate. Irregular dentition with large caniniform teeth. ?12-22 cervical vertebrae. Most forms dichranopleurous, and with long epipodial bones."

(Attributed genera range from the Upper Jurassic to Lower Cretaceous.)

Family "Polycotylidae"

"Pliosauroideans of the same type as the Pliosauridae, but more specialized. Skull very long and slender, neck not longer than skull. Number of cervical vertebrae 11-26. Cercidopleurous. An interclavicular foramen present. Postero-lateral part of the coracoids elongate. Epipodial bones broader than long. Accessory epipodials present."

(Attributed genera are Cretaceous.)

Persson considered these families to represent grades of a single phyletic line. The early rhomaleosaurids gave rise to the pliosaurids, which in turn were ancestral to the "polycotylids". Only two such grades (Pliosauridae and Leptocleididae), having a combined range from the Upper Jurassic to the Upper Cretaceous, have been recognised by Romer and Welles.

In Section 2 (below), the genera and species of the British Upper Jurassic plesiosaurs are described without reference to families. Evidence is presented which enables the taxonomic characters used by Welles, Romer, Persson and myself to be discussed with respect to the development and ageing of individuals and to the probable evolution of the group. A scheme of classification is then formulated, and the genera attributed to each family are listed.

SECTION 2 REVIEW OF BRITISH UPPER JURASSIC PLESIOSAURS

(i) DESCRIPTION OF VALID SPECIES: Group I. Oxford Clay plesiosaurs

Note on the Leeds Collection

Before proceeding to describe the British specimens of plesiosaurs from the Oxford Clay, tribute must be paid to Mr. Alfred N. Leeds, through whose efforts and enthusiasm the majority of specimens were collected. Throughout the late nineteenth century and first decade of the present century, Leeds accumulated possibly the largest ever private collection of fossil reptiles. These were recovered almost exclusively from brick-pits in the Oxford Clay, in the neighbourhood of Peterborough, not far from his home in Eyebury, Huntingdonshire.

The best and most complete specimens were sold to the British Museum (Natural History) during Leeds' lifetime, and upon his death in 1917 much of what remained was sold to the Hunterian Museum, University of Glasgow. Other material was purchased by the National Museum of Wales, Cardiff; the University Museum, Liverpool; a small amount of disarticulated material to Kendal Museum, Westmorland; and somewhat uncertain quantities to museums in Germany, particularly at Sturz.

The British Museum specimens were described and catalogued by Andrews (1910, 1913). Most of the material in Germany is now in the University Museum, Tübingen; that sold to Liverpool University (and catalogued there by Neaverson, 1935) is now in the British Museum (Natural History), and some (but not all) of the fragmentary material sold to Kendal Museum has since been purchased by Liverpool City Museum.

Leeds left a catalogue (to be referred to as the "Eyebury Catalogue") of part of his collection, which is now located in the library of the British Museum (Natural History). This lists the bones of many specimens found to which Leeds gave catalogue numbers, and there is sometimes a record of the pit from which individual specimens were recovered. Unfortunately there have been many erasures from the catalogue, and examination of the catalogue numbers reveals that they were sometimes duplicated, usually when a specimen had been sold abroad. As a result, it is impossible to determine how much of the Leeds Collection was in fact sold to institutions outside the British Isles, and in many cases there is no record of the exact site of finds, other than the general locality, namely, Oxford Clay of the Peterborough district.

The Leeds Collection is now of special scientific interest, since mechanisation in the brick-pits now prevents the collection of almost all specimens from these sites.

A historical and biographical account of the Leeds Collection was published by the collector's son, E. T. Leeds (1956).

Genus *Cryptoclidus* Seeley, 1892

Cryptoclidus Seeley, 1892 (as a subgenus); Andrews 1895a (as a genus).
Cryptocleidus Andrews, 1909 (Incorrect subsequent spelling).
Apractocleidus Smellie, 1915 (Subjective-objective synonym, *sensu* Blackwelder, 1967).

Type-species:

C. eurymerus (Phillips, 1871).

Additional British species:

C. richardsoni (Lydekker, 1889).

Diagnosis:

(Diagnostic features of the skull are taken only from the type-species).

Plesiosauroids in which

tooth ornament is reduced;

the dentary bears 24-26 teeth on each ramus;

the premaxillae bear 6 teeth each, of which the 1st (most anterior) is small, and the 2nd to 6th 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 usually 32 cervical vertebrae with relatively amphicoelous centra, the length of which very rarely exceeds the height;

the clavicles are triangular and well developed, and lie visceral to the ventral rami of the scapulae;

the interclavicle is absent or rudimentary;

the coracoids meet the scapulae in the mid-line 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 2 epipodials in the manus;

a foramen only appears between the epipodials in specimens showing advanced ossification.

Cryptoclidus eurymerus (Phillips, 1871)

Plesiosaurus oxfordiensis Seeley, 1869 (Published as *Plesiosaurus oxfordiensis* Phillips, MS).

Plesiosaurus oxoniensis Phillips, 1871; Lydekker 1888a, 1888b (*Nomen vanum*, *sensu* Simpson, 1945).

Plesiosaurus eurymerus Phillips, 1871; Lydekker 1888a, 1888b.

Muraenosaurus oxoniensis (Phillips, 1871) Seeley, 1874(b).

Cimoliosaurus oxoniensis (Phillips, 1871) Lydekker, 1889b. (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852).

Cimoliosaurus eurymerus (Phillips, 1871) Lydekker, 1889b.

Cimoliosaurus eumerus ("Phillips, 1871") Seeley, 1892. (*Lapsus calami*).

Plesiosaurus durobrivensis (Lydekker, 1889) Seeley, 1892 (in part).

Muraenosaurus (Cryptoclidus) platymerus Seeley, 1892.

Cryptoclidus oxoniensis (Phillips, 1871) Andrews 1895a, 1895b, 1896a; Bogolubov, 1909; Welles, 1962.

Cryptoclidus platymerus (Seeley, 1892) Andrews, 1895a; Bogolubov, 1909.

Cryptoclidus eurymerus (Phillips, 1871) Bogolubov, 1909.

Cryptocleidus oxoniensis (Phillips, 1871) Andrews, 1909, 1910; Delair, 1959; Persson, 1963.

Apractocleidus teretipes Smellie, 1915, 1916; Persson, 1963.

Cryptocleidus eurymerus (Phillips, 1871) Delair, 1959; Persson, 1963.

Discussion of synonymy

In 1871, Phillips (pp. 307-312) described various dissociated plesiosaurian remains from the Oxford Clay of Long Marston, Oxfordshire, under the new name *Plesiosaurus oxoniensis*. The type material, now in the Geological Collections of the University of Oxford, consists of 6 cervical and several dorsal and caudal vertebrae, some rib fragments, a pectoral girdle (figured upside down and described as a pelvis) and a hind limb including a femur. Seeley (1874b) noted the mistaken identity of the girdle, and Lydekker (1888a) referred it to *Pliosaurus philarchus* Seeley, 1869, a species subsequently transferred to the genus *Peloneustes* by Tarlo (1960). Later (1888b) he referred it, and also the hind limb, to *Plesiosaurus plicatus* Phillips, 1871. Andrews (1895a) at first thought Phillips correct in associating the girdle with the vertebrae, but in 1910 he agreed with Lydekker, and included *Plesiosaurus plicatus* in his synonymy of the genus *Muraenosaurus* Seeley. Both limb and girdle are in fact plesiosaurian, but generically non-diagnostic. Andrews (1910) concluded that the only parts of Phillips material to which the name *Plesiosaurus oxoniensis* could still be applied were the vertebrae.

In the same work of 1871, Phillips (pp. 315-316) described and figured a humerus and fore-paddle from the Oxford Clay of Bedford as *Plesiosaurus eurymerus*, identifying it as a hind-limb. Lydekker (1888a) visited the private collection of Mr. A. N. Leeds at Eyebury, near Peterborough, and took with him the type cervical vertebrae of *P. oxoniensis*. He was shown several almost complete skeletons of plesiosaurs, and discovered that the type material of *P. eurymerus* was a fore-limb. Furthermore, fore-limbs of this kind were associated with vertebrae similar to the type vertebrae of *P. oxoniensis*. He at first concluded that both names referred to the same species. In a second publication (1888b) he retained the name *P. eurymerus* to refer to Mr. Leeds' specimens as they were of larger size, but was unable to find any further differences between them and *P. oxoniensis*. In his British Museum catalogue (1889b) he transferred both species to the genus *Cimoliasaurus* Leidy (a *nomen vanum*, see Welles, 1962), and figured as *C. eurymerus* a cervical vertebra and associated forelimb of a specimen acquired by the Museum from Mr. Leeds.

In 1892 Seeley described Lydekker's figured specimen as representing a new subgenus and species, which he named *Muraenosaurus (Cryptoclidus) platymerus*. 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 type of *P. eurymerus*, and so his introduction of a new specific name was unjustified.

During the succeeding two decades, the British Museum (Natural History) received a considerable quantity of associated material from the Leeds Collection, which was examined and catalogued by Andrews. He believed (1895a) that the material before him represented sexual dimorphs of one species, differing from each other only in size. This opinion was reiterated in 1910, and he concluded that *P. oxoniensis* and *P. eurymerus* were synonyms. He chose to call the species *Cryptoclidus oxoniensis*, but gave no reasons for his preference, as the type material, for the vertebrae from Oxfordshire rather than the forelimb from Bedford. This latter was found geographically much nearer to Peterborough, from whence Mr. Leeds' material was collected, but the former was published with page priority, which may have influenced Andrews' choice.

The specific name *oxoniensis* Phillips, together with Andrews' misspelling of the generic name (*Cryptocleidus*), have been the most frequently used names for this species since then. However, a second species of the genus *Cryptoclidus* (*C. richardsoni*) has been distinguished, and will be the next to be described. This differs from the present species in the form of its forelimb, but the vertebrae of the two species are indistinguishable. Furthermore, the vertebrae of *Tricleidus seeleyi* are so similar to those of *Cryptoclidus* that confusion is possible between all but fully adult forms. Consequently, the type vertebrae of *P. oxoniensis* are dubiously diagnostic at the generic but not the specific level. *Plesiosaurus oxoniensis* Phillips, 1871, is a *nomen vanum* (*sensu* Simpson, 1945), and so the correct and valid name for the present species is *Cryptoclidus eurymerus* (Phillips, 1871).

In 1915, Smellie described a Leeds Collection plesiosaur, acquired by the Hunterian Museum, University of Glasgow, under the new generic and specific names *Apractocleidus teretipes*. Welles (1943) believed *Apractocleidus* and *Cryptoclidus* to be congeneric. It will be argued below that the type specimen is no more than an old individual of *Cryptoclidus eurymerus*.

Lost holotype:

A humerus, radius, ulna and remaining bones of a forelimb formerly in the Woodwardian Museum (now the Sedgwick Museum), Cambridge. The specimen, which was described and figured by Phillips (1871) from a plaster cast then in the University Museum of Oxford, was misidentified as a hindlimb (e.g. Lydekker, 1888a; Andrews, 1910), and was named *Plesiosaurus eurymerus*. Andrews (1910) states that vertebrae similar to those of *P. oxoniensis* were associated with the limb.

Locality of lost holotype:

Bedford, England.

Horizon of lost holotype:

Taken from Oxford Clay, and therefore of Callovian or, improbably, Lower Oxfordian age. No British remains of plesiosaurs are known to me which are of certain Oxfordian age.

Note on the missing holotype.

Dr. C.L. Forbes, Curator of the Sedgwick Museum, Cambridge, has told me that the holotype of *Plesiosaurus eurymerus* Phillips was realised to be missing approximately fifteen years ago, at a time when Tarlo was undertaking a review of British pliosaurs (published 1960). At Tarlo's request a search was made, but the specimen could not be found, nor could any record be found relating to its existence in the Museum. Since that time a watch has been kept for it, but it is still missing.

As Andrews had evidently seen the holotype, and might possibly have borrowed it for study in the British Museum (Natural History), I have searched for it there without success during many visits over the last four years.

Finally, I must record that the plaster cast in the University Museum of Oxford is also lost. Mr. H. P. Powell, Assistant Curator of Geology in the Museum, has kindly searched for the cast at my request, realising its importance. He was able to find almost all the fossil material which was described by Phillips in 1871, often having to recognise Phillip's handwriting on the labels, or use ultraviolet light to read faded markings on the bone; but the cast is not to be found.

I am therefore obliged to propose a neotype.

Proposed neotype:

B.M.(N.H.) specimen R.2860, which is one of the most complete adult plesiosaur skeletons known. Andrews (1910) based his description of the species (which he called Cryptocleidus oxoniensis) upon this specimen (pp. 165-191); extensively figured it (frontispiece; text-figs. 78C, 78D, 91A, 91B; Pl. IX figs. 1, 1a, 2, 3) and used it as the basis for his reconstruction (text-fig. 94). It is mounted in a show-case, and was only recently removed from exhibition. Its forelimbs show the same characters as Phillips' figure of the lost holotype (1871, p.315, diagram CXX); these are included in the diagnosis below. The specimen was collected by Mr. A. N. Leeds.

Neotype locality:

Near to and to the South of Peterborough. The precise locality is nowhere recorded, but is within the area and from one of the pits shown on a map published in E. T. Leeds (1956) (opposite p.16).

Neotype horizon:

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, p. vii).

Diagnosis:

Members of the genus Cryptoclidus in which

the teeth have a characteristic ornament of longitudinal ridges. Two opposing axial ridges rise from the base of the crown and almost meet over the apex. Between these rise from 4-7 lingual ridges, which extend from the base to approximately one-third of the height of the crown. There are usually no buccal ridges.

there are 55 presacral vertebrae;

the humerus is greatly expanded distally by 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, causing the anterior margin to describe a sigmoid curve;

the ulna is much wider than long.

Distribution:

Diagnostic material is known only from the counties of Northamptonshire, Huntingdonshire, Bedfordshire and Cambridgeshire.

Range:

Upper Jurassic; Callovian stage.

Referred specimens:

See catalogue in Appendix.

Description of material

The description given by Andrews (1910, pp. 164-202, text-figs. 78-94, Pls. IX-X) is extensive and, for the most part, accurate. Most of his work does not need to be repeated. My intention, therefore, is to supplement and occasionally to emend his description.

1. The skull

Andrews described the skull by comparative reference to that of Muraenosaurus. From a study of all known material I have been able partially to reconstruct the skull, which differs in several important respects from those of its contemporaries. This reconstruction (figs. 1 and 2) was based on the neotype (R.2860) with the addition of teeth and details of their interlock taken from the right side of the skull of R.3730 (fig. 6). These skulls will now be described, together with additional skull material.

(a) The skull of R.2860 (the neotype)

This is the most complete skull of C. eurymerus known, and is preserved as 12 separate fragments (to be referred to as frags. A-L). Fragment A consists of portions of premaxillae together with an anterior portion of the left maxilla, the whole having been repaired with pink plaster. The dorsal surface of these bones is much roughened by an irregular ornament of pits and ridges. The median suture has been eroded away. The right maxilla shows part of the first (most anterior) tooth socket, which is small, and the much larger 2nd, 3rd and 4th sockets. Most of the 5th socket is broken away, and the 6th, which is also large, is preserved on fragment B. The left premaxilla is incomplete anteriorly, with the 1st and 2nd sockets missing or obscured by plaster. However, part of the midline margin is preserved higher up the bone, permitting the missing outline to be restored on the plaster. The 3rd-6th sockets are preserved, the 5th containing the only tooth present with this skull. The tooth tip 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 only. It is thus certainly of the same characteristic type as the teeth of R.2417, R.3730 and R.8621. Immediately posterior to the 6th upper socket is the suture between the premaxillary and the maxillary. It is quite distinct, and rises diagonally backwards from the tooth-row. The left maxillary portion of fragment A contains the anterior 5 and part of the 6th maxillary tooth sockets. Fragment B contains the anterior 3 and part of the 4th right maxillary sockets. The snout is incomplete medially, only the more massive parts of the bone surrounding the sockets being preserved, and there is no evidence of the position of the nares.

Posterior portions of both maxillae are preserved (frags. C and D). Fragment C, a portion of the right maxilla, contains the outer parts of 13 tooth sockets, which appear as grooves due to the loss of the lingual halves. The fit of the anterior margin with the posterior margin of fragment B cannot be exactly made, as the surfaces have been eroded. An anterior dorsal process rises to form the anterior lower quarter of the orbital margin. This margin is preserved from the suture with the frontal, there being no evidence of a prefrontal or a lachrymal element.

Fragment D has been built up by repairing numerous smaller pieces, and now includes the posterior part of the left maxilla, the anterior margin of the left orbit, the paired frontals and parietals, and the supraoccipital. The left maxillary portion appears to abut onto the posterior part of fragment A, in which case the complete maxillary tooth-row is preserved. As in fragment C, the sockets appear as grooves because of the loss of their lingual halves. 15 sockets are preserved on fragment D, which with the 6 sockets on fragment A makes 21 maxillary sockets, and an upper tooth row totalling 27 teeth.

The antorbital process of the maxilla extends dorsally to suture squamously with the frontal. From this suture, the orbital margin is preserved downwards and backwards in an arc for 3 cms, but posterior to this point the edge of the bone is continuously broken back to the posterior end of the tooth-row. Thus no further evidence of the shape of the orbital margin or of posterior sutures of the maxilla with other elements is preserved. The anterior margin of the antorbital process is also irregularly broken. There is therefore no evidence of the suture with the premaxilla above the tooth-row, or of the position of the external naris.

Portions of the left and right frontals are preserved. Their median suture is straight, and posteriorly they unite with the parietals by complex interlaminating sutures. The frontals form the anterior border of the pineal foramen when viewed dorsally, but ventrally are almost excluded from its margin by the parietals. Anteriorly they suture with the maxillae; this suture is easily traced on the left side, and there is no evidence of any additional elements in this region. The prefrontal (or lachrymal) described by Andrews (1910) in the skull of Muraenosaurus, and reported by Welles (1943, 1952, 1962) in the skulls of elasmosaurs, is either absent or indistinguishably fused with the frontal or the maxilla. Anterior and lateral to the pineal foramen the outer margins of the frontals are damaged, but it is possible to restore their outline. They were relatively narrow between the orbits (a distance of about 3 cms), but more anteriorly they expanded to carry the orbital margins outwards and upwards in an arc to a height of about 1 cm. above the median suture, before continuing in descent to the suture with the maxilla. The right frontal is better preserved than the left, though incomplete anteriorly. The anterior expanded part of the bone is thin, but ventrally it is strengthened by two bars set at an angle of about 40°. One bar follows the median suture; the other runs outwards and forwards in an arc to form the anterior margin of the orbit.

The parietals are largely fused, the line of the median suture being visible only on the occipital surface. Dorsally they were produced into a high sagittal crest, which is now partly broken off but can be restored. Anteriorly they border the pineal foramen, and meet the frontals in a complex suture. They are expanded laterally, opposite the posterior margin of the pineal foramen, and formed the bases of the post-orbital bars. These latter are missing, but their position is indicated by broken surfaces on the parietals, and by ridges on the parietals and posterolateral margins of the frontals which indicate the position of the squamous suture of the postfrontal. The evidence suggests that this was thin, and that its plane was tilted downwards and backwards at an angle of about 30° to the dorsal outline of the skull.

Posterior to the bases of the post-orbital bars, the parietals are greatly excavated on either side of the median sagittal crest for the accommodation of powerful muscles to the jaw. Behind these excavations each parietal is produced into a posterior lateral process which unites with the squamosal to form the post-temporal bar. On the left side a portion of the dorsal margin of this arch is preserved to within 3 mm. of the midline, and is formed by the squamosal. The suture between this element and the underlying parietal is clearly visible, the squamosal being a very thin strand of bone tapering towards the midline, where it probably just met its opposite above the parietals. The parietals form the uppermost 2.5 cm. of the occipital face of the skull, and in this part the median suture is still visible. Ventrally, the parietals unite with the supraoccipital.

The supraoccipital has at some date been glued onto the parietals. Its form is that of an arch over the dorsal half of the foramen magnum. Its upper margin is the suture line with the parietals, and the bases of the arch are the facets for the exoccipitals. In the midline of the suture with the parietals is a small foramen, which has been observed in all the plesiosaur skulls studied. Its function is unknown; it may have carried nutritive blood-vessels to the parietals, or it may have contained a ligament running to the neural arch of the fused atlas and axis. The facets for the prootics are grooved for the reception of the dorsal part of the posterior vertical semicircular canals.

Fragment E consists of both the fused exoccipital-opisthotic elements together with the basioccipital and the basisphenoid, all of which were once separated, but have at some time been glued together along their sutures. These bones were described and figured by Andrews (1910, p.166; Pl. IX figs. 1, 1a and 2) in union with the supraoccipital and a posterior portion of the parietals. The most noteworthy feature of the occipital part of the skull in *Cryptoclidus eurymerus* is the form of the occipital condyle, which differs markedly from all contemporary species. In the present species it is formed largely from the basioccipital, but includes a small part of the pedicles of the exoccipitals. It is not elongated posteriorly. In the genera *Muraenosaurus* and *Tricleidus*, and also in all Cretaceous elasmosaurs described by Welles (1943, 1952, 1962), it is formed entirely from the basioccipital, which in these genera extends further posteriorly. This posterior extension is marked by a groove which rings the condyle, and separates it off from the suture with the exoccipitals. The fusion of the exoccipital and opisthotic appears to be usual in all plesiosaurs. The opisthotic contains half the utriculus (identified as the ampulla of the posterior semicircular canal by Andrews, 1910) and parts of the posterior vertical and horizontal semicircular canals, and does not appear to show much variation.

Parts of the left and right squamosals are preserved (frags. F and G). These are triradiate in structure, the rami being the post-temporal bar (the dorsal median end of which sutures with the parietals), the zygomatic arch and a vertical ramus extending downwards almost to the jaw articulation, largely obscuring the quadrate in lateral view. The post-temporal bars of both squamosals are eroded and cannot be fitted directly to the parietals. The right squamosal (see Andrews 1910, Pl. IX fig. 3) is the most complete, and a missing part of the zygomatic ramus has been restored in plaster in mirror image of the left. The right quadrate is preserved *in situ* with the right squamosal.

The present specimen (frag. G) displays a feature of plesiosaurian osteology which has not hitherto been recorded, but which I have observed in all British Upper Jurassic plesiosaurs in which this part of the skull is preserved. Andrews (1910) believed that the paroccipital process of the opisthotic articulated with the quadrate in plesiosaurs, although he was unable to demonstrate this in any specimens. Welles (1952) suggested this articulation in a reconstruction of the elasmosaur Styxosaurus browni. However, this does not appear to be the case in British forms. In the squamosals of the present specimen a flange is produced on the inner side of the bone, just ventral to the junction of the post-temporal bar with the other rami. The effect of this flange is to produce at the base of the post-temporal bar a ventrally-directed socket into which the dorsal end of the quadrate fits. The flange thus extends across the upper inner end of the quadrate. On its inner side is a large oval facet which matches in size and shape the head of the paroccipital process. The opisthotic therefore articulates with the squamosal, and not with the quadrate. This fact is believed to have a bearing on a theory of Andrews' concerning the homologies of the plesiosaurian squamosal.

The element which is normally termed the squamosal in the plesiosaur skull is almost certainly a compound bone, as was first suggested by Andrews (1896b). He interpreted the post-temporal bar of this bone as homologous with the supratemporal of lizards, and the remainder as homologous with the true squamosal. In support of this theory he referred to the work of Owen (1840b) who had figured a suture separating the post-temporal ramus from the remainder of the squamosal in a young individual of Plesiosaurus Macrocephalus. It may be added that Welles (1943, 1952) has suspected, with varying degrees of doubt, the presence of a suture in this position in the skulls of American Cretaceous elasmosaurs. If this bone is in fact formed from the fusion of two elements, then the post-temporal bar, together with the flange mentioned above probably represents the tabular rather than the supratemporal. Tabulars are found extending from the parietals to an articulation with the paroccipital process in, for example, the pelycosaurs (see Romer and Price, 1940), and in primitive lepidosaurian reptiles such as Youngina (Broom, 1914). In Sphenodon, on the other hand, the paroccipital process articulates with both the squamosal and the quadrate, at their point of suture. In nothosaurs the squamosal is triradiate as in plesiosaurs, and their ancestry is not known. The articulation of the paroccipital process with the plesiosaurian squamosal cannot be taken as proof of the squamosal's original formation from separate squamosal and tabular elements, but I believe that the evidence strongly favours this conclusion.

The sutures between the right squamosal and quadrate in fragment G are quite obvious. The quadrate fits dorsally into a socket in the squamosal, as described above, at which point it is a strong element with a triangular cross-section. 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. The outer condyle is slightly larger than the inner. The process for suture with the pterygoid is broken away close to the inner margin of the inner condyle. The posterior face of the quadrate is flat, and the inner face concave such that the outer edge of the bone, which is overlapped by the lower ramus of the squamosal, is much thicker than the inner part. Fragment G has been flattened out a little in preservation. As a result, when it is orientated with the quadrate vertical and at right-angles to the skull axis, the zygomatic ramus points forwards and outwards from the skull axis instead of lying almost parallel to it (by comparison with other plesiosaur skulls). This has been taken into account in the reconstruction (fig. 1).

A further skull fragment is preserved (fragment H), but it has been badly eroded, and is difficult to interpret. It consists of portions of the median bones between the frontals (as preserved in fragment D) and the snout. It can be fitted directly to the median strengthening bar of the right frontal described above, the broken surfaces (which are triangular) being too small to permit a satisfactory repair to be made. The ventral (internal) surface of the fragment is sufficiently well preserved to permit the identification of part of the fused vomers, which were probably similar in form to those of *Tricleidus seeleyi* (described below). A part of the margin of the right internal naris is preserved, in the same position relative to the vomers as that of *Muraenosaurus* (Andrews 1910, text-fig. 47). The dorsal (external) part of fragment H is very badly worn, and attempting to trace sutures is very difficult and inconclusive. It does appear, however, that parts of the premaxillae and frontals have been squashed onto the dorsal surface of the vomers.

The lower jaw is preserved in four pieces; the left ramus of the dentary and anterior 5½ sockets of the right ramus (fragment I); the remainder of the right ramus of the dentary (frag. J), and the angular, surangular and articular of the left and right sides (frags. K and L). Small gaps in both rami of the dentary make estimation of the number of tooth sockets a little difficult, but 26 is the most probable figure. This compares with a count of 24 sockets in each lower jaw ramus in R.8621; 24 with possibly a 25th developing at the posterior end of the ramus in R.2417, and 25 in R.3730, these being the only specimens with this part of the skull preserved (see below for additional description).

(b) The skull of R.8621

With the exception of one small fragment of bone which I have been unable to identify, only the lower jaw and two isolated teeth were found with this specimen. However, the material is very well preserved, and has been fully prepared by the staff at the British Museum (Natural History).

The dentary is slightly crushed dorsoventrally, but its shape as seen from above has not been altered. In lateral view, parts of the posterior margins of both rami are seen to have been broken away, but it is otherwise complete. In dorsal view (fig. 3) the dentary exhibits the characteristic structure of the sauropterygian tooth-row in which the large (secondary) tooth sockets, which hold the functional teeth, are paired on the lingual side with small (primary) alveoli in which the replacement teeth develop. These primary alveoli usually appear on the surface of the bone as small pits or sometimes elevated bumps, the surfaces of which are evenly "textured", resembling in appearance the surface of fine sandpaper (a similar "texturing" is found on surfaces which in life were cartilage-covered, such as the articular faces of vertebral centra and the ends of paddle bones). This surfacing contrasts with the surrounding bone, which is smooth and shows "grain". Each alveolus is connected to the socket by what must be a thin vertical lamina of soft bone, which shows on the dorsal surface as a fine line or a superficial groove. Replacement teeth appear to pass from the alveolus outwards along this line until they occupy the secondary socket; stages of this process are exhibited in the specimen.

There are 24 tooth sockets on each ramus of the dentary. No mature teeth are preserved <u>in situ</u>, but the developing left 2nd, 4th and 7th, and the right 1st, 2nd, 4th, 9th and 14th teeth are visible in either the alveolus or the socket, or between these. The largest sockets (implying that these held the largest mature teeth) are the 4th, 5th and 6th, decreasing very slightly forwards. Posteriorly the sockets decrease regularly in size from the 6th to the 22nd, then reduce abruptly to the small 24th socket. It seems probable that further teeth may have been added at the back of the tooth-row later in life, since up to 26 dentary teeth are known to occur in this species (in R.2860).

The sockets are not directed upwards, but are inclined outwards at an angle of from 40° from the vertical in posterior sockets increasing to 60° or more from the vertical anteriorly (this outward tilt is partly compensated by curvature towards the vertical in the teeth; see discussion of teeth of R.3730 below). They are also inclined forwards, this inclination being only slight in posterior sockets but becoming more pronounced anteriorly. The primary alveoli appear on the surface of the bone lingual and posterior to their associated sockets. Due to the inclination described above, they actually occur immediately above the socket bases. It is evident that developing teeth actually move downwards into the secondary 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.

In dorsal view, the dentary ramus is divided into two distinct areas: (i) an outer tooth-bearing area, which has a generally pitted or spongy appearance and contains the primary alveoli and secondary sockets, and (ii) an inner (lingual) area of solid bone, smooth in appearance, which also encloses the spongy tooth-bearing area ventrally and externally. The alveoli and the solid supporting bone are separated along most of the rami by a shallow groove, which, however, crosses the supporting bone at the posterior margin of the dorsal surface of the symphysis. The effect of this is to separate off an equilateral triangular portion of the supporting bone in the symphysis, which is bordered posteriorly by the groove, and left and right anterolaterally by the spongy tooth-bearing area including the alveoli of the 1st and 2nd teeth (cf. with Muraenosaurus and Tricleidus, in which this area is diamond-shaped, the grooves of the left and right rami meeting in a backward-pointing V). Lingual to the 7th socket a small foramen is visible in the supporting bone, opening anteriorly and perhaps was associated with nutritive blood-vessels. From this foramen a shallow groove leads forward for the distance of 3 sockets.

The dorsal length of the symphysis is 3.2 cm., and the length of the left ramus is 22.4 cm. The symphysis is therefore very short compared with that of the lower jaws of pliosaurs (see measurements given by Andrews, 1913). In ventral view the symphysis has a median notch in its posterior margin which is 7 mm. long and 5 mm. wide. This may mark a place of attachment of ligaments associated with the tongue. The ventral length of the symphysis to the anterior margin of this notch is 2.9 cm.

In external lateral view, the slight dorsoventral post-mortem crushing of the specimen can be seen to affect principally the anterior end of the jaw. Numerous small foramina (perhaps for blood-vessels) are visible on the external dentary surface, mostly opening posteriorly. The internal surface is deeply grooved for the reception of the surangular and possibly, anteriorly, a splenial. Thin broken fragments possibly of this latter element remain in place on both rami.

The posterior bones of the right lower jaw ramus are preserved united in a second piece (fig. 4). This is composed of the articular, angular and surangular. No coronoid ossification is preserved, nor has this element been observed in any plesiosaur remains examined. It does not appear to have been retained, unless it is indistinguishably fused to the surangular.

The articular and surangular are fused in this specimen, as they appear to be in all plesiosaurs. The combined element forms the glenoid for articulation with the skull. This is laterally expanded, and has two concavities to fit the double condyles of the quadrate. There is a hint - it may be called no more - that the articular forms the entire glenoid, and that the fused suture between it and the surangular may lie in the position indicated on the figure by a dashed line. In other specimens of plesiosaurian lower jaws it appears equally or more likely that this line of fused suture lies along the floor of the glenoid, and that the quadrate articulates posteriorly with the articular and anteriorly with the surangular.

In the present specimen, the articular-surangular is in the process of fusing with the angular. This fusion has been completed posteriorly, but the line of fusion can still be traced by observing differences in the "grain" or growth-pattern of the elements. Anteriorly the suture is clearly visible. Posteriorly, the angular is a thin lamina in plesiosaurs, which is wrapped round the sides and ventral surface of the massive and conical articular. Anteriorly it takes the form of a thin vertical lamina of bone, uniting externally with the internal surface of the dentary. Its internal surface is folded to produce a dorsally orientated meckelian groove for the insertion of the jaw musculature. A fragment consisting of parts of the left angular and surangular is also preserved.

Two isolated teeth were found near the jaw. The larger of these is somewhat eroded, the apex is broken off and much of the ornamental ridging is missing. Sufficient remains, however, for this to be diagnostic. The smaller tooth is well preserved (fig. 5), and shows clearly the highly characteristic and diagnostic ornament found in this species. There are no wear facets visible on this tooth, and it belongs to the anterior right side of the jaw (see discussion of orientation of teeth under R.3730 below).

(c) The skull of R.3730

The skull of this specimen has been considerably flattened by pressure acting in a dorsoventral direction. Only the jaws and the dorsal midline of the skull back to the supraoccipital is preserved. The suture between the premaxillae is preserved in the midline, and is straight. The frontals, parietals and supraoccipital (which comprise a separate fragment) can be fitted onto the broken posterior midline of the left premaxilla, but the area of contact is too small to be repaired. Furthermore, such a repair would cause the frontals and parietals to hide from view the internal aspect of the left lower jaw. The frontals and parietals add nothing to further the description of these bones given above for R.2860, except that in the present specimen the frontals are separated in the midline by a narrow gap (a situation which was found to occur in most plesiosaur skulls examined). The remainder of the skull, however, has proved to be very useful in assisting with the reconstruction of the skull of this species (see figs. 6 and 7).

The jaws and teeth have been squashed together *in situ*, retaining what is assumed to be the original interlock (figs. 6 and 7). Most of the teeth have been preserved, either entire or in part. There are 25 teeth in each ramus of the lower jaw, the largest being the anterior six. As in R.8621 (described above) 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 1st teeth are very close together. The remaining 5 premaxillary teeth are large, being as large as the dentary teeth with which they interlock. Each maxilla bears 18 teeth of which the first 8 (i.e. 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 the detailed interlocking of the teeth has been very well preserved. The most anterior teeth in the combined jaws are the small 1st upper teeth, which together bite inside the 1st lower teeth. Behind these bite the 2nd upper teeth, then the 2nd lower, and so on in a one-to-one fashion until halfway back along the tooth-row. At this point, two lower teeth (10th and 11th) bite together between the upper 10th and 11th teeth. It is noteworthy that both the 11th (upper and lower) are small replacement teeth, not yet having achieved their full size. Passing backward from these, the lower teeth now bite in front of the upper until the 16th lower tooth, behind which bite the 16th and 17th upper teeth.

In the specimen the 16th upper socket is actually empty, and in the reconstruction I have drawn a diminutive replacement tooth in this socket to facilitate interpretation. The interlock is now with the upper teeth again biting in front of the lower teeth, as at the front of the skull, until at the posterior end of the jaw the 24th and 25th lower teeth bite together since there is no interposed tooth present in the upper jaw. The details of interlock of the left teeth could not be satisfactorily determined owing to the degree of displacement and fracture of the teeth, but it was apparent that the places of changeover of interlock did not coincide with the right side.

A consideration of the orientation of empty sockets in the lower jaw of R.8621 (described above) enabled the teeth of the present specimen to be orientated on the jaws. The teeth leave the sockets at an angle which is inclined outwards at about 60° to the vertical in anterior teeth reducing to about 40° posteriorly. However, the teeth themselves curve towards the vertical (i.e. the lingual side is shorter), the total curvature of the crown being about 40°, and rather less than this figure in the most anterior teeth. The tooth apex is thus almost vertical in posterior teeth, but is still inclined outwards at an increasing angle anteriorly, reaching a maximum inclination from the vertical of about 40° in the most anterior teeth. The sockets direct the teeth forward with respect to the jaw ramus. It was found that anterior teeth also tended to curve very slightly forwards, and could, if isolated, be orientated as to the side of the jaw to which they belong. (By holding the tooth with its axial ridges to left and right and the lingual side facing the observer, the apex points to the front of the jaw.) Anterior sockets direct the teeth more anteriorly than posterior sockets. In lateral view, therefore, the teeth would be seen to point forwards, the angle of forward inclination increasing from the posterior to the anterior of the jaw.

The appearance of the closed jaws, with teeth interlocking, was reconstructed from this specimen (R.3730) using the observed details of tooth interlock on the right side (fig. 6), together with a knowledge of their orientation for which reference was made to R.8621. This reconstruction was reversed (so as to appear to face to the left) and very slightly reduced until it fitted a toothless skull restoration based upon R.2860 (the neotype, described above). In this way the composite reconstruction (fig. 1) was produced.

(d) The skull of R.2417

This specimen is an almost complete skeleton of a juvenile individual, at present on display. The skull, unfortunately, is very fragmentary, and has been mounted on thin steel bars to which the fragments have been glued. It is not so complete as that of R.2860, and adds very little to the description given there, save for a few details in which ossification is less complete than in the adult.

Three teeth, preserved *in situ* on the premaxillae, show the specifically diagnostic ornamentation. Fragments of the frontals and parietals are preserved, and the supraoccipital, exoccipitals, basioccipital and basisphenoid were figured by Andrews (1910, Pl. IX, figs. 4, 4a and 5). The median foramen in the basisphenoid figured and labelled *for*. (*ibid*., fig. 5) is a hole that has been drilled to facilitate mounting on a steel peg. Fusion of the exoccipitals with the opisthotics is not quite complete, and the bones are still separate ventral to the jugular foramina. The form of the occipital condyle, in which the exoccipitals are involved, is exactly as in R.2860. Part of the pterygoid facet of the right quadrate is preserved, and almost touches the inner condyle at its base. Parts of the right squamosal and left quadrate are also preserved. The lower jaw (figured Andrews 1910, Pl. IX, fig. 6) is rather badly eroded, but the sockets could be counted on the right ramus. There are 24, with posteriorly a small pit suggestive of a 25th developing. The retroarticular process was completed posteriorly in cartilage, and in this specimen the ossified angular extends slightly posterior to the ossified part of the articular.

Summarising the above descriptions of skull material, it may be said that the jaws and teeth are well-known; the dermal roofing bones are imperfectly known but sufficiently so to enable a lateral (but not a dorsal) reconstruction to be made; most of the neurocranium except the pterygoids and prootics are known, whereas the palate is not preserved in any specimens. In the lateral reconstruction (fig. 1) it was necessary to restore the outlines of the postorbital bar and the jugal from the reconstruction of Muraenosaurus given by Andrews (1910, text-fig. 46B) and from a consideration of reconstructions of elasmosaur skulls given by Welles (1943, 1952, 1962). The remainder of this and the occipital reconstruction (fig. 2) were based on the material described above.

2. Postcranial skeleton

Andrews (1910, pp. 168-202) described the postcranial skeleton of this species in detail, and accompanied his description with numerous figures (ibid., text-figs. 78-94; Pl. X). A restudy of his material in the British Museum (Natural History) together with a comparative study of undescribed material in Cardiff and Glasgow (see Appendix 1, (iv) and (v)) has confirmed the general accuracy of Andrew's descriptive work. A complete redescription is therefore unnecessary.

In Cryptoclidus eurymerus almost complete specimens are known of individuals ranging from half-grown to full-grown. To facilitate description I have divided these specimens into three categories which represent growth stages. A study of comparative growth or development of characters necessarily involves a comparison of individuals from all three growth categories, which are 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.

Reference to these three growth categories is made for all species described below. In the following comparative account of C. eurymerus several details are added to Andrews' description concerning ageing and osteological development; emphasis is placed upon those features which I consider to be of taxonomic importance, and the reconstruction presented by Andrews (1910, text-fig. 94) is modified (fig. 8).

(a) Vertebrae

In the past, plesiosaur taxonomists have placed too much emphasis on the comparative details and proportions of vertebral centra. Much confusion has arisen from a lack of understanding of the variation of these characters both with the age of the individual and with the position of the centra on the vertebral column. The problem is discussed below (Section 3(i)a), and the importance of understanding this variation is emphasised.

Five types of vertebrae are usually distinguished in describing the vertebral column of plesiosaurs, these being termed cervical, pectoral, dorsal, sacral and caudal. In cervical vertebrae the articulation of the rib is with the centrum only, whereas in dorsal vertebrae the rib articulates with a transverse process formed solely by the neural arch. Pectoral vertebrae (defined by Seeley, 1874a) are transitional between cervicals and dorsals; in these the rib articulates with both the centrum and the neural arch, which are raised into a short transverse process. In sacral vertebrae the centrum and neural arch form a very large facet for the modified sacral rib, and in caudal vertebrae the rib articulates only with the centrum, which usually has additional ventral facets for the articulation of chevrons.

Pectoral vertebrae can be easily identified and counted in 'juveniles' since the neural arches and centra are free, but in 'adults' these elements fuse to such a degree that the line of suture cannot be traced. In such cases the numbers of cervical, pectoral and dorsal vertebrae cannot be reliably determined.

In Cryptoclidus eurymerus there are 55 presacral vertebrae, and usually 32 of these are cervicals. In R.2417 (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. The relative position of the pectorals seems to be subject to some variation, for in the 'old adult' V.1091 there are an estimated 29 cervicals, 3 pectorals and 23 dorsals. In this latter specimen the total number of presacrals remains 55, but the pectorals occur three places further forward than in R.2417 and R.2860. The above three specimens are the only ones in which the column is believed to be complete from the atlas to the sacrals.

One of the problems encountered when working with Leeds Collection material is that one cannot be certain that the entire specimen was collected. In R.2416 (a 'juvenile') a total of 48 presacrals are preserved, there being 28 cervicals (including the atlas and axis), 3 pectorals and 17 dorsals. The sacrals and most of the caudals are missing, and so it is reasonable to assume that the presacral series is also incomplete, and to postulate that by comparison with the specimens above there are seven presacrals missing. The same assumption is less easily justified in the case of R.2862 (an 'old adult') in which 53 presacrals are preserved (approximately 31 cervicals, 3 pectorals and 19 dorsals) since the full complement of 4 sacrals is present together with 26 caudals. However, the total of 55 presacrals is not known to be exceeded and can be counted in three specimens. I therefore believe this to be the normal total for the species, but cannot entirely discount the possibility of minor variation.

The atlas and axis (see fig. 9) were described by Andrews (1910, p.168). In 'juveniles' they remain separate (ibid., text-fig. 78A, B), but are fused in 'adults' (ibid., text-fig. 78C, D).

The vertebral column shows several features which have sometimes been used as taxonomic characters but are here recognised as applying to all the plesiosaurs studied. 'Nutritive foramina' are present in all vertebral centra, but are most obvious in presacrals, in which they are paired, one on each side. In the most anterior cervicals they are very close together and are separated by a mid-ventral ridge. They may even coalesce into a single midventral foramen, as in cervical "5" of V.1104 (fig. 10A). They become progressively farther apart in posterior cervicals, and are laterally rather than ventrally placed in pectorals (fig. 11, i-iii), dorsals (figs. 11, iv-vi; 12 and 13, i-iii) and sacrals (fig. 13, iv-vii). In caudals the 'nutritive foramina' again become progressively ventral, but in these they tend to divide into several smaller foramina instead of the paired larger foramina of more anterior vertebrae.

The largest vertebrae are always the mid-dorsals, and these also have proportionally longer neural spines. From the atlas and axis the neural canal gradually increases posteriorly, reaching a maximum in the posterior dorsals. Between the most posterior dorsal and the first sacral the neural canal diminishes to about one-half of its cross-sectional area, indicating that large sciatic nerves left the spinal cord at this point. The diameter decreases greatly in the caudals, becoming insignificant at the end of the tail.

The zygapophyses of cervical vertebrae are large and well-developed, whereas in dorsal and caudal vertebrae they are reduced and weaker, and the extent of overlap is small. Williston (1914) thought that the large cervical zygapophyses indicated a relative lack of flexibility of the neck. However, when consecutive vertebrae are placed together with their zygapophyses articulating it is found that the gap between consecutive cervical centra is much greater than between consecutive dorsal or caudal centra. This suggests a much greater flexibility between vertebrae of the neck than between those of the back or tail.

Proportions of vertebral centra of plesiosaurs vary from species to species, and hence are of taxonomic interest. Their use as taxonomic characters is, however, limited, and differences must be expressed in relative rather than absolute terms. Welles (1952, 1962) devised a 'vertebral index' which he hoped would simplify the comparison of vertebral proportions. His index consisted of three figures, of which the first was the actual length of the centrum in millimetres. The second and third figures expressed the relative proportions of the height and width of the centrum, the length being taken as 100. Welles found that in elasmosaurs the vertebral proportions vary with the position on the column and with the age of the individual. In practice his indices were useful in distinguishing plesiosauroid from pliosauroid material, but the considerable variation of proportions within each species severely limited further use. He did not attempt to plot his indices on a graph.

I have tried to demonstrate the range of variation of vertebral proportions within the present species by using a 'vertebral length index'. This index is produced by dividing the midventral centrum length by the average posterior centrum diameter (the average of posterior height and width). The resulting figure is multiplied by 100 and is expressed as a percentage. The indices of one individual are then plotted against the vertebral number (counting the atlas as No. 1), and the resulting graph shows the variation in relative centrum length with position in that individual. If individuals from all three growth categories are plotted together (see fig. 14) the resulting compound graph indicates the minimal range of variation in relative length of each vertebral centrum for the age-range represented, and in addition illustrates the uniformity of the shape of the graphs of individual specimens. This technique is found to facilitate the comparative description of vertebral proportions. 'Height indices' and 'width indices' could be used in a similar way, but this is found to be unnecessary since all the plesiosaurs studied show the same pattern of variation in cross-sectional shape of the centra. Furthermore, variations of relative height and width are comparatively unimportant, affecting to a small extent the strength and possibly the mobility of the column, whereas variations in the relative centrum length are cumulative, and can considerably affect the proportions of the animal.

In C. eurymerus the vertebrae with the greatest length indices are the anterior cervicals. The index is not known to exceed 100% and is considerably less in 'juvenile' individuals (see fig. 14). The vertebrae become proportionally shorter posteriorly, reaching a minimal proportional length in the region of the pectorals. Thereafter they increase in proportional length, reaching a peak index at or just before the anterior sacrals. The posterior sacral and anterior caudals are proportionally the shortest vertebrae, and the length index again increases towards the tip of the tail. This sequence of variation of the vertebral length index is exhibited by individuals of all growth categories. In addition, fig. 14 shows the extent to which the vertebrae of 'juvenile' individuals are proportionally shorter than those of more mature specimens (up to 20 index points in the specimens recorded), and illustrates the point that anterior cervicals of 'juvenile' individuals may have the same central proportions as posterior cervicals of 'old adults'. A table of actual measurements of the centra of the three individuals recorded in fig. 14 is given in the appendix (pp.157-9).

As in all plesiosaurs studied, the width of the centrum in C. eurymerus always exceeds the height. In cervical, sacral and anterior caudal vertebrae the centra are oval in section, but become more rounded in the dorsals and posterior caudals.

In the present species the centra are always amphicoelous, and there is sometimes a small central pit in the articular faces. The vertebrae of 'juvenile' specimens are smoother and neater in general appearance than those of older individuals, in which the centra especially have a rougher and more wrinkled surface.

(b) Ribs

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

The anterior cervical ribs develop an anterior flange halfway along their length, giving them a "hatchet-shaped" appearance (Andrews, 1910). This flange is developed to its fullest extent in 'old adults' such as specimen V.1091 (see Smellie, 1915 text-fig. 2), but is a variable feature, and may be developed to markedly differing extents in adjacent ribs. Posterior cervical ribs are proportionally longer and straighter, and are considerably dorsoventrally flattened.

In the pectoral region the ribs become more elongate and curved. Anterior and (more distally) posterior facets on the curved distal portions of these ribs indicate that they overlapped one another, forming a strengthened area for the ligamentous attachment of the scapulae.

The anterior and median dorsal ribs are long, and were tipped with cartilage even in 'old adults'. The shape of the articulation with the transverse process changes with position on the column. The articular facets of anterior dorsal transverse processes and ribs tend to be somewhat rectangular or ovoid in outline, with the long axis almost vertical. Middorsal articular facets are almost circular, and posterior facets again become ovoid, but with the long axis almost horizontally orientated. The size of these facets also decreases posteriorly. Posterior dorsal ribs become much shorter and straighter than those occupying a more anterior position (see figs. 8 and 13). Regional variations in the form of the rib and the shape of the articular facet enable a reasonably accurate orientation of isolated ribs to be made with respect to position on the column. When ribs are held in articulation with the respective transverse processes they can be spacially orientated. By this means it was found that the anterior and median dorsal ribs were inclined much more horizontally than was indicated by Andrews (1910, frontispiece and text-fig. 94), and in lateral view the distal tip of the rib appears barely half a centrum's diameter beneath the level of the ventral surface of the centrum. The ribs are also inclined diagonally backwards at their distal ends, due both to the curvature of the rib and to the form of the transverse processes. These observations have been taken into account in the drawing of the reconstructed skeleton (fig. 8).

The four pairs of sacral ribs are short and massive bones. Proximally they articulate with both the neural arch and the centrum of the sacral vertebrae by a single large convex facet. Distally they terminated in cartilage, and anteriorly and posteriorly they bear facets or depressions where they contacted or rubbed against the distal ends of the adjacent sacral ribs. Six sacral ribs and all four sacral vertebrae are preserved in specimen V.1104 and the form of the sacrum can be reconstructed (see fig. 13). The 1st and 4th sacral ribs are longer than the 2nd and 3rd, and are orientated by the facets of the 1st and 4th sacral vertebrae so as to converge on the other ribs. The shape of the dorsal end of the ilium matches the outline of the four proximated sacral ribs, and it seems probable that an articulation was achieved by the employment of cartilage and ligaments.

The caudal ribs are free in 'juveniles', but become fused to the centrum in 'adults'. They are thin, straight and dorsoventrally flattened, and are orientated in a horizontal position, with the distal ends pointing slightly posteriorly. The most anterior caudal ribs are slightly longer than the sacral ribs, but decrease in size posteriorly, and are not present on the final three or four centra of the tail.

(c) Chevrons

The chevrons are paired bones which do not unite ventrally to form a haemal arch. They are somewhat shorter than the corresponding caudal ribs, and are slightly curved. They are orientated downwards and slightly outwards from the caudal vertebrae, and their curvature causes the distal ends to point slightly backwards. They decrease in size posteriorly, and are proportionally longer in 'adults' than in 'juveniles'.

There are no chevrons associated with the most anterior two caudal vertebrae, but they are present from the third to within about four centra from the tip of the tail. At first the chevrons articulate only with facets on the posterior ventral side of the centrum, but posteriorly the 8th or 9th and subsequent caudal centra also bear anterior chevron facets. Here the chevrons articulate, still by a single head, between posterior and anterior facets on adjacent centra.

(d) Pectoral girdle

The pectoral girdle has been described and figured by Andrews (1895a, pp. 335-346, figs. 1-4; 1910, pp. 176-181, text-figs. 87-89 and Pl. X) and by Smellie (1915, pp. 616-620, text-fig. 7 and Pl. 1). It consists of three paired elements, these being the clavicles, scapulae and coracoids. An interclavicle is known only in one specimen (R.3538), in which it is a rudimentary Y-shaped splint of bone wedged between the clavicles (see Andrews, 1910, text-fig. 88). The glenoid is formed equally by the scapulae and coracoids, and in 'adults' these elements also meet in the ventral midline to form a bar which separates the two large scapulo-coracoid foramena. As in all plesiosaurs, the coracoids meet in the ventral midline and are expanded to form a large ventral plate.

The clavicles are well-developed triangular plates of bone which lie visceral to the ventral rami of the scapulae and meet in the midline. Their shape is quite variable. At their simplest they may take the form of a right-angled triangle, with the right-angle at the posterior median corner, as in R.2616 (see Andrews, 1910, text-fig. 87 and Pl. X). Frequently the posterior border is concave, and the lateral posterior part is elongated into a short process which fits into a small depression on the visceral surface of the scapula, as in R.2860, R.3533, R.3730 and V.1091. Usually the outer margin is straight, but sometimes it bears a small protuberance half-way along its length, corresponding to the outline shape of the underlying part of the scapula (in V.1091).

The development of the elements of the pectoral girdle from small 'juveniles' to 'adults' was described by Andrews (1895a). The clavicles are comparatively large in 'juveniles', but grow at a much slower rate than the ventral rami of the scapulae, which meet between them in 'adults'.

The scapulae are triradiate in form, as is usual in plesiosaurs. The ventral (anterior) rami form large expanded anterior plates in 'adults', meeting mid-ventrally in a long suture and continuing backwards to meet an anterior prolongation of the coracoids. The scapulocoracoid bar so formed is at a lower level than the posterior (glenoid) rami of the scapulae, and is somewhat keel-shaped. In 'old adults', when ossification is complete and fusion of the elements takes place (see below), this keel is continued forwards to the anterior of the girdle by a slight downward growth at the line of suture of the ventral rami. This is well shown in specimen R.2862. On the outer margin of the ventral ramus, just in advance of the base of the dorsal ramus, projects a well-marked prominence which may indicate the origin of a muscle.

The dorsal ramus of the scapula is strongly constructed, and bears prominent rugosities along its posterior edge, marking a major muscle origin. When the skeleton is reconstructed (see fig. 8) the dorsal ramus is found to be situated dorsal to and slightly in advance of the glenoid, a relatively higher position than that suggested by Andrews (1910) and especially by Watson (1924), in whose reconstructions of plesiosaurs it is placed anterior to and only slightly above the glenoid.

The posterior ramus of the scapula is short and massive, and triangular in section. It bears the anterior half of the glenoid, and unites with the coracoid by a triangular sutural surface.

The glenoid is a large oval facet which is only shallowly cupped. Its posterior half is formed by the coracoid. On both the dorsal and ventral surfaces of the scapula and coracoid near the glenoid 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 housed the ends of the numerous ligaments necessary to hold the humerus into the glenoid. Comparison of the relatively small head of the humerus with the size of the glenoid shows that even in 'old adults' the synovial capsule was large, and the joint must have been very flexible. In old age this may have become liable to arthritic disease, as is evidenced by the pectoral girdle and left humerus of V.1807. This specimen shows severe arthritis, and the humerus is virtually immobilised.

The coracoids are developed into large plates which are thin in section over most of their area. The most massive region lies between the glenoids, where a strong horizontal bar is formed. This functioned as a compression strut, resisting the inward forces produced by the paddles in locomotion. The lateral margins of the coracoids are also thickened, and those parts therefore form bars which curve posteriorly and laterally from the glenoids to terminate in the posterior cornua. When fully developed in the 'adult' and 'old adult' stages, these cornua are up to 40% wider from tip to tip than the distance across the posterior margins of the glenoids, a feature which distinguishes the genus <u>Cryptoclidus</u> from its contemporaries. In 'juveniles', however, the posterior part of the coracoids, including the cornua, is not developed, neither does the anterior median prolongation meet the scapula to form the scapulocoracoid bar.

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. This development is best shown by specimen V.1807, but is beginning to develop in V.1091 (see Smellie, 1915, text-fig. 7A) in which the position of these notches is visible. It seems probable that the median posterior growth was visceral to the most anterior gastralia, which then curved upwards and outwards through the notches. In this way a fairly firm union would be formed between the pectoral girdle and the plastron.

Progressive fusion of the elements of the pectoral girdle takes place with advancing age. In 'juveniles' all six elements are quite separate, the scapulocoracoid bar is not formed, and the ventral rami of the scapulae do not meet in the midline. In the 'adult' stage, the ventral rami meet and continue to grow backwards in the midline to meet the anterior prolongation of the coracoids, so completing the scapulocoracoid bar, but the elements still remain separate. In the 'old adult' stage progressive fusion of the elements takes place. In V.1091 (which Smellie, 1914, made the type of the genus <u>Apractocleidus</u> largely for this reason) the coracoids are fused, the scapulae are fused, and the suture of the scapulae and coracoids in the scapulocoracoid bar is largely fused, while their unions behind the glenoids remain open. The single clavicle preserved in this specimen is quite free. Specimen V.1807 takes this progressive fusion further, and in this specimen the scapulocoracoid sutures behind the glenoids are also fused. Unfortunately the clavicles are not preserved, but their absence suggests that they were still free. Fusion is taken still further in specimen R.2362, in which the clavicles are fused to each other, and are also fused at least posteriorly onto the visceral surface of the ventral rami of the scapulae. Laterally and anteriorly the sutures of the clavicles with the scapulae are still visible.

(e) Gastralia

The gastralia, which are thought to be dermal scale derivatives (Romer, 1953) are frequently but misleadingly called "ventral ribs" (e.g. by Andrews, 1910). In plesiosaurs they form a well-developed plastron which functioned as a ventral carapace. The plastron in the present species consists of approximately 8 rows of elements, each row consisting of a median element and three pairs of lateral elements (to be called 1st, 2nd and 3rd laterals), together with a further two posterior and shorter rows which lack the median element.

Median elements are easily recognised by their symmetry, and are the most massive. Viewed from above they are very slightly V-shaped, the apex of the V pointing forwards along the mid-ventral line. The angle of the rami from one another is about 165°.. The median part of the bone is the thickest, and is circular in section. Towards the ends of the bone the anterior surface becomes progressively hollowed by large concave facets into which the 1st lateral elements fit, and the tips of the bone are often pointed. When seen in anterior or posterior view the median element is only slightly curved, giving the ventral surface of the animal a very gently convex shape.

The 1st and 2nd lateral elements are very similar to each other and are difficult to distinguish. Viewed from above they appear twisted into a very gentle S-shape, but much of this appearance is the result of excavations for the articulation of adjacent elements. The 1st lateral has a large posterior facet which occupies almost half the posterior surface of the inner end, and which fits a similar facet on the median element. The outer end of the 1st lateral is hollowed on the anterior side for the reception of the 2nd lateral. Similarly, the 2nd lateral has a large inner facet on the anterior surface for the inner end of the 3rd lateral element.

1st and 2nd lateral elements can be orientated by examining them in anterior or posterior view, with the convex ventral surface downwards. A left element will then present a facet towards the observer on the right side, and a right element a facet on the left. The most gently tapering and pointed end is that nearest the midline; the most abruptly terminating end is the outermost, and this end is also the most curved. When 1st and 2nd laterals are compared in anterior or posterior view, the 2nd laterals are more curved, and the outer ends are more tapered. 2nd lateral elements therefore present a more slender and curved appearance.

3rd lateral elements are easily distinguished as there is only one facet, this being on the posterior surface of the inner end, for articulation with the 2nd lateral. The outer end is somewhat laterally flattened, and tapers to a blunt ending. This element is more strongly curved than the other laterals.

In specimen R.2362 the major part of the plastron has been preserved <u>in situ</u> due to an unusual concretion of the surrounding clay matrix (see Andrews, 1910, text-fig. 86). This preservation shows that not only are the elements of each row closely associated, but also the tips of the individual elements of adjacent rows tend to interlock, and so form a strong and compact plastron. In R.2362 are also preserved the "9th" gastralial row, which consists only of the lateral elements, and a forked piece of bone representing the inner end of a "10th" row. These posterior rows are preserved overlapping the anterior ventral margin of the pubis. The forked gastralium is preserved almost entire in V.1104, and is probably the only element in the row.

The specimen, from the right side, has a small anterior facet towards the outer end, but this does not extend to the tip of the element. Instead of articulating with a further lateral element, the outer end of the '10th' row closely contacted the posterior surface of the '9th' row laterals.

(f) Pelvic girdle

The pelvic girdle has been adequately described and figured by Andrews (1896a; 1910, pp. 183-186, text-fig. 92 and Pl. X). It is very similar to the pelvic girdles of its contemporaries, and presents no characteristic features. The pubes and ischia are large 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. In Jurassic plesiosaurs this bar is not known to ossify, but it is sometimes ossified in Cretaceous elasmosaurs (Welles, 1962). The ilium is reduced to a bar which is orientated diagonally backwards and upwards between the acetabulum and the sacrum. The acetabulum is an elongated oval shape, its posterior margin being formed by the ilium, which sutures only with the ischium. Andrews (1896a) drew an interesting parallel between the structure of the plesiosaur pelvis and that of marine turtles; probable functional similarities are discussed in Section 3(ii)(a).

(g) Fore paddle

The fore paddle has been described and figured by Andrews (1910, pp. 181-183, text-figs. 90, 91A) and by Smellie (1915, pp. 620-622, text-fig. 8B, Plate fig. 4). The humerus, radius and ulna are highly characteristic in this species, whereas the distal parts of the paddle cannot be distinguished from those of contemporary plesiosaurs. The length of the entire paddle may be well in excess of 1 metre, and the overall paddle-span from tip to tip of the outstretched paddles may be 3 metres in a specimen of overall length 4 metres.

The 'adult' humerus (see figs. 15, 16,A and 17, A-B) is a stout and massive bone which is characteristically expanded at its distal end. This unusually great expansion is the result of the disproportionate enlargement of the distal anterior portion of the humerus which bears the radial facet. In 'juveniles' the distal expansion is not developed sufficiently for this feature to be diagnostic.

Rugosities on the surface of the bone indicate the positions of muscle insertions on the humerus. These show that a very powerful muscle inserted onto the median part of the anterior border of the humeral shaft (see fig. 15,C). A similarly large muscle insertion appears along the posterior border of the shaft (fig. 15,A). On the dorsal surface of the humerus, between these insertions, the bone of the shaft is quite smooth (fig.16,A), and without muscle attachment. In contrast, the ventral surface of the shaft bears a band of rugosities marking a muscle insertion centred at about one third of the humeral length from the proximal end. This insertion runs continuously between the more prominent anterior and posterior insertions, but is most developed at the middle of the ventral surface of the shaft.

The prominent tuberosity of the humerus also shows evidence of muscle insertions. These are most evident on the anterior and posterior edges of the tuberosity (see figs. 15,C and 15,A), implying the insertion of muscles with the function of rotating the humerus. Additional markings on the dorsal surface of the tuberosity indicate the insertion of muscles and ligaments which may have functioned primarily to hold the humerus into the glenoid. They may be too near the head to have been the site of insertion of powerful elevators, though some elevation was no doubt brought about by muscles inserting on the tuberosity.

A reconstruction of the muscles inserting onto the proximal half of the humerus, and their function, is discussed in Section 3(ii)(a).

On both the dorsal and the ventral surfaces of the distal end of the humerus are extensive areas of shallow grooves and ridges, which become more prominent distally. In addition there are present in this area numerous small foramina, the apertures of which face towards the radial and ulnal facets. These foramina are also present on the epipodials and mesopodials, and their apertures always face towards the peripheries of the bones. All the distal paddle bones have roughened surfaces. These ridges and grooves, foramina and roughened surfaces are taken as evidence for a thin but tough covering of ligaments and small muscles, whose function was to strengthen and stiffen the paddle, making it a firm, streamlined and only slightly flexible appendage.

The radius of this species is of a characteristic shape, being greatly expanded proximally and anteriorly to match the expansion of the humerus, This gives the bone a sigmoid anterior outline, which is convex proximally and concave distally. All other contemporary species have this anterior radial margin concave throughout. These contrasting features are developed in each case even in small 'juveniles', and are thus of considerable diagnostic value.

The ulna is generally very short and wide, its antero-posterior width being approximately twice its length. Occasionally, as in V.1091, there is evidence that it may ossify from two distinct centres; however, perfectly normal ulnae are known associated with skeletons exhibiting all other 'old adult' features (e.g. R.2362), showing V.1091 to be aberrant in this respect.

The combined shape of the radius, ulna, and the 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. The unusually expanded portions of the radius and humerus form, as a consequence, a prominent 'elbow' in this species (cf. description of the fore paddle of Muraenosaurus leedsii).

In most plesiosaurs the radius and ulna are clearly separated by a gap or foramen. The present species differs from its contemporaries in that this foramen is only visible when the advanced ossification of the 'old adult' stage is reached, as in V1091, V.1809 and R.2862. A further feature of the fore paddle which only becomes clear in the 'old adult' involves the proximal end of the humerus; the tuberosity may become separated from the head by the development of a strip of finished bone surface which divides the usually single proximal cartilaginous area into two, as in V.1835.

The carpals (sometimes termed "mesopodials", esp. by Welles) are essentially six in number and arranged in two rows of three, the proximal row consisting of the radiale, intermedium and ulnare. There is a considerable and very variable tendency to develop additional elements ("accessory ossicles", auct.) which may be preaxial or postaxial or both, and which may remain free or fuse to an adjacent epipodial or mesopodial. They may result in assymmetry between the left and right paddles of an individual, and are of no taxonomic significance.

The first (most anterior) metacarpal is generally flattened, resembling a distal carpal, but the second to fifth are cylindrical, resembling the phalanges. The fifth metacarpal, characteristically for plesiosaurs later than the Lower Jurassic, has moved proximally into the distal metacarpal row and articulates with the ulnare.

It is not known exactly how many phalanges there were present in each digit, as the paddles were frequently found disturbed, or collected without due attention being paid to their position. The recently found specimen R.8621 was carefully photographed before collection, and every bone was numbered, but at the present time it is still undergoing preparation in the British Museum workshop. The longest digits (3rd and 4th) were probably composed of about 15 phalanges, whilst the 2nd, 5th and 1st contained decreasingly less. In the reconstruction (fig. 8) the number of phalanges in the fore limb is taken from R.2864, which is a specimen of Muraenosaurus leedsii (Andrews, 1910, text-fig. 63B).

(h) Hind paddle

The hind paddle has been described and figured by Andrews (1910, pp. 186-189, text-fig. 93). The distal portion (tarsals, metatarsals and phalanges) closely resembles the corresponding part of the fore paddle in structure, but the proximal portion differs, and is very similar to the hind paddle of contemporary species. It is slightly shorter and a little more slender than the fore limb.

The femur (figs. 16,B; 17, C & D, and 18) resembles the humerus in general shape, but is readily distinguished in the adult. The distal anterior portion is not so expanded; it is, nevertheless, more expanded in the 'adult' than in 'adults' of contemporary species (but not sufficiently so for this feature always to be diagnostic). The trochanter is not so well developed as the tuberosity of the humerus, and does not form such a prominent angle at its posterodorsal margin. The proximal portion of the femoral shaft is circular in section, whereas that of the humerus is oval, with definite anterior and posterior margins. In young specimens the femur may be indistinguishable from the humerus, and is indistinguishable from the femora of contemporary species.

The evidence for muscle insertions on the proximal portion of the femur differs from that of the humerus in several respects. There is a relatively small muscle insertion on the median part of the anterior surface of the shaft, weaker in appearance than the corresponding insertion on the humerus (cf. fig. 18,C and fig. 15,C). This insertion is completely surrounded and delimited by an area of smooth bone. The ventral surface of the shaft is much pitted and ridged for muscle attachment, and these surface markings are in many specimens aggregated around two centres, one on either side of the ventral midline of the shaft, thereby differing from the humerus in which there is one median centre of surface markings (cf. fig. 18,B and fig. 15,B). The posterior surface of the femoral shaft (see fig. 18,A) is covered with pits and ridges which extend from the base of the distal expansion to the proximal margin of the posterior surface of the trochanter. It is not possible to delimit the insertions of individual muscle blocks within this large area, which in its ventral part is continuous with the ventral muscle insertions. There may be a small muscle insertion on the anterior surface of the trochanter, but this is not so clearly developed as on the humerus.

The femur shows evidence of ligaments and muscles holding the head into the acetabulum such as was described for the humerus and pectoral glenoid. Similarly, markings on the distal portion of the femur, together with surface markings on the paddle bones, suggest the presence in the living animal of a thin but tough covering of ligaments and small muscles whose function was to strengthen and stiffen the paddle. Several deep posterior foramina at the base of the distal expansion probably held the origins of large postaxial strengthening ligaments.

In the 'old adult' the trochanter may become separated from the head by the development of a strip of finished bone surface which divides the usually single cartilaginous area into two, as in V.1810.

The tibia is a rectangular, almost square bone, differing from the radius in that it lacks the proximal anterior expansion. The fibula generally resembles the ulna. As in the fore limb, a foramen between the tibia and fibula is only evident when the full ossification typifying the 'old adult' stage is reached, as in R.2616.

The mesopodials, metatarsals and tarsals resemble the corresponding bones of the fore limb. The left hind paddle of R.3703 (see Andrews, 1910, text-fig. 93) is believed to be complete, and has three phalanges (plus the phalange-like metatarsal) in the first (most anterior) digit, 9 phalanges in the second, 13 in the third, 13 in the fourth (and longest) digit and 12 phalanges in the fifth digit.

Note on the reconstruction

Figure 8, which represents a reconstructed lateral view of the skeleton of a swimming 'adult' individual, was based so far as possible on the neotype specimen R.2860. The skull is a direct and proportional reduction of fig. 1. The outlines of the vertebrae were redrawn from the frontispiece in Andrews, 1910 (a lateral photograph of the mounted skeleton), which was itself used by Andrews in the production of his reconstruction (ibid., text-fig. 94). As the vertebrae are mounted in close contact, they have been spaced to allow for cartilage. The orientation and reconstruction of the ribs (which are incorrectly 'hung' in the mounted exhibit) was based on observations of the neotype, on examination of the ribs and vertebrae of V.1104, and on a photograph of the mounted exhibit of specimen V.1091 (in the Hunterian Museum, Glasgow), which is correctly mounted in this respect. The pectoral and pelvic girdles were drawn from telephotographs of the girdles of specimen R.2616, which is correctly mounted, with slight reduction to match measurements of the girdles of R.2860. The gastralia were reconstructed from R.2860, R.2862 (Andrews, 1910, text-fig. 86) and V.1104. The proximal portions of the paddles were drawn from R.2860, with the full complement of phalanges of the fore limb taken from R.2364 (a specimen of Muraenosaurus leedsii; from Andrews, 1910, text-fig. 63), and phalanges of the hind limb from R.3703 (Andrews, 1910, text-fig. 93).

The body shape of this animal is flatter and wider than in Andrews' reconstruction, and is closer to the shape of a mounted skeleton in the U.S.A. which was figured by Williston (1925). The neck length should not be considered as 'mesodeiran' (sensu Seeley, 1892, applied to this species by Persson, 1963). In fact, the neck has the same proportional length and contains the same number of vertebrae (32) as Plesiosaurus dolichodeirus, which has been cited (e.g. by Watson, 1924) as possibly ancestral to the elasmosaurs.

The significance of the body shape and proportions is discussed in Section 3.

Cryptoclidus richardsoni (Lydekker, 1889)

Plesiosaurus plicatus (Phillips, 1871) Mansel-Pleydell, 1888.

Cimoliosaurus richardsoni Lydekker, 1889b; Mansel-Pleydell, 1889.

(*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Cryptoclidus richardsoni (Lydekker, 1889b) Bogolubov, 1909.

Cryptocleidus richardsoni (Lydekker, 1889b) Delair, 1959; Persson, 1963.

(*Lapsus calami* for *Cryptoclidus* Seeley, 1892)

Holotype:

B.M.(N.H.) specimen R.6696, which was discovered and collected by Mr. Nelson M. Richardson of 'Montevideo', near Weymouth, and consists of an almost complete postcranial skeleton. The pectoral girdle was figured by Lydekker (1889b) and the whole (then mounted) skeleton was described and figured by Mansel-Pleydell (1889) as *Cimoliosaurus richardsoni*.

Type locality:

A label with the holotype states that it was found "in a brick-field between Montevideo House and Chickerell ... " (near Weymouth, Dorset), "at a depth of 30 feet".

Type horizon:

Upper Jurassic, Callovian or Oxfordian Stage. From the Oxford Clay, which includes the 6 ammonite zones from the zone of *Kosmoceras jason* to the zone of *Cardioceras cordatum*.

Referred specimens:

The only known specimen is the holotype.

Diagnosis:

Members of the genus Cryptoclidus in which

there are about 54 presacral vertebrae;

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 sub-square.

Description

Specimen R.6696 is an 'old adult' which closely resembles C. eurymerus in all details except those listed in the diagnosis. It is of similar size and proportions, and was probably a little less than 4 metres in overall length. Unfortunately no part of the skull was recovered, but the remainder of the skeleton was found articulated. The right hind paddle is missing.

The vertebrae have to a variable extent been crushed, distorted and broken. They bear numbers in white paint in two series, numbered 1-34 followed by 1-38, but several mistakes and misidentifications have been made and the numbering is neither original nor reliable. The general features of these vertebrae are largely determinable, but some are so badly damaged that they cannot be identified or orientated.

Parts of 73 vertebrae are preserved of which probably 54 are presacral. Only two sacrals can be positively identified, and there are probably 19 caudals. The presacral series consists of about 32 cervicals (including the fused axis and atlas, jointly numbered '1'), about 3 pectorals and about 19 dorsals. It is quite possible that a few vertebrae in the sacral region are missing, in which case the sacral number may have been the normal 4, the number of presacrals may have been 55, and there may have been one or two anterior caudal vertebrae lacking chevron facets, all as in C. eurymerus. The neural arches were fused throughout, as were the cervical and caudal ribs, but these are now largely broken away and missing. A caudal vertebra (numbered '24') has both chevrons almost complete, and fused to the centrum. They were similar to those of C. eurymerus, were more than 4 cm. long and are inclined downwards and backwards at an angle of 45° or more from the vertical. The most anterior 8 caudal vertebrae have chevron facets or the remains of fused chevrons only at the posterior ends of the centra, whereas the posterior 11 vertebrae have both anterior and posterior chevron facets developed. Only the final 3 or 4 terminal caudal centra are missing.

A box of broken rib fragments and gastralia is present. These show no unusual features.

The pectoral girdle has been broken into several pieces which can be reconstructed like a jig-saw puzzle. Most of the lateral parts of the left and right scapulae are preserved. These are of the same form as in C. eurymerus, and were fused to the coracoids. Their anterior median surface is missing, as is the scapulocoracoid bar. The specimen has suffered from a decay of the spongy bone of the anterior part of the girdle, and the outer lamellar parts of the bones are separated. A piece of bone (numbered '7' in white paint) which has suffered in this way, and is now tied together with gut, appears to be part of the right clavicle. If this identification is correct, the clavicle was of the large triangular form found in C. eurymerus. It is concave dorsally and convex ventrally to lie on the ventral ramus of the scapula.

The thickened glenoid portions and the outer margins of the coracoids are preserved. The base of the scapulocoracoid bar has been heavily eroded, but the evidence which remains suggests that this was fully developed. The posterior cornua are not quite complete to their tips. The right is the best preserved, and extends laterally to just beyond the level of the glenoid, giving the coracoid a superficial resemblance in its present state to that of Muraenosaurus. However, near the broken tip (which has been squashed a little) are preserved the outer margin and part of the posterior margin. Extrapolation of these margins lengthens the horn outwards by at least 3 cm, giving the coracoid a shape similar to that of C. eurymerus. A portion of the median suture of the coracoids is preserved which shows that these elements were ~~more~~ fused posteriorly.

The preserved pelvic girdle consists of most of the ilia and ischia, and portions of the pubes. The pubes and ischia do not differ from the corresponding parts of C. eurymerus, but the ilia are smaller dorsally, and the shaft and dorsal articulation is more rounded. It is therefore possible that only two sacral ribs articulated with this small head, and that the two sacral vertebrae are in fact the full complement in this species.

The humerus does not have the characteristic expanded shape of that of C. eurymerus, and closely resembles that of Muraenosaurus leedsii. Both humeri are preserved, and have been slightly squashed, making the shaft appear a little too wide in dorsal aspect. Their posterior distal margins have been broken, but it is possible to estimate the extent of these broken portions by extrapolation of the existing margins. The distal expansion was produced very largely by the expansion in a posterior direction of the posterior distal portion. The radial facet is larger than the facet for the ulna, and their junction is posterior to the mid-line of the shaft.

The radius and ulna resemble those of Muraenosaurus leedsii. The foramen between them is clearly formed, as in 'old adult' specimens of C. eurymerus, and is not of diagnostic consequence.

The femur (only the left is preserved) has not been crushed, and the shaft retains its cylindrical shape. Largely as a result of the difference in preservation of the humeri and the femur, the latter appears much more slender in comparison with the humeri than it actually was. It is not quite so expanded distally, as in the femur of C. eurymerus, and this expansion is greater posterior to the axis of the shaft.

The tibia and fibula resemble those of all contemporary species. A foramen is formed between them as between the radius and ulna.

Numerous assorted phalanges were collected with this specimen, and are now mixed in a box. They belong to all three preserved paddles, as is shown by the plate of this specimen in Mansel-Pleydell, 1889, a plate made when the specimen was mounted and still in the collection of Mr. Nelson M. Richardson.

Genus *Muraenosaurus* Seeley, 1874

Muraenosaurus Seeley, 1874a.

Picrocleidus Andrews, 1909. (Subjective synonym)

Tremamesacleis White, 1940. (Subjective-objective synonym, *sensu* Blackwelder, 1967).

Type species:

M. leedsii Seeley, 1874a.

Additional British species:

M. beloclis Seeley, 1892.

Diagnosis:

Plesiosauroids in which

- the teeth are ornamented by many longitudinal ridges;
- the dentary bears 19-22 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 very large;
- the parietals form a sagittal crest;
- the inner margin of the quadrate overlaps the quadrate ramus of the pterygoid internally and posteriorly;
- the paroccipital process of the exoccipital-opisthotic is relatively long and slender;
- the occipital condyle is ringed by a groove, and is formed only from the basioccipital;

there are usually 44 cervical vertebrae with relatively platycoelous centra, the length of which exceeds the height in anterior vertebrae, and exceeds or is subequal to the height in posterior vertebrae;

the clavicles are absent or reduced;

the interclavicle is developed and may be large and 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 subequal 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 2 epipodials in the manus;

a foramen is present between the epipodials even in 'juveniles'.

Muraenosaurus leedsii Seeley, 1874

Plesiosaurus plicatus Phillips, 1871; Lydekker, 1888a. (*Nomen vanum*, *sensu* Simpson, 1945)

Muraenosaurus leedsii Seeley, 1874a.

Plesiosaurus leedsii (Seeley, 1874a) Whidborne, 1881.

Muraenosaurus leedsii ("Seeley, 1874a") Lydekker, 1888a; Andrews, 1909, 1910; White, 1940; Delair, 1959; Persson, 1963. (*Lapsus calami*)

Cimoliosaurus plicatus (Phillips, 1871) Lydekker, 1889b. (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Cimoliosaurus durobrivensis Lydekker, 1889b. (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Muraenosaurus platyclis Seeley, 1892; Andrews, 1909, 1910.

Muraenosaurus plicatus (Phillips, 1871) Andrews, 1895c; Delair, 1959; Persson, 1963.

Muraenosaurus durobrivensis (Lydekker, 1889b) Andrews, 1909, 1910.

Tremamesacleis durobrivensis (Lydekker, 1889b) White, 1940; Persson, 1963.

Tremamesacleis platycleis ("Seeley, 1892") White, 1940. (*Lapsus calami*)

Tremamesacleis platyclis (Seeley, 1892) Persson, 1963.

Discussion of synonymy

In 1871 Phillips described 13 vertebrae from the Oxford Clay of St. Clements, near Oxford, under the name *Plesiosaurus plicatus* (the vertebrae are now in the University Museum, Oxford, Nos. J.25929-J.25941). These were distinguished from other vertebrae (variously named) by their greater relative length and by the flatness of their articular faces. The centra were described as "ellipsospondylian" (i.e. elliptical in transverse section).

In 1874(a), Seeley described an almost complete plesiosaur skeleton in the Leeds Collection (now in the British Museum, specimen R.2421) as

Muraenosaurus leedsii. This specimen is an 'adult', in which the ossified scapulocoracoid bar is preserved. Unfortunately, the dermal elements of the pectoral girdle are missing; this absence was later apparently regarded by Seeley (1892) as a feature distinguishing M. leedsii from a second species, M. platyclis, in which they are present.

In 1888(a) Lydekker visited the collection of Mr. A. N. Leeds at Eyebury, taking with him the type vertebrae of Plesiosaurus plicatus Phillips. He found that these were indistinguishable from the vertebrae of Muraenosaurus leedsii Seeley, and, rejecting also Seeley's generic distinction, referred the Leeds Collection specimens to P. plicatus. In 1889(b) the species was included in the genus Cimoliasaurus Leidy, 1852 (mis-spelt Cimoliosaurus by Lydekker).

In 1889(b) Lydekker referred to drawings (sent to him by Leeds) of a specimen numbered '28' in the Leeds Collection (now British Museum specimen R.2428). This specimen is a 'juvenile', and lacks the skull. Lydekker distinguished it from material referred to C. plicatus (which he states it otherwise resembles) on account of its slightly shorter vertebrae and the absence of an ossified scapulocoracoid bar, and proposed for this specimen the new name C. durobrivensis. The "distinguishing features" are features typical of 'juvenile' specimens of M. leedsii and other contemporary species.

In 1895(c), Andrews, having examined the type specimens of C.durobrivensis and M. leedsii together with several more or less complete Leeds Collection specimens, concluded that "apart from variations in size and in the extent to which the arches and ribs have fused with the centra, no important differences are to be found". This variation he thought due to age and possibly to sexual dimorphism, and referred all specimens to Muraenosaurus plicatus.

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

In 1909 Andrews reversed his opinion of 1895(c), and recognised *leedsii* (which he mis-spelt *leedsi*), *durobrivensis* and *platyclis* as separate species of the genus *Muraenosaurus*. In 1910 he published diagnoses purporting to distinguish these species from each other, using as his criteria comparative size; comparative proportions and superficial features of the cervical vertebrae; proportions of the humerus, and the structure of dermal elements of the pectoral girdle. It is argued in the description below that for varying reasons Andrews' distinctions are invalid or even erroneous. His features involving comparative proportions of vertebrae and humeri are characters indicating the relative age and degree of ossification of individuals. The recognition of an interclavicle associated with the type specimen of *M. durobrivensis* and a reinterpretation of the structure of this element in the type specimen of *M. platyclis* shows the structure of the pectoral girdles to be the same. The size of individuals is variable and cannot be correlated with any other characters.

When in 1910 Andrews distinguished three species of the genus *Muraenosaurus*, he concluded that the type vertebral centra of *Plesiosaurus plicatus* Phillips, 1871, were non-diagnostic. Thus he effectually reduced the latter name to *nomen vanum* status (*sensu* Simpson, 1945). This finding is now upheld, but for different reasons. Isolated vertebral centra of *M. leedsii* and *M. beloclis* are indistinguishable except possibly by size, the latter species being the smaller. The size range of *M.beloclis* is insufficiently known, but almost certainly there is overlap between the largest specimens and the smallest specimens of *M. leedsii*.

Plesiosaurus plicatus cannot be regarded as a *nomen oblitum* as in 1959 Delair stated his opinion that "although *M. leedsii* and *M. plicatus* are undoubtedly nearly related they nevertheless present certain differences and are here regarded as distinct forms". The nature of these supposed differences was not indicated.

The earliest name applied to diagnostic material is *Muraenosaurus leedsii* Seeley, 1874(a), and this is the valid name for the species.

Holotype:

B.M.(N.H.) specimen R.2421, which is an almost complete 'adult' skeleton lacking parts of the skull, the anterior part of the pectoral girdle (with the possible exception of the interclavicle), the left pubis, the posterior extremity of the tail, and several phalanges and gastralia. It was collected by Mr. A. N. Leeds, and was described by Seeley (1874a), who figured several vertebrae (Pl. XXI). The description of the genus *Muraenosaurus* which was given by Andrews (1910, pp. 78-119) was based largely upon this specimen, and it was extensively figured (Pl. III, figs. 1, 1a, 2, 2a, 3, 3a, 6; Pl. IV, figs. 1-10). (Plate III, figs. 4, 4a and 5 in Andrews, 1910, stated to be teeth belonging with this specimen, are crocodylian and probably referable to the Oxford Clay genus *Metriorhynchus*)

Type locality:

In the Peterborough area, and south of the city. The precise locality is nowhere recorded, but is within the area and from one of the pits shown on a map published in E. T. Leeds (1956) (opposite p.16).

Type horizon:

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, p.vii).

Diagnosis:

Muraenosaurs 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 450 to 520 cm.

Distribution:

Diagnostic material is known only from the type locality.

Range:

Upper Jurassic; Callovian Stage. Known only from the type horizon.

Referred specimens:

See catalogue in Appendix.

Description of material

The description of material given by Andrews (1910, pp. 77-139; text-figs. 43-60, 62-63, 65-69; Pl. III, figs. 1-3 and fig. 6, Pl. IV and Pl. V figs. 1-9, 11-12) is extensive and accurate, with the exception of a few errors which are rectified below. He noted much variation in the size and extent of ossification of individuals, but interpreted this in terms of taxonomic characters by which he distinguished three separate species ("*M. leedsi*", *M. durobrivensis* and *M. platyclis*). This variation is now reinterpreted as a manifestation of the growth stages of a single species, and the terms 'juvenile', 'adult' and 'old adult' (as defined on page 46) are used to distinguish individuals of differing age.

The following description is intended to supplement and where necessary to emend Andrews' (1910) account.

1. The skull

Skull material is preserved with several specimens, the most complete skull being that of R.2678. It was largely upon this skull that Andrews based his description and his reconstruction (text-figs. 47 and 48). Unfortunately, this skull (which consists of numerous fragments and disarticulated elements including the only good palate so far known of an Upper Jurassic plesiosaur) has since been set in plaster for exhibition, and could not be adequately examined. I have therefore not attempted to produce a reconstruction from much less complete material, but hope to reconstruct the skull of this species from specimen R.2678 at a later date. In the present description a general account of the skull is given by comparison with the skull of Cryptoclidus eurymerus and with reference to most of the material. Emphasis is placed upon those features which I consider to be of taxonomic importance.

(a) 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) more closely resemble those of Lower Jurassic plesiosaurs and Cretaceous elasmosaurs than they do the teeth of C. eurymerus, and are ornamented by numerous longitudinal ridges. These are more prominent on the lingual side, several may rise almost to the apex, and they are closely spaced such that about 20 ridges are simultaneously visible from the lingual side. Unlike the teeth of C. eurymerus there are no especially prominent axial ridges, and the buccal side is also ridged, though here the ridges are fewer in number, especially in younger specimens, and may be largely confined to the basal half of the crown.

There are fewer teeth in the present species than in *C. eurymerus*. The complete tooth-row of at least one premaxilla, together with most or all of the maxillary tooth-row and the lower jaw, is preserved in all the above specimens except R.2863. The sizes of the teeth can be estimated from the diameter of the empty sockets or broken tooth bases.

There are five premaxillary teeth, of which the 1st (most anterior) is very small. Sometimes the small 1st tooth sockets of the left and right premaxillae may be confluent, as in the holotype (R.2421). The 2nd, 3rd and 4th upper teeth are large, and the 5th is much smaller (except in R.2427 in which the 5th tooth is only slightly smaller than the 4th). 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 teeth are very large, and the 10th is enlarged but to a lesser degree. Thereafter the teeth decrease posteriorly forming a more or less evenly graded series. Complete maxillary tooth-rows are preserved in specimens R.2422 and R.2678, and in both of these specimens the maxilla bore 16 teeth, making a total of 21 teeth in the upper jaw. In specimen R.2861 (which is an 'adult' or even an 'old adult') the premaxillae and maxillae have fused with obliteration of the suture, and there are 19 tooth sockets on either side with perhaps only the most posterior 2 sockets broken away and missing. In the holotype (R.2421) the maxillae are less complete, the best being the right with the most anterior 11 maxillary sockets preserved.

The tooth-row 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 the holotype (R.2421), and in specimen R.2861 there are 21 teeth on the left ramus and 22 on the right. Two further specimens (R.2427 in which there are 18 sockets preserved and R.2864 in which there are 20) are lacking an estimated one or two lower sockets only. In all cases the 1st (most anterior) lower tooth is of medium size, and the 2nd to 6th are large, being of similar size when fully grown to the large upper 8th and 9th teeth. The lower 7th tooth is smaller, about equalling in size the 1st, and the 8th is smaller still. From here backwards the teeth form an evenly graded series, gradually decreasing in size.

The jaws of specimen R.2678 are virtually undistorted, and it is possible to superimpose them and obtain a reasonable impression of the way in which they must have occluded. As in C. eurymerus, the upper 1st teeth bit in advance of and between the lower 1st teeth, and from here backwards to the lower 7th tooth the upper and lower teeth interlocked with each other in a one-to-one fashion. At this point, however, the width of the lower jaw decreases slightly, and above it the maxillary tooth-row bulges outwards, such that when the occluded jaws are seen in ventral view the sockets for the enlarged 8th and 9th maxillary teeth project laterally completely clear of the lower jaw rami. It is evident that the upper 8th and 9th teeth were powerful fangs which bit outside the much smaller lower teeth, resulting in an overlapping rather than an interlocking occlusion. Behind these fangs the bone outlines of the upper and lower jaws coincide, and the 10th to 13th teeth are of similar size. Here the upper and lower teeth again engaged in an interlocking occlusion. Posteriorly, the reduction in tooth size is greater in the upper than the lower jaw, but these teeth probably continued to interlock as in the reconstruction of C. eurymerus (fig. 1).

It is interesting to note that where Welles (1943, 1952, 1962) gives details of relative tooth size in Cretaceous elasmosaurs, he indicates that the first one or two maxillary teeth are small and peglike, 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 would therefore seem probable that Kuraenosaurus shows the same occlusion as that of 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 the holotype. In this specimen they fuse anteriorly in the symphysis, and extend on the inner surface of each ramus posteriorly to the position of the 16th or 17th tooth socket. At this point the splenial lies deep in the Meckelian groove, interposed between the anterior portions of the angular and surangular. These latter elements extend forwards respectively below and above the splenial to the position of the 10th or 11th tooth sockets.

The element labelled "splenial" in Andrews' (1910) figure of the posterior portion of the right lower jaw ramus of R.2678 (ibid, text-fig. 48) is not part of that element but a fragment of the dentary. The surangular and the dentary appear to interlaminate considerably at their suture, but this is only revealed when the bone is broken at this point, as in R.2678 and R.2427.

In the description of the lower jaw of C. eurymerus (p.39) reference was made to a shallow groove which separates the spongy tooth-bearing part of the dentary from the smooth and solid inner supporting bone. In the present species the grooves from the left and right rami cross part of the supporting bone in the symphysis to meet medially in a backward-pointing V. The effect of this is to separate off a diamond-shaped portion of the supporting bone in the symphysis, which is bordered left and right posterolaterally by the grooves, and left and right anterolaterally by the spongy tooth-bearing area including the alveoli of the 1st and 2nd teeth. This structure is shown in Andrews' figure of the lower jaw of R.2678 (1910, Pl. VI, fig. 2), and differs from C. eurymerus in which this area of enclosed supporting bone is triangular (cf. my fig. 3).

(b) Neurocranium

The general form of the braincase was described by Andrews (1910, pp. 78-84; text-figs. 43-45; Pl. III, figs. 1, 1a) and is very similar to that of C. eurymerus, the principal difference being in the structure of the occipital condyle. The present species resembles Tricleidus and also all Cretaceous elasmosaurs described by Welles (1943, 1952, 1962) in that this is formed entirely from the basioccipital without any participation by the exoccipitals. The articular surface of the condyle is almost perfectly hemispherical, without a median pit, and is ringed by a constriction or groove which separates it from the basioccipital-exoccipital sutures. This groove is more fully developed in 'old adults' (e.g. R.2422, see Andrews, 1910, text-fig. 44) than in 'adults' (e.g. R.2861 and R.2421, ibid., text-fig. 43 and Pl. III, figs. 1, 1a).

The fused basisphenoid and parasphenoid, the supraoccipital and the fused exoccipital-opisthotic elements are closely similar to those of Cryptoclidus, the only constant difference being the rather longer and slightly slimmer form of the paroccipital process in the present species. In the 'old adult' specimen R.2422 the basioccipital and basisphenoid have largely fused, but the dorsal median pit remains in this suture, which was traced vertically downwards to a smaller median opening between these elements on the ventral surface. The function of this pit is not known; it may have been cartilage-filled, and failed to ossify.

The prootic is not known in Cryptoclidus, and Andrews (1910, p. 84) knew of only one crushed prootic among the Muraenosaurus skull material (belonging with R.2861). However, an almost entire (though somewhat crushed) left prootic and part of the right are preserved with specimen R.2422, and were prepared to enable the semicircular canals to be traced. The element is essentially 4-sided in lateral view, but the lower posterior corner is 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 the short and almost vertical facet for the supraoccipital faces obliquely upwards and backwards, and is of about the same length as the supraoccipital facet of the exoccipital-opisthotic (2.0 cm, in specimen R.2422). The rounded anterior margin of the prootic is the longest side and was probably almost vertical.

The outer surface of the prootic is smooth and convex, and appears to be marked by three small foramena, in a horizontal row. Unfortunately, the complete left specimen has been crushed and 'telescoped' at this point, and it is not possible to trace these into or through the bone. The inner surface of the prootic is concave, and the posterior edge is hollowed for the utriculus which is shared equally with the opisthotic. The prootic also houses the anterior half of the horizontal semicircular canal, and the ventral half of the anterior vertical semicircular canal.

The left prootic and exoccipital-opisthotic elements of specimen R.2422, together with the supraoccipital and the fused basioccipital and basisphenoid, can be placed together enabling the positions and orientation of the fenestra ovalis, semicircular canals and utriculus to be ascertained. Welles (1962), in his diagnosis of the suborder Plesiosauria, stated that the fenestra ovalis and stapes are absent in the group. However, upon assembling the neurocranial elements of R.2422 the position of the fenestra ovalis becomes at once apparent. It has the form of a short duct of circular section, and its walls are formed in approximately equal thirds by the prootic, the opisthotic and the combined basioccipital and basisphenoid. Proximal to the fenestra ovalis there is no evidence of ossification around the cochlea, and this must have been encased in cartilage. Distally, a columella auris has never been found preserved in a plesiosaur skull, but judging from the well-developed state of the fenestra ovalis it was almost certainly present in some form. This conclusion is in general agreement with Andrews (1910, p. 83), who believed the columella auris to have lain in a groove on the anterior surface of the opisthotic (labelled 'c.a.' in his text-fig. 45C), which groove is now identified as the posterior wall of the fenestra ovalis. It is difficult, however, to see where the tympanum and the distal end of the columella auris might have been situated, as there is no development of an otic notch in plesiosaur skulls.

On the inner surface of the prootic and opisthotic, and immediately above the fenestra ovalis, is a spherical concavity formed equally by both elements. The opisthotic half of this cavity was identified by Andrews as the site of the ampulla of the posterior semicircular canal, but it is evidently for housing the utriculus, as it receives all three semicircular canals.

The horizontal semicircular canal lies in a horizontal plane lateral to the utriculus, and is contained equally within the prootic and opisthotic. It passes anteroposteriorly through the centre of the faces of union of these two elements. The posterior vertical semicircular canal lies in a vertical plane obliquely backwards and outwards from the utriculus. It enters the opisthotic, becomes vertical and passes upwards into the supraoccipital. In this element it completes a forward and inward U-turn to pass almost vertically downwards back towards the utriculus just below the inner angle of the junction of the supraoccipital and opisthotic, at which point its path is marked by a groove on the opisthotic. The anterior vertical semicircular canal lies in a vertical plane obliquely forwards and outwards from the utriculus; this plane is at right angles to that of the posterior vertical semicircular canal. From the utriculus it passes within the prootic in an anterior, upward and lateral direction, emerging vertically from the prootic on the face which articulates with the supraoccipital. It does not enter the latter element, but runs between the two bones in cartilage. In this part of its course it turns to continue in a horizontal, backward and inward direction towards the inner posterior angle of the supraoccipital-prootic interface, at which point it is marked by a groove on the prootic. It passes backwards, inwards and downwards from this angle to return to the utriculus. This last part of its path, and also of the posterior vertical semicircular canal, is continued in cartilage, and it is not possible to determine whether a crus commune was formed before these canals reentered the utriculus.

The three semicircular canals are of equal length. There is no preserved osteological evidence for the positions of the ampullae.

(c) The skull roof and palate

The remaining parts of the skull were described, figured and reconstructed by Andrews (1910, pp. 84-89, text-figs. 46-47, Pl. III, figs. 2, 2a and Pl. V, fig. 1). Very little can at present be added to this description as it was largely based upon the skull of R.2678 (which is much the best specimen for the preservation of these parts), and, as was previously stated, this skull has since been set in plaster which permits only a superficial study. Furthermore, the skull roof and palate of Cryptoclidus eurymerus, so far as this is known, does not differ from that of the present species except in the structure of the tooth-row, which has already been described. The most interesting part of Andrews' description is therefore that relating to the form of the postorbital bar, the jugal and the complete palate, as these are not preserved among the Cryptoclidus material.

In specimen R.2678 the postfrontal elements are preserved on both sides, and are in good condition. They are orientated in an almost horizontal plane. Only the left postorbital and jugal are preserved, and form part of a squashed and distorted fragment which also includes the major part of the squamosal. The inner surface of this fragment has been plastered, and the sutures are largely obscured by plaster or bad preservation, so that these can be less reliably reconstructed. Furthermore, the lower end of the jugal, which

Andrews (1910, text-fig. 45B) united to the posterior end of the maxilla, is definitely not preserved.

The tapering posterior termination of the maxilla is preserved in this and several other specimens, and shows no indications of a sutural contact with a more dorsal or posterior element such as Andrews suggested in his reconstruction. This condition of the maxilla was observed in all plesiosaur material studied, and poses a problem of how the back of the upper jaw was supported. Specimen R.2678 offers a solution, for in this specimen the ectopterygoids (termed "transpalatines" by Andrews) are preserved. The ectopterygoid is a small but strongly constructed element, and sutures anteriorly with the palatine, proximally with the pterygoid and distally with the posterior terminus of the maxilla along the latter's inner margin. The dorsal surface of the left ectopterygoid is visible, and bore a thick and strong process which extended upwards and slightly backwards. This process is now broken away, the broken section being an oval of length at least 1 cm. in the lateral axis and 0.5 cm. in the shorter anteroposterior axis. This process almost certainly provided the mechanical link to the temporal and postorbital bars, and it seems most probable that the jugal united with the ectopterygoid and not with the maxilla.

I am inclined to doubt the accuracy of the shape of Andrews' lateral reconstruction of the skull (1910, text-fig. 46B). Except for the comparative length of the snout, the shapes and proportions of the skull elements do not differ substantially from those of Cryptoclidus eurymerus and Tricleidus seeleyi, both of which I have been able to reconstruct (figs. 1 and 21). Certainly the shape of the lower jaw is incorrect, and the jaw articulation was substantially below the level of the tooth-row. This in turn would give the quadrate and squamosal a more vertical orientation, and I suspect that the shape of the posterior part of the skull was similar to those of C. eurymerus and T. seeleyi. Judging from the comparative length of the tooth-row and the number of teeth, the snout was proportionally shorter than in C. eurymerus and slightly longer than in T. seeleyi. Furthermore, the jaws are distinguished from the former and to a lesser extent the latter species by the great development of the upper 8th and 9th teeth.

The overall length of the skull of 'adult' specimens is 35-45 cms.

2. The postcranial skeleton

It is appropriate at this stage in the description to emphasize two points; firstly, that individuals of differing age and osteological development are preserved together in the Leeds Collection, which thus in some respects assumes the character of a population; and, secondly, that there is always to be expected some amount of size variation within an animal population, to which general rule plesiosaurs are no exception. An understanding both of the osteological development with age and of the extent of variation must therefore be reached before such groups of differing individuals can be described together as belonging to one species. It is argued below that Andrews failed to reach such an understanding, and that the three "species" which he described (1910) must be interpreted as only one when differential osteological development and variation (principally in size) are taken into account.

Andrews took three differing individuals (R.2421, R.2428 and R.2678) which had previously been described by other authors, without cross-reference, as the type-specimens of distinct species (leedsii Seeley, 1874a; durobrivensis Lydekker, 1889b and platyclis Seeley, 1892, respectively). He attempted to group the remaining individuals around them, producing diagnoses purporting to distinguish these groups, and assigning all three "species" to the genus Muraenosaurus. His diagnoses are based entirely upon features of the postcranial skeleton, and it is argued below that those may be entirely dismissed as age-associated osteological differences or as acceptable variations in size which are to be expected in any animal population over a period of time. The three specimens are now reinterpreted as belonging to the single species M. leedsii as follows:-

R.2428 has the neural arches free from the centra, and the pectoral girdle incompletely ossified, and is therefore a 'juvenile'. By comparison with other 'juvenile' specimens (the only two adequately preserved specimens being R.2424 and R.2863) it is typical and representative of this growth stage, and is slightly smaller than the smallest 'adult' specimens (see below).

R.2421 (the holotype of M. leedsii) has the neural arches fused to the centra, and the elements of the pectoral girdle, though still free, are fully formed. It is larger than all 'juvenile' forms but smaller than several other 'adult' specimens, and therefore may be regarded as a "small 'adult'".

R.2678 is also an 'adult' and is one of the largest specimens, being about 10% larger than R.2421, and may therefore be regarded as a "large 'adult'". It is interesting to note that of the two known 'old adult' specimens (in which the elements of the pectoral girdle are fused), R.3704 is actually slightly smaller and specimen R.2426 (misprinted R.2456 in Andrews, 1910) is about the same size as R.2678.

(a) Axial skeleton

The axial skeleton was extensively described and figured by Andrews (1910, pp. 92-106; text-figs. 49-60; Pl. IV, figs. 1-6a; Pl. V, figs. 1-7a; Pl. VI, figs. 4-5b).

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 C. eurymerus, 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.

The column in this last specimen can be guaranteed to be complete from the fused atlas-axis to the sacrals as the clay matrix has consolidated around the bones, and the blocks of bones can be fitted together in their exact order. A total of 3 pectorals and 19 dorsals are also preserved in specimens R.2422, R.2424 and R.2678, but in these the cervical series is incomplete. Four sacrals are preserved in specimens R.2421 and R.2863, and the tail is complete in R.2422, in which 24 caudal vertebrae are preserved.

In the holotype (specimen R.2421) the vertebral column is complete from the atlas-axis to the 8th caudal vertebra, and the centra have been mounted in order on boards, with small gaps between them amounting to rather less than might have been occupied by cartilage. The total length of this series, as mounted, is 378 cm. The length of the missing portion of the tail (by comparison with R.2422) was approximately 50 cm., and the length of the skull of R.2421 is about 37 cm. This makes a total estimated overall length of at least 465 cm. in this specimen.

The average length of the centrum taken over the range from the 25th to the 50th vertebra in R.2421 is approximately 5.6 cm. This figure is greater than the same average in all 'juveniles' including R.2428, in which specimen it is only 5.3 cm. At the same time the figure is smaller than this average obtained in several other 'adult' specimens including R.2678 and R.2861. In these, the largest individuals known, the average centrum length over the range from the 25th to the 50th vertebra is about 6.3 cm., and if it is assumed that these individuals had the same proportions as R.2421, then their overall length may have been approximately 520 cm.

Andrews used comparative size as a feature distinguishing his three "species". M. leedsii was said to be small when adult, M. platyclis was said to be larger and more massive, and the immature type-specimen of M. durobrivensis (R.2428) was also believed to have been going to be larger and more massive when adult. It is, however, evident from Andrews' descriptions that he found difficulty in assigning other material to these "species". Specimen R.2427 was assigned to *M. durobrivensis*, but he remarked that "ossification is complete, although the animal is smaller than the type specimen .... "; conversely, R.2424 was assigned to *M. leedsii* with the comment that "in this specimen ossification is not so far advanced as in the type, although it is already larger, so that probably this individual might have attained a considerably greater size than the type." Only two large specimens in addition to the type were assigned to *M. platyclis*.

The comparative proportions of the cervical vertebrae at once serve to distinguish them from those of *C. eurymerus*. As in that species, the centrum width is always greater than the height, but the length always exceeds the height and generally also the width in at least the anterior cervicals, giving a length index (see p.49 ~~44~~) in excess of 100%. Even in 'juveniles' such as R.2428 this index reaches 105% in the anterior third of the neck, and in 'adult' specimens such as the holotype (R.2421) an index of 110% or slightly more is commonly reached in the region of the 10th to 15th cervical vertebrae.

There is a decrease in the proportional length of the centra posteriorly, the length index dropping to about 80% at the pectorals. Thereafter, the variation in proportions follows the same pattern as in *C. eurymerus*, with the dorsal vertebrae only very slightly longer and the caudals proportionally slightly shorter than in that species.

By comparison with *C. eurymerus*, the neck is proportionally almost twice as long. This length is achieved not only by the development of a larger number of vertebrae (44 compared with 32) but also by the proportional lengthening of each centrum. Conversely, the tail of *M. leedsii* is proportionally slightly shorter than in *C. eurymerus* as there are less caudal vertebrae (about 24 compared with about 30) and these are each proportionally slightly shorter.

The articular faces of the vertebrae differ in shape from those of C. eurymerus and give the general impression of being flatter. It is not, however, strictly correct to describe those of M. leedsii as "flat" and those of C. eurymerus as "concave", since the vertebrae of M. leedsii became increasingly concave with age. The difference lies in the outline of a sagittal or horizontal section across the articular face. In C. eurymerus this outline is a double sigmoid curve, the centre of the articular face being concave, whilst the borders of the face are convex and continue relatively smoothly into the sides of the centrum. This shape is distinct from that of M. leedsii, in which the outline is more truly concave or even a very open V-shape, and the borders of the face form an abrupt angle with the sides of the centrum.

In 'adults' a longitudinal crest is developed on the sides of the cervical vertebrae, particularly in the anterior half of the neck, and lies midway between the facets or sutures for the cervical rib and the neural arch. Such a longitudinal crest is not found in the shorter-necked forms C. eurymerus and T. seeleyi, but is developed in elasmosaurs (Welles, 1943, 1952, 1962) and presumably functioned to assist the neck muscles in their role of supporting a very long neck. It is absent in 'juveniles' in which the neck is not so long.

An additional feature of the vertebral centra is an ornament which Andrews (1910) terms "plications" (a term first used for plesiosaur material by Phillips, 1871, in his description of Plesiosaurus plicatus, nomen vanum). These plications are small longitudinal ridges, closely spaced, which occur in bands on the sides and ventral surface of the centrum immediately adjacent to the articular faces. These are clearly shown in his Plate V, figs. 2a, 2b, 3a and 3b, and are typical of 'juveniles' and smaller 'adults'. In the largest 'adults' and in 'old adults' they become further ossified into bands of irregular rugosities, losing the neat appearance which is characteristic of younger specimens. Plications are most strongly developed in cervical vertebrae, and continue backwards onto the dorsals with decreasing prominence, eventually to disappear before the sacrals. They are presumably associated with muscle insertions.

Andrews used the proportional length of the centrum, the presence of a longitudinal ridge on cervicals and the development of "plications" as features in the diagnoses of his three "species". M. durobrivensis was typified by relatively short cervical centra, poor development of the longitudinal crest and prominent development of "plications"; M. leedsii had proportionally longer cervical vertebrae and well-developed longitudinal crests and the plications, and M. platyclis had well-developed longitudinal crests but irregular rugosities instead of "plications". These differences relate entirely to the differences in relative age and ossification of the respective type-specimens.

The ribs and chevrons of the present species do not differ in any respects from those of C. eurymerus. It should be mentioned that the development of an anterior flange on the cervical ribs is irregular as it is in C. eurymerus, but it is seldom strongly developed, and in this it appears to differ from the next species, M. beloclis.

The gastralia, though not strictly part of the axial skeleton, were described by Andrews (1910, p. 106) after the ribs, and it is convenient to mention them here. They are not so well known as in C. eurymerus, and it is not known how many rows there were in the complete plastron. The isolated elements are identical to those of C. eurymerus, suggesting a similar arrangement. I have not seen any specimens of the forked posterior element which is present in that species.

(b) Appendicular skeleton

The appendicular skeleton was described and figured by Andrews (1910, pp. 106-119; text-figs. 62-63, 65, 67-69; Pl. IV, figs. 7-10; Pl. V, figs. 8-9a, 11-12b; Pl. VI, figs. 3, 6, 6a). The pelvic girdle and the distal portions of the limbs (mesopodials and phalanges) are indistinguishable from those of C. eurymerus and need no further description. The pectoral girdle, however, differs in several important respects, and the propodials and epipodials are also distinct.

The scapulae resemble those of C. eurymerus in the structure of the posterior and dorsal rami and the formation of the scapulocoracoid bar, but differ in the form of the median suture of the ventral rami anterior to the bar. In 'juveniles' (e.g. R.2428, see Andrews, 1910, text-fig. 67) the ventral rami first contact just in advance of the developing scapulocoracoid bar, and anteriorly are separated by a V-shaped space. Further osteological development produces the scapulocoracoid bar typifying the 'adult' stage, but unlike C. eurymerus the anterior parts of the ventral rami do not contact along their entire length. They are instead separated by an elongated U-shaped notch which persists in all 'adult' and 'old adult' specimens, the posterior part of which forms part of a foramen (termed the "interscapular foramen" by Andrews) bordered jointly by the scapulae and the overlying interclavicle.

The coracoids are similar in their general structure to those of C. eurymerus, a strong horizontal interglenoid bar being formed together with thickened and curved posterolateral bars terminating in the posterior cornua. The present species, however, differs markedly from C. eurymerus in the extent to which these cornua are developed; in the 'adult' and 'old adult' they are equal to or only just in excess of the interglenoid width, which makes them substantially less prominent than in that species. No specimens are known in which the posterior margins of the coracoids are sufficiently ossified to show them engaging with the most anterior gastralia, but in the 'old adult' specimen R.3704 (see Andrews, 1910, text-fig. 67) the thin posteromedian part of the coracoids projects posteriorly well beyond the level of the cornua in a manner reminiscent of 'old adult' specimens of C. eurymerus, and it is possible that a similar interrelationship of the coracoids and gastralia existed in cartilage in this species.

The dermal elements of the pectoral girdle differ considerably from those of C. eurymerus. The interclavicle is well-developed, and the clavicles, though poorly known, are present though probably undergoing reduction.

Andrews (1910) was confused about the structure of the interclavicle, and used supposed differences of its structure in the diagnoses of his three "species". He correctly described the structure of this element in his M. leedsii from specimen R.3704 (ibid., text-fig. 62 and Pl. VI, figs. 6, 6a), in which it is clearly an oval plate-like bone with a small notch in its anterior margin, and a peg-like posterior process. In his description of M. durobrivensis, however, he described and figured a non-plesiosaurian bone accidentally associated with specimen R. 2863 (ibid., Pl. V, fig. 10) as an interclavicle with a large anterior notch, and also a posterior notch instead of a peg-like process. This confusion led him to misinterpret the structure of the interclavicle of R.2678, which he retained as the type-specimen of M. platyclis. In this interclavicle the posterior process lay between two small notches (a structure now noted in the other specimens, see below), but has been broken away at its base. Its original structure is, however, still quite clear from the relative thickness of the broken base of this process and the growth-lines on the adjacent bone surface. Andrews overlooked the broken process and interpreted the bone as having a posterior notch in the same manner as he supposed in M. durobrivensis. He figured the anterior part of the pectoral girdle of R.2678 with the interclavicle centred slightly to the right of the midline, and his "median posterior notch" is clearly the notch to the left of the broken posterior process. Further to this confusion, White (1940), relying on Andrews' descriptions, produced a classification of plesiosaurs based entirely on features of the pectoral girdle, in which he made <u>platyclis</u> the type-species of a new genus <u>Tremamesacleis</u>. The new family Tremamesacleididae was founded for its reception.

The interclavicle has now been found preserved with five specimens (R.2426, R.2427, R.2428, R.2678, and R.3704) and it is possible that a bone fragment belonging with the holotype (R.2421) may be another specimen. Four of these are shown in outline with the surface growth-pattern indicated and broken parts tentatively restored in fig. 20. They show considerable variation in size, but the basic structure is the same. The shape is that of an irregular oval plate of bone, with the longest axis being lateral. The thickest part of the bone is the centre, and the thickness decreases towards the edge until it becomes so thin that frequently the absolute margins are broken away and not preserved. Where they are preserved they are ragged and interrupted by irregular clefts. The lateral thinning of the bone is produced in such a way that the ventral surface is convex whilst the dorsal surface is flat or even concave. There is a small but regularly occurring notch in the anterior median margin of the bone, around which the edge of the bone is smooth and rounded. In the posterior margin there is a short but persistent peg-like process which is frequently triangular in section, the apex of the triangle being ventral. On either side of this short process are small clefts or notches which are irregular in size and frequently assymetrical, as in R.2678, in which there is a large left notch and a small right cleft. The interclavicle lies dorsal to the ventral rami of the scapulae, and both scapulae and interclavicle bear rugosities marking the insertions of connecting fibres.

Parts of the clavicles are preserved in R.2678 as extremely thin sheets of bone which are fused to the dorsal surface of the interclavicle. Both they and the underlying interclavicle are broken posterolaterally, and their shape cannot be reconstructed from the fragments which are preserved. A similar fragmentary scale of bone is compressed onto the left dorsal surface of the interclavicle of R.2426 ("R.2456" in Andrews), and may represent part of the left clavicle, though without a knowledge of R.2678 it would undoubtedly have been dismissed as an unidentifiable stray fragment of bone. A very different situation exists in R.2424, in which the interclavicle is not preserved, but two bones are present which are certainly plesiosaurian clavicles. The left was figured by Seeley (1892, fig. 8), and is irregularly triradiate in form. It is, however, not of the regular triangular shape found in *C. eurymerus*, in which the clavicles met in median symphysis. Andrews (1910, p. 124) questioned whether these clavicles actually belonged with specimen R.2424, or whether they were accidentally associated and from a specimen of *Cryptoclidus*. This, however, cannot be the case on osteological grounds, and furthermore, specimen R.2424 and the clavicles show an unusual preservation and colour, being mottled white and red, and in my opinion certainly belong together. The shape of the anterior part of these clavicles is not inconsistent with the shape of the fragments preserved with R.2678, the only real differences being the greater thickness of the clavicles of R.2424 and the fact that they are free. It may be concluded that the clavicles of *M. leedsii* are variable and poorly known.

There is a tendency towards fusion of the elements of the pectoral girdle in 'old adults', as in *C. eurymerus*. In specimen R.2426 the left and right coracoids are in the process of fusing, being fused ventrally but still separate dorsally. In R.3704 the coracoids are fused to each other and to the glenoid rami of the scapulae, which are themselves fused at the junction of their ventral rami. In all places this fusion only involves the ventral parts of the sutures; dorsally the elements are still separate, and there is no fusion between the scapulae and coracoids in the scapulocoracoid bar. There are no specimens in which the interclavicle is involved in fusion with the scapulae.

The humerus has a shape which is very similar to many plesiosaurs, being indistinguishable from that of *C. richardsoni* and from that of the next species except by superior size. It is probably also indistinguishable from that of many elasmosaurs. It therefore differs from that of *C. eurymerus*, which is unique in being unusually expanded distally. In *M. leedsii* the humerus does not exhibit a disproportionate expansion of the portion bearing the radial facet, and so by comparison with the humerus of *C. eurymerus* it is more L-shaped (see fig. 38). The radial facet is only slightly larger than the facet for the ulna, and never forms a sharp angle with the anterior margin. Instead, both anterior and posterior angles of the distal expansion are considerably rounded, even in 'old adults', and at the posterior angle this rounding is frequently uneven, giving the appearance of a third and posteriorly-facing facet. The proximal end of the humerus, the shaft and the positions of muscle insertions are just as in *C. eurymerus*, except that the tuberosity is not quite so strongly prominent as in that species.

The radius and ulna closely resemble those of *C. richardsoni* and many elasmosaurs, and differ considerably from these elements in *C. eurymerus*. The radius is nearly square in shape; the humeral facet, the concave anterior border and the distal facet for the radiale are almost the same length, but the facet for the ulna is rather shorter. Between the ulnal and radialial facets is a very small oblique facet for the intermedium. This distinguishes the radius of *M. leedsii* from that of *M. beloclis*, in which the intermedial facet is much larger, and of equal size to the intermedial facet of the ulna. The ulna itself is a 5-sided bone, the longest side being the humeral facet. The fairly thin posterior edge usually remains cartilage-covered, and may have articulated with a small pisiform element, though such a bone is only known in the left fore-paddle of R.2864 (Andrews, 1910, text-fig. 63). Distally the ulna bears two facets of equal size, one facing obliquely posteriorly for articulation with the ulnare, and the second facing very slightly to the anterior of the limb axis for union with the intermedium. The fifth side of the ulna faces anteriorly, and meets the radius proximally and distally. In between the radius and the ulna is a foramen, which, unlike this foramen in C. eurymerus, is usually detectable even in the youngest individuals. The combined shape of the radius and rather smaller ulna serve to offset the distal part of the limb back at a small angle to the humeral facet; this feature is common in plesiosaurs, and is much less marked in this species than in C. eurymerus.

The distal elements of the forelimb are indistinguishable from those of C. eurymerus. The left forelimb of R.2864 is almost complete, and has a phalangeal formula of 6; 12; 14; 13; 8. The 5th metacarpal has moved proximally only half its length into the distal carpal row, thereby representing an intermediate stage between Lower Jurassic plesiosaurs (e.g. Plesiosaurus dolichodeirus) in which it is entirely level with the metacarpals, and Cretaceous elasmosaurs in which this element lies entirely in the distal carpal row.

The pelvic girdle again so closely resembles that of C. eurymerus that the elements cannot be distinguished.

The femur of 'adults' is indistinguishable from that of C. richardsoni and closely similar to that of C. eurymerus. It is not quite so expanded distally as in the latter species, and the tibial facet tends to be flat whereas in C. eurymerus it is frequently concave. These features are comparative and are taxonomically unreliable. The positions of muscle insertions are as were described for that species.

The tibia and fibula are extremely similar to those of C. eurymerus and are indistinguishable in the 'old adult'. In younger specimens they may be distinguished by the presence of an interposed foramen which, as in the epipodials of the forelimb, is sufficiently developed to be detectable even in the youngest specimens.

The distal portions of the hind limb are indistinguishable from those of C. eurymerus. The left hind limb of R.2864 is especially complete, and has a phalangeal formula of 6; 13; 15; 13; 9. As in the fore limb, the 5th metatarsal is shifted proximally by only half its length into the distal tarsal row. The hind limb is very slightly smaller than the fore limb, as is usual in plesiosaurs.

Note on Andrews' reconstruction

The general similarity of the postcranial skeleton to that of C. eurymerus has been emphasized above, and the principal large-scale differences are in the relative length of the neck and tail. The shape of the body ought therefore to be reconstructed as in my reconstruction of that species (fig. 8). This involves elevating the ribs (which in Andrews' reconstruction, 1910, text-fig. 66, are incorrectly 'hung'), closing up the gastralia into a compact plastron, moving the pectoral girdle back about four vertebral lengths (it is reconstructed with the scapulae suspended beneath the cervical vertebrae) and reducing the vertical distance between the dorsal and ventral surfaces. The body shape so produced would be flatter and more turtle-like. The tail is perhaps a little too long, and it is possible that the neck may be a little too short, as no space has been allowed for cartilage. I intend to reconstruct the postcranial skeleton of this species when it becomes possible also to reconstruct the skull.

Muraenosaurus beloclis Seeley, 1892

Muraenosaurus beloclis Seeley, 1892.

Picrocleidus beloclis (Seeley, 1892) Andrews, 1909, 1910; Persson, 1963.

Holotype:

B.M.(N.H.) specimen R.1965, which is an incomplete postcranial skeleton consisting only of six cervical and two dorsal vertebrae, several rib fragments, the pectoral girdle, both humeri and ulnae and one radius. It was collected by Mr. A. N. Leeds, and was first described by Seeley (1892), who figured the pectoral girdle, radius and ulna (ibid., figs. 10-12). It was redescribed by Andrews (1910), who figured the pectoral girdle, humerus, radius, ulna and five cervical vertebrae (ibid., text-fig. 70; Pl. VII, figs. 2-4). Note: Plate VII fig. 1 in Andrews (1910), which is part of a lower jaw, was incorrectly labelled as associated with R.1965, but was correctly described in the text as associated with R.3698.

Type locality:

In the Peterborough area and south of the city. The precise locality is nowhere recorded, but is within the area and from one of the pits shown on a map published in E. T. Leeds (1956) (opposite p.16).

Type horizon:

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, p. vii).

Diagnosis:

Muraenosaurs 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 with the ulna;
- the overall length of the 'adult' is approximately 250 cm.

Distribution:

Diagnostic material is known only from the type locality.

Range:

Upper Jurassic, Callovian Stage. Known only from the type horizon.

Referred specimens:

Of the four features listed in the diagnosis, the second and third (referring to the form of the interclavicle and of the radius and ulna) are individually diagnostic, but the first (referring to the form of the cervical ribs) is not exhibited by the holotype, and the last (comparative size) is regarded as a very useful guide for distinguishing *M. leedsii* from *M. beloclis*, but not diagnostic when taken in isolation.

The interclavicle is known only in the holotype, but at least one radius is preserved with the following, which are therefore regarded as fully diagnostic specimens:-

B.M.(N.H.) R.2739 Figured Andrews (1910, text-fig. 71)

B.M.(N.H.) R.3698 Figured Andrews (1910, Pl. VII, figs. 1, 5-6a)

An additional specimen is known and is distinguished only by its relatively small size. The specimen, B.M.(N.H.) R.2429, is an 'old adult', in which the elements of the pectoral girdle are undergoing fusion, and could therefore not have reached even the size of known 'juveniles' of M. leedsii. It is therefore referred, with reservations, to the present species.

Description of material

Muraenosaurus beloclis is extremely similar in structure to M. leedsii, from which it is only distinguished by the features listed in the diagnosis. It was described and figured by Seeley (1892, figs. 10-12) and more fully by Andrews (1910, pp. 139-148, text-figs. 70-71, Pl. VII). Andrews believed the holotype and the three referred specimens (see above) to represent two species of a distinct genus, Picrocleidus. The differences in the postcranial skeleton are, however, very small, and the fragmentary skull remains preserved with specimens R.2739 and R.3698 show no difference in structure from skull material of M. leedsii. On the contrary, similarities in the structure of the occipital condyle, tooth ornament, vertebral structure and numbers, development of elements of the pectoral girdle and the form of the fore limb indicate that M. beloclis and M. leedsii are congeneric. Andrews' second species of the genus Picrocleidus, to which he referred specimens R.2429 and R.2739, was never named, and was indicated only as "Picrocleidus, sp.".

The skull is very poorly known, but sufficient is preserved to establish similarities between itself and the skulls of M. leedsii and T. seeleyi, and differences from C. eurymerus. A small portion of the posterior part of the right ramus of the lower jaw of R.3698 contains the broken stumps of several teeth, and although the full tooth ornament cannot be reconstructed it is clear that it consisted of many longitudinal ridges which occur all round the tooth. In this specimen and in R.2739 the basioccipital is preserved, and forms the entire occipital condyle, which is ringed by a constriction or groove. Badly crushed fragments of an exoccipital-opisthotic element, a quadrate and a squamosal are also preserved with R.3698, and part of the basisphenoid and parasphenoid with R.2739, but these differ only in their smaller size from those elements of M. leedsii. No skull material is preserved with the holotype.

The vertebrae of the holotype (R.1965) closely resemble those of M. leedsii. Six posterior cervical vertebrae are preserved, together with two anterior dorsals, but there are no cervical ribs. In R.3698, however, the column is much more complete, and ribs are preserved fused to many of the cervical centra. 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. This indicates that there were at least another four cervical vertebrae before the pectorals, giving a minimum count of 41. It is therefore not improbable that there were the same number of cervical vertebrae as in M. leedsii, in which 43 or 44 cervical vertebrae are found.

The anterior faces of the vertebrae are the same shape as in M. leedsii, flattish in contour and sometimes with a small central pit. The lateral longitudinal crest is also developed on the most anterior cervical vertebrae, decreasing in prominence posteriorly and disappearing by about the 25th; this feature is better shown in R.2739 than in R.3698. The cervical centra are proportionally a little wider than in M. leedsii, and the length never exceeds the width; nevertheless, the length index again rises over 100% in anterior cervicals, and in R.3698 reaches a maximum of 106% at the 16th vertebra.

The development of a prominent anterior flange to the anterior cervical ribs was noted as irregular in C. eurymerus and uncommon in M. leedsii, but is most evident in the present specimen (R.3698), and to a lesser extent in

R.2739. Lack of anterior cervical ribs and vertebrae with the holotype (R.1965) make this feature of somewhat dubious taxonomic importance, but it was used by Andrews (1910) and is included with reservations in the present diagnosis. Several of the cervical vertebrae of R.3698 were figured by Andrews (1910, Pl. VII, figs. 5, 5a, 5b).

In specimen R.2429 only ten vertebrae are preserved, these being 6 posterior cervicals, 3 pectorals and an anterior dorsal. At least the posterior five of these are in sequence, indicating that there are the usual number of 3 pectorals in this species.

The dorsal vertebrae are inadequately known and their numbers cannot be estimated, and the largest number of sacrals preserved in a single specimen is only two (in R.2739). The tail, on the contrary, is well known from specimen R.3698, in which it is complete from the last sacral to the penultimate caudal. The matrix has consolidated around the vertebrae, which are thus preserved in such a way that they can be fitted together in their exact sequence. Twenty-two caudal vertebrae are preserved, the centra of the 20th and 21st being fused, and the shape of the diminutive 22nd indicates that only a spherical lump of bone less than 1 cm. in diameter is needed to terminate the sequence. Posterior chevron facets begin on the 5th caudal, and anterior facets on the 6th, and these continue almost to the tip of the tail. From the 14th caudal backwards a ridge develops on each side of the centra in a ventro-lateral position, and in posterior vertebrae this enlarges into a projection which resembles in shape and position a cervical rib. As was pointed out by Andrews (1910), these coexist with chevron facets and therefore cannot be fused chevrons. They have never been noted in other plesiosaurs and may perhaps be an oddity of this specimen rather than a typical feature of this species.

The estimate of the overall length of the 'adult' of M. beloclis which is given as a measure of comparative size in the diagnosis (about 250 cms) was based upon the length of the 37 cervical vertebrae of specimen R.3698. This length was compared with the length of the first 37 cervical vertebrae of R.2421 (the holotype of M. leedsii), and the overall length calculated as the same proportion of the estimated overall length of R.2421 (465 cms). This assumes a similar number of vertebrae of similar proportions in the two species.

The pectoral girdle of the holotype was described and figured by Seeley (1892, figs. 10-11) and by Andrews (1910, text-fig. 70; Pl. VII, figs. 2, 2a). The scapulae are indistinguishable from those of M. leedsii, with an identical development of the "scapular foramen", and the coracoids differ only in being proportionally very slightly slimmer midway between the glenoids and the cornua. The interclavicle, which Seeley (1892) recorded as being found in situ between the ventral rami of the scapulae, appears at first sight to differ widely from that of its cogener; in M. leedsii it is broad and plate-like whereas in R. 1965 it is lanceolate and triangular in section, with the apex of the triangle ventral and the visceral surface flat. However, its anterior and wider end is marked by a median notch, the edges of which are smooth, whereas the posterior end is developed into a stout and cylindrical process, which may have terminated in cartilage. These clearly are homologous with the anterior notch and posterior peg characteristic of the interclavicle of M. leedsii, and the element could be derived from that of M. leedsii by the loss or failure to ossify of the thin plate-like lateral sections in that species.

On the left side of the ventral surface of the interclavicle is a small compressed fragment of bone not part of the interclavicle, and a similar compressed fragment adheres to the visceral surface of the right scapula. It has been argued by Seeley (1892) and by Andrews (1910) that these may represent remnants of the clavicles. Were it not for a similar preservation of what are undisputedly the clavicles in R.2678 (M. leedsii, referred) these patches would have been overlooked or dismissed as unimportant and unidentifiable bone debris. As it is, the possibility that they do represent the clavicles must be given consideration, but it would seem rather a fortunate chance that both should have been preserved in this unusual way, and not have been lost. It is better to leave the presence or absence of clavicles in this species as an open question rather than to assert their presence on the sole basis of this evidence.

The pectoral girdle is represented in one other specimen (R. 2429) by the scapulae and coracoids only. This specimen is evidently an 'old adult', as the coracoids are partially fused in the midline, and fused to the glenoid rami of the scapulae, which latter elements also fuse at the anterior meeting of their ventral rami. It is also the largest of the four specimens, but is still much smaller than any specimens of M. leedsii. As a measure for comparison, the length of the left humerus of R.2429 is 21.8 cm, whereas the humerus of R.2424, which is the smallest 'juvenile' of M. leedsii in the British Museum, is 28.3 cm. in length.

The humerus is indistinguishable in shape from that of M. leedsii. It has almost flat facets for the radius and ulna, and the anterior and posterior angles are rounded as in that species. The radius is distinct, however, as it has a considerably larger facet for the intermedium. This also gives the bone a more elongate shape. Posteriorly it meet the ulna, enclosing between these elements the usual foramen.

In the holotype (R. 1965) the ulna is somewhat unusual in that its posterior margin bears a small facet which faces obliquely posteriorly and proximally, suggesting that a small pisiform element may have existed between it and the humerus, as is found in the next species (T. seeleyi). Unlike that species, such an element could not have articulated distally with the ulnare as the ulna clearly forms the posterior margin of the limb between them. The ulna of R.3698, however, more closely resembles the typical form of the ulna in M. leedsii, and it is probable that small "accessory ossicles" may have occurred irregularly in the present species as is found in C. eurymerus.

In *M. leedsii* only one such element was observed, being in the left fore paddle of R.2864. No distal parts of the fore limb of *M. beloclis* are known.

The hind limb is represented only in specimen R.3698, in which the left femur, tibia and fibula are preserved. Except for their smaller size they are indistinguishable from those elements in *M. leedsii*.

Genus Tricleidus Andrews, 1909

(No synonyms)

Type-species by monotypy:

T. seeleyi Andrews, 1909.

Diagnosis:

As monotypic species.

Tricleidus seeleyi Andrews, 1909

(No synonyms)

Holotype:

B.M.(N.H.) specimen R.3539, which consists of disarticulated elements representing most of the skull together with 26 cervical, 3 pectoral, 5 dorsal and 2 caudal vertebrae, the pectoral girdle, proximal portions of both fore limbs, one pubis, both femora, one tibia, one fibula, two tarsals and numerous fragments of ribs and gastralia. It was collected by Mr. A. N. Leeds and was described and figured by Andrews (1909, figs. 1-2; 1910, pp. 149-163, text-figs. 72-77, Pl. VIII).

Type locality:

E. T. Leeds (1956) records helping his father to collect the holotype "from the pit worked by Messrs. Hicks and Gardner immediately across the lane from Woodston Lodge". In the 'Eyebury Catalogue' this is recorded as "pit No. 8", and is at Fletton, near Peterborough.

Type horizon:

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, p. 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 inner margin of the quadrate overlaps the quadrate ramus of the pterygoid internally and posteriorly;

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 only from the basioccipital;

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 is 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 4 epipodials.

Note: Only the 'adult' growth-stage is known.

Distribution:

Diagnostic material is known only from the neighbourhood of the type locality, as indicated on a map published in E. T. Leeds (1956) (opposite p. 16).

Range:

Upper Jurassic, Callovian Stage. Known only from the type horizon.

Referred specimens:

The following two specimens are also diagnostic:

N.M.W. specimen 19.96.G7, not previously described, which consists of both scapulae, coracoids, clavicles and the interclavicle together with both humeri.

H.M. specimen V.1800, not previously described, which is an isolated right humerus.

Description of material

The holotype (R.3539) is a very well preserved specimen, almost completely lacking in distortion due to crushing. E. T. Leeds (1956) records that his father found the disarticulated specimen 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. Notably absent are the dorsal and caudal vertebrae, most of the pelvic girdle, the phalanges and most of the gastralia, and it follows that although the series of cervical vertebrae, 26 in number, appears complete, it is very probable that some may be lost, taken at random from the column in such a way that no obvious gaps appear in the sequence.

The unique skull is so well preserved that the disarticulated elements can be placed together and their combined shape deduced with the minimum of adjustment and reconstruction. Diagrammatic reconstructions of lateral and occipital views of the skull (figs. 21 and 22) were produced by combining a large number of scale photographs of isolated or grouped elements. The results were then checked against actual measurements, but in any case the gross outlines may be almost guaranteed since the entire dorsal midline exists from the parietals to the tip of the snout, the interlock of the teeth can be checked by superimposing the jaws, the lower jaw is complete, and only the absence of the supraoccipital prevents the lower jaw from being linked back to the parietals. In the reconstructions this element was restored by comparison with the supraoccipitals of _M. leedsii_ and _C. eurymerus_.

1. _The skull_

Andrews (1910) described the skull with reference to that of _M. leedsii_. He described and figured the neurocranium extensively (text-figs. 72-74), and this part of his description is largely accurate and complete. The remainder of the skull received only a brief description. The following account is intended to supplement and where necessary to emend that given by Andrews (1910, pp. 149-156).

The lower jaw (Andrews, 1910, Pl. VIII, figs. 1, 1a) is very similar to that of _M. leedsii_, the principal difference being the smaller number of tooth sockets. There are 17 sockets on each ramus, of which the 2nd to the 8th are the largest, but the size does not greatly diminish posteriorly, and even the most posterior may be described as of medium size. It is, however, possible that an anterior pair of very small tooth sockets may lie adjacent to the symphysis and in advance of the teeth here regarded as the first. The fine state of preservation shows that the teeth were directed well outwards. This is most marked at the front of the snout, where they are inclined at only about 20° to the horizontal at the base, and due to upward curvature of the crown by about 40° at the apex.

The right ramus is the best preserved, and contains _in situ_ eight complete teeth, these being the 2nd, 4th, 6th to 10th and the 12th. These are ornamented with many longitudinal ridges as in _M. leedsii_, which are found all round the teeth and are more concentrated on their lingual sides. There are no prominent axial ridges.

Several scale-like patches of bone on the inner surface of the right dentary may represent parts of a splenial element. The form of the fused articular-surangular and of the angular are just as in _C. eurymerus_ and _M. leedsii_. The grooves which lie between the solid and spongy alveolar regions of the dentary meet in the symphysis in a backward-pointing V as in _M. leedsii_, thereby differing from _C. eurymerus_.

Both premaxillae are preserved and are almost complete, the most posterior median part being missing from each. They are triangular in shape, with the tooth-row and the premaxillary-maxillary suture meeting at right angles. The median sutural surfaces, where the two elements met, are almost straight. Each bears 5 tooth sockets of which the first is the smallest (0.3 cm in diameter), the second to fourth are considerably larger (diameter about 0.75 cm) and the fifth is almost as small as the first. The bone is thickened around the sockets, but reduces medially and posteriorly to a thin plate which partly forms the border of the external naris. In the left specimen, in which the narial border is better preserved, the suture of the premaxilla and maxilla lateral to the external naris is complete, but the posterior edge of the bone between the naris and the dorsal midline is missing. In this region the premaxilla is extremely thin, and an examination of the underside of the bone reveals a series of ridges and grooves which suggest a squamous overlap of this element with the anterior border of the frontal. This overlap extended beneath the premaxilla almost to the anterior margin of the naris. Similarly, a groove on the anterior part of the right frontal indicates that a thin median process of the premaxilla may have extended posteriorly in the midline for a further 3 cm. beyond the broken edge of the preserved parts. In this case the median suture of the premaxillae may have been 9 cm. long. The median margin of the left external naris is 0.9 cm. from the midline, that of the right is 0.7 cm, and their anterior margins are 5.0 cm. from the anterior tip of the snout. The dorsal surface of the premaxillae is ornamented with pits and ridges as seems the case in all plesiosaurs, and the internal surface is divided by a ridge which runs on each side from the tip of the snout to the middle of the premaxillary-maxillary suture. This ridge indicates the line of union with the vomers.

Both maxillae are preserved and are complete from the premaxillary-maxillary suture to their posterior extremities, but only the left has retained the dorsal antorbital process, to which also adheres a portion of the left frontal. There are sockets for 15 teeth (6th to 20th upper teeth) on each side. The most anterior (6th upper) socket is small (diameter 0.55 cm), and the 7th upper socket is only slightly larger, whereas the 8th and 9th are the largest sockets of the upper jaw, with diameters of about 0.9 cm. The 10th to 14th decrease regularly in size, the latter being the size of the small 6th socket. The remaining sockets (15th to 20th) are small and shallow, and must have borne only small and relatively weak teeth.

Posteriorly the maxilla terminates in a short wedge-shaped projection without any apparent suturing with other bones, and it is difficult to determine how the maxilla was structurally linked to the squamosal and post-orbital bar, if at all. It is possible that a few roughened ridges on the inner surface of this projection may mark the position of overlap of a small jugal element, but such a link would be mechanically weak. This problem seems universal among British Upper Jurassic plesiosaurs, and it is possible that a solution may have been found were the ectopterygoids preserved. In M. leedsii it was suggested that it was through this element, and not through the maxilla, that the connection was made. In the lateral reconstruction (fig. 21) a jugal element is reconstructed as descending to this region, an appearance which would be seen were it to attach to the maxilla or by-pass it internally to connect with the ectopterygoid. In his reconstructions of elasmosaurs, Welles (1943, 1952, 1962) never mentions this as a problem and draws the jugal boldly attaching to the maxilla in the "normal" manner.

Dorsal to the 8th and 9th upper tooth sockets the left maxilla rises to meet a downward process of the anterior end of the frontal. These elements together form a bar which separates the external naris from the orbit. The sutures in this bar are difficult to trace, the elements being almost completely fused, but a line distinguishing the lower edge of the frontal is visible on the dorsal surface opposite the position of the posterior margin of the external naris. Very faint markings on the bone below this suture may possibly indicate that a third element is involved in the formation of the bar. Elements in this position in other plesiosaurs have been variously named as prefrontals or lachrymals by Andrews (1910) and Welles (1943, 1952, 1962), both of whom have expressed difficulty in distinguishing the sutures. Several of Welles' reconstructions show the maxilla suturing directly with the frontal (e.g. in Styxosaurus snowii and Alzadasaurus colombiensis) and this pattern has been preferred in the present reconstruction. Behind the antorbital bar the dorsal margin of the maxilla continues in an outwards, downwards and backwards curve, borne on a wide flange which extends laterally and slightly dorsally for 2.7 cm. beyond the tooth-row. The flange reduces posteriorly, its margin reaching the posterior end of the maxilla. Only small parts of the palatal flanges are preserved.

In addition to the anterior portion of the left frontal referred to above, a large part of the right frontal is preserved, suturing posteriorly with the parietals. A small portion of the border of the right naris is preserved, and a comparison of this border with the narcal border of the right premaxilla, together with a comparison of the ridges and grooves of the sutural overlap of these two bones, indicates that the preserved portions of these elements just touch. This is important as it enables the entire dorsal midline to be reconstructed.

A narrow groove continuing backwards above the midline on the right frontal probably indicates the extent of the posterior median prolongation of the premaxilla. Ventromedially the frontal is thickened into a bar, where it is probably narrowly separated from its opposite as in C. eurymerus and apparently also in M. leedsii. Posteriorly, this median bar converges upon and unites with another bar, which, from their junction, curves anterolaterally to support the anterior margin of the orbit. This supraorbital bar descends anteriorly to meet the antorbital process of the maxilla. Between the median and supraorbital bars the bone is very thin, and forms a smooth external surface to the skull. Posteriorly the frontals unite with the parietals by a complex interlaminating suture immediately in front of the pineal foramen, which is thus just contacted by the frontals.

The parietals are largely fused, but a part of the suture is still visible on the occipital surface. They are similar in structure to these elements in C. eurymerus. Anteriorly the fused bones form almost the entire border of the pineal foramen, which is elongated longitudinally into an almond-shaped aperture. Lateral to the pineal foramen the parietals are expanded into broad rami which are convex dorsally, concave ventrally, and are tilted slightly backwards and downwards. These rami form the bases of the postorbital bars.

There are no elements of the left postorbital bar preserved beyond the parietal, which bears a distinct ridge opposite the pineal foramen marking the extent of the overlapping suture with the missing postfrontal or postorbital bone. There is a fragment of this element preserved *in situ* fused onto the right parietal.

Posterior to the pineal foramen the parietals form a high and narrow sagittal crest, which lies between the deep concave excavations of the temporal opening. The post-temporal bar was probably formed from the parietals and squamosals as in other plesiosaurs, but the upper parts of both are missing, as is the dorsal edge of the parietals for the temporal bars and much of the sagittal crest. In the reconstruction of the occipital view (fig. 22) I have assumed a similar arrangement of the sutures to these in *C. eurymerus* and *M. leedsii*, with the squamosals just touching in the midline above the posterior end of the sagittal crest. Posteriorly the vertical line of the suture of the parietals is visible down the entire preserved occipital surface to the facets for the supraoccipital. These form an oval area 1.2 cm anteroposteriorly and 1.8 cm. wide which faces downwards and backwards at an angle of about 45° to the horizontal. There may have been a small median foramen between the parietals and supraoccipital such as was described in *C. eurymerus* and is well shown in the next species.

Only the dorsal (post-temporal) ramus of the right squamosal is preserved, but the left squamosal is virtually complete. The latter was described and figured by Andrews (1910, p. 156, text-fig. 75) in two pieces, the anterior and quadrate rami being labelled "sq." whilst the dorsal ramus was labelled "sq'." They were separated by a natural break, not a suture, and this has now been repaired. The single element is thus triradiate, and closely similar in form to that of *C. eurymerus* and *M. leedsii*. The quadrate ramus extended over the quadrate almost to the jaw articulation, and the extent of this overlap is clearly marked by a ridge on the latter element.

The upper part of the facet for articulation with the paroccipital process of the exoccipital-opisthotic is preserved on the right squamosal fragment but is broken away on the left.

Andrews (1910, pp. 154-156, text-fig. 75) described the "left" quadrate as consisting of two elements or fractions which he labelled "q." and "q'." The "right" quadrate was said to be similar in structure, and Andrews proposed that either a symmetrical fracture had occurred in each, or his "q." represented the quadratojugal and his "q'." the true quadrate. Upon dissolving the glue binding the two portions of each "quadrate" the adjoining surfaces were found to be covered in part with matrix. This was removed with an 'Airbrasive' machine, and it was found that the four fragments could then be exactly fitted together, but with "q'." belonging to the right quadrate and "q." to the left. Andrews' text-figure 75 and his description thus relate to parts of both quadrates incorrectly assembled. As now assembled, the right quadrate is rather more complete than the left, and is closely similar to this element in C. eurymerus. Part of the surface for union with the pterygoid is preserved as a series of pits and ridges on the anterior surface of the mesial part of the right quadrate. From an examination also of the pterygoid it is evident that the overlapping suture of these two elements was arranged with the pterygoid in advance of the quadrate, which thus obscured the posterior tip of the pterygoid in occipital view. This arrangement is also found in C. eurymerus and M. leedsii as witnessed by the structure of the pterygoids, but differs from the next species (see below).

The form of the pterygoids of this species was quite accurately described by Andrews (1910, p. 154, text-fig. 74). The slender anterior ramus projected into a small socket in the posterior margin of the vomers. Posterior to this, the pterygoids lay parallel to each other and separated by a long but very narrow interpterygoid vacuity until they contacted the parasphenoid, which contact is evidenced by a small groove on the inner margins of the pterygoids. Posterior to this, two contacts of the pterygoid with the basisphenoid were achieved; the main axis of the pterygoid bears an inward-facing facet for articulation with a facet on the basisphenoid which was labelled "f." in Andrews' (1910) text-fig. 73B, and posterior and ventral to this the second contact was made through a uniquely developed basisphenoid process of the pterygoid (labelled "pt.f'." in Andrews, *ibid.*, text-fig. 73B). The final articulation with the braincase was by a large oval facet which contacted the pterygoid process of the basioccipital. This contact has the appearance of a movable joint. The dorsal flange of the pterygoid is broken away on both sides. The present species appears to differ from *M. leedsii* in that there is no prolonged process for contact with the ectopterygoid, and it must be assumed that the missing ectopterygoid in this species was proportionally larger than in *M. leedsii*.

The vomers are totally fused to form a single element, which has the shape of an arrow-head. This element bears a deep longitudinal groove on its dorsal (internal) surface, and the ventral (palatal) surface is smooth and gently convex. The lateral margins are angled obliquely upwards and outwards for suture with the palatal flanges of the maxillae, and posteriorly are developed the antero-medial borders of the internal nares. In the posterior border, at the posterior termination of the longitudinal groove, are two short and narrow notches for the reception of the anterior ends of the pterygoids. A complete anteroposterior line from the premaxillae through the vomers, pterygoids and the right quadrate is preserved in the skull which was also useful in the production of skull reconstructions.

Welles (1952, p. 98) evidently mistook the fused vomers in this specimen for nasal elements. These latter are not preserved in any species which I have seen, with the very slight possibility of an exception in R.2860 (neotype of *C. eurymerus*), and must be either lost or fused to the premaxillae or frontals.

The preserved elements of the braincase (basioccipital, basisphenoid with fused parasphenoid and both exoccipital-opisthotic elements) were adequately and accurately described by Andrews (1910, pp. 150-152, text-figs. 72-73). The occipital condyle is formed entirely from the basioccipital, and is ringed by a groove as in M. leedsii. It is relatively small and almost perfectly spherical, with no notochordal pit. On the ventral surface of the basioccipital is a small median nutritive foramen; unlike C. eurymerus, there is no median ridge. The paroccipital process of the exoccipital-opisthotic is relatively long and slender, thereby resembling that of M. leedsii and differing from C. eurymerus and the next species.

When reconstructed (see figs. 21 and 22), the skull of T. seeleyi differs markedly in proportions from that of C. eurymerus (cf. with figs. 1 and 2). The snout is proportionally shorter, giving the skull a shorter and higher appearance. The ventral outline of the lower jaw is straighter than in C. eurymerus, in which there is a pronounced downward curvature of the posterior part. The skulls are further distinguished by differences in dentition, the form of the occipital condyle and the proportions of the paroccipital process. This high and relatively short skull with fewer teeth which is found in T. seeleyi approximates much more closely to the reconstructio of the skulls of Cretaceous elasmosaurs given by Welles (1943, 1952) than does the skull of C. eurymerus.

2. The postcranial skeleton

The axial skeleton is incompletely known, and is preserved only in the holotype (R.3539). It was described and figured by Andrews (1910, pp. 156-157, Pl. VIII, figs. 5-8d). The preserved vertebrae number 26 cervicals, 3 pectorals, 5 dorsals and 2 caudals, and as noted above it is very likely that the cervical series is incomplete despite its appearance to the contrary.

The cervical vertebrae closely resemble those of *C. eurymerus*. They are not elongated as in *Muraenosaurus*, having similar proportions to those of *Cryptoclidus*, and do not develop a lateral longitudinal crest. The articular faces are deeply concave with a convex rounded border, again as in *Cryptoclidus*, and they differ only superficially from the cervical vertebrae of 'adults' of that genus by their relatively small size. They are approximately 15% smaller than the average size of similarly ossified specimens of *C. eurymerus*.

The three pectoral vertebrae may represent the complete number as in previously described forms. The dorsals and caudals resemble those of *C. eurymerus*.

The ribs and gastralia are incomplete and show no distinguishing features. Cervical ribs show a slight and irregular development of the anterior flange as in *C. eurymerus*, but this is not developed to the extent seen in *M. beloclis.*

The distinctive pectoral girdle is complete both in R.3539 (described and figured by Andrews, 1909, fig. 1 and 1910, pp. 157-159, text-fig. 76 and Pl. VIII, fig. 3) and in 19.96.G7 (identified for the first time). The scapulae resemble those of *M. leedsii*, the ventral rami meeting in the mid-line posteriorly but remaining separated anteriorly. In both specimens this separation is V-shaped, differing from that of *M. leedsii* in which the gap is U-shaped. The ventral rami extend backwards in the midline to meet the coracoids and form the scapulocoracoid bar as in 'adults' of all species so far described.

The coracoids are in form 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 *C. eurymerus*. Specimen R.3539 is probably a little older than 19.96.G7 as the median posterior edge of the coracoids is ossified further (see Andrews, 1910, text-fig. 76).

The dermal elements of the pectoral girdle are well developed in this species. In R.3539 the interclavicle (fig. 23,A) is very large and plate-like, with a small anterior notch as in M. leedsii, but most of its area is only thin. The central part is thickened in two areas, one forming a laterally orientated bar, the other a median longitudinal thickening; these meet to form a thickened area which is T-shaped. Only a small portion of the interclavicle of 19.96.G7 is preserved (fig. 23,B), and includes part of the wide anterior notch and part of the median thickening. In this specimen it is evident that the interclavicle was structurally more like that of M. leedsii than the interclavicle of R.3539, as posteriorly the median longitudinal thickening continued as a peg which was triangular in section, the apex of the triangle being ventrally orientated. The dorsal surface of the element is relatively smooth, and the ventral surface is roughened antero-laterally for attachment to the underlying ventral ramus of the right scapula. The thin lateral parts of the specimen are broken away and it is not possible to reconstruct its entire shape. It is, however, evident that the interclavicle of 19.96.G7 was smaller than that of R.3539, indicating considerable size variation of the element in this species, as in M. leedsii.

The clavicles are elongated triangular bones with a thickened antero-lateral axis (see fig. 23,C+D). In R.3539 parts of both elements are incompletely preserved (see Andrews, 1910, Pl. VIII, fig. 3), the thinner parts of the bone being broken away. In 19.96.G7 the left clavicle is almost complete and enables the form of the entire element to be described. The postero-lateral corner consists of the thickened part of the bone only, with no thin lateral extensions, and terminates in a slightly upturned point, the underside of which is roughened for attachment to the scapula. Antero-mesially the clavicle becomes expanded and laterally thinned, the final shape of the bone being triangular with a concave posterior border, a fairly straight mesial border which may have been parallel to the body axis, and a long antero-lateral border. The expansion posterior to the thickened axis is larger than the anterior expansion. The ventral surface is almost flat, the dorsal (visceral) surface convex. A small part of the right clavicle of 19.96.G7 is preserved, which includes some of the thickened axis and anterior expansion. The preserved parts of the clavicles of R.3539 closely agree in structure with those of 19.96.G7.

The fore-paddle of R.3539 was figured and accurately described by Andrews (1909, fig. 2; 1910, pp. 160-161, text-fig. 77). The humerus is relatively short and stout by comparison with that of all other species described above and below, and has a characteristic shape since only in this species does it articulate distally with four elements. Of the corresponding four distal humeral facets the most anterior facet, that for the radius, is the largest. The second and fourth facets, for the ulna and a postaxial accessory ossicle, are smaller and of approximately equal size, and between these the facet for the pisiform is the shortest. The facet for the accessory ossicle faces posteriorly, that for the pisiform obliquely posterodistally, the ulnal facet is almost exactly distally orientated and the concave radial facet faces obliquely antero-distally. The rugosities for muscle insertion are strongly developed and are arranged as in *C. eurymerus*. Both humeri are preserved with 19.96.G7, and a further specimen, an isolated find (V.1800), is also preserved. These specimens are almost indistinguishable from those of the holotype, having the same unusually small, stout and well-ossified appearance with four distal facets.

The epipodials are preserved only in R.3539. The radius is similar in shape and size to that of *M. beloclis*, having distally a moderate facet for the intermedium in addition to that for the radiale, but the anterior border differs in being convex and not concave. The ulna is small, and characteristically shaped. Anteriorly it articulates with the radius in the usual way, a foramen being preserved between these elements, but posteriorly there is a large facet for articulation with the pisiform. The anterodistal facet for the intermedium and the posterodistal facet for the ulnare are of similar length and meet at right angles. The pisiform is smaller than the ulna and is five-sided. Anteriorly it articulates with the ulna, anteroproximally with the humerus, posteroproximally with the postaxial ossicle, distally with the ulnare, and the posterior border is rounded to form part of the posterior edge of the paddle. The accessory ossicle is a thin element with a long anterior facet for the humerus, and a short distal facet for the pisiform. Its overall shape is thus elongated along the axis of the paddle. Its presence along the posterior edge of the humerus explains the apparent reduction in the distal width of that element.

The distal carpal row contains the three small carpals together with the 5th metacarpal, which has shifted proximally for almost its entire length, as in *C. eurymerus*. The phalanges are not known.

Of the pelvic girdle only one pubis is known, associated with R.3539. This, except for its smaller size, is indistinguishable from these elements in *C. eurymerus* and *M. leedsii*. (Andrews was mistaken in his belief that the pubes of *Cryptoclidus* and *Muraenosaurus* can be distinguished by the greater proportional width to length in the former genus. He confused the girdle of an 'adult' *Cryptoclidus* with one of a less-ossified 'juvenile' *Muraenosaurus*.)

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, pp. 161-162, Pl. VIII, fig. 4). These elements are indistinguishable from those of *M. beloclis* (the femur, tibia and fibula only are preserved), and differ from those of *M. leedsii* only in their smaller size. The femur has a slimmer and less massive appearance than the humerus, and is very slightly longer.

SECTION 2(i): Group II. Kimmeridge Clay plesiosaurs

Genus *Kimmerosaurus* n.gen.

Derivation of name:

From the stratigraphical position of the type-species (Kimmeridge Clay, Kimmeridgian stage) with omission of the final syllable from the stem for ease of pronunciation, together with sauros, a lizard.

Type-species by monotypy:

K. oweni n.sp.

Diagnosis:

As monotypic species.

Kimmerosaurus oweni n.sp.

Derivation of name:

In honour of Sir Richard Owen (1804-1892), who first described British plesiosaur material from Upper Jurassic deposits.

Holotype:

B.M.(N.H.) specimen R.8431, which is a disarticulated partial skull. All or parts of the following elements are preserved; 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. It was collected and presented to the British Museum (Natural History) by R. Langham, Esq., and is now described and figured for the first time.

Type locality:

Endcombe Bay (about 0.5 km. north-west of Egmont Point), 5 km. to the south of Corfe Castle, Dorset. (Also known as Egmont Bay.)

Type horizon:

Upper Jurassic, Kimmeridgian Stage. From the Kimmeridge Clay. The exposed section at Endcombe Bay consists lithologically of the Crushed Ammonite Shales, which are included (Arkell, 1933) in the zone of Pavlovia rotunda.

Diagnosis:

Plesiosauroids in which

- tooth ornament is absent;
- the teeth are greatly recurved, sharply pointed and bucco-lingually 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 inner margin of the quadrate overlaps the quadrate ramus of the pterygoid externally and anteriorly;
- 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 unknown in this genus and species.

Referred specimens:

The only known specimen is the holotype.

Description

The skull is preserved in eight pieces and an additional nine isolated teeth. The frontals, parietals, postorbital bar and squamosals are preserved associated in a single piece, and the right angular and fused surangular-articular are associated in a second piece, on the outer surface of which have been compressed two isolated teeth and an unidentifiable skull fragment. The remaining elements listed above are preserved completely disarticulated. A small fragment of bone compressed onto the left anterior part of the dentary represents a portion of the left premaxilla.

An occipital view of the skull was reconstructed (fig. 25) by combining the posterior elements of the skull, producing the right quadrate and left exoccipital-opisthotic by mirror image of the preserved opposite elements, and by restoring only the missing supraoccipital. From this reconstruction can be determined the posterior height of the skull from the parietals to the jaw articulation, and the distance between the left and right articulations on the lower jaw. As the entire right ramus of the lower jaw is preserved, the skull length can be restored; furthermore, the dorsal outline of the skull is preserved almost to the anterior margin of the orbit. It was therefore possible to reconstruct a lateral view of this skull (fig. 24) by restoring the missing outlines from the reconstruction of C. eurymerus (fig. 1). The tooth number is known for the lower jaw from empty sockets, and several teeth are preserved, and so their interlock was reconstructed on a one-to-one basis, approximately as in other forms, by assuming a similar 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).

The material was presented almost clear of the clay matrix, and the last traces were removed with an industrial 'Airbrasive' machine. This revealed the suture lines, bone growth lines and surface ornament. The specimen is remarkably well preserved, and will now be described in detail.

The dentary (fig. 26) is remarkably slender and lightly built, and in dorsal view the "spongy tooth-bearing area" (see description of C. eurymerus, p. 39) is prominent, the "solid supporting bone" being considerably reduced from the state found in Cryptoclidus, Muraenosaurus and Tricleidus. The grooves between these areas meet directly in the symphysis as in C. eurymerus, and not in a backward-pointing V as in Muraenosaurus and Tricleidus. The bone has been somewhat eroded, and the dorsal portions of the tooth sockets have been lost. However, all the ventral parts remain and as a result the sockets appear as grooves which are orientated horizontally and outwards, and only slightly upwards. In many cases the primary alveoli are clearly visible lingual to the sockets. There are 34 well preserved sockets on the right ramus, and the most posterior of these blends into a space large enough to have contained a further 2 sockets, making a total of 36. On the left ramus the posterior sockets are confused owing to erosion of the bone, and the total here is 35 or more probably 36 sockets, as in the right ramus. Ventrally the dentary has been crushed, but there appear to be no fragments of other elements of the lower jaw preserved.

A small fragment of bone which represents part of the left premaxilla (judging from its position and close fit with the dentary) is compressed onto the dentary over the 3rd to 7th left tooth sockets, and shows a series of regular convexities marking the internal bases of tooth sockets. This fragment suggests that in life the premaxilla extended posteriorly at least to the level of the 7th lower socket. As the 1st upper tooth interlocks in advance of the 1st lower tooth in all genera so far described (including elasmosaurs described by Welles, 1943, 1952, 1962), and the interlock of teeth is on a one-to-one basis at least for the length of the premaxilla, it follows that there must have been at least 8 premaxillary teeth in the present species. This figure, and also the number of dentary teeth, exceeds that recorded for all plesiosaurs except one, that being the hitherto considered "aberrant" (Welles, 1962) form Aristonectes parvidens Cabrera, 1941, which is from the Cretaceous of South America. In that genus and species there are no fewer than 15 premaxillary teeth and 58 teeth on the right ramus of the dentary.

The teeth (fig.28) are unique among 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 crowns are not circular but eliptical, being bucco-lingually compressed. They are, nevertheless, very sharply pointed, and it is notable that even in the largest teeth this point shows no sign of wear. Lack of wear on the tooth apex is a feature by which the teeth of plesiosaurs and pliosaurs can generally be distinguished, as wear almost invariably occurs on pliosaur teeth. The implications of this are discussed below (Section 3: ii,b).

The posterior part of the right ramus of the lower jaw (fig. 27) is almost complete and is not crushed. The articular and surangular appear to be fused as in other forms, but a probable line of fusion is traceable along the base of the jaw articulation as indicated in the figure. The suture between these elements and the angular is fully traceable except where it is covered, on the external surface, by unidentifiable fragments of the skull and by two teeth which have become compressed upon it; but this part of the suture is linear. Anterior to these compressed fragments the lower part of the surangular is reduced to an exceedingly thin film of bone covering the angular externally. Its outline, however, is quite distinct. Above this area the surangular is divided by a long anterior cleft which has the effect of making this a forked element, with the dorsal and ventral rami closely compressed except at the place of forking, at which a small foramen is produced between the internal and external (dentary) surfaces of the bone. This may perhaps have permitted the passage of blood vessels to the posterior part of the dentary. The position of the posterior edge of the overlapping dentary, on the external surface, is indicated by ridges which are partly overlain by the compressed fragments and teeth, and is in the same position as in Cryptoclidus, Muraenosaurus and Tricleidus. The articular is of the usual massive structure, and forms most of the retroarticular process, the part overlying the angular being thin. The angular itself is of the usual shape and anteriorly is a long and thin vertically oriented lamina of bone. It is notably curved anteroposteriorly, with the ventral edge concave, and this has the effect of lowering the jaw articulation with respect to the tooth-row. This occurs to a slightly lesser extent in C. eurymerus and hardly at all in T. seeleyi.

The largest single piece of the skull includes portions of the frontals, right postorbital and postfrontal, the parietals and the squamosals (figs. 29 and 30). Only the posterior portions of the frontals are preserved, and show the complex interlaminating sutures with the parietals. A part of the thin median portion of the right frontal above the orbit is missing and has been restored on the specimen in plaster. Insufficient space between the preserved portions has been allowed on this restoration, and in the figure the anterior portion of the right frontal is shown moved forward a further 6 mm. The frontals form the anterior border of the pineal foramen, in advance of which they suture ventrally. Dorsally they are separated by a groove in the midline which continues the lines of the dorsal border of the pineal foramen forwards between the frontals. The dorsal surface of the frontals is smooth and convex. The lateral margins form the dorsal border of the orbit, which must have been relatively large (see lateral reconstruction, fig. 24). In ventral view a shallow groove runs anterolaterally on either side of the median suture, diminishing anteriorly just before the anterior ends of the preserved parts. In section the frontals form roughly triangular bars at their narrowest parts between the orbits. Anteriorly they are expanded and become excavated by large ventral concavities. This excavation has the effect of producing two thickened bars which diverge anteriorly and are separated by thin bone. One of these bars continues forwards, meeting its opposite in the midline and continuing the line of the ventral anteroposterior grooves. The other bar curves outwards, forwards and downwards in an arc to form the anterior border of the orbit. The ventral concave surface of the anterior portion of the right frontal is marked by three shallow grooves leading to foramina which were presumably for nutrient blood vessels.

A proximal part of the postorbital bar is preserved _in situ_ on the right side. It is flat and thin, and its distal extremity has suffered much damage and repair, being extremely fragile. Nevertheless, it is quite clear that parts of two distinct elements are preserved which are probably the postfrontal and postorbital. When complete the postfrontal element probably met the posterolateral corner of the frontal in the region of its suture with the parietal; at this point the frontal overlaps the parietal dorsally. However, in the specimen this part of the postfrontal is broken away and missing, and must be reconstructed by forward extrapolation of its broken surface, which is 2 mm. thick. The remaining portion of 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 postorbital fragment is also laminate, and is exceedingly thin, being only 0.5 mm. in vertical section.

In lateral view the plane of the postorbital bar dips downwards and backwards at an angle of about 30° to the dorsal surface of the frontals and parietals. The distal end of the bar is broken and not preserved. The preserved portion shows no downward curvature, and it is not possible to determine the form of its connection, if any, with the squamosal or a missing jugal element. Accidental breaks across the bar (now repaired with plastics soluble in chloroform) showed a section which confirmed beyond any doubt the presence of the two distinct lamellar postfrontal and postorbital elements. On the left side these elements are missing, and the lateral flange of the parietal shows dorsal ridges and grooves which mark the sites of the sutures.

The parietals appear to be in the process of fusing with each other. Their suture is visible in the dorsal midline, extending from the posterior border of the pineal foramen to the posterior midline suture of the squamosals, but it cannot be traced ventrally. Anteriorly the parietals meet the frontals in a complex interlaminating suture. This extends further forwards ventrally than dorsally such that in dorsal view the frontals somewhat overlap the parietals. The pineal foramen is approximately almond-shaped, and in dorsal view is bordered equally by the frontals and parietals.

Each parietal expands to produce a flange which lies lateral to the posterior end of the pineal foramen and forms the base of the postorbital bar. The plane of this flange curves downwards and backwards reaching a maximum angle of about 45° to the dorsal surface of the parietals. Its anterior edge, together with the overlying postfrontal element, forms the upper part of the posterior border of the orbit, and continues the curve established by the lateral margin of the frontal. Behind this flange, the lateral surface of the parietal is concavely excavated for the temporal musculature.

Unlike any previously described plesiosaurian there is no development of a sagittal crest between the temporal excavations, which are separated by at least 1 cm. of dorsal surface at their closest approach. There is no possibility that this is a 'juvenile' feature and due to lack of ossification, as all known 'juveniles' of other species have a sagittal crest developed, and the shape of the concave excavations in the present specimen produce a slight "overhang" of the dorsal margin, which is clearly fully formed. In lateral view the dorsal outline of the parietals is approximately linear, and continues the lines of the frontals, whereas in most plesiosaurs the sagittal crest is elevated well above this line. The dorsal surface of the parietals is irregularly pitted, and is delineated by a sharp angle where it meets the lateral excavated surfaces.

The ventral surface of the parietal flanges is smooth, with small nutritive pits near the posterior border of the pineal foramen. Behind this, the roof of the braincase is divided into three distinct areas. In the ventral midline is a deep groove, widening and deepening into a roughened pit halfway along its length. This is surrounded by a smooth area which may possibly have been covered with cartilage. This in turn is bordered laterally by areas of roughened bone which curved downwards to form part of the walls of the braincase and united ventrally with the prootics. The margins of the latter areas are broken, and their original extent cannot be determined. The posterior part of the smooth area is inclined backwards at a slight angle to the anterior part, and forms two facets, divided by the groove, for union with the supraoccipital. With this element in place, the groove would form a mesial posterior channel leading from the occipital surface of the skull to the pit. A mesial foramen between the parietals and the supraoccipital was noted above in *C. eurymerus*, and also occurs in *M. leedsii* and *T. seeleyi*, and it was concluded that this may have held a ligament running to the neural arch of the fused atlas-axis and functioning to support the skull. Such a ligament would have its origin in the pit described above, which is roughened to provide a firm anchorage.

Posteriorly the parietals suture with the squamosals. This suture extends further forwards dorsally than it does ventrally, where the parietals are produced into posterolateral processes and play a part in the formation of the post-temporal bar. The occipital surface of the parietals is small by comparison with the other forms described above.

The squamosals are large and have been subjected to a certain amount of crushing. This has resulted in somewhat straightening the post-temporal rami and consequently spreading apart the quadrate rami. Symmetrical cracks have developed along lines of weakness which superficially suggest the presence of several fusing elements; however, close inspection reveals their true nature. Each squamosal consists of only one large ossification of the usual triradiate form. The two squamosals meet mesially above the posterior end of the parietals, where they are bulbous and form the highest part of the skull profile. They are much thicker and stronger in this region than are those of *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*, in which genera they are more neatly spliced into the upper margin of the broad occipital face of the parietals. The post-temporal ramus is strong, being more or less circular in section, with a minimum diameter of 1 cm. It expands ventrolaterally into a large plate of bone which forms the quadrate and anterior (zygomatic) rami. The anterior ramus terminates in a large sutural surface perpendicular to its axis. This sutural surface gives no indication of the nature or direction of the element or elements with which it was united.

The quadrate ramus of the squamosal is fully preserved only on the right side. It bears on its inner surface a large flat vertical facet for union with the quadrate. The dorsal (primary) head of the quadrate was housed in a socket at the end of the thickened post-temporal ramus, and a process of the squamosal descends from this for some distance along the upper border of the quadrate. On its inner surface is a facet for articulation with the paroccipital process of the exoccipital-opisthotic. The possible significance of this feature of the plesiosaur squamosal was discussed in the description of this element in *C. eurymerus* (p. 35), and it was concluded that the squamosal may be a compound bone formed by the fusion of the squamosal proper with a tabular element.

Only the left quadrate is preserved (fig. 31) and is relatively larger and proportionally longer than in *Cryptocleidus*, *Muraenosaurus* and *Tricleidus*. It has been somewhat flattened in preservation. The large vertical facet for union with the internal surface of the squamosal is 5.7 cm. long and 1.5 cm. wide and is at right-angles to the plane of the two large ovoid condyles with which the lower jaw articulated. The outer condyle is slightly the larger, and projects perpendicularly downwards a little further than the inner condyle when the squamosal facet is vertically orientated. The dorsal end of the quadrate (the primary head) is to the outer side of the bone and above the squamosal facet. It forms a strong projection, oval in section, which fitted into a socket at the lower end of the post-temporal ramus of the squamosal. It was capped with cartilage. From this projection the dorsal edge of the quadrate describes an inward, forward and downward arc which terminated along the upper edge of the pterygoid facet. The pterygoid continues the lines of this arc when the articulated elements are viewed from above.

The pterygoid facet of the quadrate is very large, vertically orientated, and faces inwards and backwards at approximately 45° to the axis of the skull. It occupies the entire inner surface of the bone from the dorsal edge to the internal margin of the inner condyle, a vertical distance of 4.8 cm. Its surface is much ridged and pitted, and measures 1.3 cm. anteroposteriorly at its widest point. The posterior margin of the pterygoid facet is straight and nearly parallel to that for the squamosal. The anterior and innermost margin is thin and broken, and may possibly have continued as a thin film of bone further forwards across the outer surface of the pterygoid, its ultimate extent being indicated by a ridge on the pterygoid. The mechanism of overlap of the quadrate and pterygoid in the present specimen is quite different from that of previously described species, in which the posterior end of the pterygoid fits into a notch in the quadrate, which overlaps the quadrate internally.

The anterior and posterior surfaces of the quadrate are smooth and concave, except where slight squashing of the bone has opened up thin cracks particularly on the anterior surface. Without this squashing the pterygoid facet would have been more parallel to the facet for the squamosal.

Parts of both pterygoids are preserved, but the right pterygoid is the most complete (fig. 32). It is an elongated element consisting essentially of a long, thin and flattened anterior (palatal) ramus and a more massive posterior portion (quadrate ramus) which is inclined downwards and backwards at an angle of about 50° to the anterior ramus and bears the facets for articulation with the quadrate and basioccipital.

The quadrate facet of the pterygoid is large, and its surface is much pitted and ridged. It is confined to the outer surface of the bone, and the posterior margin is relatively straight and even, thereby differing in form from the pterygoids of *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*. The anteroventral margin of the facet is bounded by a thickening of the bone, which forms a ridge and rises diagonally forwards and upwards across the lateral surface of the pterygoid. The upper part of this ridge is well in advance of the apparent anterior limit of the quadrate facet as indicated by the rugosities, and reaches the dorsal margin of the pterygoid at a position which was probably level with the anterior margin of the missing basisphenoid. It is possible that this ridge could mark the anterior limit of the overlap of the quadrate. However, the roughening of the pterygoid is confined to the area of overlap observable from the specimens (the anterior edge of the quadrate is broken), and it could equally be that the ridge represents the limits of a temporal muscle insertion upon the outer surfaces of the pterygoid and quadrate.

The facet for articulation with the basioccipital takes the form of an oval concave depression on the inner surface of the pterygoid, and has a much roughened floor. It faces backwards and inwards, and is in line with the axis of the anterior ramus. It is also on the opposite side of the bone from the upper end of the quadrate facet. At this point, therefore, the basioccipital and the quadrate are 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 vertical crest of bone, beyond which it again falls to the posterior end of the palatal ramus. Just posterior to this point and about 2 cm. anterior to the basioccipital facet is a crescentic depression with a roughened floor, which is a facet for union with the basisphenoid. A similar facet is found on the pterygoids of the previously described genera. There is no development of a process marking a second and more posterior contact with the basisphenoid such as is found in T. seeleyi.

Immediately in front of the basisphenoid facet the pterygoid expands to twice its lateral thickness, the increase being produced on the outer surface of the bone. From here forwards the pterygoid extends as a long flattened rod. At first this is inclined in a plane 45° to the horizontal, with the dorsal surface facing upwards and outwards, but further forwards spiralling increases this angle until at the anterior end of the pterygoid, so far as it is preserved, the plane of the bone is vertical. The bone is very thin and fragile in this area and has been broken and repaired many times, and so the twist may result from cumulative small errors in joining the very thin bone. There may also have been some post mortem distortion which would be difficult to detect in so thin an element. Whatever the cause, it is most probable that the present flat inner surface should be ventrally orientated and play a normal part in the formation of the palate as in other plesiosaurs. It is not possible, however, to judge how the anterior ramus connected to 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 (fig. 33) is proportionally a little larger than in *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*. Posteriorly it forms approximately nine-tenths of the occipital condyle, the remaining tenth being borne on the pedicles of the exoccipitals as in *C. eurymerus*. In consequence the condyle is not ringed by a groove, and a shallow groove delineates only the ventral and lateral parts of the basioccipital portion. The condyle is not circular in outline, as the dorsal concavity of the floor of the foramen magnum together with the exoccipital portions serve to make it reniform. Furthermore, its surface is not spherical as in all the above genera, but is marked by a well-developed pit slightly dorsal to the centre, which marks the position of the embryonic notochord.

The dorsal surface of the basioccipital is similar in structure to other plesiosaurs and bears two large lateral facets for the exoccipital-opisthotic element, 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 had not completely ossified. The ossified part of the braincase floor is thus Y-shaped.

The ventral surface of the basioccipital is marked by a gentle median ridge, on either side of which are two small nutritive foramina; it thus resembles the ventral surface of a plesiosaurian cervical vertebra. The anterior surface is the facet for union with the basisphenoid, and is of relatively small size, being equal only to the facets for the exoccipital-opisthotics. It is marked by a vertical median groove which, together with the missing basisphenoid, may have formed a small dorsoventral channel such as was noted in the *M. leedsii* specimen R.2422. The outline of the basisphenoid facet is elliptical, being more dorsoventrally compressed than is usual in other forms. Thus the basioccipital tapers anteriorly.

Laterally the basioccipital produces the pterygoid processes, which are short and massive. Terminally these bear facets which face obliquely anterolaterally for union with the pterygoids. They are well formed and are completely isolated from the basisphenoid facet by finished bone surface, whereas in *Cryptoclidus*, *Muraenosaurus* and *Tricleidus* they are confluent except in fully ossified 'old adult' specimens.

The exoccipital and opisthotic are fused as in other plesiosaurs. Only the right combined element (fig. 34) is preserved, but it is in almost perfect condition. The line of fusion of the two parts is indicated on the internal surface by a ridge, and at the dorsal and ventral margins by notches. The main bodies of these elements (disregarding the paroccipital process) are of a similar shape, which is almost that of a right-angled isosceles triangle, and they are fused along the hypothenuses so as to form a combined element which is approximately square in lateral view. Ventrally the exoccipital-opisthotic united with the basioccipital by a facet formed almost entirely from the exoccipital portion, whereas the dorsal facet for union with the supraoccipital was formed almost entirely from the opisthotic portion. It is not clear which part formed the paroccipital process, which in this genus is comparatively shorter and more massive than in *Cryptoclidus*, and considerably more so than in *Muraenosaurus* and *Tricleidus*. Distally this process bears a facet for union with the process of the squamosal which lies internal to the primary head of the quadrate.

As in other genera, the opisthotic portion contains the posterior half of the utriculus and portions of the horizontal and posterior vertical semicircular canals. The exoccipital portion is pierced by a large anterior jugular foramen and behind this two smaller foramina for branches of the hypoglossal nerve. Above and between these latter foramina on the internal surface is a pit or foramen which apparently terminates within the bone and was presumably for nutritive blood vessels.

The exoccipital-opisthotic, basioccipital, quadrate rami of the pterygoids and the quadrate are so well preserved and uncrushed that they can be placed exactly together. During the preparation of the reconstructions (figs. 24 and 25) it became obvious that it was necessary to orientate the basioccipital with its anteroposterior axis inclined at about 30° to the horizontal and the posterior end uppermost in order to enable the paroccipital process of the exoccipital-opisthotic to articulate with the facet on the squamosal when the quadrate and squamosal are vertical. This orientation of the basioccipital and exoccipital-opisthotic is indicated in the figures of those elements (figs. 33 and 34), and is substantiated by further osteological evidence. Only with this orientation are the horizontal and vertical semicircular canals truly horizontal and vertical; this observation also applies to the other genera described. Furthermore, it is evident from the orientation of the basisphenoid facets of the basioccipital and of the pterygoid that the basisphenoid and basioccipital form an angle of about 30° with each other (Andrews, 1910, figured these elements so orientated in *T. seeleyi*, see his text-fig. 73B). The ventral surfaces of the basisphenoid and the fused parasphenoid should be almost horizontal as they form the posterior roof of the palate; this is shown by *M. leedsii* specimen R.2678 to be flat.

The present specimen is truly remarkable and unique, being quite unlike any previously reconstructed plesiosaurian in the proportional length of the snout and the dentition. Several peculiarities (including increase in numbers of teeth, reduction in dental ornament, form of the occipital condyle, reduction in length of the paroccipital process, curvature of the angular) suggest a closer affinity to *Cryptoclidus* than to *Muraenosaurus* or *Tricleidus*. The systematic position of *Kimmerosaurus* and other genera is discussed in detail in Section 3(i).

Genus *Colymbosaurus* Seeley, 1874

Type-species by monotypy:

C. trochanterius (Owen, 1840).

Diagnosis:

As monotypic species.

Colymbosaurus trochanterius (Owen, 1840)

Plesiosaurus trochanterius Owen, 1840a; Hulke, 1870; Phillips, 1871; Lydekker, 1888a; Watson, 1924.

Plesiosaurus (Pliosaurus) trochanterius (Owen, 1840) Owen, 1841.

Pliosaurus trochanterius (Owen, 1840) Owen, 1869 (in part).

Pliosaurus portlandicus Owen, 1869; Hulke, 1870.

Plesiosaurus megadeirus Seeley, 1869, 1871; Hulke, 1870; Sauvage, 1879b; Watson, 1924.

Plesiosaurus macrodeirus Seeley, 1869. (Alternative original spelling for *P. megadeirus*; rejected by Lydekker, 1889b).

Plesiosaurus manselii Hulke, 1870.

Plesiosaurus portlandicus (Owen, 1869) Seeley, 1871.

Muraenosaurus manselli ("Hulke, 1870") Seeley, 1874b; Andrews, 1895c. (*Lapsus calami*)

Colymbosaurus megadeirus (Seeley, 1869) Seeley, 1874b, 1892; Persson, 1963.

Muraenosaurus manselii (Hulke, 1870) Sauvage, 1879a, 1879b.

Plesiosaurus manseli ("Hulke, 1870") Hulke, 1883; Lydekker, 1888a, 1889a, 1889b. (*Lapsus calami*)

Plesiosaurus megadirus ("Seeley, 1869") Lydekker, 1888a, 1889b. (*Lapsus calami*).

Muraenosaurus manseli ("Hulke, 1870") Lydekker, 1889b. (*Lapsus calami* after Hulke, 1883).

Plesiosaurus macrodirus ("Seeley, 1869") Lydekker, 1889b. (*Lapsus calami* cited in synonymy).

Colymbosaurus megadirus ("Seeley, 1869") Lydekker, 1889b. (*Lapsus calami*).

Cimoliosaurus trochanterius (Owen, 1840) Lydekker, 1889b. (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852).

Cimoliosaurus portlandicus (Owen, 1869) Lydekker, 1889b. (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852).

Colymbosaurus manselli ("Hulke, 1870") Seeley, 1892. (*Lapsus calami*).

Plesiosaurus manselli ("Hulke, 1870") Seeley, 1892; Watson, 1924. (*Lapsus calami*).

Colymbosaurus portlandicus (Owen, 1869) Seeley, 1892; Delair, 1959; Persson, 1963.

Cryptocleidus trochanterius (Owen, 1840) Sauvage, 1911. (*Lapsus calami* for *Cryptoclidus* Seeley, 1892).

Colymbosaurus trochanterius (Owen, 1840) Delair, 1959; Persson, 1963.

Colymbosaurus manseli ("Hulke, 1870") Delair, 1959; Persson, 1963. (*Lapsus calami* after Hulke, 1883).

Discussion of synonymy:

In 1840(a) Owen described a large propodial bone then in the collection of Viscount Cole (later 3rd Earl of Enniskillen) under the new name *Plesiosaurus trochanterius*. The species was subsequently referred by Owen (1841) to the subgenus *Pliosaurus*, which he raised to generic rank in 1869. All subsequent authors have recognised the type material as plesiosauroidean.

Owen's type specimen, which is a right humerus, is now in the British Museum (Natural History) and is numbered 31787. It was figured by Phillips (1871, Diagram CLXII), who correctly identified it as a humerus. The specimen was later erroneously described as a femur by Hulke (1870, 1883) and by Lydekker (1889b). Hulke mistook it for the type specimen of Pliosaurus brachydeirus, apparently due to incorrect labelling of the specimen (Lydekker, 1889b), and named another specimen (31795) as the type of Plesiosaurus trochanterius. Fortunately the real type (31787) shows several distinguishing features (see below) which were described by Owen (1840a) and Phillips (1871), and confusion of the specimens is not possible.

In 1869 Seeley described two specimens in the Woodwardian Museum (now the Sedgwick Museum), Cambridge, under the new name Plesiosaurus megadeirus. The first specimen, from the Kimmeridge Clay of Ely, was presented to the Museum by Stead Jones, Esq., and the second specimen, presented by Rev. S. Banks, came from the Kimmeridge Clay of Haddenham. The Ely specimen (now numbered J.29596-J.29691 and J.59736-J.59743, every bone being separately numbered) consists of a series of cervical, pectoral and dorsal vertebrae, portions of the coracoids and the proximal parts of both hind limbs including the femora. The Haddenham specimen (now missing) consisted of "an almost perfect vertebral column".

Seeley's description of Plesiosaurus megadeirus did not extend beyond a list of the bones preserved for each specimen, and their locations in the Museum. This led Lydekker (1888a, 1889b) to regard it as inadequate to establish a new species (the personal feud between Seeley and Lydekker has been noted elsewhere, e.g. by Tarlo, 1960). However, though the bones themselves were not described, the type-series consisting of the associated remains of two specimens clearly was. Descriptions of new species of plesiosaurs published in the mid-nineteenth century very seldom purported to distinguish the new form from all forms previously described. Seeley's description included the number of cervical vertebrae (stated as 42 in the Haddenham specimen) which in 1869 was sufficient to establish that the specimens were plesiosaurian rather than pliosaurian; as such this was the first description of associated plesiosaurian remains from the British Kimmeridge Clay. Subsequent authors including Hulke (1870, 1883) and Watson (1924) have admitted the inadequacy of the original description for subsequent comparative purposes, but at the same time have treated the name P. megadeirus as either a valid name or as a junior synonym of P. trochanterius (in either case as an 'available name' in the modern taxonomic sense). It is important to emphasise the availability of this name, as it could become the valid name for the present species if further discoveries of more complete specimens were to demonstrate that Owen's humerus (31787) is non-diagnostic (see below).

Also in 1869, Owen described a small right femur and associated paddle bones (preserved in articulation) from the Portland Stone of Portland Island, Dorset, as the type specimen of Pliosaurus portlandicus. An unusual feature of this paddle is that the distal end of the femur articulates with three epipodial bones. The relative lack of ossification of the elements, with large intervening spaces for cartilage, indicates quite clearly that the individual was a 'juvenile'; this has not previously been realised. The specimen is now in the British Museum (Natural History) and is numbered 40640.

In 1870 Hulke described and figured a large incomplete postcranial skeleton from the Kimmeridge Clay of Kimmeridge Bay, Dorset, under the new name Plesiosaurus manselii. This specimen includes most of the vertebral column, proximal parts of both left limbs including the humerus and the femur (which were confused by Hulke) and fragments of the girdles of which only the anterior parts of the coracoids are identifiable (Hulke confused their dorsal and ventral surfaces). An important feature shown by this specimen is the structure of the humerus ("femur" of Hulke), which also articulates distally with three epipodial elements. These are preserved in articulation in the specimen, and although the postero-distal part of the left humerus is missing, its shape can be partly restored (Hulke, 1870, Pl. XLI, fig. 3).

In his discussion, Hulke commented on the apparent general similarity between his specimen and those referred to *P. megadeirus* by Seeley (1869), but was prevented from making a detailed comparison by the lack of adequate description of the latter specimens. Drawings of Seeley's Ely specimen (in Hulke's possession) and a figure of the atlas of the Haddenham specimen published by Barrett (1858) indicated strong resemblances, but Hulke was advised by Mr. Davies, sen., of the British Museum (who had seen all the specimens involved) that *P. manselii* was a different species from *P. megadeirus*.

Hulke then noticed a strong similarity between the humerus ("femur") of *P. manselii* and the type humerus ("femur") of *P. trochanterius* (mistakenly calling it the type specimen of *Pliosaurus brachydeirus*, see above). He realised that the posterodistal part of the latter specimen had been broken away and the broken edge smoothed with plaster of Paris, and he implied that the entire bone would have been very similar to that of *P. manselii*. Believing both these propodials to be femora, Hulke then engaged upon a comparison between them and the type specimen of *Pliosaurus portlandicus* (which is truly a hind limb). (The latter name is now included in the synonymy of the present species, but not through the similarity of the epipodials as discussed by Hulke.)

Phillips (1871) figured the type humerus of *P. trochanterius* (from a cast) (Diagram CLXII) and also another humerus (apparently then in the collection of the Earl of Enniskillen) said to be from the Kimmeridge Clay of Foxcombe or Wheatley (Diagram CLXIII). The latter specimen (the present location of which is not known) was complete, and Phillips' description and figure clearly indicates the three distal articular facets. Independently realising that the former specimen was incomplete, he restored the missing part in dotted outline on his Diagram CLXII, indicating a third distal articular facet. He thereby unknowingly agreed with Hulke's (1870) deduction.

(Phillips did not refer to Hulke's work or to *P. manselii*, probably because of the close timing of their two publications.) Phillips' Diagram CLXIII was later copied by Lydekker (1888a, fig. 2; 1889b, fig. 63), who synonymised *P. manselii* and *P. megadeirus* with *P. trochanterius* and transferred the species to the genus *Cimoliasaurus* Leidy, 1852 (a *nomen vanum*, see Welles, 1962).

Seeley (1874b) distinguished several British genera of plesiosaurs using as his principal criterion the structure of the pectoral girdle. A pectoral girdle in the private collection of Marshall Fisher, Esq., of Ely, was described (p. 447) and figured (fig. 12) under the new generic name *Colymbosaurus*, and it was stated that this genus was "to be indicated by *Plesiosaurus megadeirus*, of the Kimmeridge Clay, in the Woodwardian Museum and in that belonging to Marshall Fisher, Esq., of Ely." Seeley also stated that these plesiosaurs "have very long necks", a feature which must have been taken from the Woodwardian Museum specimens since the girdle in Marshall Fisher's Collection was an isolated find (Lydekker, 1888a). Unfortunately the present whereabouts of the Collection of Marshall Fisher is unknown (Sherborn, 1940), and Seeley's figure and text are insufficiently explicit to be of descriptive value.

In 1892, Seeley modified his diagnosis to enable *Colymbosaurus* to be distinguished from *Muraenosaurus*. In this publication features of the pectoral girdle were not used since the then known elements of the *Colymbosaurus* girdle were indistinguishable from those of *Muraenosaurus*. Instead, the diagnosis rested upon 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, these being *C. megadeirus*, *C. manselii* and *C. portlandicus*, and Seeley evidently believed that these could be distinguished by the comparative form and number of the epipodials (he misinterpreted *C. manselii* as having four epipodials, and distinguished *C. portlandicus* by features which are now held to indicate that the type specimen is a 'juvenile').

It is here argued that *Colymbosaurus megadeirus*, *C. manselii* and *C. portlandicus* are synonyms, and that because of the identity of form of the humeri of the type specimens of *C. manselii* and *P. trochanterius*, the latter and earlier specific name is also a synonym and has priority. The holotype of *C. trochanterius* is therefore an isolated and imperfect humerus, whereas the diagnosis (which in essence is similar to that given by Seeley in 1892 for the genus *Colymbosaurus*) lists characters shown by the humerus, femur, epipodials, vertebral column and pectoral girdle (see below). It is felt that such a diagnosis is justified at the present time since it is based upon many specimens which, though individually incomplete, do overlap by their preservation of at least one diagnostic propodial, as follows:-

The holotype humerus (31787) is identical in form with that of the type of *P. manselii* (40106). The latter specimen is the most complete known, and also includes diagnostic epipodials and a femur, together with most of the vertebral column. The surviving syntype of *P. megadeirus* (J.29596, etc., see above) includes both the femora and a major part of the vertebral column, which are indistinguishable from those of 40106. Two humeri in the Manchester Museum (L.3165 and L.3166), are identical in form with those of 31787 and 40106, and are associated with a pectoral girdle (without a catalogue number) including a scapula which displays a further diagnostic feature. No other complete scapulae are known.

The type specimen of *P. portlandicus* (40640) consists of a femur associated with two epipodials and the impression of a third together with several additional paddle bones of a 'juvenile' specimen. The presence of three epipodials is in agreement with the structure of *P. megadeirus* (J.29596 etc.) and with material in the Castle Museum, Norwich (no catalogue numbers). This specimen (40640) is from the Portland Stone, a higher horizon than the Kimmeridge Clay, but I have included its name in the synonymy of the present species since the material cannot be osteologically distinguished.

It must be emphasized that Colymbosaurus trochanterius is poorly known by comparison with the species so far described. There are no complete specimens upon which to base the description; indeed, there is no skull material known which can in any way be associated with diagnostic material. Further finds of complete specimens may well indicate that more than one species is represented by the presently referred specimens. In such an event, much currently known material would prove to be non-diagnostic, and the name Colymbosaurus trochanterius would become a nomen vanum (sensu Simpson, 1945).

Holotype:

B.M.(N.H.) specimen 31787, which is a large and probably 'old adult' right humerus. The specimen is incomplete posterodistally, the broken surface having been smoothed over with plaster. The shaft has also been broken medially and joined with excessive plaster, this probably lengthening the specimen by about 2.5 cm. It was collected by Viscount Cole (later 3rd Earl of Enniskillen), described by Owen (1840a) and figured from a plaster cast in the Oxford Museum by Phillips (1871, Diagram CLXII).

Type locality and type horizon:

Owen (1840a) said that the type specimen came from the Kimmeridge Clay of Shotover Hill, Oxfordshire; but in 1871, Phillips recorded that the Earl of Enniskillen had informed him that this statement was incorrect, and that although several specimens similar to the type had been collected from that locality and horizon, the type specimen described by Owen was taken from the Oxford Clay of Christian Malford, Wiltshire. Lydekker (1889b) expressed doubt that the specimen could have come from the Oxford Clay, since there were no similar specimens known from that horizon, but he then unsatisfactorily compromised the statements of Owen and Phillips by giving the horizon and locality as the Kimmeridge Clay of Wiltshire. In view of the fact that many specimens similar to 31787 are known, all of which are from the Kimmeridge Clay, it seems more reasonable to accept the locality and horizon given by Owen in 1840(a) 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 border;
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, is 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 approximately 500-660 cms.

(Note: The skull is unknown in this species.)

Distribution:

Diagnostic material is known from several sites in England ranging from Kimmeridge Bay, Dorset, through Oxfordshire and Cambridgeshire to Downham Market, Norfolk.

Range:

Upper Jurassic, Kimmeridgian and Portlandian Stages. Almost all the referred specimens were taken from the Kimmeridge Clay, but of these only one specimen (40106) can be more accurately placed. This specimen was stated by Hulke (1870) to have been found in the cliffs to the east of Clavell's Tower in Kimmeridge Bay. These cliffs are composed of "clay with stone bands" (Arkell, 1933) and are stratigraphically part of the Upper Kimmeridgian Stage, zone of *Pectinatites pectinatus*.

Specimen 40640, which was originally purchased by the British Museum from a Dorset dealer, is said to be from the Portland Oolite of Portland Island (Owen, 1869). The adherent matrix is Portland Stone rather than Portland Sand and this specimen is therefore from the zone of *Titanites giganteus* (of Arkell, 1933).

Referred specimens:

See catalogue in Appendix.

Description of material

Colymbosaurus trochanterius is the largest of the British Upper Jurassic plesiosaurs, reaching a probable overall length of 660 cm. The propodials, which are the most frequently recovered elements, are readily distinguished by their large size and relative length, as well as by their development of three distal articular facets. The largest single specimen is the holotype (31787), with a total actual length (discounting the plaster involved in a repair to the shaft, see above) of 57.5 cm. This compares with 39.5 cm. and 36.1 cm. for the longest humeri of *Cryptoclidus eurymerus* (R.8621) and *Muraenosaurus leedsii* (R.2425).

The overall length was estimated for the two specimens in which a considerable part of the vertebral column is preserved, these being specimens 40106 and J.29596, etc. In the former specimen the column is almost complete (see below), and the numbers and length of the missing vertebrae were estimated. The length of all vertebrae was totalled, and this figure was increased by 10% to allow for intervertebral cartilage (as was the practice in estimates for other species). This gave an estimated length for the postcranial skeleton of 570 cm. The assumption was made that this species would have the same skull-length to postcranial-length ratio as *Muraenosaurus leedsii* (which has 44 cervical vertebrae, compared with 42 in *C. trochanterius*), and so by comparison with R.2421, the skull of specimen 40106 could have been 45 cm. long. This gives a total estimated length in the specimen of 615 cm. A similar procedure with specimen J.29596, etc. gives an estimated length for that specimen of 500 cm. If the humeral length to overall length ratio was the same in specimens 40106 and 31787, then the overall length of the latter specimen (the holotype) may have been as great as 660 cm.

The vertebral column is known only in specimens 40106 and J.29596, etc. In the latter specimen the column is apparently complete anteriorly from the fused atlas-axis to the middle of the dorsal series. There are 42 cervical vertebrae (including the atlas-axis as two) followed by 3 pectorals and 11 dorsals. The articular faces are concave, especially so in the most anterior vertebrae, but this concavity is never as strongly developed as in the vertebrae of *Cryptoclidus eurymerus*. The proportions of the centra are similar to those of *Cryptoclidus*, and unlike *Muraenosaurus* the length of the cervical centra never exceeds the height. The neck of *Colymbosaurus* is therefore lengthened (by comparison with *Cryptoclidus* or *Tricleidus*) by an increase in the number of vertebrae but not by increasing their proportional length.

Specimen 40106 complements specimen J.29596, etc., being relatively complete posteriorly. Unfortunately, however, many of the centra are badly chipped or damaged and a few have been badly distorted, so that it is not easy to assign every centrum to its place on the column. The fused atlas-axis is preserved, posterior to which there is a large gap followed by a further 30 cervicals. The gap could well have contained 10 vertebrae, which would then have given a count of 42 cervicals as in J.29596, etc. There are 22 vertebrae which can be positively identified as dorsals, 3 which are certainly sacral, and a further 7 badly preserved centra which may represent 3 pectorals, 3 dorsals and another sacral. If this determination is correct, there are 3 pectorals, 25 dorsals and 4 sacrals. Posterior to these are 20 well-preserved caudal vertebrae, and it is evident that between two of them there is a small gap for perhaps a further 3 centra. The caudal series is incomplete posteriorly, but it is unlikely that any more than 6 or 7 vertebrae are missing. The tail is thus of similar relative length and proportions to that of <u>Cryptoclidus</u>. Posterior chevron facets begin on the fourth caudal, and posteriorly from the tenth caudal vertebra both posterior and anterior chevron facets are present.

A few fragments of ribs and gastralia are preserved with Specimen 40106, and are similar to the corresponding parts of all other plesiosaurs.

The best pectoral girdle is that (un-numbered) in the Manchester Museum which is associated with L.3165 (see catalogue in Appendix and fig. 39,E). Both coracoids and the left scapula are preserved. The coracoids are similar in form to those of <u>Tricleidus</u>, the width across the posterior cornua being slightly in excess of the interglenoid width. The posterior cornua are therefore porportionally slightly longer than in <u>Muraenosaurus</u>, but not developed to the extent seen in <u>Cryptoclidus</u>. Anteriorly, the coracoids meet backwardly extending processes of the ventral rami of the scapulae to form a scapulocoracoid bar, as in the 'adults' of all other Upper Jurassic species in which the pectoral girdle is known.

The scapula of the Manchester specimen is of a distinctive form (see fig. 39,E), and was described by Watson (1924). The ventral ramus ("anterior ramus" of Watson) is greatly expanded anteroposteriorly, not only in the midline, as is predominantly the case in previously described genera, but laterally where it meets the base of the dorsal ramus. The dorsal and ventral rami are thus confluent, and their combined anterior margin is convex, thereby differing from Cryptoclidus, Muraenosaurus and Tricleidus in which the base of the ventral ramus is constricted into a bar. The extremity of the dorsal ramus is broken off, but the major part remains and forms an upright strengthened projection as also in the above genera. It is not "of very small size, being thin and weak in consonance" as was stated by Watson (1924, p. 903), and the scapula of Colymbosaurus differs from that of Muraenosaurus only in the relative development of the ventral ramus. The ventral rami meet in the midline throughout most of their length, being separated in only their most anterior parts by a small V-shaped notch. There are no ridges, depressions or other indications of the position of clavicles or an interclavicle in this specimen. It is possible that the reduction of these elements which was noted in the descriptions of species from the Oxford Clay may have resulted in their elimination in Colymbosaurus, as is probably the case in many Cretaceous elasmosaurs.

Only the anterior interglenoid portions of the coracoids are preserved with specimens 40106 and J.29596, etc., and no other pectoral girdle remains associated with diagnostic material are known. The pelvic girdle is not known from any specimens, except that a few indeterminable bone fragments associated with 40106 were described by Hulke (1870) as probably parts of the pelvic girdle.

Of both the forelimb and hindlimb only the propodials and epipodials are adequately known. The humerus (fig. 38,F) is a proportionally large element, strongly built with a cylindrical shaft. The holotype (31787), is the humerus of an 'old adult' individual, and shows the 'old adult' character which was noted in previously described genera, namely that the cartilage-covered areas of the head and the tuberosity are separated by a strip of finished bone surface. The tuberosity lies obliquely dorsal and posterior to the head, and forms a prominent posterior angle when seen in proximal view, as in the humeri of other plesiosaurs. This relationship of the tuberosity to the head always provides the best means of distinguishing humeri from femora, in which the trochanter is dorsal but never posterior to the head (cf. fig. 17,A and C of Cryptoclidus eurymerus).

Distally the humerus is expanded in a manner similar to that described in Muraenosaurus, almost all the expansion being posterior to the axis of the shaft. Three distal facets are formed for articulation with the epipodials. The radial and ulnal facets are approximately equal in size, the radial facet facing distally and obliquely slightly anteriorly. The ulnal facet makes a small angle with the radial facet and faces distally and obliquely very slightly posteriorly. Posterior to this the smaller facet for the pisiform faces obliquely postero-distally. Specimens L.3165, L.3166 and specimen 46479 (the latter is rather small and probably 'juvenile') are entire and show the complete form of the distal facets, whereas the remaining specimens including 31787 and 40106 have the postero-distal part of the humerus partly broken away.

Three epipodials have been found only with specimen 40106, and only a further two ulnae are known, these being associated with the Manchester specimen and numbered L.3177. Specimen 40106 has suffered badly from pyritic decay since its original description (Hulke, 1870), and all that now remains of the epipodials of the forelimb are the anterior parts of the radius and ulna. These have been fortified with cement and varnish to prevent further crumbling, and little can now be made of their structure. Fortunately, however, Hulke's description is detailed and the specimens were figured (Hulke, 1870, Pl. XLI, fig. 3, and 1883, fig. 7). Both the radius and the ulna ("tibia" and "fibula" of Hulke in 1870, who confused the fore and hind limbs) were described as pentahedral, and the pisiform (Hulke did not give this element a name in 1870) was five or six-sided and approximately equal in size to the radius and the ulna. The three epipodials were evidently held together by matrix, and from their combined shape Hulke was able to estimate the original posterodorsal outline of the humerus ("femur").

In 1870, Hulke (in a footnote) wondered if a crack in the pisiform was a natural suture, indicating a total of four epipodials; but in 1883 he returned to his original description of three elements. He revised his nomenclature calling the elements "tibia", "intermedium" and "fibula", but it is evident from a knowledge of Oxford Clay plesiosaurs that where more than two epipodials are formed the additional elements occur as postaxial ossifications, posterior to the ulna or fibula. It is now customary to call the most anterior of these elements the "pisiform" (e.g. Andrews, 1910; Watson, 1924; Welles, 1943, 1952, 1962).

Except for the usual and characteristic difference in the development of the humeral tuberosity and the femoral trochanter mentioned above, the femur of C. trochanterius is very similar to the humerus. The distal end is expanded to only slightly less than the width of the humerus, and three articular facets are also developed. Two specimens of femurs are preserved entire, these being the left femur (not numbered) on display in the Castle Museum, Norwich (an 'adult'; fig. 35), and specimen 40640 (a 'juvenile' individual) (see Owen, 1869, Pl. IV), but specimens 40106 and J.29596, etc. have femorae which are almost entire and whose shape may be easily reconstructed. The size and relative orientation of the three epipodial facets is as in the humerus.

The three epipodials of the hind limb are known only in specimen 40640, in which they are retained in situ by the matrix, and the pisiform (termed the "fabella" by Owen, 1869) is preserved only as an external mould, the bone itself having been lost. Tibiae and fibulae are also preserved with the Norwich specimen and with J.29596, etc. The tibia and fibula (fig. 35) are 5-sided as are the radius and the ulna. The facet on the tibia for the intermedium is less than half the length of that facet on the fibula. The fibula is an almost bilaterally symmetrical element with a long femoral facet, short facets for the tibia and pisiform, and almost equal facets for the intermedium and fibulare. The pisiform impression in 40640 is only 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 are preserved, and also the first (most anterior) three metatarsals. There is space between these elements for a great deal of cartilage, and the bones themselves have rather rounded outlines, this testifying to the 'juvenile' nature of the individual. The tibiale articulates with the first, and by a small facet also the second distal tarsal. The intermedium articulates with the second and to a lesser extent the third distal ~~facet~~ tarsal. The fibulare bears two almost equal distal facets, one facing obliquely anterodistally and articulating with the third distal tarsal, and a second facing obliquely posterodistally, evidently for articulation with the fifth metatarsal (which element is either missing or covered by the matrix). The fifth metatarsal has therefore completed its proximal migration into the distal tarsal row in this species.

Miscellaneous additional plesiosaurian material

The following specimens from the Kimmeridge Clay or later Jurassic deposits cannot be referred with certainty to either *Kimmerosaurus oweni* or *Colymbosaurus trochanterius*, and may represent additional species or be evidence of the survival into Kimmeridgian times of species known from the Oxford Clay.

(a) Isolated teeth

Three teeth in the Sedgwick Museum and numbered J.30069, J.30070 and J.30071 were collected and presented by J. Carter, Esq., from the Kimmeridge Clay of Ely. The crowns were approximately 3 cm. long, and J.30070 (fig. 36) is complete almost to the apex. It is ornamented with a large number of longitudinal ridges which are confined largely to the lingual side, and are absent from the buccal side. The tooth therefore resembles in size and ornament the teeth of 'juvenile' specimens of *Muraenosaurus leedsii* (in 'adult' specimens of that species buccal ridges are also present). In section the crown is somewhat flattened bucco-lingually. These teeth differ considerably from those of *Kimmerosaurus oweni*, and it is not possible to assign them to any genus. They may be referrable to *Colymbosaurus trochanterius*; they may equally represent a hitherto undescribed species, or be an indication that the range of the genus *Muraenosaurus* extends upwards into the Kimmeridge Clay.

A single isolated tooth in the Sedgwick Museum, numbered J.14270a, was labelled "from the Portland Oolite" (with no other data), and was recently freed from a piece of matrix (now numbered J.14270b) by Dr. Forbes. The matrix is a hard pale-coloured sandy limestone, which is in keeping with its original label. The tooth itself (fig. 37) has a crown approximately 4 cm. long, which is cylindrical in section. It is ornamented by numerous longitudinal ridges which are longer and more pronounced on the lingual side. The longest ridges do not extend from the base more than two-thirds up the cusp, and so the apical third of the cusp is smooth and without ornament. This tooth resembles the teeth of *Muraenosaurus leedsii* or *Tricleidus seeleyi* in general form, except in the degree of lack of ornament near the cusp. It differs markedly from the teeth of *Cryptoclidus eurymerus* and *Kimmerosaurus oweni*, but is generically non-diagnostic, and the comments made above for J.30070 also apply here.

(b) Lower jaw symphysis

Specimen L.9412, in the Manchester Museum, is the anterior portion of a dentary collected by K. C. F. Manning and said to be from the Kimmeridge Clay. It consists of the symphysis together with the left ramus posteriorly to the fifth tooth socket and the right ramus posteriorly to the eighth socket. The mature teeth are broken off and only their bases remain, but two immature teeth are present and are ornamented by longitudinal ridges. The specimen is indistinguishable from lower jaws of *Muraenosaurus leedsii* and *Tricleidus seeleyi*, but differs widely from *Cryptoclidus eurymerus* and *Kimmerosaurus oweni*. As with the isolated teeth above, it may be referrable to *Colymbosaurus trochanterius*, to the genus *Muraenosaurus* or *Tricleidus* or to an undescribed form.

(c) Vertebrae

Several large vertebrae in the Castle Museum, Norwich (un-numbered), and collected by C. B. Rose from the Kimmeridge Clay of Downham Market, almost certainly represent an undescribed species. There is no guarantee that any of the specimens are associated. The largest specimen is an 'adult' cervical centrum, which 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. It is thus, to the best of my knowledge, the largest plesiosaurian vertebra from the British Upper Jurassic. Furthermore, it is quite distinct from the vertebrae of *Colymbosaurus trochanterius* since it has flat articular facets, and each end is ringed by an ornament of "plications" such as were described in the vertebrae of 'juvenile' specimens of *Muraenosaurus leedsii*. It would, however, be folly to name the species on the evidence of only these vertebrae. They differ from those of *M. leedsii* only in size and known geological range, and they will probably ultimately prove to be non-diagnostic or at the best referable only to a genus, as is the case with all other isolated vertebrae from the British Upper Jurassic.

Several vertebrae in the Castle Museum, Norwich, and in the Sedgwick Museum, Cambridge (un-numbered except for one, specimen J.29717) are indistinguishable from those of *Cryptoclidus* and *Tricleidus*, being of small size with strongly concave articular facets. These specimens, however, are recorded as taken from the Kimmeridge Clay. They could be referable to either of those genera, indicating that their ranges extend upwards into the Kimmeridge Clay. They could also be referable to *Kimmerosaurus oweni*, in which the postcranial skeleton is unknown but the skull is known to be similar in size and several other details to that of *Cryptoclidus eurymerus*. A third possibility is that they represent part of an undescribed species.

SECTION 2(ii) REJECTED NAMES

The rejection of all names in this section is subjective. The rejected generic names (a) and specific names (b) are listed in alphabetical order. Synonymies are limited to usage (such as binomial combinations and spelling variants) only of the name under review, and only when this is not now a junior synonym.

The type-speci~~es~~men or type material is briefly indicated, and then the current (subjective) status of the name is given. Where the name is now regarded as a junior synonym, no further remarks are given as these appear in the discussion of the synonymy of the senior synonym (q.v).

A frequent cause for the rejection of a name is that it is a *nomen vanum*. Such names (Simpson, 1945) are published and described so as to satisfy the criteria of availability (*sensu* Stoll, *et al*, 1964), but are founded upon non-diagnostic type material. In one case where there is doubt about the diagnostic nature of the type material, and yet it cannot be demonstrated to be non-diagnostic (because the material has been lost), I have treated this name as a *nomen dubium* (a *nomen dubium* is defined, e.g. by Blackwelder, 1967, as a name of doubtful validity). As this name also proved to be a *nomen oblitum* I have included it as a rejected name.

Nomina oblita (*sensu* Stoll *et al*, 1964) are forgotten names which have "remained unused as senior synonyms in the primary zoological literature for more than fifty years", and are not to be used unless the International Commission on Zoological Nomenclature so directs. In my interpretation of the key words "primary literature", I have discounted mere listing of a name in a taxonomic catalogue, but have included any further remarks with reference to a name which indicate that the author has positive reasons for regarding the name as valid.

(a) Rejected genus-group names

Apractocleidus Smellie, 1915

Type-species:

A. teretipes Smellie, 1915.

Status:

Subjective-objective junior synonym (*sensu* Blackwelder, 1967) of *Cryptoclidus* Seeley, 1892; the synonymy of the genera is objective so long as the synonymy of their type-species (*A. teretipes* and *C. eurymerus*) is subjectively maintained.

Picrocleidus Andrews, 1909

Type-species:

P. beloclis (Seeley, 1892).

Status:

Subjective junior synonym of *Muraenosaurus* Seeley, 1874.

Tremamesacleis White, 1940

Type-species:

T. platyclis (Seeley, 1892).

Status:

Subjective-objective junior synonym of *Muraenosaurus* Seeley, 1874; the synonymy of the genera is objective so long as the synonymy of their type-species (*T. platyclis* and *M. leedsii*) is subjectively maintained.

(b) Rejected species-group names

Plesiosaurus affinis Owen, 1840(a)

Holotype:

A small humerus or femur from the Kimmeridge Clay of Headington pits, Oxford, and originally in the Collection of Viscount Cole. Present location unknown, presumed lost.

Status:

Nomen dubium; *nomen oblitum*.

Remarks

Viscount Cole's Collection was sold to the British Museum (Natural History) in the mid-nineteenth century, and was included in the catalogue of Lydekker (1889b), where, however, the type of *P. affinis* is not recorded.

Plesiosaurus brachistospondylus Hulke, 1870.

Cimoliosaurus brachistospondylus (Hulke, 1870) Lydekker, 1889(b). (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852).

Colymbosaurus brachistospondylus (Hulke, 1870) Bogolubov, 1912; Delair, 1959; Persson, 1963.

Holotype:

B.M.(N.H.) specimen 45869, which consists of five dorsal vertebrae, several rib fragments, a distal phalanx and an indeterminate carpal or tarsal, preserved in three slabs of Kimmeridgian Clay-stone from Kimmeridge Bay, Dorset. The specimen was collected by J.C. Mansel-Pleydell and described and partly figured by Hulke (1870, Pl. XLI, figs. 7-9).

Status:

Nomen vanum.

Remarks

The rib fragments and distal limb bones are diagnostic only to the suborder Plesiosauria. The vertebrae have centra with concave faces which appear four times as high and wide as they are long. Dorsal vertebrae appear particularly prone to crushing and distortion, and it is evident that these have undergone crushing in an axial direction. This has had the effect of spreading out the articular faces and compressing the length, both effects being individually relatively slight but combining to produce a relatively greater distortion. Restored, the vertebrae would probably have been half as long as wide, and thereby had similar dimensions to the dorsal vertebrae of *Colymbosaurus trochanterius* or *Cryptoclidus richardsoni*. Lydekker (1888a) suggested that they had been crushed in this way, but then reversed his opinion in 1889(b).

Cimoliosaurus brevior Lydekker, 1889(b). (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)
Cimoliasaurus brevior Lydekker, 1889(b). Corrected spelling used by Persson, 1963.
Muraenosaurus brevior (Lydekker, 1889) Sauvage, 1911.

Holotype:

B.M.(N.H.) specimen 41955, which consists of six associated mid-cervical vertebral centra of a 'juvenile' individual from the Kimmeridge Clay of Weymouth, Dorset. Described and figured by Lydekker (1889b, fig. 75).

Status:

Nomen vanum.

Remarks

The centra have similar general proportions to the 'adult' centra of *Colymbosaurus trochanterius*, but 'juvenile' centra of that species are not known in association with more diagnostic material. The centra are also very similar to 'juvenile' cervical centra of *Muraenosaurus leedsii*, but it is not known whether the range of the latter species extends beyond the Oxford Clay.

Plesiosaurus brevis Owen, 1854

Holotype:

The centrum of a cervical vertebra from the Oxford Clay of Wiltshire, once in the Museum of the Royal College of Surgeons of London and numbered 249 by Owen (1854). Subsequently destroyed by a fire in the museum.

Status:

Nomen vanum; *nomen oblitum*.

Remarks

Owen (1854) described the centrum as "twice as broad as long, and slightly concave at both ends: the costal surfaces are continuous with those for the neural arch". The absence of the neural arch indicates that the specimen was 'juvenile', and the concave articular facets imply that it may have been referrable to the genus *Cryptocleidus* or to *Tricleidus seeleyi*.

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

Holotype:

See under *Plesiosaurus phillipsi* Sauvage, 1879(a).

Status:

Junior homonym of *P. carinatus* Cuvier, 1824, and replaced by *P. phillipsi* Sauvage, 1879(a). (q.v.)

Plesiosaurus doedicomus Owen, 1840(a)

Holotype:

B.M.(N.H.) specimen R.273, which is an indeterminate non-plesiosaurian bone of elongated shape, heavily eroded at each end, and with a superficial resemblance to a plesiosaurian propodial.

Status:

Nomen vanum. (Not plesiosaurian.)

Remarks

Lydekker (1889b) regarded the holotype as an immature propodial, and referred it to *P. truncatus* (q.v.), which was without justification since the syntypes of that name are vertebrae. My finding is in agreement with that of Persson (1963).

Cimoliosaurus durobrivensis Lydekker, 1889(b). (*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Holotype:

B.M.(N.H.) specimen R.2428.

Status:

Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874. (q.v.)

Plesiosaurus ellipsospondylus Phillips, 1871

Holotype:

Nine cervical vertebrae in the Oxford Museum and numbered J.12083 and J.25942-J.25949. From the Kimmeridge Clay of Shotover, Oxfordshire. Described by Phillips (1871) who said that they were associated.

Status:

Nomen vanum; *nomen oblitum*.

Remarks

Phillips (1871) gave the author of this name as Owen, and Lydekker (1889b) cited it as "ex Owen, MS." Owen in fact never published the name, but there still exists with the specimens a label reading "*Pl. elliptospondylus*" in Owen's handwriting.

The vertebrae are extremely similar in form to the posterior cervical vertebrae of *Cryptoclidus eurymerus* or *C. richardsoni*, having concave articular facets and being relatively short, although they are marginally larger than the largest size usually attained by these Oxford Clay species. Lydekker (1889b) retained the name, but as generically indeterminable. Persson (1963) rejected it without giving his reasons.

Plesiosaurus hexagonalis Phillips, 1871

Holotype:

Oxford Museum specimen J.12068, which is a worn mid-caudal vertebral centrum from the Kimmeridge Clay of Cowley Pit, Oxfordshire.

Status:

Nomen vanum; *nomen oblitum*.

Remarks

The "hexagonal" shape of this centrum is typical of the centra of 'juveniles' of most species of plesiosaurs, including all British Upper Jurassic forms in which the tail of the 'juvenile' is known. There are no further distinguishing features, and the centrum is diagnostic only to the suborder Plesiosauria.

Plesiosaurus infraplanus Phillips, 1871

Syntypes:

Three isolated cervical vertebral centra from the Kimmeridge Clay of localities in Oxfordshire, and preserved in the Oxford Museum. They are numbered J.12069 (from Stanford), J.12087 (from Brill) and J.12088 (from Shotover).

Status:

Nomen vanum; *nomen oblitum*.

Remarks

Features shared by these three centra include their relative length (length exceeds height), their flat articular faces, the presence of "plications" and the fact that they are from 'juvenile' individuals as witnessed by the lack of fusion with the neural arches. They are indistinguishable from 'juvenile' cervical centra of *Muraenosaurus leedsii* and *M. beloclis*, and were they from the Oxford Clay they could be attributed to that genus with reasonable confidence. Similar vertebrae, but larger in size than any of *M. leedsii*, are known from the Kimmeridge Clay of Norfolk (see above, under "Miscellaneous additional plesiosaurian material"), which may or may not belong to the same species as the present vertebrae. Should such a species be proved to be new by the finding of a complete skeleton, differing osteologically as well as by superior size from *M. leedsii*, then their vertebrae in isolation may not even be generically diagnostic.

Plesiosaurus levis Owen, 1854

Syntypes:

Two dorsal centra and a neural arch from the Kimmeridge Clay of Shotover Hill, Oxfordshire, once in the Museum of the Royal College of Surgeons of London and numbered 245 and 246 by Owen (1854). Subsequently destroyed by fire.

Status:

Nomen nudum; *nomen oblitum*.

Plesiosaurus manselii Hulke, 1870

Holotype:

B.M.(N.H.) specimen 40106.

Status:

Subjective junior synonym of *Colymbosaurus trochanterius* (Owen, 1840) (q.v.).

Plesiosaurus megapleuron Owen, 1854

Colymbosaurus megapleuron (Owen, 1854) Delair, 1959; Persson, 1963

Holotype:

"Four cervical vertebrae in natural sequence, slightly dislocated, and united by petrified lias clay" (Owen, 1854) from an unknown locality, once preserved in the Museum of the Royal College of Surgeons of London and numbered 233. Subsequently destroyed by fire.

Status:

Probably a *nomen vanum*; not from Upper Jurassic deposits.

Remarks:

Delair (1959) listed this as a valid species from the Portland Stone of the Isle of Portland, since the name was applied by Damon (1860) to vertebrae from this horizon (the whereabouts of Damon's material is unknown). However, Owen's reference to "lias clay" implies that the holotype came from Lower Jurassic deposits. Until the Lower Jurassic plesiosaurs have been reviewed the status of this name will not be known; but, being based solely upon vertebrae, it is almost certain to prove to be a *nomen vanum*.

Plesiosaurus oxoniensis Phillips, 1871

Syntypes:

Several isolated finds of material from various Oxford Clay sites in Oxfordshire, originally and probably still preserved in the Oxford Museum. Phillips (1871) mentioned (a) six cervical vertebrae from Long Marston; (b) various dorsal vertebrae; (c) rib fragments; (d) eight caudal vertebrae; (e) a pectoral girdle (described as a pelvis); (f) a femur; (g) various isolated paddle bones.

Status:

Nomen vanum.

Remarks

The type material apparently consists of an assemblage of bones referable in part to all Oxford Clay species. No parts are diagnostic of a single species. The syntypes cannot now be identified amongst a mass of unlabelled isolated plesiosaurian bones in the Oxford Museum.

The name Cryptoclidus oxoniensis (Phillips), or the mis-spelt form Cryptocleidus oxoniensis, has been used incorrectly by several authors (including Andrews, Welles and Persson) for the species here described as Cryptoclidus eurymerus (Phillips, 1871) (q.v.).

Plesiosaurus phillipsi Sauvage, 1879(a)

Holotype (or syntypes):

One cervical, two pectoral and six dorsal vertebrae of a 'juvenile' individual (or individuals) in the Oxford Museum, and numbered J.12070 (the cervical) and J.25920-J.25927 (the pectorals and dorsals). Phillips (1871) gave the locality as Quainton, Buckinghamshire, and added that they were probably, but not certainly, from Portland Rock.

Status:

Nomen novum for Plesiosaurus carinatus Phillips, 1871 (non Cuvier, 1824). Nomen vanum; nomen oblitum.

Remarks

The vertebrae are clean and completely clear of the matrix. It is therefore most unlikely that they came from a hard matrix such as Portland Stone. More probably they were found in Kimmeridge or Oxford Clay, which could be washed off the specimens without the need for acid (a technique not known to Phillips).

The vertebrae are similar to those of Muraenosaurus leedsii or M. beloclis, being relatively long and having flat articular facets and "plications", and may possibly be referable to that genus.

Plesiosaurus planispondylus Damon, 1860

Syntypes:

"Saurian bones" (unidentified) from the Oxford Clay of Radipole backwater and Greenhill, Dorset. Delair (1959) recorded that this material had been lost or misplaced, but is believed to have been originally in the Dorset County Museum, Dorchester.

Status:

Nomen nudum.

Muraenosaurus platyclis Seeley, 1892

Holotype:

B.M.(N.H.) specimen R.2678.

Status:

Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874 (q.v.). Named by White (1940) as the type-species of his genus *Tremamesacleis* (q.v.).

Muraenosaurus (Cryptoclidus) platymerus Seeley, 1892

Holotype:

B.M.(N.H.) specimen R.2412.

Status:

Subjective junior synonym of *Cryptoclidus eurymerus* (Phillips, 1871) (q.v.). *Nomen oblitum*.

Plesiosaurus plicatus Phillips, 1871

Cimoliosaurus plicatus (Phillips, 1871) Lydekker, 1889b.

(*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Muraenosaurus plicatus (Phillips, 1871) Andrews, 1895c

Holotype (or syntypes):

Eight cervical and five dorsal vertebrae from the Oxford Clay of St. Clements, Oxfordshire, numbered J.25929-J.25941 (and not necessarily associated) which are preserved in the Oxford Museum.

Status:

Nomen vanum.

Remarks

Phillips (1871) also described, under a separate heading "*Plesiosaurus plicatus*", eight cervical vertebrae from the Kimmeridge Clay of Shotover, Oxfordshire. It is however, evident that Phillips intended the type material to be the Oxford Clay specimens, as he said (p. 313), with reference to these specimens, "If not identical with species in the Kimmeridge Clay, they are very closely allied to them". The type locality was not given, but faded labels on the specimens, readable only in ultra-violet light, indicate that they were from St. Clements (note: Delair, 1959, incorrectly gave the locality as Summertown, and the number of vertebrae as six).

The vertebrae, which are from an 'adult' individual (or individuals) are relatively long with flat articular faces and show "plications", which, however, are not so pronounced as in 'juvenile' individuals of the genus *Muraenosaurus*. They may be referable to *Muraenosaurus* but are specifically non-diagnostic.

Pliosaurus portlandicus Owen, 1869

Holotype:

B.M.(N.H.) specimen 40640.

Status:

Subjective junior synonym of Colymbosaurus trochanterius (Owen, 1840) (q.v.).

Plesiosaurus subdepressus Owen, 1854

Holotype:

The centrum of a cervical vertebra from the Kimmeridge Clay of Nuneham, Oxfordshire, once preserved in the Museum of the Royal College of Surgeons of London and numbered 248. Subsequently destroyed by fire.

Status:

Nomen nudum; nomen oblitum.

Apractocleidus teretipes Smellie, 1915

Holotype:

Specimen V.1091 in the Hunterian Museum, University of Glasgow.

Status:

Subjective junior synonym of Cryptoclidus eurymerus (Phillips, 1871) (q.v.). Type-species of the genus Apractocleidus Smellie, 1915 (q.v.).

Plesiosaurus truncatus Owen, 1854

Cimoliosaurus truncatus (Owen, 1854) Lydekker, 1889b.

(*Lapsus calami* for *Cimoliasaurus* Leidy, 1852)

Muraenosaurus truncatus (Owen, 1854) Sauvage, 1911

Holotype:

The centrum of a cervical vertebra of a 'juvenile' individual from the Kimmeridge Clay of Shotover, Oxfordshire, once preserved in the Museum of the Royal College of Surgeons of London and numbered 228. A second centrum, numbered 229, was named but not described. Both specimens were subsequently destroyed by fire.

Status:

Nomen vanum.

Remarks

Owen's description of 228 was sufficient only to indicate that the centrum was free from the neural arch (not preserved), and was therefore from a 'juvenile' individual. In 1888(b) Lydekker mentioned the existence of a large Kimmeridgian form "allied to *Plesiosaurus plicatus*", for which he proposed to adopt Owen's name *P. truncatus*. In 1889(b) he synonymised two further names with it (*P. subdepressus* and *P. doedicomus*), produced an elongated diagnosis from the material so obtained, and (in a footnote, p. 230) took as the type material not Owen's original centrum but several vertebrae from the Kimmeridge Clay of Oxfordshire to which Phillips (1871) had applied the (Oxford Clay species) name *P. plicatus*. This unorthodox action caused all subsequent authors, including Sauvage (1911), Delair (1959) and Persson (1963) to list *P. truncatus* as a valid specific name.

Plesiosaurus validus Phillips, 1871

Syntypes:

Phillips (1871) based this name upon several series of vertebrae from the Kimmeridge Clay of Oxfordshire and preserved in the Oxford Museum. This included two sets of cervicals (one of which included 26 vertebrae), a few dorsals and "lumbars" and a series of caudals. The only details of their localities given was that nine caudals came from Baldon. The majority of the original syntypes cannot now be distinguished, except for a series of 15 cervicals (numbered J.28542-J.28556) which are labelled "Plesiosaurus validus. Cumnor."

Status:

Nomen vanum; nomen oblitum.

Remarks

Lydekker (1888a) compared the type vertebrae of P. validus with those of P. manselii Hulke, and found "an absolute identity between the two." In 1889(b), he formally synonymised this species with Colymbosaurus trochanterius (calling it Cimoliosaurus trochanterius). The surviving vertebrae do indeed resemble those of that species, but they are also extremely similar to those of the genus Cryptoclidus. Isolated vertebrae of British Upper Jurassic forms cannot be regarded as specifically diagnostic.

Plesiosaurus winspitensis Seeley, 1871

Holotype:

Two cervical vertebrae preserved associated in a piece of Portland Stone from Winspit, Isle of Purbeck, Dorset. Preserved in the Sedgwick

Museum, Cambridge, and numbered J.5345 and J.5346. Seeley (1871) also mentioned a pectoral vertebra, but this cannot be found.

Status:

Nomen vanum; nomen oblitum.

Remarks

The vertebrae are relatively elongated with relatively flat articular faces, and therefore similar to those of the genus Muraenosaurus (and also many American elasmosaur species from Cretaceous deposits according to Welles (1943, 1953, 1962). Isolated vertebrae such as these are non-diagnostic.

SECTION 3 DISCUSSION

(i) TAXONOMY, EVOLUTION and CLASSIFICATION

(a) Characters employed in taxonomy

The history of the classification of plesiosaurs, and the principal characters employed by previous taxonomists in the production of their classifications, was reviewed in Section 1 (iv) and (v). Early classifications based on a single or a very few characters (such as the classification proposed by White in 1940 and based entirely upon features of the pectoral girdle) were discredited, and the importance of considering together all the features available for observation (first emphasised by Welles in 1943) was stressed. Welles (1943) listed and discussed twenty-two features of the plesiosaur skeleton which vary and may therefore be employed as taxonomic characters. However, he was not always able to recognise and distinguish between ontogenetic variants and variants of real evolutionary (and hence taxonomic) significance; the American species which he studied are not adequately represented by specimens of differing and intergrading developmental stages. Fortunately, as has been shown in Section 2 above, this handicap does not apply to British material. Moreover, it has been possible to observe the variation of further osteological features and so to add to Welles' list. Before proceeding to a discussion of the probable evolution within the Plesiosauria, and the presentation of a classification, I will list and comment upon the characters employed in taxonomy in the present and in previous work.

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 from 3 to 5 metres, whereas late Cretaceous forms may reach a length of 8 to 12 metres, and be proportionally more massive.

2. Relative skull size.

The skull may remain relatively small, or show a chronological trend towards increase in size. The skull size has frequently been indicated by expressing its length as a proportion of the length of the neck, but this is inclined to be misleading as neck length tends to decrease with relative increase in size of skull in many, but not all forms. Comparison of skull size with trunk size overcomes this difficulty.

3. Tooth form.

Teeth of forms with a relatively large skull have relatively large roots, and a relatively short, wide-based and slightly curving crown which usually shows considerable wear at its tip. Forms with a relatively small skull have teeth with proportionally slimmer crowns which are slightly more curved and show little or usually no wear on their tips. Usually teeth are circular in section, but may be sub-triangular (in pliosaurs from the Kimmeridge Clay reviewed by Tarlo in 1960), and exceptionally (in Kimmerosaurus) may be bucco-lingually compressed and show a curvature of up to 90°.

4. Tooth ornament.

The teeth of almost all plesiosaurians (except Kimmerosaurus) are ornamented by numerous longitudinal ridges. The pattern of these ridges is distinctive and therefore taxonomically useful in some genera (pliosaurs from the Oxford Clay reviewed by Tarlo, 1960, and the genera Cryptoclidus and Kimmerosaurus in the present work), but little attention has been paid to this feature in forms outside the Upper Jurassic, and the extent of its usefulness is not known. There is some ontogenetic variation in tooth ornament, the 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 correlated with a small skull, and is only as thick as the thickness of more posterior parts of the mandibular rami. A long symphysis is one which is expanded anteroposteriorly, and bears the alveoli of several pairs of teeth. This type of symphysis is correlated with a relatively large skull, and varies considerably in form and in the number of teeth borne.

6. Number of teeth on lower jaw ramus.

The number of teeth borne by each ramus of the dentary varies slightly within each species, and generally an old individual will have one or two teeth more than a juvenile. There are, however, considerable differences in the number of teeth from genus to genus. The range of variation in lower tooth numbers is much less in Lower Jurassic genera than in those from the Upper Cretaceous, and trends to increase or decrease the toothrow are evident. The tooth-row of Lower Jurassic plesiosaurs has seldom been accurately counted and described, but from my own observations Plesiosaurus dolichodeirus has about 24 teeth in each lower ramus, whereas Macroplata longirostris and Rhomaleosaurus zetlandicus (both large-skulled forms with a 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 American Upper Cretaceous genus Dolichorhynchops has 26 (D. osborni) or 34 (D. willistoni) (Welles, 1962). There is therefore no obvious trend in these large-skulled forms to increase or decrease the tooth-row. The small-skulled long-necked forms, on the other hand, show a definite trend to decrease the tooth-row; the Upper Jurassic genus Muraenosaurus has about 22 pairs of lower teeth (present work), and in Upper Cretaceous forms this is reduced to between about 18 (in Styxosaurus) and 14 (in Thassalomedon) (Welles, 1952). Only two genera with a short symphysis do not follow this trend. These are *Kimmerosaurus*, with 36 pairs, and the South American Upper Cretaceous genus *Aristonectes*, which has 53 pairs of lower teeth (Cabrera, 1941).

7. Number of teeth on the premaxilla.

There are usually 5 teeth borne by each premaxilla, and this number is probably primitive for the group. Five premaxillary teeth appears to be normal for large-skulled short-necked types, but this needs to be checked in Lower Jurassic forms and was not recorded by Tarlo (1960) in Upper Jurassic pliosaurs. The small-skulled long-necked forms of the Jurassic appear always to have 5 premaxillary teeth. In the Upper Jurassic genera *Muraenosaurus* and *Tricleidus* the most anterior tooth is reduced in size as in most Cretaceous forms, and in the Cretaceous genera *Thassalomedon* and *Styxosaurus* this tooth is lost, reducing the count to four (Welles, 1952). Welles (1943) recalled that Williston (1903) had noted 6 alveoli in the premaxilla of the long-necked genus *Brancasaurus*; but unfortunately this specimen had never been examined by himself (Welles, 1962). Apart from this reference, there are only three genera in which the premaxilla bears more than 5 teeth. These are *Cryptoclidus* with 6, *Kimmerosaurus* with at least 8, and *Aristonectes* with 15.

8. Regularity of dentition.

Forms with a large skull and a long symphysis tend to develop large "caniniform" teeth towards the tip of the snout around the symphysis and on the premaxillae, posterior to which the teeth are smaller and form a regularly decreasing series. Early small-skulled forms with a short symphysis have a regular dentition, without any precocious development of "caniniform" teeth. Upper Jurassic and Cretaceous forms with a short symphysis and showing a tendency to increase the tooth number (i.e. the genera *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes*) retain this regularity, but in the majority of genera showing a trend towards reduction in tooth number it becomes disrupted to a varying extent. Except for the small anterior premaxillary teeth, the remaining teeth on the premaxilla tend to become enlarged. The most anterior maxillary teeth are generally small, posterior to which are borne one or more very large teeth in a position beneath the anterior margin of the orbit. The most posterior maxillary teeth are very small. The lower tooth-row is generally more regular, the largest teeth occurring beneath the premaxillary-maxillary suture.

9. Parietal crest.

Williston (1903) stated that the parietals may form a high thin crest or be without such a crest, but almost certainly the feature to which he referred was the ontogenetic development of the sagittal crest which occurs in virtually all forms. In the juvenile the crest is the last part of the parietals to ossify, but it is nevertheless apparent from the shape of the ossified basal part of the parietals of such juveniles that a crest will be developed. In Kimmerosaurus, however, a crest is never developed, and the lateral excavations of the parietals are separated by at least 1 cm. of dorsal surface, which actually overhangs the dorsal edge of the excavations. Kimmerosaurus appears to be unique in this respect.

10. Pterygoid structure.

The structure of the pterygoid is adequately known for only a few genera, but in these there is considerable variation. The manner of contact with the quadrate varies. Usually the pterygoid is overlapped posteriorly by the quadrate, which develops a rough socket for its reception; but in Kimmerosaurus the pterygoid overlaps the quadrate posteriorly, and the latter element produces a large flange which extends forward along the lateral surface of the pterygoidal quadrate ramus. There is also variation in the manner of contact with the braincase, and the form of facets and processes on both the pterygoid and the braincase elements differs from genus to genus. Knowledge of pterygoidal variation is limited outside British Upper Jurassic small-skulled genera, and so wide-ranging conclusions cannot be drawn.

11. Paroccipital process.

In his diagnosis of the suborder Plesiosauria, Welles (1962) included as a character "paroccipital processes long and slender, meeting quadrate." The relative length and thickness of the process, however, is variable. Those of Muraenosaurus and Tricleidus are truly long and slender, resembling those of the Cretaceous genera figured by Welles (1943, 1952, 1962), but those of Cryptoclidus are shorter (first noticed by Andrews, 1910), and those of Kimmerosaurus can reasonably be described as short and massive by comparison with most genera. Unfortunately this feature is inadequately described for many genera, and wide-ranging conclusions cannot be drawn. The latter part of Welles' character is probably incorrect; the paroccipital process meets the squamosal and not the quadrate in all genera studied.

12. Occipital condyle.

Welles (1962) recognised two types of occipital condyle, and correlated them with other characters in the diagnoses of his two superfamilies. These were given as "occipital condyle projecting, hemispherical, marked off by constricting groove" (in the Plesiosauroidea), and "occipital condyle short and close to skull" (in the Pliosauroidea). In fact, the constricting ring around the occipital condyle develops ontogenetically in at least the genus Muraenosaurus, being most prominent in the oldest individuals, but it is indeed characteristic of small-skulled long-necked forms. In the genera known to Welles the occipital condyle was invariably formed from the basioccipital only; but in the British Upper Jurassic genera Cryptoclidus and Kimmerosaurus its formation is shared by the pedicles of the exoccipitals. It is also very short, and not ringed by a groove. A similar condyle formation may be found in the Upper Cretaceous genus Aristonectes, in which the exoccipitals are not preserved, but the basioccipital part of the condyle is described as very short, without a separating groove (Cabrera, 1941). The occipital condyles of most forms with a long symphysis and a large skull have not been adequately described, and a detailed comparison cannot be made.

13. Atlas.

In 1943, Welles recalled that Linder (1913) had distinguished between two types of atlas formation, viz: "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". In adults the atlas and axis components fuse solidly with complete obliteration of the sutures, and in juveniles in which fusion has not occurred the atlas intercentrum and neural arch are very small and frequently lost. In consequence, these details are known in only a very few specimens and, though apparently variable, they are of only dubious taxonomic value at the specific or generic level.

14. Relative neck length

Relative neck length has been recognised as of major taxonomic significance since the publications of Owen (1869), Lydekker (1889b) and Seeley (1892), but there has been much confusion of what are here regarded as three interrelated features, namely, true relative neck length (i.e. relative to the length of the trunk), which is itself a function of the number of cervical centra and their individual relative length. Thus, the Lower Jurassic species Plesiosaurus dolichodeirus has always been regarded as a long-necked "dolichodeiran" form, whereas Cryptoclidus is frequently regarded (e.g. by Delair, 1959, and Persson, 1963) as "mesodeiran", since in relative neck length it is supposed by these authors to be between "dolichodeiran" forms like Muraenosaurus and "brachydeiran" forms such as Pliosaurus. In fact, Cryptoclidus and P. dolichodeirus both have 32 cervical vertebrae which are similarly proportioned. If direct evolution be involved between these forms, then Cryptoclidus shows a retention of primitive features and not an evolutionary change such as is implied by the terms "dolichodeiran" and "mesodeiran". The terms "long-necked" and "short-necked" ("dolichodeiran" and "brachydeiran") are useful shorthand for referring to the extreme forms within a particular period of geological time, but should be avoided in strictly taxonomic work and substituted by reference to the two component factors of neck length. The term "mesodeiran" is meaningless and misleading, and should cease to be used.

15. Number of cervical vertebrae

The primitive number of cervical vertebrae for the suborder Plesiosauria is probably around 30 to 32 (with the atlas and axis, though fused, counting as two). The Lower Jurassic forms Plesiosaurus dolichodeirus, Macroplata longirostris (specimen in the collections of the Department of Geology, University of Manchester) and Rhomaleosaurus zetlandicus have 32, 32, and 28 respectively. There is relatively little range of variation about this figure in Lower Jurassic genera, but by the Cretaceous the number of cervical vertebrae ranges from 71 (in Elasmosaurus) to 13 (in Brachauchenius). Trends to increase or decrease the number of cervical vertebrae are correlated with small skulls with a short symphysis and large skulls with a long symphysis respectively. Only one Cretaceous genus is known which apparently retains the primitive number of cervical vertebrae, that being Aristonectes with 25 preserved and an estimated 5 missing (Cabrera, 1941).

16. Proportions of vertebral centra.

Isolated vertebral centra are the most frequent finds of plesiosaurian material, and it is therefore understandable that much emphasis was placed on their proportions by early writers. Welles (1952) devised a system of vertebral indices based upon comparative measurements of centrum length, height and breadth, but after much experimentation found that they were of limited use. Not only do comparative proportions of centra vary with the position on the column, but they also vary ontogenetically, being comparatively shorter in younger individuals. However, he showed quite clearly that there is relatively little variation in the ratio of height to breadth except in a fairly regular manner according to position on the column (dorsals are more circular in section), and not of much consequence from genus to genus. From my own observations the breadth is always greater than, or subequal to the height, but the length to height ratio varies considerably.

Dorsal, sacral and caudal vertebrae are relatively conservative in their variation of proportions, long-necked forms having only slightly longer centra than short-necked forms, but cervicals vary greatly. Proportional length is correlated with the number of cervical centra. Thus, a relatively long neck is usually produced both by increasing the number of vertebrae and by increasing the proportional length of each; and where the numbers are reduced their relative length is also decreased. In a long-necked form the vertebrae with the greatest proportional length are those in the anterior third of the neck, whereas in short-necked forms these tend to become the shortest, and are proportionally shorter than dorsal centra. In forms such as *Cryptoclidus* in which the primitive vertebral number is retained, the pattern of vertebral proportions is as in long-necked forms, but to a lesser extent. Thus in this genus the length of cervicals approaches but never exceeds the height, whereas in most long-necked forms with an increased cervical count, the height is exceeded by the length for most of the neck, and the breadth may also be exceeded by the length in the anterior cervicals.

17. Lateral "keel" on cervical centra.

A "lateral keel" (Welles, 1952, 1962), also called a "lateral longitudinal ridge" by Welles (1943) and 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. It is presumably associated with the strengthening of neck muscles which is required for the efficient mechanical management of the elongated neck. It is absent in all short-necked forms.

18. Articular faces of centra.

The centra of early 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, the centra of juveniles tending to have flatter articular faces. In the past, much attention has been paid to the exact shape of articular faces of isolated vertebrae, and also to such features as the presence or absence of a central pit, and whether the edges are angular or smoothly rounded. These, however, appear quite variable, not only ontogenetically and intraspecifically but also within a single individual. A central pit may be evident in the vertebrae of many juveniles, which also frequently have angular edges to the articular faces, whereas in adults the pit may frequently fill and the edges become more rounded.

19. 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 emphasised by early writers. Such features are very variable, and also vary ontogenetically, 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 surfaces of 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 minor or secondary use in some cases, as with the forms described by Tarlo (1960).

20. Fusion of neural arches and ribs to centrum.

In Upper Jurassic forms this is an ontogenetic feature, neural arches, cervical and caudal ribs being free in juveniles, but fusing, usually with complete obliteration of the sutures, in the adult. Welles (1962) regards fusion, especially of neural arches, as of minor taxonomic importance in Upper Cretaceous forms, but this is probably due to the lack of juvenile and adult specimens of each of the species which he studied. However, he gave "arches not fused to centra" as a feature in his diagnosis of the Lower and Middle Jurassic family Plesiosauridae. It is 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.

21. Height of neural spine.

Welles (1943) included "neural spines high or short" in his list of variable characters available for taxonomic consideration. It is, however, very doubtful that proportional length of the neural spine will prove to be anything other than an ontogenetic character. Neural spines are proportionally shorter in juveniles, their extremities being terminated in cartilage.

22. Cervical rib heads.

The cervical ribs of all Lower Jurassic forms 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 cervical rib heads into a single structure (cercidopleurous ribs). In forms with a short symphysis this is achieved by the Upper Jurassic, whereas in forms with a long symphysis it is delayed until the Cretaceous. Welles (1962) based the horizontal division of his two superfamilies (into two families each) upon the number of cervical rib heads (according to his diagnoses), but did not strictly apply this division, and included the British Upper Jurassic cercidopleurous genera in his dicranopleurous family Plesiosauridae.

23. Interclavicle.

The structure and comparative size of this element is extremely variable, as is the structure and size of the clavicles. The dermal elements of the pectoral girdle are considered together, below.

24. Clavicles.

The size and structure of the clavicles and the interclavicle have been the subject of much debate, and have frequently been overemphasised in taxonomic discussion. Variations in the development and shape of these elements, which are typically very conservative in other reptile groups, have been taken as of taxonomic importance at generic and even family level, regardless of the similarity of other features of the specimens involved. Thus Andrews (1910) distinguished three species of the genus *Muraenosaurus* (all now *M. leedsii*) on minor differences of dermal girdle structure, and separated *M. beloclis* at the generic level as the genus *Picrocleidus* (his supporting characters were largely ontogenetic differences between the type specimens); and White (1940) distinguished nine families using features of the pectoral girdle, one of these families (Tremamesacleididae) containing the two *Muraenosaurus* species now considered to be junior synonyms of *M. leedsii*.

It is important that variations of the interclavicle and clavicles be put into their proper perspective. In other reptile groups, these elements play an important functional role for which they are structurally adapted. Thus any change in their form reflects a change in their function, and is therefore of importance at a relatively high taxonomic level. In all but the earliest plesiosaurs, however, the ventral rami of the scapulae become greatly increased in size and meet in the ventral midline external to the interclavicle and clavicles. It follows that the muscles which once had their origin on the ventral surfaces of these dermal elements must have transferred to the ventral rami of the scapulae, which thus largely replace the interclavicle and clavicles functionally.

In plesiosaurs, therefore, these elements are no longer functionally important, and cease to be structurally adapted to the lost function. Tendencies to modify, reduce and even to lose the dermal elements 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 these elements within a single species, as, for example, in *Muraenosaurus leedsii* (see fig. 20).

Clavicles and an interclavicle are retained in a moderately well-developed state in several Upper Cretaceous genera (e.g. *Thalassomedon*, *Morenosaurus*), and so the supposition that they had been lost in many of the genera in which they are unknown must be regarded with suspicion. Owing to their relatively small size, frequently thin and delicate nature, and dermal membranous development, it is probable that they easily became fragmented or detached and separated from the decaying corpse, which might explain their absence from many specimens. Conversely, 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 feature which should be used with much caution in taxonomic discussion.

25. Ventral process of scapula.

In all but the earliest plesiosaurs the ventral processes of the scapulae meet in the ventral midline beneath the clavicles and interclavicles in the adult. In juveniles they were separated to a varying degree by cartilage, as was demonstrated by Andrews (1895a) in Cryptoclidus eruymerus. This, however, has not always been taken into account by taxonomists, several of whom have used ontogenetic characters in their diagnoses. The relative width of the adult ventral process is, however, of some taxonomic use. The process is relatively narrow in many early forms, and tends to remain so in short-necked large-skulled species. In the long-necked forms the ventral process tends to become progressively broader.

26. Scapulocoracoid bar.

The presence or absence of a scapulocoracoid bar, formed by the union of anterior median processes of the coracoids with posterior median projections from the ventral rami of the scapulae, has frequently been over-emphasized and misunderstood by taxonomists. In many Lower Jurassic plesiosaurs this bar certainly does not form even in the adult, but in

Upper Jurassic genera its development is typically ontogenetic, being absent or forming in the juvenile and completed in the adult. In old adults the scapulae and coracoids may even fuse, with loss of the sutures. It is probable that many of the Upper Cretaceous forms which have been described (e.g. by Welles, 1962, subfamily Alzadasaurinae) as lacking the scapulocoracoid bar are in fact based upon individuals which had not reached full maturity.

27. 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 (in which the width across the cornua may be up to 45% more than the interglenoid width).

28. Median suture of coracoids.

The coracoids unite mesially along their entire length in all Jurassic forms, and also in Cretaceous large-headed short-necked forms, but are characteristically separated posteriorly by a wide intercoracoid foramen in Cretaceous long-necked forms.

29. Anterior border of pubis.

Welles (1943) listed "Pubes ... may become convex anteriorly or concave" as a variable feature for consideration. This, however, is almost certainly an ontogenetic feature. Juveniles tend to 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.

30. Relative length of ischia.

The ischia are relatively short anteroposteriorly in long-necked forms and relatively long in short-necked large-skulled forms. This correlation was first recognised by Mehl in 1912.

31. Pelvic bar.

Welles (1962) divided his family Elasmosauridae into the subfamilies Elasmosaurinae and Alzadasaurinae upon the presence or absence of a scapulocoracoid ("pectoral") bar and a median puboischial ("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 onotgenetic feature. Thus it is probable that the two species included in the former family (*Elasmosaurus platyurus* and *Brancasaurus brancai*) which show a mesial pelvic bar which is more or less fully formed, are based upon adult and well-ossified individuals. This feature is probably not of widespread taxonomic importance.

32. Ilia.

Welles (1943) included "Ilia becoming narrow proximally or remaining broad" in his list of variable features, but without further comment. No major trends in ilial development have been demonstrated, and irregularities in the form of this element are therefore of only minor taxonomic importance.

33. 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 elongate 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.

34. Capitulum and tuberosity (in humeri) or trochanter (in femora).

In the list given by Welles (1943) it was stated that these "... may remain connected or show changes leading up to complete separation". These changes are in fact entirely ontogenetic. 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 completely separated by a strip of finished bone.

35. 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, but this is not of taxonomic importance above the generic level.

36. Relative length of epipodials.

The epipodials of primitive forms are elongate and dumbel-shaped, reflecting the shape of the epipodials of a terrestrial ancestor. There is a trend throughout the whole group to shorten and widen the epipodials until they resemble mesopodials in shape, and may be considerably broader than long.

37. 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 forms (and notably in the genus <u>Cryptoclidus</u>) it is not revealed until ossification of the epipodials reaches an advanced stage in old adult individuals; in younger individuals the epipodial foramen is entirely surrounded by cartilage. It is not possible to prove its absence in any species, as in no individual apparently lacking the foramen are the epipodials actually fused together.

38. Proximal shift of 5th metapodial.

Distal to the epipodials are 6 mesapodials (with occasional additional postaxial ossifications), which are arranged in proximal and distal rows containing three each. Beyond the distal mesapodial row in primitive forms are the five phalangiform metapodials. There is a trend throughout the entire group to shift the 5th (most posterior) metapodial proximally into the distal mesapodial row, and this is fully achieved in many Upper Jurassic forms and almost all Cretaceous forms.

39. Extent of hyperphalangy.

In association with other progressive features (here numbered 35, 36 and 38) which together improve the limb as a paddle for aquatic locomotion, is a 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

With the omission of character 14 above (relative length of neck), which it is argued should be treated in taxonomic discussions by separate reference ~~to~~ its two component factors (number of cervical vertebrae and relative length of their centra), 38 variable characters of plesiosaurian osteology are now recognised as available for the purposes of classification. It is probably true to say that constant variants of any of these could, in appropriate circumstances, prove sufficient for the taxonomic distinction of species, and several in combination might distinguish genera. Classification above the generic level is considerably more complicated. A satisfactory classification must be phyletic, and it is therefore necessary to establish which variable characters are of phylogenetic significance; to assess their relative importance; and to formulate a hypothesis of probable evolution within the group.

The 38 characters may be grouped together into four categories (i - iv) of differing phylogenetic significance, as follows:-

(i) Eight characters (9, 19, 20, 21, 26, 29, 31 and 34) may be dismissed as of no phylogenetic significance since their variations are due largely or entirely to ontogenetic growth. For this reason, taxonomic use of these characters is likely to prove unsatisfactory, and should in any case be limited to specific and generic diagnoses.

(ii) The variation of six characters (10, 11, 13, 27, 32 and 37) is either apparently random (i.e. shows 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 (character 4, tooth ornament) largely belongs in this category, except that there may 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 possible exception mentioned), their use should be limited at the present time to specific and generic diagnoses.

(iii) Eight characters (1, 22, 23, 24, 35, 36, 38 and 39) show progressive unidirectional evolutionary change which affects the entire suborder. These changes (general increase in size, reduction of the dermal elements of the pectoral girdle and improvements to the structure of the paddles) are largely associated with the adaptation of a once-terrestrial body form to an aquatic mode of life, and occur irrespective of other changes which cause 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.

(iv) The remaining fifteen characters (2, 3, 5, 6, 7, 8, 12, 15, 16, 17, 18, 25, 28, 30 and 33) 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 such associated variants and trends will lead to the recognition of phyletic lineages and enable 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 will be produced which is phylogenetic.

It is interesting to note that, of these fifteen characters, seven (2-12) 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 of the skull has never before been given is explained by the relative lack of good skull material compared with the relative abundance of postcranial remains.

(b) Evolution

It is argued above that phyletic lineages within the Plesiosauria will be recognised only by an analysis and correlation of the fifteen characters listed in category (iv). If the genera Cryptoclidus, Kimmerosaurus and Aristonectes are omitted from consideration, such an analysis clearly indicates the presence of two distinct lineages which agree in essence with those recognised by Welles (1943, 1962) and are defined by him as the two superfamilies Plesiosauroidea and Pliosauroidea.

The first lineage (the "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 premaxillary-maxillary suture; to increase the number of cervical vertebrae, and to increase the length of each individual cervical centrum. Advanced members of this lineage also develop platycoelous rather than amphicoelous vertebrae; a lateral keel on cervical centra, and a wide posterior inter-coracoid vacuity.

The second lineage (the "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 usually show considerable wear on their tips; a relatively narrow scapular ventral ramus; relatively long ischia, and propodials which are "pendulous" (term used by Welles, 1962) 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 length of individual cervical centra.

The known geological range of both these lineages extends from the base of the Jurassic to the Upper Cretaceous. Their origin in the Triassic must for the present remain an unanswered question. Much has been suggested relating the pistosaurs to the "plesiosauroidean" lineage (e.g. Edinger, 1935; Welles, 1943; Romer, 1956), but the relationships of the "pliosauroidean" lineage have largely been overlooked. Welles (1943) doubted that all plesiosaurians could have descended from the pistosaurs, since the "plesiosauroidean" and "pliosauroidean" lineages do not show sufficient retrospective convergence. Skull reconstructions of other nothosaurs, e.g. *Ceresiosaurus* (by Meyer, 1931, reproduced in Romer, 1966) 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.

There now remains to be considered the three genera *Cryptoclidus*, *Kimmerosaurus*, and *Aristonectes*. *Cryptoclidus* (Upper Jurassic; Oxford Clay) and *Kimmerosaurus* (Upper Jurassic; Kimmeridge Clay) have been described above; *Aristonectes* (Upper Cretaceous of South America) was described from an incomplete skull and partial postcranial skeleton by Cabrera (1941). They 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 characterise the "plesiosauroidean" and "pliosauroidean" lineages. The dentition is regular, lacking the precocious development of certain premaxillary and maxillary teeth characteristic of the former lineage, and also the large symphysial teeth of the latter lineage. The number of cervical vertebrae (known in *Cryptoclidus* and *Aristonectes*) remains about thirty, which seems to have been the primitive number in all lineages, and 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 the three 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 chronological trend to increase the premaxillary tooth number, which is 6 in *Cryptoclidus*, at least 8 in Kimmerosaurus and 15 in Aristonectes. (ii) There is similarly 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 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 characterises 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. There is good reason to believe that this may also be the case in Aristonectes, for although the exoccipitals are not preserved and the basioccipital was not figured by Cabrera (1941), it was stated that the condyle is short and not separated off from the body of the basioccipital by a groove. In this respect, the condyle of Aristonectes differs from contemporary "plesiosauroids" and resembles those of Cryptoclidus and Kimmerosaurus.

The evidence cited above indicates that the genera Cryptoclidus, Kimmerosaurus and Aristonectes are representatives of a third and **distinct** phylogenetic lineage. This lineage has a known geological range from the Upper Jurassic to the Upper Cretaceous. Cryptoclidus, with only 6 premaxillary teeth and 24-26 pairs of dentary teeth, is seen as a primitive representative, whereas Aristonectes, with 15 and 58 pairs respectively, is an advanced form.

Several characters shown by these genera (such as those of the neck indicated above) 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 shown by primitive members only of the "plesiosauroidean" lineage. These are (i) a relatively small skull; (ii) a short mandibular symphysis; (iii) teeth with slim crowns not showing wear on their tips; (iv) a relatively large ventral process of the scapula; (v) a relatively short ischium, and (vi) propodials which are "massive", and of which the humerus is larger than the femur. The post-cranial features (iv) to (vi) in this list are known only for Cryptoclidus; but as this is the most primitive representative of the newly recognised 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.

The possible functional and adaptive significance of the structural changes characterising the three lineages is discussed below in Section 3(ii).

(c) Classification of the Plesiosauria

Welles (1943) described the two principal~~e~~ phylogenetic lineages (referred to, above, as "plesiosauroidean" and "pliosauroidean") and ranked them as separate superfamilies, Plesiosauroidea and Pliosauroidea. Using the single or double-headed form of the cervical rib, he then divided each superfamily into two families, distinguishing in both cases an early dicranopleurous family from a later cercidopleurous family. Welles interpreted these as representing primitive and advanced grades of each lineage.

In 1962, Welles 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 strictly adhere to his diagnoses, and in the same paper referred 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 cercidopleurous British Upper Jurassic genera with the Cretaceous elasmosaurs can only be explained by a consideration of their relative neck length. Undeniably, the British Upper Jurassic genera have shorter necks; even _Muraenosaurus_, with 44 cervical vertebrae, has fewer such vertebrae than the shortest-necked Cretaceous elasmosaurs. As the elasmosaurs are generally considered to be long-necked forms, the question naturally arises, "How long is a long neck?" The answer is not difficult to find, for if it is accepted that the primitive number of cervical vertebrae for all the Plesiosauria is of the order of 30 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 moderate length.

Neck length, however, is only one of several characters which show progressive evolutionary change and may be used to divide the plesiosaur-elasmosaur lineage (or, indeed, the "pliosauroidean" lineage) into grades. The eight characters listed above under Section 3(i)(a), category (iii) (these include the reduction in the number of cervical rib heads from two to one) may all be employed~~,~~ but as they apply equally to all phylogenetic lineages, they are of lesser taxonomic importance when only one particular lineage is under consideration. Of greater importance and significance for the distinction of primitive and advanced grades are those evolutionary trends which are manifested only in the lineage in question. Some characters limited to the plesiosaur-elasmosaur lineage, such as the development of platycoely and of lateral crests on 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 trend which shows a gradual development in this lineage 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 British Upper Jurassic genera, *Muraenosaurus* has from 19-22 teeth on each dental ramus, whereas *Tricleidus* has only 17, which is less 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 lengths of their necks.

Past attempts to divide the plesiosaur-elasmosaur and the "pliosauroidean" lineages into primitive and advanced grades have met with considerable problems. The formation of diagnoses which can be rigidly applied and which draw upon all characters showing a progressive evolutionary change is made extremely difficult by the extent of interaction and the chronological overlap of development of these characters. Only by heavily weighting one character with respect to all the others could a diagnosis of this form be successfully applied in practice.

Historically (as in the classification of Welles, 1943, 1962), the character chosen for this weighting has been the nature of the cervical rib head. In practical terms this character has the advantage of providing two clear-cut and indisputable possibilities; the cervical rib head can be double (primitive grade) or single (advanced grade), with no known borderline cases. This method of diagnosis construction, however, has an inherent weakness. The reduction in number of cervical rib heads from two to one involves all lineages, and, although of undoubted evolutionary importance to the suborder as a whole, it is of less significance than other more restricted characters when considering single lineages (as was argued above). The arbitrary 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 the various lineages. One must therefore seriously question the necessity or desirability of producing such arbitrarily based divisions.

In the case of the Pliosauroidea, which is currently understood to represent a single unbranched lineage, the reduction in the number of the 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 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 much more closely resemble. It is generally accepted that 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 distinctions.

In the case of the Plesiosauroidea the issue is now changed by the recognition of a third phylogenetic lineage which has evolved from primitive members of the plesiosaur-elasmosaur lineage. In order that the classification may reflect the phylogeny it is clearly desirable to recognise the elasmosaurs and the new lineage as separate families, and to distinguish these from their common stock. Furthermore, the difficulties of making taxonomic divisions are greatly reduced by the new situation. The descendant families are mutually distinct; and the primitive parental family can be objectively defined 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 new 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), which is therefore the correct name for the family. In addition to the progressive trends discussed above, the family is clearly distinguished from all others by two characters, namely, increase in the number of pairs of premaxillary teeth above 5, and involvement of the exoccipital in formation of the occipital condyle. Two negative characters 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 (subject to revision) (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 30 to 32 (subject to revision).

Characters which will distinguish all members of the family Elasmosauridae from those of other families are a decrease in the number of pairs of lower teeth below the primitive number of about 24, and an increase in the number of cervical vertebrae above 32. Negative features, of importance in distinguishing the family from the Cryptoclididae, are the retention of the primitive number of pairs of maxillary teeth (5), and the structure of the occipital condyle, which is formed from the basioccipital only.

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 (here taken as about 24 and 30-32 respectively, subject to revision). Such forms would not then be debarred from ancestry to either the Elasmosauridae or the Cryptoclididae.

A consequence of this action is considerably to reduce the size and chronological range of the family Plesiosauridae, and at the same time to enlarge and extend the Elasmosauridae. In particular, the British Lower Jurassic genus *Microcleidus* Watson, 1909, which has hitherto always been included with the Plesiosauridae because of the double-headed condition of the cervical ribs, must now be recognised as a primitive elasmosaur since it has increased the number of cervical vertebrae to 40 and proportionally elongated each cervical centrum. This genus also demonstrates that the reduction in number of cervical rib heads from two to one evolved by convergence, not only in the two superfamilies Plesiosauroidea and Pliosauroidea, 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*. It must, however, be emphasised that this genus has in the past been made a "catch-all" group which still remains diverse and is in need of review. When such a review has been undertaken it is likely that more than the present single genus will be recognised, and in addition several species currently placed in this genus must be removed to the Pliosauroidea. For the present it need only be said that, of the better-known species, the type-species *P. dolichodeirus* and also *P. guilelmiimperatoris* belong in the Plesiosauridae, whereas "*Plesiosaurus*" *hawkinsii* and *"P." rostratus* belong in the Pliosauroidea.

A second Lower Jurassic genus, *Sthenarosaurus*, 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 increased in number; but as the skull is not preserved, the presence or absence of cryptoclidid trends cannot be demonstrated. The genus is therefore placed as Plesiosauroidea, *incertae sedis*. All other named plesiosaurian genera may be assigned to a family.

There yet remains to be considered the taxonomic position of the genus Pistosaurus, which has in the past been variously placed in the Nothosauria or the Plesiosauria as a family or as a superfamily (see Section 1). Whereas it is generally assumed (e.g. by Romer, 1956; Welles, 1962; Persson, 1963) that these forms were in some way ancestral to at least the Plesiosauroidea, it is true that the phylogenetic nature of this relationship, and the relationship to nothosaurs, is not understood. In consequence, the genus cannot be classified in either suborder as a result of phylogenetic arguments, but only for reasons of taxonomic convenience. A thorough review of the Lower Jurassic plesiosaurs, of the genus Pistosaurus and of the Nothosauria, is necessary before this problem can be satisfactorily resolved. For the present, an arbitrary line must be drawn which separates the Nothosauria from the Plesiosauria. I propose that the retention or loss of nasals be made the decisive criterion, which thereby causes the genus Pistosaurus to be retained in the Nothosauria, and permits a classification of the Plesiosauria which is entirely based upon current theories of phylogeny.

The classification of the Plesiosauria which I propose may now be formalised:

Order SAUROPTERYGIA

Suborder PLESIOSAURIA de Blainville, 1835

Diagnosis:

Sauropterygia in which the nasals are absent; paroccipital processes long and slender, meeting quadrate; posttemporal fenestrae large; stapes absent; thecodont with new teeth developing lingually to old and moving laterally to replace them; overall length up to 14 metres; vertebral centra with paired ventral nutritive foramena; 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 suborder:

? Upper Triassic; Lower Jurassic, Hettangian Stage, to Upper Cretaceous, Maestrichtian Stage.

Superfamilies included:

Plesiosauroidea and Pliosauroidea.

Superfamily PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

Diagnosis:

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

Range of superfamily:

Lower Jurassic, Hettangian Stage, to Upper Cretaceous, Maestrichtian Stage.

Families included:

Plesiosauridae, Elasmosauridae, and Cryptoclididae.

Incertae sedis:

Sthenarosaurus Watson, 1909.

Family PLESIOSAURIDAE Gray, 1825

Diagnosis:

Plesiosauroidea with five pairs of premaxillary teeth; not less than twenty-four pairs of dentary teeth; teeth ornamented with numerous longitudinal ridges; occipital condyle formed from the basioccipital only; overall length not known to exceed three metres; not more than thirty-two 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.

Genera included:

The single genus *Plesiosaurus* Conybeare, 1821. (Subject to revision.)

Family ELASMOSAURIDAE Cope, 1869(b)

Diagnosis:

Plesiosauroidea with a maximum of five pairs of premaxillary teeth; upper tooth row of advanced forms characterised 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 metres in primitive forms to a maximum of 14 metres in advanced forms; number of cervical vertebrae primitively 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 from the metapodial row in advanced forms; hyperphalangy of up to 17 phalanges in the longest digit.

Range of family:

Lower Jurassic, Toarcian Stage, to Upper Cretaceous, Maestrichtian Stage.

Genera included:

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; tooth-rows regular, teeth decrease in size anteroposteriorly 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 the exoccipitals and not ringed by a constricting groove; overall length probably does not exceed 8 metres; number of cervical vertebrae remains about 30 to 32; cervical centra remain of moderate relative length; cervical ribs are 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 mesopodial row; hyperphalangy of up to at least 15 phalanges in the longest digit.

Range of family:

Upper Jurassic, Callovian and Kimmeridgian Stages; Upper Cretaceous, Maastrichtian Stage.

Genera included:

Cryptoclidus Seeley, 1892 and Kimmerosaurus n. gen. (Upper Jurassic genera); Aristonectes Cabrera, 1941 (Upper Cretaceous genus).

Superfamily PLIOSAUROIDEA (Seeley, 1874) Welles, 1943

Diagnosis, etc.:

As for the single family Pliosauridae.

Family PLIOSAURIDAE Seeley, 1874

Diagnosis:

Plesiosauria with relatively large skulls; premaxillae bear five pairs of teeth; mandibular symphysis long, including several pairs of alveoli which bear enlarged teeth; from 25 to 40 pairs of dentary teeth; teeth relatively broad and strong and usually show wear on their apices; teeth ornamented with longitudinal ridges and may also be keeled; occipital condyle formed from basioccipital only; overall length from about 3 metres in primitive forms to about 12 metres 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 relatively narrow; ischia relatively long antero-posteriorly; propodials relatively 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 mesopodial row in advanced forms; hyperphalangy of up to about 16 phalanges in the longest digit.

Range of family:

Lower Jurassic, Hettangian Stage, to Upper Cretaceous, Senonian Stage.

Genera included:

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, and *Stretosaurus* Tarlo, 1959 (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).

SECTION 3(ii) FUNCTIONAL MORPHOLOGY

(a) Locomotion

Discussion of published work

In 1924, Watson compared and discussed the morphology of the pectoral girdle and humerus of several plesiosaurs, attempted to reconstruct the pectoral musculature, and produced a theory of the locomotion of plesiosaurs. His paper represents the only serious attempt to analyse the mechanics of plesiosaurian pectoral structure, and to explain certain progressive evolutionary changes of structure in functional terms. Several new ideas were expressed in his paper and will be discussed below. Watson's princip~~le~~al conclusion, however, was that plesiosaurs swam by a method comparable with "rowing"; according to this theory the humerus was moved backwards and forwards in a horizontal plane, the backward power-stroke being made with the transverse axis of the paddle in a vertical plane and the return stroke with the paddle "feathered", the axis horizontal.

Watson's theory has never been opposed in print. At the Symposium on Vertebrate Palaeontology and Comparative Anatomy which took place at Queen Elizabeth College, University of London in 1967, Mr. B. H. Newman showed film of sea-lions swimming with an up and down "flapping flight" movement of the forelimbs and suggested the possibility of similar movement in pliosaurs; but in a brief publication (Newman and Tarlo, 1967) it was held that whereas a certain amount of up and down movement of the pliosaur forepaddle was possible in addition to the fore and aft movement, this was not possible in long-necked plesiosaurs. It was concluded that, as a result of the greater freedom of movement in pliosaurs, only these short-necked forms were capable of diving for prey. No structural arguments were given to support their claim.

A recent publication by W. F. Walker (1971) has substantially improved upon knowledge of the "flapping flight" locomotion of living marine turtles of the family Cheloniidae. This publication, together with film of marine turtles by Jacques Cousteau (kindly made available to me for study in Bristol by the B.B.C.) has enabled me to prepare a reconstruction of the locomotion of plesiosaurs in which it is suggested that their locomotion resembled that of marine turtles. However, before proceeding to that part of my discussion, it is necessary to discuss and evaluate Watson's (1924) theory.

Watson's approach was to examine the pectoral girdle and humerus of selected forms, and to identify areas of muscle origin and insertion. Then, using his knowledge of the musculature of living vertebrates, he stated which origin was associated with which insertion, and named the interposed muscles. Thus in *Plesiosaurus dolichodeirus* the origins on the girdle and insertions on the humerus of nine different muscles were identified, associated and named, as follows:- deltoid; coracobrachialis brevis; coraco-branchialis longus; subcoracoideus; supracoracoideus; subscapularis; scapulo-humeralis anterior; pectoralis and latissimus dorsi. Once this muscle reconstruction had been achieved, Watson was able to determine the effect of each muscle, and to give an account of how the muscles operated to produce a "rowing" action of the limb. This same muscle reconstruction and function was identified in the genera *Microcleidus*, *Muraenosaurus*, *Colymbosaurus* and *Elasmosaurus*, and much of the latter part of Watson's paper was concerned with establishing the functional cause for the enlargement of the ventral ramus of the scapula and apparent shortening of the coracoids throughout this evolutionary series. It was concluded that this imparted the ability in later forms to "back water" with the fore-paddles, thus increasing manoeuvrability.

Watson's entire argument rests upon the accuracy of his original muscle reconstruction. Unfortunately this does not stand the test of a close and detailed analysis. The principal elements of the pectoral girdle in plesiosaurs are large flattened or gently curved plates, and although it is obvious that their external surfaces must have provided the origins of the locomotor muscles, their appearance is of a large and continuous surface for origins rather than a surface divided into several separate areas for the insertion of discrete muscle blocks. Only two discrete muscle origins can be separately distinguished, these being on the posteroventral edge of the dorsal ramus of the scapula (marked by very prominent rugosities) and on the posterior part of the lateral edge of the coracoid (marked by less prominent rugosities). Of the remaining surface of the scapula and coracoid, the most strongly rugose area is the lateral surface of the mid-ventral "keel" produced by the coracoids, and lying between the glenoids.

The humerus, likewise, does not show as many discrete insertions as Watson suggested (see description of the humerus of Cryptoclidus eurymerus). There is no evidence from any specimens which I have studied that the prominent rugosities along the anterior edge of the humerus represent the insertion of two muscles ("deltoid" and "pectoral" of Watson) rather than a single muscle; likewise the ventral surface of the shaft exhibits a large and continuous rugose surface for muscle attachment. There is some variation between specimens, but this variation is neither species-specific nor bilaterally symmetrical within a single specimen. There is also no evidence from rugosities to permit a deduction of the direction of pull of the muscle whose site of insertion they mark.

Close examination of some of Watson's figured material reveals the mistaken identity of some surface features which he interpreted as muscle insertions. In his text-fig. 8 (Watson, 1924, p. 903), which represents a left humerus of Colymbosaurus trochanterius (specimen L.3166 in the Manchester Museum) a feature on the dorsal surface of the tuberosity was identified as the insertions of the scapulo-humeralis anterior and subscapularis muscles, whereas in fact it is post-mortem damage comparable with a miniature "rift valley" produced by the sinking of an area of the surface between two parallel cracks in the bone.

Watson's approach of comparing the musculature of living vertebrates with that of plesiosaurs is suspect. The osteological structure of the plesiosaurian pectoral girdle and humerus is unique, and cannot be directly compared with any living vertebrate form. Amongst reptiles only the turtles have developed the humerus and forelimb into a comparable paddle, but here the structure of the pectoral girdle is highly modified, and the locomotor muscles have their origins largely on the visceral surface of the plastron. In sea lions the pectoral girdle is modified from that of mammalian ancestors and comparison with totally unrelated reptiles from the Mesozoic is tenuous. Furthermore, these mammals have seldom been studied, and their musculature is inadequately known. Watson did not in fact name the animal or animals with whose musculature that of plesiosaurs was compared.

In practice, it is possible to examine the pectoral girdle and humerus of plesiosaurs and to locate the areas of muscle insertions. In a few cases, where very prominent rugosities are confined to a small area of bone, it is probable (but never certain) that the origin or insertion of a single muscle is involved; but over much of the bone surface it is possible only to distinguish areas of insertion from areas without powerful muscle attachment. There are no grounds for associating precise origins on the girdle with precise insertions on the humerus, but one may argue on general grounds about probabilities. For example, it is probable that the muscles inserting on the ventral surface of the humerus had their origins on the coracoid, and it is also probable that those inserting on the anterior edge of the humerus had their origins on the scapula, by reason of their juxtaposition. The use of exact comparative anatomical terms for the muscles cannot be justified, since direct homology of plesiosaurian with living reptilian or mammalian musculature cannot be demonstrated, and is evolutionarily very tenuous. Terms of a general descriptive nature and which may refer to single muscles or to muscle systems (such as "scapulohumeralis" and "coracohumeralis") are acceptable for descriptive purposes provided these are not taken to imply homologies outside the context of plesiosaurs.

It follows from the above argument that no single muscle reconstruction can be proved accurate and that many differing reconstructions are possible. Watson's (1924) reconstruction is one of several possibilities, and would produce a "rowing" manner of locomotion. It is, however, possible to reconstruct the musculature to a different pattern, and produce differing movements of the forelimb.

One such alternative pattern is outlined below, and would produce locomotive movements similar to those of the paddles of marine turtles. A descriptive account of marine turtle locomotion is given, after which follows a comparative review of the structure of the plesiosaurian pectoral and pelvic girdles and their propodials. An arrangement of the principal muscle systems is then suggested, after which follows an account of how turtle-like locomotion might have been achieved. This reconstruction is then compared with, and assessed relative to, that given by Watson (1924).

<u>Locomotion of cheloniid marine turtles</u>

The swimming movements of the forelimb in cheloniid marine turtles is unique among living reptiles. It has been likened to the movement of a bird's wing in flight (e.g. Carr, 1952; Gray, 1953), and was briefly analysed by Zangerl (1953) and Parrish (1958).

In 1971, Walker studied four genera and species of marine turtles at the Marine Studios, Marineland, Florida. Specimens were filmed at 32 frames/second, the film was analysed frame by frame, and limb movements plotted. The angles and extent of movement of the humerus and the paddle were calculated, and the description was accompanied by figures (reproduced here, see fig. 41). Walker found that the four species studied (Chelonia mydas, Eretmochelys imbricata, Lepidochelys kempii, and Caretta caretta) showed no significant differences in major aspects of limb movement, and so a composite description was given. This was summarised as follows:-

"Cheloniid turtles swim by moving the blade of their pectoral flipper up and down along a line inclined from 40° to 70° from the horizontal plane. The leading edge of the blade is inclined anteroventrally on the down-stroke and anterodorsally on the upstroke, and the tip of the blade usually inscribes a figure 8. The downstroke is the main propulsive stroke, but some propulsive components are generated on the upstroke. The blade, composed of the antebrachium and manus is driven largely by movements of the humerus that include on the downstroke a retraction of 70°-80°, a 60°-70° rotation, and a 30°-50° adduction. A shift in the axis of the articular surface of the humeral head, relative to the axis of the shaft, enables a retraction of the humerus to bring about concurrently most of the adduction and much of the rotation observed. The crus and pes extend posteriorly beyond the edge of the shell close to the horizontal plane. They act as rudders and elevators, and aid in steering and changing depth".

The shift in the axis of the articular surface of the humeral head relative to the axis of the shaft (by comparison with living fresh-water turtles and terrestrial tortoises) which Walker noted, results in reducing the angle of these two axes with respect to each other from about 90° (in non-marine forms) to about 20° (in marine forms), and the head is thereby placed much nearer to the proximal end of the humeral shaft. Walker interprets this as an adaptation for improving locomotion. In the cheloniid humerus, rotation of the head results in the inscription by the distal end of a much smaller circle than in non-marine forms. Since the blade of the flipper makes a backward angle with the humerus at the elbow, a simple rotation of the humerus will result in elevation or depression of the distal tip of the blade. In the complete swimming movement the flipper blade is thus elevated and depressed through a greater arc than the humerus, and this increases the efficiency of the locomotive strokes.

The flexibility of the marine turtle flipper is limited, but it does flex to the pressure of the water during locomotion, and in an advantageous way. The posterior edge of the flipper trails behind the anterior edge, which results in inclining the plane of the flipper blade at an angle to the horizontal. This angle increases towards the distal tip of the flipper, and Walker likens both its shape and its effect to that of a propellor blade. He concludes that, since the distal end of the flipper travels through the water at a greater speed than more proximal parts, this differential twisting probably compensates for differences in speed, and equalises the forces generated along the blade.

The forces produced by the up and down movements of the flipper resolve into a posterior component and a vertical component (the direction of the latter depends on the direction of the stroke). The upward and downward vertical components produced during a complete locomotive cycle cancel each other, and the posterior component results in forward movement of the animal.

Walker did not make a detailed study of the movements of the hind limb, but nevertheless recorded its function in general terms. In an attempt to supplement this description, I was permitted, through the kindness of the B.B.C. Natural History Unit, Bristol, to examine a film about the Green Turtle (Chelonia mydas) (entitled "Search in the deep"; a volume in the series "The undersea world of Jaques Cousteau". B.B.C. copyright). This was studied with the aid of a Keller 16 mm. film viewing machine, which permits frame by frame analysis with tracing facilities.

When commencing from rest on the sea bottom, the turtles perform rather awkward clambering movements with all four limbs, crawling and kicking to gain momentum and clear the ground. Once in clear water, the "flying" movement of the forelimbs commences. The downstroke is performed with considerable force, and by comparison the upstroke appears to be performed almost passively. This difference between the two strokes is most clearly marked when the animal is accelerating or escaping from a potential predator. When not hurried, the turtle "cruises" in a seemingly effortless manner, with a gentle and almost evenly timed raising and lowering of the forelimb in the manner described by Walker (1971). At no stage was a forceful and rapid upstroke observed.

The hindlimbs are passive during normal straight swimming, and are held backwards and only slightly outwards, with the plane of the blades parallel to the direction of movement (the longitudinal axis). They are orientated at approximately 45° to the horizontal when seen in posterior view, with the inner (posterior) edges uppermost (see fig. 42). They may be raised or lowered slightly to aid in elevation or diving, but their principal use is in turning. Both hind flippers are used for any turn, and are operated with opposite surfaces pressed against the water.

To make a turn to the left, both hind flippers are pushed to the left from their normal resting position. Thus the left flipper presents its dorsal surface to the pressure of the water, and the right flipper its ventral surface. The flippers are not, however, held in a perpendicular plane, but remain nearer to their 45° rest position. The left flipper therefore produces a force with a horizontal component (acting to the right) and also a downward component, whereas the right flipper produces a force with a horizontal component (to the right) and an upward component. The horizontal components have the normal effect of the rudder of a boat, rotating the axis of the animal anticlockwise (in dorsal view) and producing a left turn. In addition, the left downward and right upward components rotate the animal along its longitudinal axis to produce "banking", as in an aeroplane. It is likely that the hind flippers also produce a force which depresses the posterior and thereby causes elevation. The combined effect of these forces is to produce a left turn into which the animal banks. Such a turn resembles the turning of birds and aeroplanes, and takes advantage of the flattened body form. It is mechanically efficient, involving the minimum amount of drag. The tail appears to have negligible effect in locomotion and steering.

Comparative morphology of plesiosaurian girdles and propodials

The following account is largely based upon a study of *Cryptoclidus eurymerus*. In most respects the general structure of the girdles and propodials of this species is representative of all Upper Jurassic and Cretaceous forms, and, except where stated, the account may be taken as composite. It is not possible to give a detailed comparison with turtle structure at the present time; such a comparison, which I hope to undertake at a future date, would involve the study of fresh turtle material, and is outside the scope of the present work.

The pectoral and pelvic girdles of plesiosaurians each largely consist of two paired elements, these being the scapulae and coracoids, and the pubes and ischia, respectively. In plesiosaurians these elements have become expanded into plate-like structures which meet in the ventral midline. In addition, the pectoral girdle of most forms retains elements of dermal origin (the interclavicle and clavicles), but in Upper Jurassic and later forms these are reduced in size and lie visceral to the anterior (ventral) rami of the scapulae. Their position is such that they may reasonably be excluded from a consideration of the probable sites of origin of pectoral locomotor muscles. The pelvic girdle includes a further pair of elements, the ilia. Each ilium, usually large and prominent in reptiles, has undergone considerable reduction in plesiosaurs, and is represented by a rod of bone which rises diagonally upwards and backwards from the ischia at an angle of up to 45° from vertical, and braces the acetabulum to the sacrum. Its external surface is smooth and rounded, and it is evident that this element may reasonably be excluded from discussion of the sites of origin of the principal pelvic locomotor muscles. In plesiosaurs the principal locomotor muscles probably originated only on the scapulae, coracoids, pubes and ischia.

The pectoral and pelvic girdles differ considerably in several respects:-

(i) The anterior portion of the coracoids is thickened and strengthened, and this strengthening functions as a compression strut between the glenoids (Watson, 1924). Such a strut is necessary to resist inward pressures which are produced by the humeri during a complete swimming stroke, whether the humeral movement be in a horizontal plane (as was postulated by Watson, 1924) or in a more or less vertical plane, as in marine turtles. A similar compression strut is not found in the pelvic girdle. Indeed, inward pressure upon the acetabuli would probably cause them to move inwards, pushing the pubes anteriorly and the ischia posteriorly. It is quite possible that some movement of this sort could have taken place, for the pubo-ischial junctions contained much cartilage, and rigidity of the junction was reduced by the lack of contact of the pubis with the ilium.

(ii) In the pectoral girdle the glenoids lie very slightly anterior to the coracoidal compression strut. There is, however, a second and anterior line of compression resistance which runs along the glenoid and anterior rami of the scapulae. The anterior scapular rami are enlarged into a median symphysis for the transmission of these forces, and forward movement of these rami with respect to the coracoids is prevented by the development of the median scapulocoracoid bar (n.b. these details only become ossified in the 'adult'). In the pelvic girdle, both the pubes and the ischia tend to become expanded into median symphyses, but a mesial pubo-ischial bar is developed only in one genus (Elasmosaurus).

(iii) In the pectoral girdle, the glenoid fossae face outwards at 90° to the animal's longitudinal axis, whereas in the pelvic girdle the acetabuli face diagonally backwards at an angle of about 70° to the longitudinal axis. This difference in angles of orientation of the pectoral and pelvic glenoids suggests a difference between the normal orientations of the humerus and the femur.

(iv) In the pectoral girdle, the scapula is triradiate, there being produced a dorsal ramus which extends dorsally and anteriorly to the glenoid. The degree to which the process is orientated dorsal to the glenoid is accentuated by the natural orientation of the scapula, whose main antero-posterior axis is inclined at an angle to the horizontal (see fig. 8). This dorsal process bears prominent rugosities marking a major muscle origin. In the pelvic girdle the pubis is a simple plate and there is neither a dorsal ramus nor any other ossified site for muscle origins dorsal and anterior to the acetabulum.

The above four differences between the pectoral and pelvic girdles combine to imply that these girdles and their respective limbs differ in function. Furthermore, it is probable that the femur was normally orientated in a more posterior direction than the humerus, as in marine turtles.

It was argued above that the principal locomotor muscles in plesiosaurs had their origins on the ventral surfaces of the scapulae, coracoids, pubes and ischia. It is unlikely that the ventral (anterior) rami of the scapulae held the origins of powerful muscles running to the humerus since they are orientated at an anteriorly-inclined angle, and only become strongly ossified in the 'adult'. The posterior margin of this ramus may, however, have provided a surface for the origin of a relatively weak muscle (which may for convenience of description now be termed the 'anterior scapulohumeralis'). The dorsal ramus of the scapula, on the contrary, bears prominent rugosities on its posterior edge, is strongly built, and evidently bore the origin of a powerful muscle to the humerus ('dorsal scapulohumeralis').

The ventral surface of the coracoids is concave, and was probably completely covered with muscle. A mid-ventral keel is produced (somewhat reminiscent of the sternal keel of a bird) which is most prominently developed in the region of the median compression strut (see above). Its development suggests that the muscle was thickest here, and was capable of exerting a strong pull upon the humerus along the lines of the strut. The muscle or muscles in question ('anterior coracohumeralis') were certainly the largest in volume, and it is envisaged that they produced the principal locomotive force. Subsidiary muscles ('posterior coracohumeralis') ran to the humerus from more posterior parts of the coracoids, the compression forces from these being absorbed by the thickened lateral coracoid bars. The combined effect of the 'coracohumeralis' muscles upon the humerus would be to pull it in a ventral and slightly posterior direction.

It is probable that the entire ventral surface of the pubes and ischia were covered by the origins of muscles running to the femur ('pubofemoralis' and 'ischiofemoralis'). These may have been divided into anterior and posterior blocks as suggested for the 'coracohumeralis' muscles, since each pubis and ischium consists of thickened lateral and acetabulo-medial bars connected by thin sheet bone as in the coracoid.

The structure of the propodials and the development and position of the rugosities marking muscle insertions has been described in detail for Cryptoclidus eurymerus (see above, Section 2,1, pp.60, 63-64). Except that in that form the distal expansion of the humerus is unusually broad, the description given there may be taken as composite for most Upper Jurassic and probably also Cretaceous forms. The humerus and femur are broadly similar, except that the tuberosity of the humerus is inclined more posteriorly than the femoral trochanter (cf. figs. 17,A and 17,C), and in consequence the posterior face of the humeral tuberosity is visible in ventral view (cf. figs. 15,B and 18,B).

On the shaft of each propodial there are three areas of muscle insertion, these being on the anterior and posterior edges and a broad area on the ventral surface. The anterior insertion is much more prominent in the humerus than in the femur. The ventral shaft insertion in the femur frequently has a double appearance, whereas in the humerus only a single large area of insertion is discernable. On the tuberosity or trochanter there are likewise three areas of muscle insertion indicated by rugosities, these being on the anterior and posterior edges and at the proximal end of the dorsal surface. These areas are comparatively smaller and less rugose than the insertions on the shaft. Judging from the area and prominence of rugosities, the most powerful insertions upon the humerus are, firstly, the ventral insertion and, secondly, the insertion upon the anterior edge of the shaft. In the femur the apparently most powerful insertions are, firstly, the (?double) ventral insertion and, secondly, the insertion on the posterior edge of the shaft.

Reconstruction of the principal pectoral and pelvic musculature

The shafts of both the humerus and the femur are roughly cylindrical and are devoid of flanges or protuberances (other than the tuberosity or trochanter). It may therefore be assumed that rotation of the propodials is the primary function only of the muscles inserting upon the anterior or posterior edges of the tuberosity or trochanter. The primary function of muscles inserting upon the shaft or the ~~proximal end~~ dorsal surface of the tuberosity is to move the limb in an arc, and any rotation caused by these muscles is a secondary function. It is therefore logical that muscles inserting upon the shaft will have their origins in a reasonably juxta position to the insertion, whereas the origin of muscles causing rotation will be more speculative.

Following upon this argument, the principal locomotor muscles identified above from evidence of their origins on the girdles may now be arranged so as to insert upon the propodial shafts according to juxta position of the origins with insertions upon the shaft.

When the humerus is orientated in the glenoid in the "rest position" (i.e. extending outwards in a horizontal plane with the dorsal surface uppermost), it is evident that the large and powerful ventral insertion is for the 'coracohumeralis' muscles. Operation of the 'anterior coracohumeralis' alone would depress the humerus, with only a very small amount of retraction, and operation of the 'posterior coracohumeralis' would both depress and retract the humerus and also cause some rotation (anti-clockwise in the left limb).

The relatively smaller insertion on the posterior edge of the humerus is probably for a muscle running from the rugose lateral edge of the coracoid, the function of which would be to retract the humerus with minimal rotation. This muscle may for convenience be termed the 'lateral posterior coracohumeralis'.

The insertion of the powerful 'dorsal scapulohumeralis' muscle must be that which is prominent on the anterior edge of the humerus. Starting with the humerus in the "rest position", the function of this muscle is to elevate and protract the humerus, and also to produce some rotation of the limb (clockwise in the left limb).

The position of insertion of the relatively weak 'anterior scapulohumeralis' muscle is obscure, but must have been between the insertions for the 'dorsal scapulohumeralis' and the 'anterior coracohumeralis'. In such a position its function would have been to protract the humerus. It is doubtful that powerful "backing of water" was possible such as was suggested by Watson (1924).

The origins of muscles inserting on the well-developed tuberosity must remain speculative. It is, nevertheless, quite safe to assume that reasonably powerful rotation of the limb in both directions was achieved through muscles inserting anteriorly and posteriorly upon the tuberosity. Elevation of the limb was supplemented by a muscle whose insertion was upon the dorsal surface of the tuberosity and whose origin must have been either upon the visceral surface of the coracoids or, more probably, upon the dorsal ribs and vertebrae (in the latter case such a muscle may reasonably be regarded as homologous with the latissimus dorsi of other vertebrates).

Turning now to a consideration of the pelvic musculature, it seems probable that the principal muscles from the pelvic girdle (the 'pubofemoralis' and the 'ischiofemoralis') both inserted upon the ventral surface of the femoral shaft. This would account for the double appearance of this insertion in several specimens (including V.1104, see fig. 18,B). Inserted in this position, the 'pubofemoralis' would depress and protract the femur, and also produce slight rotation (clockwise in the left limb). The 'ischiofemoralis' would retract and slightly depress the femur, and slight rotation (in an anticlockwise direction in the left limb) might also have been produced.

The well-developed rugose area of insertion on the posterior edge of the femoral shaft probably represents the position of insertion of a muscle originating around the sacrum or the base of the tail ('caudifemoralis'). The function of this muscle was to retract and slightly elevate the femur.

The small area of rugosity on the anterior side of the femur probably represents the insertion of a relatively weak muscle whose origin lay along the lateral edge of the pubis ('lateral pubofemoralis'). The function of this muscle was to protract the femur, without rotation.

The remarks made above concerning the muscles inserting upon the humeral tuberosity apply equally to those inserting upon the femoral trochanter. It is reasonable to assume that rotation of the limb was produced by muscles inserting upon the anterior and posterior edges of the trochanter. It is also probable that the limb was elevated by a muscle inserting upon the dorsal surface of the trochanter, but it is difficult to judge where such a muscle might have had its origin.

The production of turtle-like locomotory movements

The reconstruction of the principal locomotory muscles of plesiosaurs outlined above was argued as that which most easily and logically fitted the known osteological structure. It was produced without reference to marine turtles or "flapping flight" locomotion. It is, however, a relatively easy matter to outline how the muscles thus arranged might have been used to produce cheloniid turtle-like locomotion. It is argued below that this ease is a measure of the probability that such locomotion in fact took place.

The locomotory stroke of the forelimb of cheloniid turtles was described by Walker (1971) and was summarized above. If the forelimb of plesiosaurs were to produce a similar movement then, commencing with the limb at its highest elevation at the beginning of a complete propulsive cycle, the operation of the large 'anterior' and 'posterior coracohumeralis' muscles would cause a powerful downward and slightly backward movement of the limb. Some rotation of the limb, placing the leading edge of the paddle slightly lower than the trailing edge (as in the flippers of turtles at this stage) would also be produced by the operation of these muscles, without the need for assistance by the rotator muscles inserting on the tuberosity.

At the conclusion of the downstroke an initial protraction of the humerus, quickly followed by elevation and protraction of the limb on the returning upstroke, would be produced by the powerful 'dorsal scapulohumeralis' muscle. Again, some rotation of the limb would be caused, this time bringing the leading edge uppermost as in the same stage of the turtle locomotory cycle. Elevation might be assisted by contraction of the muscle inserting on the dorsal surface of the tuberosity, and would also be assisted by water pressure on the inclined limb due to forward motion of the animal (this would amount to a reduction in the overall force required to elevate the limb). At the top of the upstroke slight forward movement might have been produced by action of the 'dorsal scapulohumeralis' perhaps assisted by the 'anterior scapulohumeralis' before commencement of a second locomotory cycle.

Throughout the locomotory cycle the horizontal orientation of the limb as produced by the principal locomotory muscles ('coracohumeralis' and 'dorsal scapulohumeralis') is essentially correct, and needs only slight modification by the rotator muscles. As in turtles, the downstroke would be substantially more powerful than the upstroke. The flexibility of the plesiosaur paddle, the slight backward orientation of the paddle with respect to the brachis, and the orientation of the humeral head relative to the shaft are all closely similar to these characters of the cheloniid turtle flipper, and indicate that the plesiosaur paddle would have functioned in the same way.

The hind limb of plesiosaurs was incapable of moving as does the fore limb since it lacks a major elevator muscle corresponding to the 'dorsal scapulohumeralis'. It again probably functioned as do the hind limbs of turtles. During normal straight swimming they were probably held in a backwardly orientated position by action of the 'ischiofemoralis' and 'caudifemoralis' muscles. Excess use of the former or the latter muscle would produce diving or elevation respectively. Turning was probably achieved by use of the pubofemoralis muscles. Herein may lie the only noteworthy functional difference between the hind limbs of plesiosaurs and turtles; operation of the 'pubofemoralis' would cause "backing water", in which operation the ventral face of the paddle would be pressed against the oncoming water, and the tip of the paddle would be moved outwards. It is difficult to envisage how at any stage the dorsal surface of the paddle might have been pressed against the water, since no powerful muscles inserted on the dorsal surface of the femur. To turn left, therefore, a plesiosaur would have used only the left hind limb, with the ventral face inclined forwards, whereas a turtle would use both hind flippers, pressing against the water the dorsal face of the left flipper and the ventral face of the right flipper. The turtle's method is undoubtedly more efficient, and it is quite probable that in plesiosaurs turning was assisted by the use of the neck and tail.

As with turtles, locomotion on land was probably cumbersome and laborious since the main locomotor muscles could not have been used to their best advantage, and the fore-and-aft muscles ('anterior scapulohumeralis' and 'lateral posterior coracohumeralis') of the fore limb are relatively weak. On land the most powerful fore-and-aft muscles would be those of the hind limb ('pubofemoralis', and the 'ischiofemoralis' and 'caudifemoralis') and these may have been used to push the anterior part of the animal in a sledge-like fashion. As a result, only sandy and muddy shores would have been visited, and probably then only to lay eggs as do the turtles (note: unlike ichthyosaurs, in which embryo young have been found, there is no evidence of viviparity in plesiosaurs).

Critical comparison with Watson's theory

A close examination of Watson's muscle reconstruction (1924) and a comparison with the structural conclusions reached above, reveals numerous and serious flaws in his argument that the muscles served to bring about a form of locomotion in which the principal movements of the humerus were in a backwards and forwards horizontal direction. In the following discussion of Watson's reconstruction, the names used by him are quoted only as labels to refer to the muscles which he envisaged, and (as was argued above) these should not be taken to imply homologies with similarly named muscles in living vertebrates.

According to Watson, the powerful backward swimming movement of the forelimb (in which the axis of the paddle is vertical, the anterior edge of the paddle being downwards) is produced by the action of five muscles. Only one of these (the "coraco-brachialis brevis" of Watson, which is the equivalent of my 'posterior coracohumeralis') inserts on the ventral surface of the humeral shaft, the other four inserting on the anterior edge in two opposing blocks. These all tend to produce rotation as well as backward movement; the "subcoracoideus" (Watson's name; originating on the visceral surface of the coracoid) and the "latissimus dorsi' (Watson's name; arising from the dorsal part of the trunk) tend to rotate the anterior margin of the humerus upwards, whereas the "supracoracoideus" (the equivalent of my 'anterior coracohumeralis') and the "pectoralis" (Watson's name; drawn originating on the gastralia) tend to rotate the anterior margin of the humerus downwards. Watson commented (p. 895) that "the two pairs of muscles balance one another so that the rotation which would ensue from the action of any one of them alone is prevented by the action of the other member of the pair".

It may be commented at this point that two of Watson's principal locomotory muscles, those which he called the "latissimus dorsi" and the "subcoracoideus" are unlikely to have contributed much power, since he reconstructed them originating dorsal to the humerus and yet inserting upon the edge of the humerus which was ventral in the swimming stroke. The effect of muscles in this position would have been to elevate and rotate the humerus, and only thirdly to retract the limb. Furthermore, as was stated earlier, the humeral shaft is cylindrical in section and is devoid of flanges which might normally be expected at the point of insertion of muscles with a rotatory effect. It is probable that any muscles originating dorsal to the humerus inserted in a different place from that suggested by Watson, and hence had a different function. The most probable site is the dorsal surface of the tuberosity (the only insertion on the dorsal side of the humerus), and the appearance of this insertion indicates that such muscles were relatively weak. Their function when reconstructed in this way would be to elevate the humerus with the axis of the distal expansion in a horizontal and not a vertical plane.

A muscle which Watson labelled as the "pectoralis" and which he showed originating on the gastralia, is most unlikely to have existed. Gastralia are primitively derived from dermal scutes, and therefore would be primitively external to any musculature originating in this position. It is unlikely that the gastralia, developed as they are into a protective plastron, could have sunk through this muscle. Certainly there is no osteological evidence to suggest the origins of any musculature on their smooth and rounded ventral surfaces. It is probable, therefore, that the true homologue of the pectoralis muscle, an important locomotory muscle in virtually all tetrapods, shifted its origin onto the ventral surface of the coracoid and is now represented by the muscle which I am calling the 'posterior coracohumeralis'.

Watson envisaged a large muscle, which he called the "deltoid", as the principal muscle pulling the humerus forward in the "feathered" position. According to his reconstruction, this muscle had its origin upon the whole of the clavicle, interclavicle and dorsal part of the scapula. He placed no special functional emphasis upon the dorsal ramus of the scapula; on the contrary, he argued that it showed a trend towards reduction, and made special reference to the "reduced" dorsal process in Colymbosaurus. This conclusion was reached through two errors of interpretation. Firstly, the dorsal process of the specimen which Watson studied is broken distally, but was taken to be complete by him (see description of C. trochanterius in Section 2(i) above). Secondly, the reconstructed girdle (Watson's text-fig. 11D) is shown misorientated by approximately 45°, in which position the scapular dorsal process appears horizontally in front of the glenoid instead of diagonally above it.

In my reconstruction the principal locomotor muscles have their origins on the ventral surface of the coracoid and the dorsal process of the scapula. It is evident that Watson realised that the muscles in this position were large and powerful. He also appreciated that muscles having their origins on the ventral surface of the coracoid ought normally to depress the humerus in addition to contributing to retraction, and he argued around this point with some difficulty. Referring to his "supracoracoideus" (equivalent to my 'anterior coracohumeralis') he admitted (p. 895) that such a muscle would draw the humerus "backward and downward" but added the dubious comment that "its action is not applied to the bone in a mechanically efficient way". This supposed lack of efficiency in a powerful muscle is surely an adverse reflection upon Watson's reconstruction (in which the muscle is inserted on the anterior and not the ventral surface of the humerus) rather than the result of devious and improbable evolution.

Watson further recognised that muscles from at least the dorsal process of the scapula would cause elevation of the humerus in addition to protraction. The probability of movement of the humerus in a vertical plane clearly worried him, and he was led (p. 895) to eliminate these unwanted movements and forces in an unorthodox manner, as follows:-

> "The humerus tends to be depressed by the action of all muscles arising from the body below the glenoid cavity and raised by those which arise from the dorsal part of the scapula and trunk. The muscles serving to depress the humerus act at a considerable mechanical disadvantage owing to their oblique insertion on the humerus, and can thus be counterbalanced by the comparatively less powerful muscles opposed to them which have a more favourable insertion."

It would therefore appear that Watson's theory may depend upon cancelling the forces of the most powerful muscles through a permanent state of tetanus, which then allows weaker muscles to produce retraction and protraction of the limb. Assuming that such an interpretation was not Watson's intention, it is nevertheless evident that a cheloniid "flapping flight" method of locomotion is substantially easier to reconstruct in plesiosaurs than is a "rowing" method.

"Flying" is a more efficient method of underwater locomotion than "rowing". Although the downstroke is the principal force-producing movement, the upstroke is also effective (Walker, 1971), whereas in "rowing" the forward "feathering" movement is counterproductive. Furthermore, the entire length of the forelimb is efficiently used in "flying" and is differentially twisted (like the blade of a ship's propellor) to this end; whereas in the backward power-stroke of the "rowing" method the axis of the entire limb has to be held in a vertical plane, whereby the fast-moving distal extremity of the paddle produces thrust but the proximal part of the brachis acts as a brake.

The relative efficiency of the "flying" method is witnessed by the evolution of modern forms. All recent vertebrate marine forms which use the manus for locomotion rather than the tail employ the "flapping flight" method (e.g. cheloniid turtles, sea lions, penguins). There are no examples of vertebrate animals which "row".

From the above discussion it is concluded that plesiosaurs swam by a "flapping flight" method, using the forelimbs for producing forward thrust and the hind limbs for steering as do cheloniid turtles.

(b) Teeth

The Plesiosauria have a dentition of numerous pointed and recurved teeth which intermesh when the jaws are closed. This character they share with several other groups, notably the ichthyosaurs, mosasaurs and mesosaurs (all of which were aquatic) and also with some pterosaurs (e.g. Pterodactylus) (which is believed to have been coastal in occurrence and fish-eating). It is generally accepted that this tooth arrangement is useful for capturing and retaining fish, and hence the term "piscivorous" is frequently applied to it. Some modern cetaceans have developed a comparable dentition.

In most marine higher vertebrates the "piscivorous" dentition serves a dual purpose. Firstly, the prey is captured and retained underwater, being either pierced by the teeth or trapped behind the enmeshed tooth-row; secondly, the animal surfaces and, with the teeth acting as a sieve, the water which was engulfed with the prey is drained off before the prey is swallowed. Such behaviour avoids an excessive intake of salt water, and very probably occurred in plesiosaurs.

In the descriptive and taxonomic sections (above) it was mentioned that teeth of pliosaurs can almost invariably be distinguished from those of plesiosaurs by the fact that pliosaur teeth show considerable wear on the tips of their crowns, whereas plesiosaur teeth remain sharply pointed and do not show apical wear. This difference, together with the fact that pliosaur teeth are less recurved and more strongly built, indicates a difference in function and diet.

Pliosaurs show numerous developments of structure which indicate that they were active predators and that their prey was relatively large. The jaws are relatively much larger and stronger than those of plesiosaurs, and the teeth were differentiated into enlarged anterior caniniform teeth and smaller posterior ones. The jaws were quite capable of biting off a limb of such smaller animals as plesiosaurs and crocodiles, and these may well have formed part of their diet. This being so, a pliosaur's teeth would have been used to chew and cut sizeable carcases into mouth-sized pieces for swallowing. Such action would involve grinding through bone, and this would produce apical wear on the pliosaur's teeth.

Plesiosaurs, on the other hand, have relatively small and weak jaws. Furthermore, as they had relatively long necks they would not have been able to use the weight of their bodies to suppress large prey. It may safely be assumed that their prey was of a relatively small size, including perhaps small to medium-sized fish and squid. These could be swallowed whole without the need for chewing and biting into bone, and so the apices of the teeth remained sharp.

The Cryptoclididae show a trend towards the development of a large number of smaller teeth. The most likely explanation for this development is that their prey was of a smaller size still, and that the use of the jaws as a sieve became more important than their use for direct penetration and retention of the prey. Shoals of immature or very small fish and crustaceans were their probable diet, and here the relatively fine sieve produced by the intermeshing of many small teeth was an advantage. The contents of the mouth, perhaps many small fish at a time, would be swallowed whole without wear to the teeth.

The characteristic pattern of tooth replacement found in plesiosaurians, in which juvenile teeth develop in alveoli which are lingual to the mature teeth, may be of considerable advantage to plesiosaurs. If the teeth were replaced from beneath as in most reptiles, then there would necessarily be a period of time immediately following the loss of an old tooth in which a gap would exist in the tooth-row. Several such gaps could adversely affect the efficiency of the sieving mechanism and result in the loss of prey. In plesiosaurs, however, the juvenile tooth is relatively well developed and is able to fill the gap immediately when an old tooth is shed. Also, as teeth tend to space themselves according to the positions of the teeth which surround and oppose them, it may well have been important for the overall maintenance of the intermeshing of the jaws that the old tooth's position be immediately reserved by the replacement tooth.

(c) Gastroliths

Gastroliths, or "stomach stones", have been frequently found associated with plesiosaurian remains. They are usually somewhat rounded and worn, having the appearance of beach pebbles, and are generally composed of a relatively hard rock. In specimens which have been remarkedly little disturbed after death and before preservation the gastroliths tend to be aggregated into a clump in the mid-ventral part of the belly.

Several theories accounting for their occurrence have been tentatively suggested. These include the accidental swallowing of stones by plesiosaurs whilst foraging on the sea bed for food, and the deliberate swallowing of stones for ballast (Brown, 1904).

In view of the fact that a plesiosaur's food was probably bolted whole, it would seem more likely that the gastroliths had a positive function to perform, assisting in the breaking up of food in a bird-like gizzard.

(d) General conclusions on mode of life of plesiosaurians

The Pliosauroidea, with their relatively short and thick neck, powerful limbs and streamlined body shape, were undoubtedly good swimmers. These large predators must have run down their prey by superior speed and general manoeuvrability.

The Plesiosauroidea, on the other hand, were less streamlined and powerful. The longer neck would produce a greater drag under water. The shorter-necked forms (Plesiosauridae and Cryptoclididae) were probably quite active swimmers, and were quite able to run down their smaller and less speedy prey. Greater mobility of the head and neck would allow lateral darting movements to be made in the final stages of capture. It is envisaged that these two families, together with the pliosaurs, persued their prey entirely under water.

The elasmosaurs developed a long neck to the point where the animals must have been quite ungainly underwater. Prey must have been persued by wide sweeping and darting movements of the head and neck in an arc around the body, with the body remaining relatively stationary in the water. Such activity may have taken place on the surface of the water, prey being searched for and attacked from above, as in the air a faster movement of the head could have been achieved. It is also possible that these animals may have lain in waiting for their prey, the long neck being darted forward towards unsuspecting victims.

Although the sea was obviously the principal habitat of plesiosaurs and pliosaurs, it is quite possible that they may have occasionally ventured out onto land, perhaps to lay eggs. They would have found the same difficulties of locomotion on land as do cheloniid turtles; but the well-developed plastron of gastralia would have protected the belly and supported its shape, thereby allowing breathing to continue normally.

If plesiosaurs did indeed lay their eggs on land, then this stage of their life-cycle would be the most vulnerable. It is possible that at this stage they became subject to conditions similar to those which caused the eventual extinction of the terrestrial dinosaurs. This may conceivably account for their disappearance from the fossil record at the same time.

SUMMARY

After a brief introduction and a synopsis of relevant British Jurassic stratigraphy, there follows a historical review of the taxonomy and classification of the suborder Plesiosauria down to the level of family. Three distinct classifications are currently in use, having been proposed by Welles (1943, 1962), Romer (1953, 1966) and Persson (1963). Taxonomic errors and oversights in these classifications are emended, and the emended classifications compared. The characters used by each author are listed.

The British Upper Jurassic plesiosaurs (members of the Plesiosauroidea) are reviewed in detail. Of the seven generic and thirty-two specific names which have been published for British Upper Jurassic plesiosaurs only four generic names and six specific names are found to be valid. In addition, a skull from the Kimmeridge Clay of Dorset is described as Kimmerosaurus oweni, new genus and species. Of these, five species belonging to three genera are recognised from the Oxford Clay and two species and genera from the Kimmeridge Clay.

After a formal listing and discussion of the synonymy of each valid species, a diagnosis is given and referable material is listed and described. The plesiosaur Cryptoclidus eurymerus is described in the greatest detail and is subsequently taken as a model for comparison with other species. A reconstruction of the entire skeleton of this form is offered, and the skulls of Cryptoclidus eurymerus, Tricleidus seeleyi and Kimmerosaurus oweni are reconstructed for the first time.

A list of rejected generic and specific names is given, with reference to the type material and the reasons for rejection, as appropriate.

The characters employed by previous taxonomists are discussed in the light of the present work. Thirty-nine characters currently or previously used in plesiosaurian taxonomy are distinguished and evaluated, and are

sorted into four categories according to their phylogenetic significance. It is concluded that only fifteen of these characters are of importance in distinguishing phylogenetic lineages.

The evolution of plesiosaurians is discussed, and three phyletic lineages are distinguished. The classification of plesiosaurs is then discussed, and a new classification is proposed which reflects the phylogeny. The suborder Plesiosauria is divided into two superfamilies, these being the Plesiosauroidea and the Pliosauroidea. It is believed that they may have had separate origins from the Nothosauria.

The Plesiosauroidea contains two major divergent families, the Elasmosauridae and the Cryptoclididae, together with a much reduced family Plesiosauridae which is considered to have been ancestral to both the former families. The Pliosauroidea is represented by a single family, the Pliosauridae. Diagnoses of the superfamilies and families are given, and the genera included within each family are listed.

The locomotion of plesiosaurs is discussed in detail. A theory advanced by Watson (1924), in which it was suggested that plesiosaurs used a "rowing" method of locomotion, is critically reviewed. A descriptive account is given of the locomotion of cheloniid marine turtles; these animals swim with their forelimbs in a manner comparable with "flapping flight" and use their hind limbs for steering. A comparative review of plesiosaurian pectoral and pelvic girdles and the associated propodials is given, and an arrangement of the principal muscle systems is then suggested. Using this reconstruction there follows an account of how turtle-like locomotion might have been produced in plesiosaurs. The reconstruction is then compared with and assessed relative to that given by Watson (1924). It is concluded that plesiosaurs swam by operating their forelimbs in an up-and-down manner resembling the "flapping flight" locomotion of cheloniid turtles, and their hind limbs were used for steering.

Further selected aspects of the functional morphology of plesiosaurs are discussed. Differences in tooth form in the three phyletic lineages, together with other morphological differences including general body shape, proportions and size, are accounted for by differences in diet and life habit. Gastroliths are considered to be evidence for the existence of a bird-like gizzard. It is believed possible that plesiosaurians came onto land to lay eggs as do marine turtles.

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APPENDIX

Catalogue of specimens referred to *Cryptoclidus eurymerus* (Phillips)

(i) The following specimens in the British Museum (Natural History) were catalogued by Andrews (1910), and are specifically diagnostic:-

R.2412	Figured Seeley (1892, figs. 13-15) as the type of *Muraenosaurus (Cryptoclidus) platymerus* Seeley. Figured Andrews (1910, text-figs. 79, 80, 83, 84 and 90,C).
R.2416	Figured Andrews (1895a, fig. 3,B; 1910, text-figs. 89,A and 90,B)
R.2417	Figured Andrews (1895b, Pl. ix; 1910, text-figs. 78,A,B; 90,A; 92; Pl. IX, figs. 4, 4a, 5 and 6).
R.2420	
R.2431	
R.2862	Figured Andrews (1910, text-fig. 86).
R.3703	Figured Andrews (1910, text-fig. 93).
R.3730	Figured Andrews (1910, Pl. IX, fig. 7).

(ii) The following specimens in the British Museum (Natural History) were catalogued by Andrews (1910), and are generically diagnostic. As the areas of distribution of the two species of *Cryptoclidus* are not known to overlap, these specimens are referred as *Cryptoclidus cf. eurymerus* since they are from within the known range of that species:-

R.2418	Figured Andrews (1910, text-figs. 81 and 82).
R.2616	Figured Andrews (1895a, figs. 1 and 2; 1896a, fig. 1; 1910, text-fig. 87 and Pl. X).
R.3533	Figured Andrews (1910, text-fig. 88).
R.3705	Figured Andrews (1910, text-fig. 85).

(iii) The following specimens, now in the British Museum (Natural History), were catalogued by Neaverson (1935). (Numbers are those of the Geological Collection of the University of Liverpool).

(a) Specifically diagnostic specimens:-

4532; 4534; 4538.

(b) Indeterminate material catalogued as Cryptoclidus oxoniensis:-

4533; 4535; 4536; 4537.

(iv) The following described specimen in the Hunterian Museum, University of Glasgow, is specifically diagnostic:-

V.1091 Figured Smellie (1915, 1 fig; 1916, figs. 1-9 and 1 plate) as the type of Apractocleidus teretipes Smellie. Now mounted and exhibited incombination with the caudal vertebrae of V.1104.

(v) The following specifically diagnostic specimens have not been listed in published catalogues:-

(a) In the British Museum (Natural History):-

R.8621 Figured Charig and Horrell (1971). This specimen was discovered in 1970 in the No. 1 pit of the London Brick Company at Fletton, near Peterborough. Its horizon was established as the zone of Kosmoceras jason, Middle Callovian, Upper Jurassic. The postcranial skeleton is almost complete, lacking only the atlas and axis, a few anterior cervical vertebrae, and part of the right forepaddle. Of the skull only the lower jaw and 2 teeth were recovered.

(b) In the National Museum of Wales, Cardiff:-

19.98.G1 An immature post-cranial skeleton consisting of an incomplete column of 60 vertebrae; a few rib fragments; scapulae; coracoids; the right clavicle; the left ilium; the right humerus; one radius; both femora, tibia and fibulae, and 55 indeterminable paddle bones. The specimen has been mounted, with the mising parts restored in plaster, and thus reconstructed has a length of 240 cm.

19.98.G5 Very incomplete adult skeleton consisting of 20 vertebrae; rib and gastralial fragments; 1 ilium, 1 humerus, 1 femur and several indeterminable paddle bones.

(c) In the Hunterian Museum, University of Glasgow:-

V.1090 A partial postcranial skeleton of an adult individual, consisting of 44 vertebrae; several ribs and gastralia; both ilia; both humeri; 1 radius; 14 mesopodials and 47 phalanges.

V.1104 A partial postcranial skeleton of an adult individual, consisting of 20 cervical, 14 dorsal, 4 sacral and 19 caudal vertebrae; an almost complete series of dorsal ribs; numerous gastralia; both scapulae and coracoids; the pelvic girdle; both humeri; 1 radius and 1 ulna; both femora; 4 mesopodials and 19 phalanges. The caudal vertebrae have been incorporated as an exhibited "complete" skeleton with V.1091, which lacked a tail.

V.1105 A partial postcranial skeleton of a juvenile individual in which the neural arches are not fused to the centra. 2 cervical, 22 dorsal, 4 sacral and 5 caudal vertebrae; both coracoids, pubes and ischia; the left ilium; the right humerus and both femora.

V.1128	A right humerus of a juvenile.
V.1614	2 scapulae, 2 coracoids and 1 humerus (on exhibit).
V.1692	A right humerus of a juvenile.
V.1753	Both humeri and femora of an adult.
V.1803	A right humerus of an adult.
V.1807	2 coracoids and 2 scapulae which are fused into a single plate, and both humeri. An old adult individual.
V.1809	Right humerus, radius, ulna and associated paddle bones of an old adult individual.
V.1810	Right humerus, left femur, both tibia and fibulae with associated paddle bones of an old adult individual.
V.1827	Right humerus.
V.1828	Left humerus, which could belong with V.1827.
V.1830	Right humerus.
V.1835	Right humerus of an old adult.
V.1840	Left humerus.

(d) In the Sedgwick Museum, Cambridge. The plesiosaur collection of the museum is at present undergoing curation and restoration. The Oxford Clay plesiosaurs have not yet been given catalogue numbers, and it is not possible to give an account of diagnostic material, save to note that this exists in the Museum collections.

Tables of measurements used in fig. 14

Measurements are of the centra and are in centimeters.

Vertebrae are numbered in sequence from anterior to posterior.

Length (L) is the maximum mid-ventral length.

Width (W) is the maximum width of the posterior face.

Height (H) is the minimal height of the posterior face to the floor of the neural canal.

Length Index = $\frac{2L}{(2+H)} \times 100$

Table 1 Vertebrae of BM.V.1091

Type	No.	L	W	H	Index	Type	No.	L	W	H	Index
Atl/Axis	1+2	4.42	2.93	2.42	-	Cervical	29	3.92	6.15	4.75	71.9
Cervical	3	2.43	3.12	2.51	86.5	Pectoral	30	4.00	6.14	4.82	73.0
"	4	2.73	3.42	2.68	89.5	"	31	4.02	6.23	4.93	72.0
"	5	2.82	3.40	2.84	90.4	"	32	4.08	6.26	4.96	72.7
"	6	2.89	3.62	2.95	88.1	Dorsal	33	4.24	6.15	5.18	74.9
"	7	2.99	3.71	2.97	89.5	"	34	4.08	6.12	5.19	72.2
"	8	3.12	3.82	3.03	91.2	"	35	4.32	6.02	5.25	76.7
"	9	3.21	3.85	3.07	92.8	"	36	4.43	6.19	5.20	77.8
"	10	3.20	4.11	3.18	87.9	"	37	4.43	6.22	5.32	76.8
"	11	3.23	4.10	3.25	88.0	"	38	4.74	6.37	5.35	80.8
"	12	3.30	4.27	3.36	86.6	""	39	4.75	6.40	5.45	80.2
"	13	3.36	4.36	3.38	87.3	"	40	4.77	6.50	5.50	79.5
"	14	3.47	4.46	3.48	87.4	"	41	4.82	6.55	5.43	80.5
"	15	3.55	4.63	3.58	86.6	"	42	4.70	6.48	5.62	77.7
"	16	3.55	4.70	3.69	84.7	"	43	4.74	6.57	5.60	78.0
"	17	3.67	4.87	3.79	84.7	"	44	4.88	6.55	5.58	80.5
"	18	3.68	4.96	3.93	82.9	"	45	4.83	6.48	5.67	79.6
"	19	3.63	5.10	3.96	80.1	"	46	4.82	6.37	5.45	81.5
"	20	3.70	5.34	4.08	78.5	"	47	4.85	6.35	5.33	83.0
"	21	3.73	5.37	4.20	78.0	"	48	4.81	6.30	5.27	83.2
"	22	3.65	5.38	4.28	75.6	"	49	4.84	6.31	5.28	83.6
"	23	3.73	5.50	4.30	76.1	"	50	4.60	6.15	5.14	81.6
"	24	4.00	5.65	4.64	77.8	"	51	4.58	6.07	5.02	82.7
"	25	3.80	5.70	4.34	75.7	"	52	4.70	6.00	5.13	84.5
"	26	3.82	5.84	4.50	73.9	"	53	4.62	6.00	4.97	84.3
"	27	3.82	5.90	4.55	73.2	"	54	4.57	6.04	4.90	83.5
"	28	3.84	6.00	4.62	72.3	"	55	4.67	6.09	5.01	84.1
						Sacral	56	4.73	6.12	4.92	85.7

Table 2 Vertebrae of HM.V.1104

Type	No.	L	W	H	Index	Type	No.	L	W	H	Index
Cervical	5	2.65	3.45	2.67	86.6	Dorsal	49	4.47	6.34	5.75	73.9
"	6	2.72	3.55	2.72	86.6	"	50	4.43	6.60	5.64	72.4
"	7	2.77	3.67	2.74	86.3	(Small gap)		-	-	-	-
"	8	2.98	3.87	2.94	87.4	Dorsal	52	4.34	6.07	5.32	76.3
"	9	3.00	3.98	2.93	86.7	"	53	4.23	6.06	5.15	76.3
(Small gap)		-	-	-	-	"	54	4.25	6.40	5.30	72.6
Cervical	11	3.20	4.13	3.17	87.7	"	55	4.25	6.03	5.14	76.0
"	12	3.28	4.26	3.25	87.2	Sacral	56	4.15	5.69	5.10	76.9
"	13	3.30	4.38	3.34	85.5	"	57	4.07	5.74	5.24	74.1
"	14	3.34	4.53	3.42	83.9	"	58	4.10	5.90	5.08	74.7
"	15	3.38	4.62	3.58	82.4	"	59	3.74	6.62	5.00	64.4
"	16	3.43	4.68	3.64	82.5	Caudal	60	3.60	6.70	4.95	61.8
"	17	3.38	4.80	3.73	79.2	"	61	3.50	6.50	4.92	61.3
"	18	3.48	4.94	3.85	78.0	"	62	3.48	6.30	4.79	62.8
"	19	3.50	5.03	3.88	78.5	"	63	3.45	6.28	4.84	62.0
"	20	3.56	5.09	4.04	77.9	"	64	3.40	6.23	4.76	61.9
"	21	3.56	5.26	4.10	76.1	"	65	3.37	6.08	4.73	62.4
"	22	3.52	5.30	4.17	74.3	"	66	3.39	5.95	4.58	64.4
"	23	3.60	5.45	4.23	74.4	"	67	3.23	5.86	4.56	62.0
"	24	3.55	5.56	4.32	71.9	"	68	3.25	5.78	4.46	63.5
"	25	3.49	5.75	4.39	68.8	"	69	3.23	5.84	4.56	62.1
(Gap)	-	-	-	-	-	"	70	3.10	5.75	4.39	61.1
Dorsal	41	4.09	5.90	5.50	71.8	"	71	2.98	5.74	4.43	58.7
"	42	4.25	6.26	5.58	71.8	"	72	2.96	5.70	4.30	59.2
"	43	4.17	6.16	5.63	70.7	"	73	2.93	5.50	4.25	60.2
"	44	4.30	6.19	5.60	72.9	"	74	3.03	5.30	4.20	63.8
"	45	4.37	6.12	5.65	74.2	"	75	2.99	5.20	4.12	64.2
"	46	4.40	6.31	5.72	73.2	"	76	3.05	4.97	3.98	68.2
"	47	4.33	6.20	5.72	73.5	"	77	2.95	4.56	3.80	70.6
"	48	4.25	6.32	5.52	71.8	"	78	2.85	4.33	3.57	72.1

Note: Vertebral numbers 5-50 are estimated.

Table 3 Vertebrae of BM(NH). R.2417

This specimen is mounted and on exhibition, and could not be measured.

The following measurements were given by Andrews (1910).

Type	No.	L	W	H	Index
Cervical	5	1.6	2.4	1.7	78.0
"	10	1.7	2.8	2.0	70.8
"	20	2.0	3.6	2.5	65.6
"	25	2.1	3.9	3.0	60.9
"	30	2.1	4.2	3.1	56.0
'Anterior dorsal'		2.4	4.4	3.6	60.0
'Posterior "		2.4	4.1	3.3	64.9
'Anterior caudal'		1.9	4.2	3.0	52.8
'Middle caudal'		1.6	3.4	2.7	52.5

Catalogue of specimens referred to *Muraenosaurus leedsii* Seeley

Of the four characters listed in the diagnosis (p.78) the second and third (referring to the form of the interclavicle and the intermedial facet of the radius) are individually diagnostic of the species, and the first and to a lesser extent the fourth are somewhat variable supporting characters. Thus, specimens in which the interclavicle or a radius or both are preserved are referred with certainty to *M. leedsii* (section 1 below), whereas specimens which exhibit only the supporting characters are tentatively referred (section 2 below).

1. The following specimens are referred with certainty to *M. leedsii*:-

(a) Specimens in the British Museum (Natural History) which were catalogued by Andrews (1910) as *M. leedsii*, *M. durobrivensis* or *M. platyclis*:-

R.2422	Figured Andrews (1910, text-fig. 44).
R.2423	
R.2424	Figured Seeley (1892, fig. 8).
R.2425	Figured Andrews (1910, text-fig. 58).
R.2426	Figured Seeley (1892, fig. 9).
R.2427	
R.2428	Figured Andrews (1895c, figs. 1-3; 1910, text-figs. 65 and 67, Pl. V, figs. 1-9, 11-12). Type-specimen of *Muraenosaurus durobrivensis* (Lydekker, 1889a).
R.2678	Figured Seeley (1892, fig. 7) and Andrews (1910, text-figs. 48, 68, 69, Pl. VI, figs. 1-5; also basis of reconstructions text-figs. 46, 47 and 66). Type-specimen of *Muraenosaurus platyclis* Seeley, 1892.
R.2864	Figured Andrews (1910, text-figs. 59 and 63).
R.3704	Figured Andrews (1910, text-fig. 62; Pl. VI, figs. 6 and 6a).

(b) One specimen now in the British Museum (Natural History) was catalogued by Neaverson (1935):-

4539 (Catalogue number is that of the Geological Collections of the University of Liverpool).

(c) Specimens in the National Museum of Wales, Cardiff, which have not been listed in published catalogues:-

19.96.G17 A 'juvenile' specimen consisting of an almost complete vertebral column of 90 centra (including the axis and atlas but lacking all neural arches and ribs); both humeri, femora and ilia; one radius, one ulna, a few paddle bones and a posterior portion of the left lower jaw. A basi-occipital labelled as belonging with this specimen is not in fact associated according to correspondence in the museum from Mr. E. T. Leeds.

21.44.G3 An 'adult' specimen consisting of 25 vertebrae, the right humerus, the left femur, 1 radius, 2 carpals, 1 tibia, 1 fibula and 6 tarsals.

(d) One specimen in the Hunterian Museum, University of Glasgow, has not been listed in a published catalogue:-

V.1092 An 'adult' specimen consisting of parts of 66 vertebrae, both fore paddles, the pectoral girdle, numerous broken rib fragments, a few isolated teeth and a small portion of the lower jaw. The left fore paddle has been mounted on a board. This specimen has suffered badly from pyritic decay.

2. The following specimens are tentatively referred to *M. leedsii*:-

(a) Specimens in the British Museum (Natural History) which were catalogued by Andrews (1910) as *M. durobrivensis*:-

R.2861 Figured Andrews (1910, text-figs. 43 and 45).

R.2863 Figured Andrews (1910, text-figs. 49-57 and 60). An unidentifiable bone fragment accidentally associated with this specimen was also figured (*ibid.*, Pl. V, fig. 10) and was described as an interclavicle.

(b) One specimen in the National Museum of Wales, Cardiff, has not been listed in a published catalogue:-

19.96.G6 A 'juvenile' specimen consisting of 28 cervical, 2 pectoral, 3 dorsal and 6 caudal vertebrae, together with the right humerus, both femora, portions of both coracoids, ischia, ilia and the right pubis, a few mesopodials and phalanges and a box of broken rib fragments.

Catalogue of specimens referred to *Colymbosaurus trochanterius* (Owen)

(a) In the British Museum (Natural History):-

31785 A left femur from the Kimmeridge Clay of Shotover, Oxford. History unknown. Catalogued as a generically undetermined "humerus" by Lydekker (1889b, p. 148).

31787 The holotype of *C. trochanterius*, described by Owen, 1840a; figured Phillips, 1871; and catalogued by Lydekker (1889b, p. 198) as a "femur". The specimen is actually a right humerus, and is probably from the Kimmeridge Clay of Shotover Hill, Oxfordshire. Enniskillen Collection.

31795 A left humerus from the Kimmeridge Clay of Shotover. Incorrectly noticed by Hulke (1870) as the type specimen. Catalogued by Lydekker (1889b, p. 199) as a "right femur". Enniskillen Collection.

40106 A partial postcranial skeleton of an 'adult' individual from the *Pectinatites pectinatus* zone of the Kimmeridge Clay of Kimmeridge Bay, Dorset. Described and figured as the type specimen of *Plesiosaurus manselii* Hulke, 1870, since which time several parts have suffered badly from pyritic decay. This specimen was originally catalogued (Lydekker, 1889b) under the numbers 40106, 40107a, 40107b, 40108a, 42496 and 42496a. Collected by J. C. Mansel-Pleydell.

40107 A left femur from the Kimmeridge Clay of Kimmeridge Bay, Dorset. Originally numbered 40107c, not catalogued by Lydekker (1889b). Collected by J. C. Mansel-Pleydell.

40640 A right femur with associated epipodials, tarsals and proximal phalanges of a 'juvenile' individual which are preserved *in situ* by the matrix of Portland Stone.

Described and figured as the type specimen of *Pliosaurus portlandicus* by Owen (1869, Pl. IV). Also figured by Hulke (1883, fig. 8). From the zone of *Titanites giganteus*. Portlandian Stage, Portland Island, Dorset.

46479 A right humerus of a 'juvenile' individual from the Kimmeridge Clay (locality unknown). Figured Lydekker (1889b, fig. 62), which figure is not an accurate representation.

(b) *In the Sedgwick Museum, Cambridge*:-

J.29596-J.29691 together with J.59736-J.59743.

A partial postcranial skeleton of an 'adult' individual (each bone is separately numbered). This specimen is one of the two syntypes of *Plesiosaurus megadeirus* Seeley, 1869 (the second syntype is missing), and consists of 42 cervical, 3 pectoral and 11 dorsal vertebrae (J.29598-J.29653), anterior portions of both coracoids (J.29596 and J.29597), the left femur, tibia, fibula, 5 tarsals and 30 phalanges (J.29654-J.29691) and the right femur, tibia, fibula and 5 tarsals (J.59736-J.59743). The specimen was collected from the Kimmeridge Clay of Ely, Cambridgeshire, and presented to the Museum by Stead Jones, Esq.

(c) *In the Manchester Museum*:-

L.3165, L.3166, L.3177 and a pectoral girdle without catalogue numbers.

An associated series consisting of the right and left humeri (L.3165 and L.3166), 2 ulnae, 1 ulnare and one indeterminable carpal (jointly numbered L.3177), the left scapula and both coracoids (without catalogue numbers). The left humerus (L.3166) was figured by Watson (1924, text-fig. 8) who also gave an outline figure of the whole specimen (text-fig. 10D).

Collected by K. C. F. Manning from the Kimmeridge Clay of Coppock's Pit, Shotover, Oxfordshire, and presented to the Manchester Museum in 1895. Six cervical vertebrae numbered L.3171 may also be associated with this specimen.

(d) In the Castle Museum, Norwich:-

(No catalogue numbers)

A left femur, tibia, fibula, two distal tarsals and several phalanges on display in the gallery and associated with a right femur (in two pieces) in the store. This specimen was collected from the Kimmeridge Clay of Downham Market, Norfolk, by C. B. Rose, Esq.

CHECK-LIST OF BRITISH UPPER JURASSIC PLESIOSAURS

Names are arranged in alphabetical order of specific epithet.

(i) The following are valid names for species:-

Muraenosaurus beloclis (Seeley, 1892)
Cryptoclidus eurymerus (Phillips, 1871)
Muraenosaurus leedsii Seeley, 1874
Kimmerosaurus oweni gen. et sp. nov.
Cryptoclidus richardsoni (Lydekker, 1889)
Tricleidus seeleyi Andrews, 1909
Colymbosaurus trochanterius (Owen, 1840)

(ii) The following names are rejected for the reason(s) given:-

Plesiosaurus affinis Owen, 1840	*nom.dubium*; *nom.oblitum*.
Plesiosaurus brachistospondylus Hulke, 1870	*nomen vanum*
Cimoliasaurus brevior Lydekker, 1889	*nomen vanum*
Plesiosaurus brevis Owen, 1854	*nom.vanum*; *nom.oblitum*.
Plesiosaurus carinatus Phillips, 1871 (*non* Cuvier, 1824).	see *P. phillipsi*
Plesiosaurus doedicomus Owen, 1840	*nomen vanum*
Cimoliasaurus durobrivensis Lydekker, 1889	syn. with *M. leedsii*
Plesiosaurus ellipsospondylus Phillips, 1871	*nom.vanum*; *nom.oblitum*
Plesiosaurus hexagonalis Phillips, 1871	*nom.vanum*; *nom.oblitum*
Plesiosaurus infraplanus Phillips, 1871	*nom.vanum*; *nom.oblitum*
Plesiosaurus levis Owen, 1854	*nomen nudum*
Plesiosaurus manselii Hulke, 1870	syn. with *C.trochanterius*
Plesiosaurus megadeirus Seeley, 1869	syn. with *C.trochanterius*
Plesiosaurus megapleuron Owen, 1854	*nom.vanum*; *nom.oblitum*
Plesiosaurus oxoniensis Phillips, 1871	*nomen vanum*
Plesiosaurus phillipsi Sauvage, 1879	*nom.vanum*; *nom.oblitum*
Plesiosaurus planispondylus Damon, 1860	*nomen nudum*

Muraenosaurus platyclis Seeley, 1892	syn. with *M. leedsii*
Muraenosaurus (Cryptoclidus) platymerus Seeley, 1892	syn. with *C. eurymerus*
Plesiosaurus plicatus Phillips, 1871	*nomen vanum*
Pliosaurus portlandicus Owen, 1869	syn. with *C.trochanterius*
Plesiosaurus subdepressus Owen, 1854	*nomen nudum*
Apractocleidus teretipes Smellie, 1915	syn. with *C. eurymerus*
Plesiosaurus truncatus Owen, 1854	*nomen vanum*
Plesiosaurus validus Phillips, 1871	*nom.vanum*; *nom.oblitum*
Plesiosaurus winspitensis Seeley, 1871	*nom.vanum*; *nom.oblitum*

Figure 1

Cryptoclidus eurymerus: Skull reconstruction, x1. Lateral view.

A	angular
D	dentary
F	frontal
J	jugal
MX	maxilla
P	parietal
PMX	premaxilla
po.b	postorbital bar (postorbital and/or postfrontal)
PT	pterygoid
Q	quadrate
SA-ART	fused surangular-articular
SO	supraoccipital
SQ	squamosal


P
SO
F
po.b.
F
SQ
PMX
MX
J
PT
D
SA-ART
Q
A

Figure 2

Cryptoclidus eurymerus: Skull reconstruction, x1. Occipital view

A	angular	PT	pterygoid
BO	basioccipital	Q	quadrate
EO-OP	fused exoccipital-opisthotic	SO	supraoccipital
P	parietal	SQ	squamosal

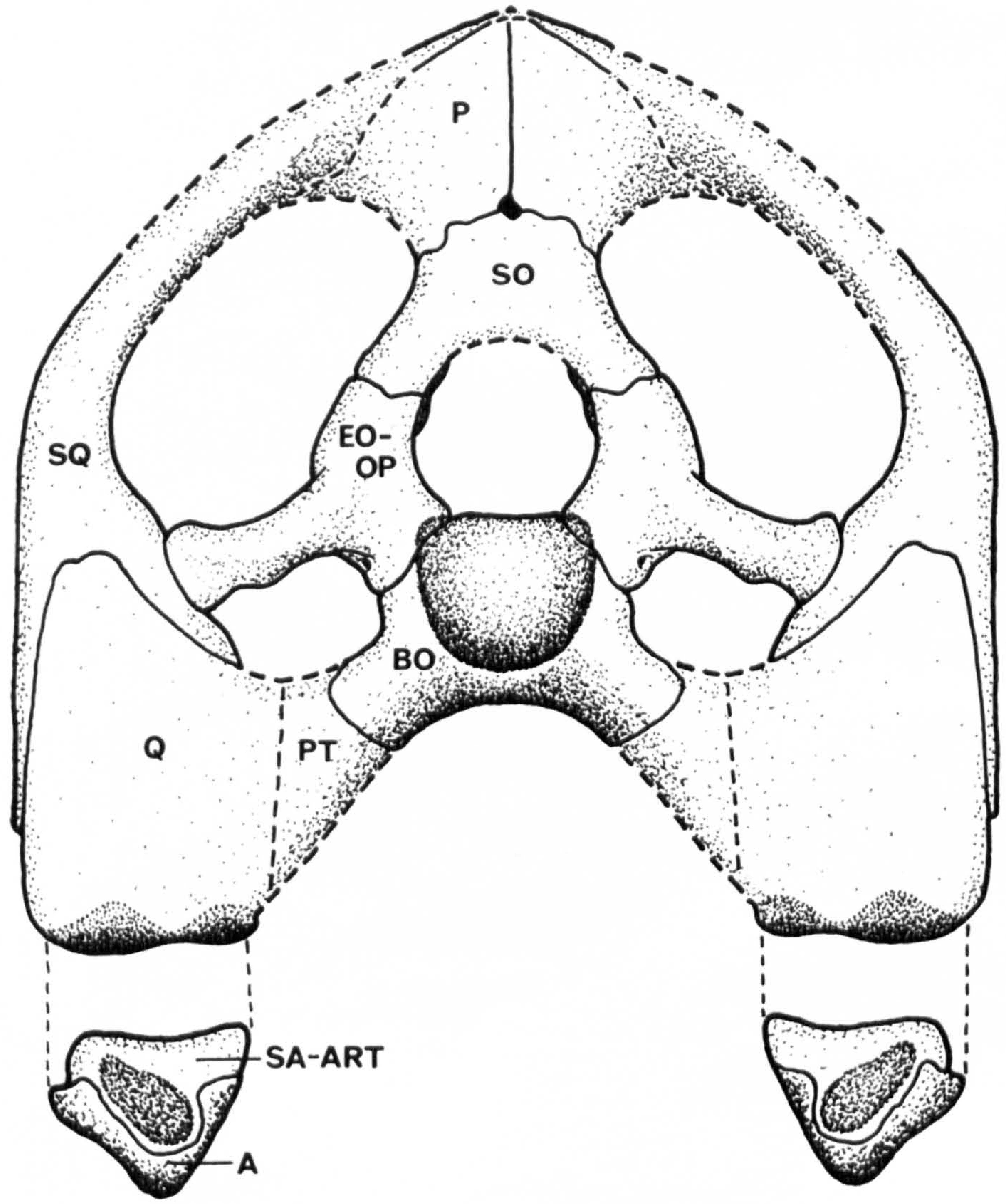

P
SO
SQ
EO-
OP
BO
Q
PT
SA-ART
A

Figure 3

Cryptoclidus eurymerus: Dentary of R.8621, x0.8. Dorsal view. Outline of posterior part of lower jaw added to scale in outline from fig. 4B.

prim. alv.	primary alveoli
sec. soc.	secondary sockets

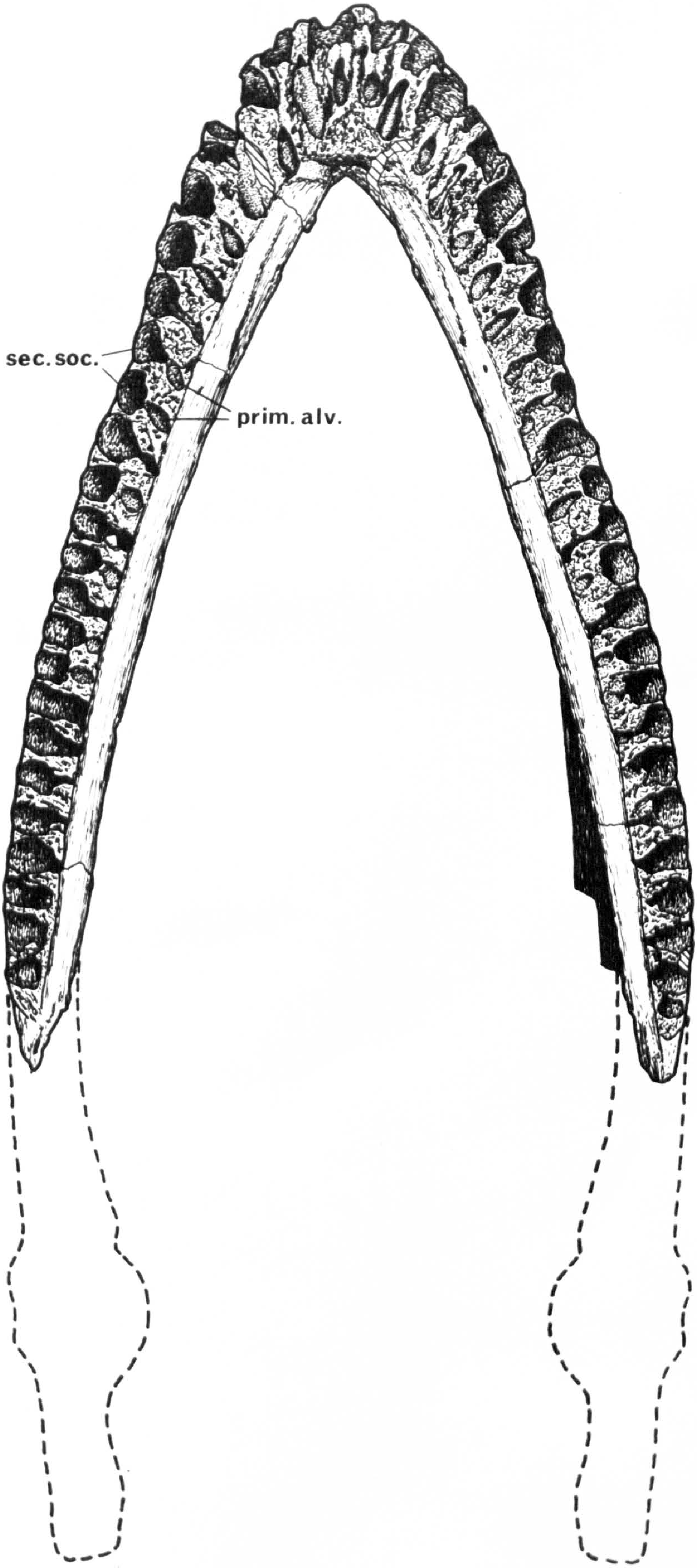

sec. soc.
prim. alv.

Figure 4

Cryptoclidus eurymerus: Posterior part of right lower jaw ramus of R.8621, x0.8. A mesial view; B dorsal view; C lateral view

A	angular	SA	surangular
ART	articular	s.d.	surface for union with dentary

The articular and surangular are fused: the probable line of suture is indicated in fig. 4B by a dashed line. A similar dashed line between the articular and angular represents the line of fusion between these elements, which is clearly discernable from growth-lines.

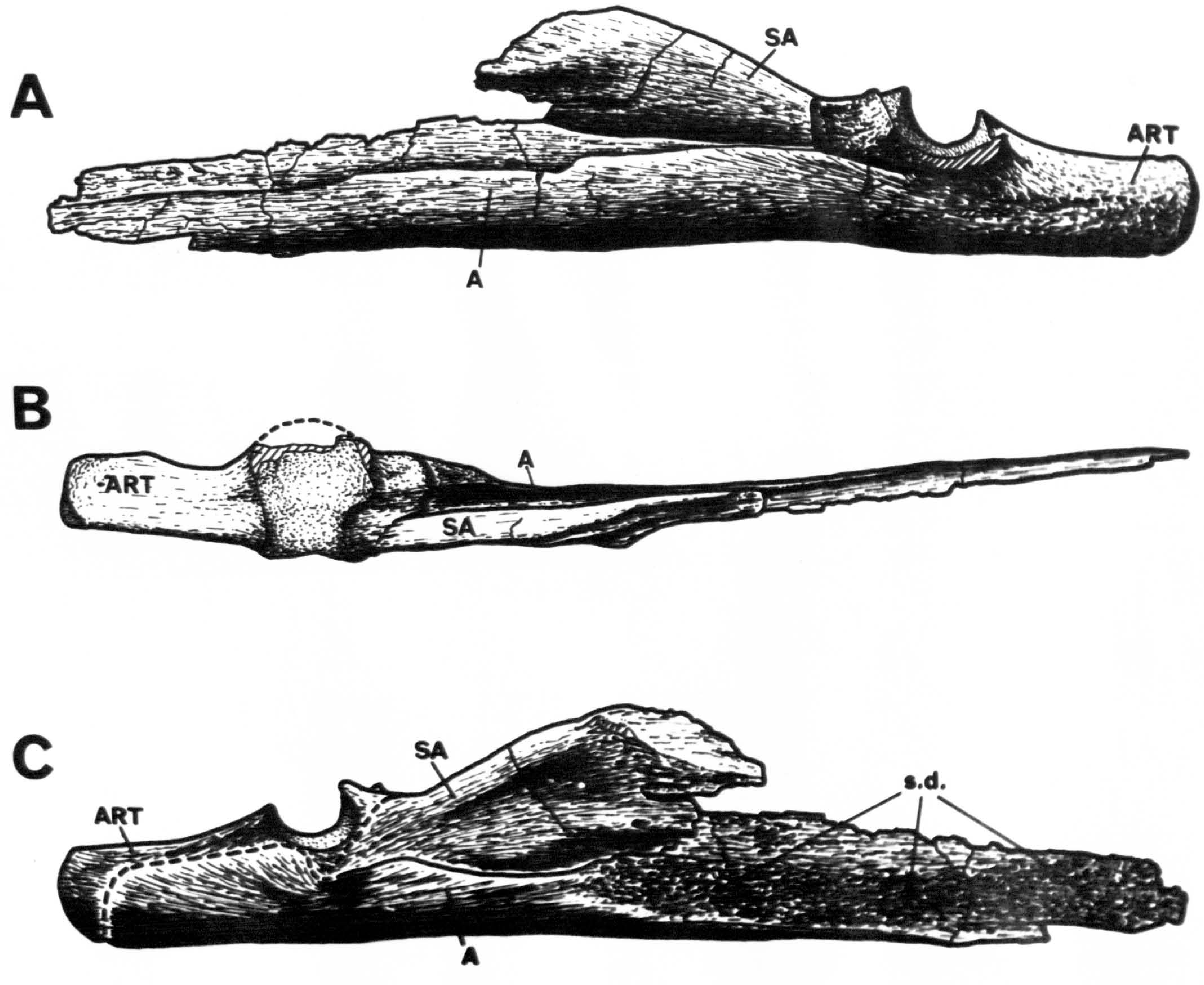

A
SA
ART
A
B
A
ART
SA
C
SA
ART
s.d.
A

Figure 5

Cryptoclidus eurymerus: Isolated right tooth of R.8621, showing ornamental ridges. a anterior axial view; b lingual view; c posterior axial view; d buccal view.

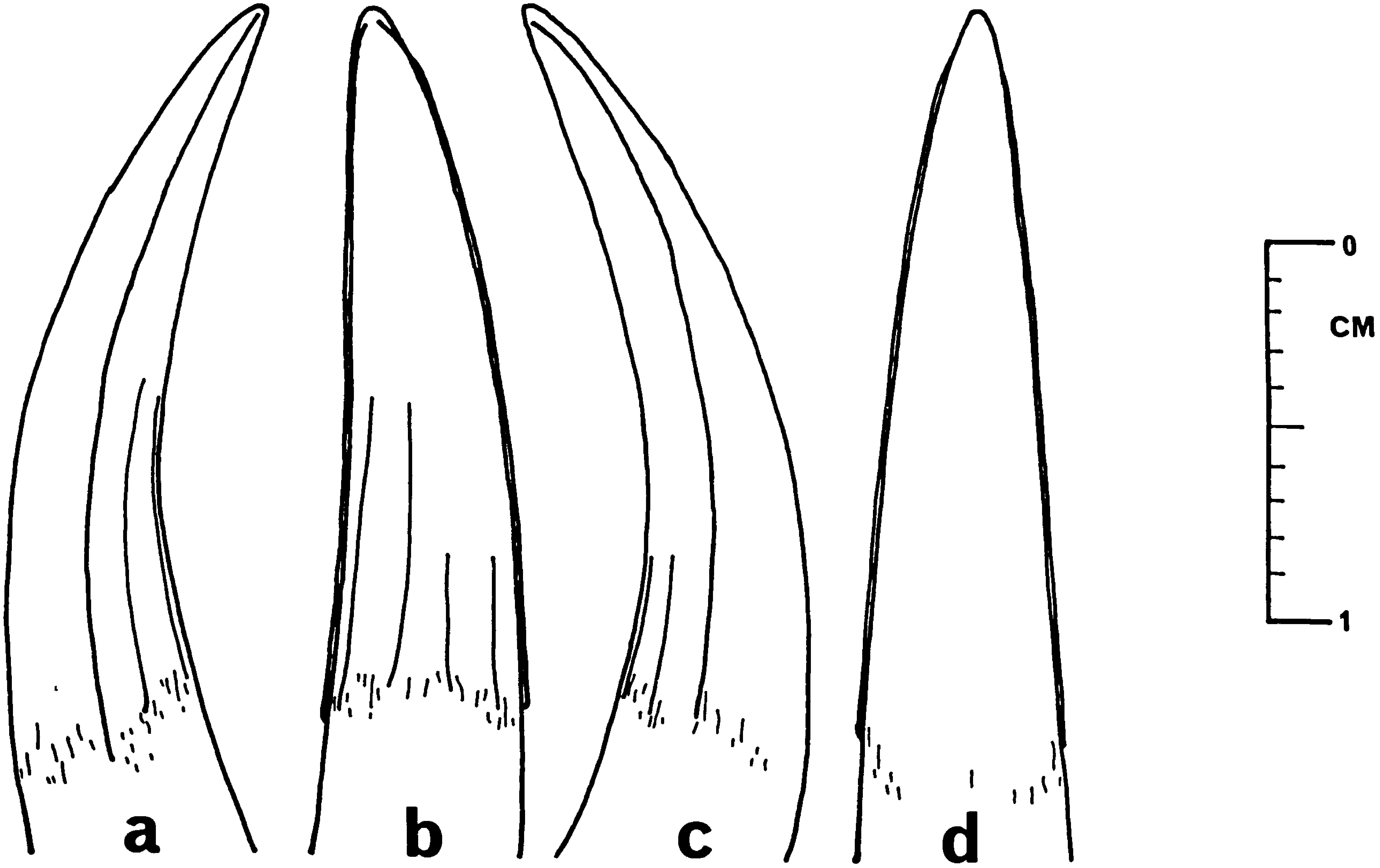

a
b
c
d
0
CM
1

Figure 6

Cryptoclidus eurymerus: Skull of R.3730, x0.8. Right dorsolateral view.

A	angular
D	dentary
MX	maxilla
PMX	premaxilla
PT	pterygoids
Q	quadrate
SA-ART	fused surangular-articular

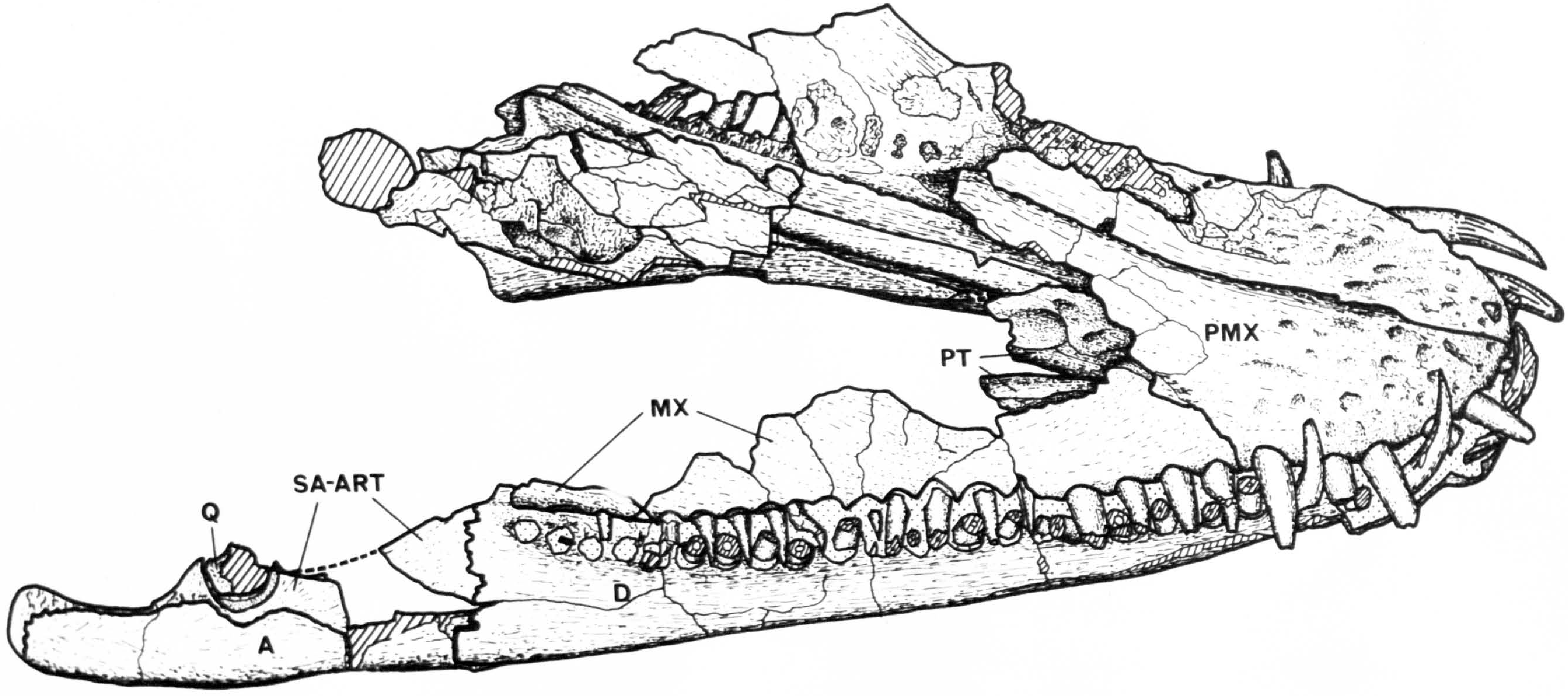

PMX
PT
MX
SA-ART
Q
D
A

Figure 7

Cryptoclidus eurymerus: Skull of R.3730, x0.8. Left ventrolateral view

A	angular
D	dentary
MX	maxilla
PT	pterygoids
SA	surangular portion of surangular-articular

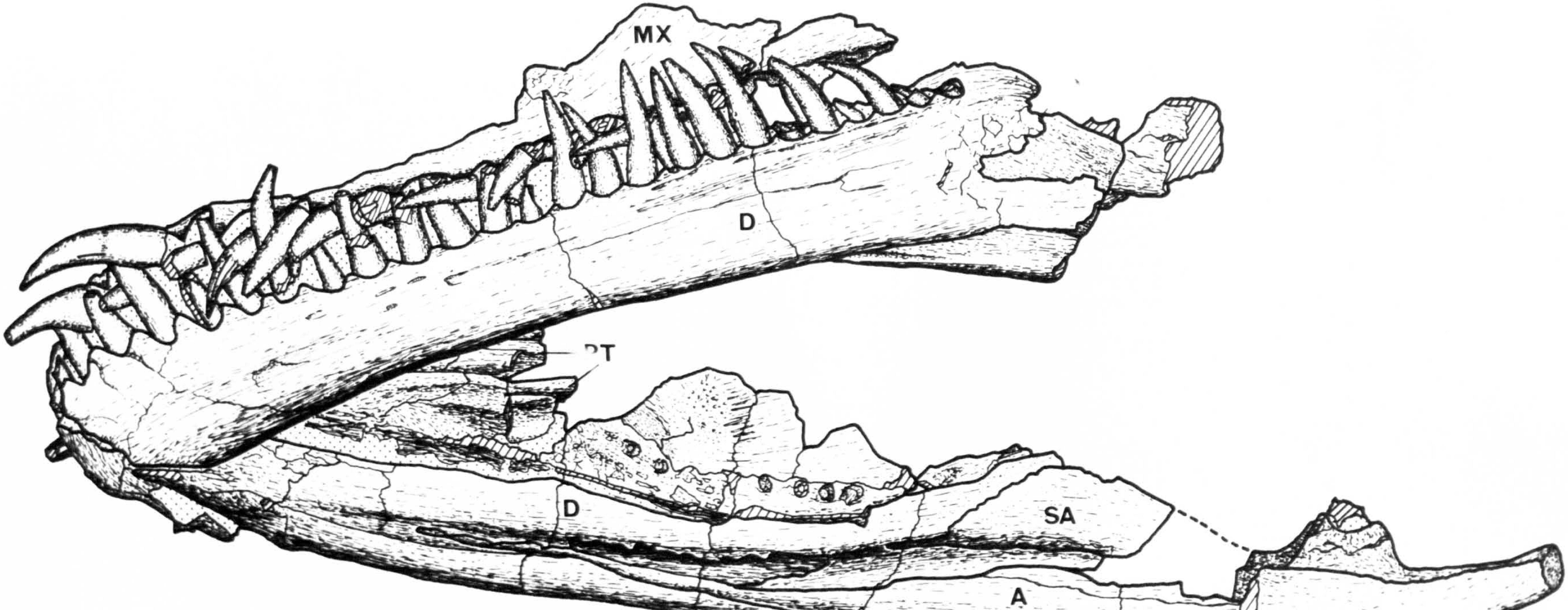

MX
D
PT
D
SA
A

Figure 8

Cryptoclidus eurymerus: Composite reconstruction (see p. 65). Lateral view. Overall length about 4 metres.

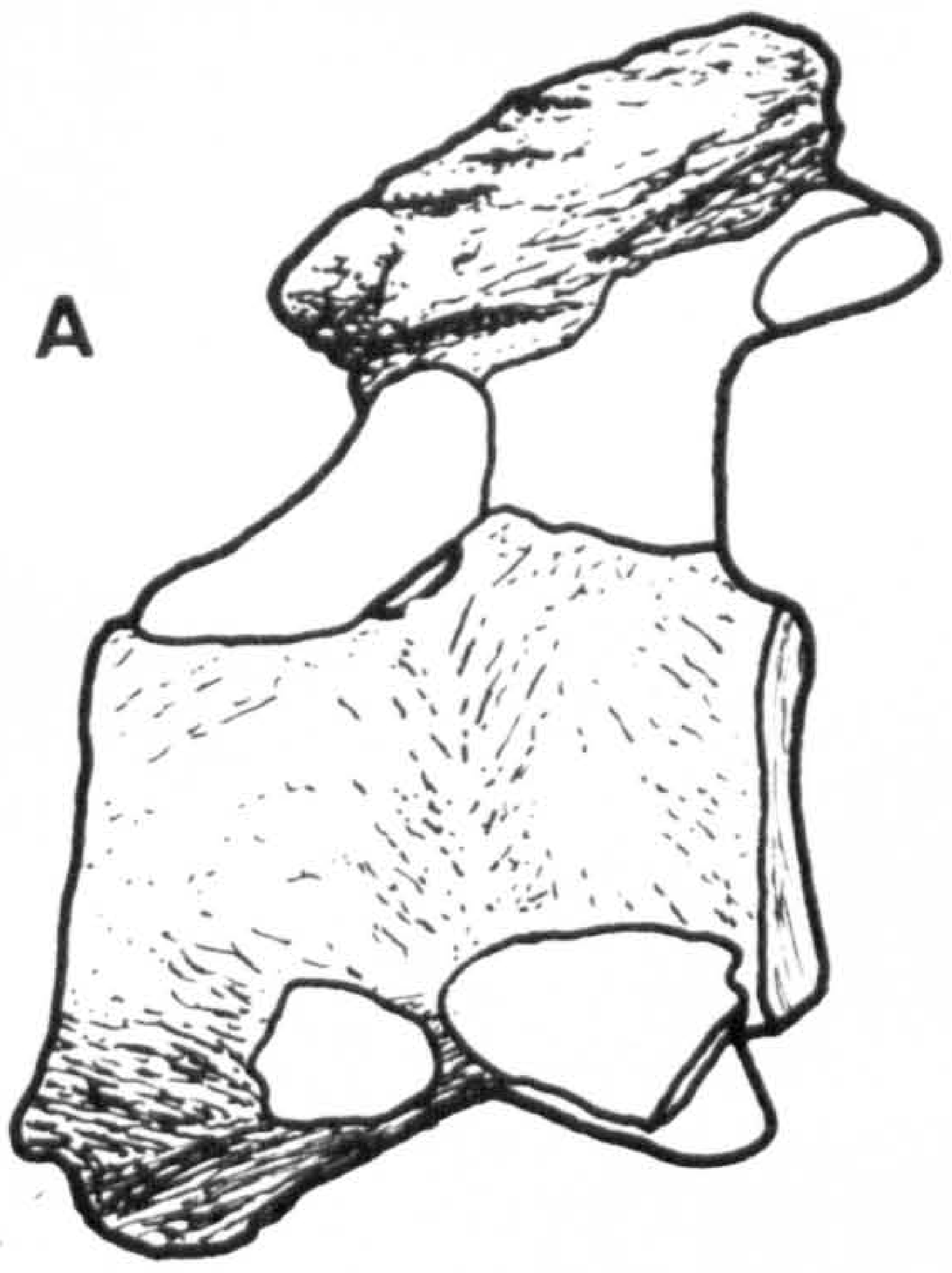
Figure 9

Cryptoclidus eurymerus: Fused atlas-axis of V.1091, x1.

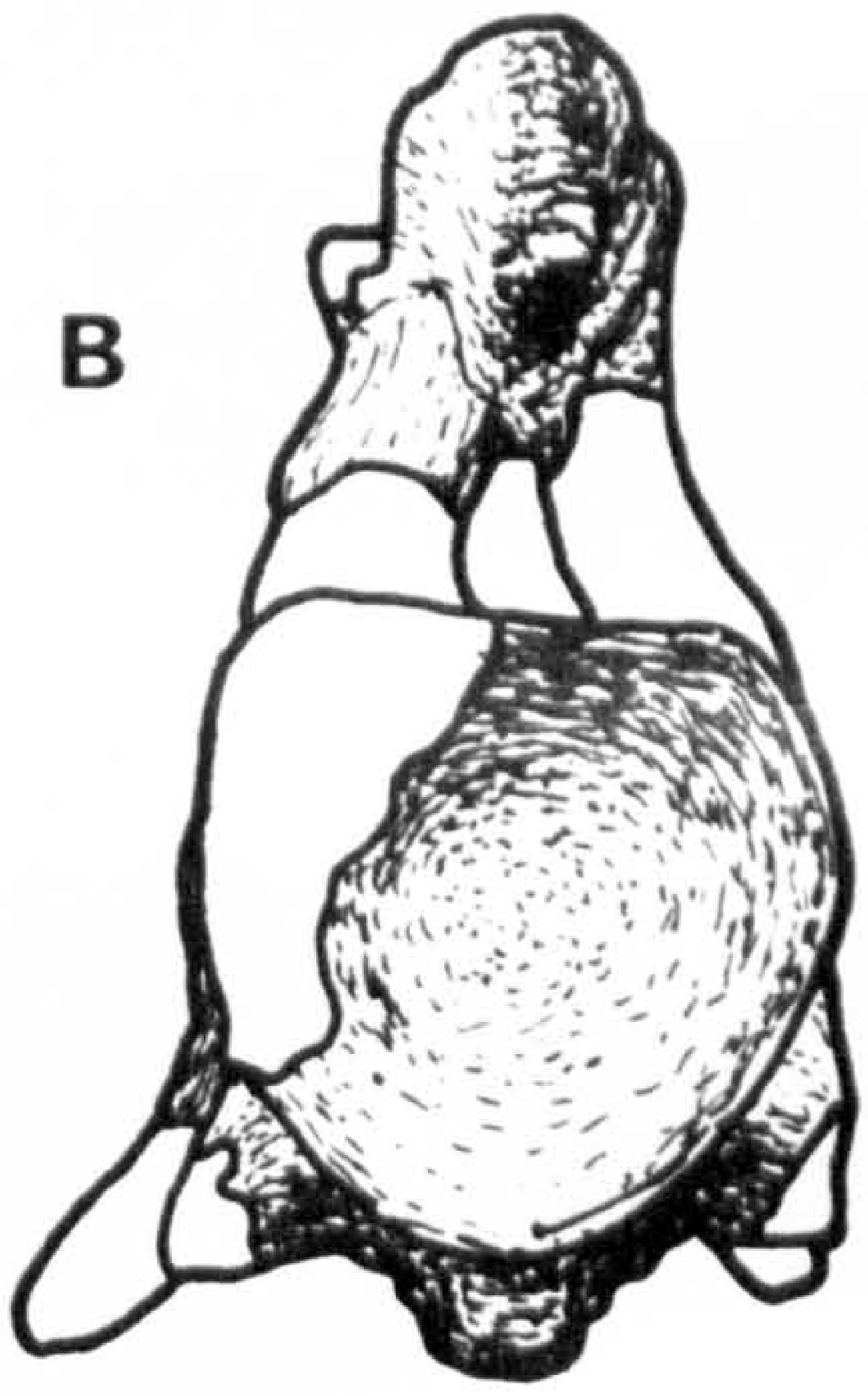
a left lateral view; b anterior view; c right lateral view;

d posterior view.

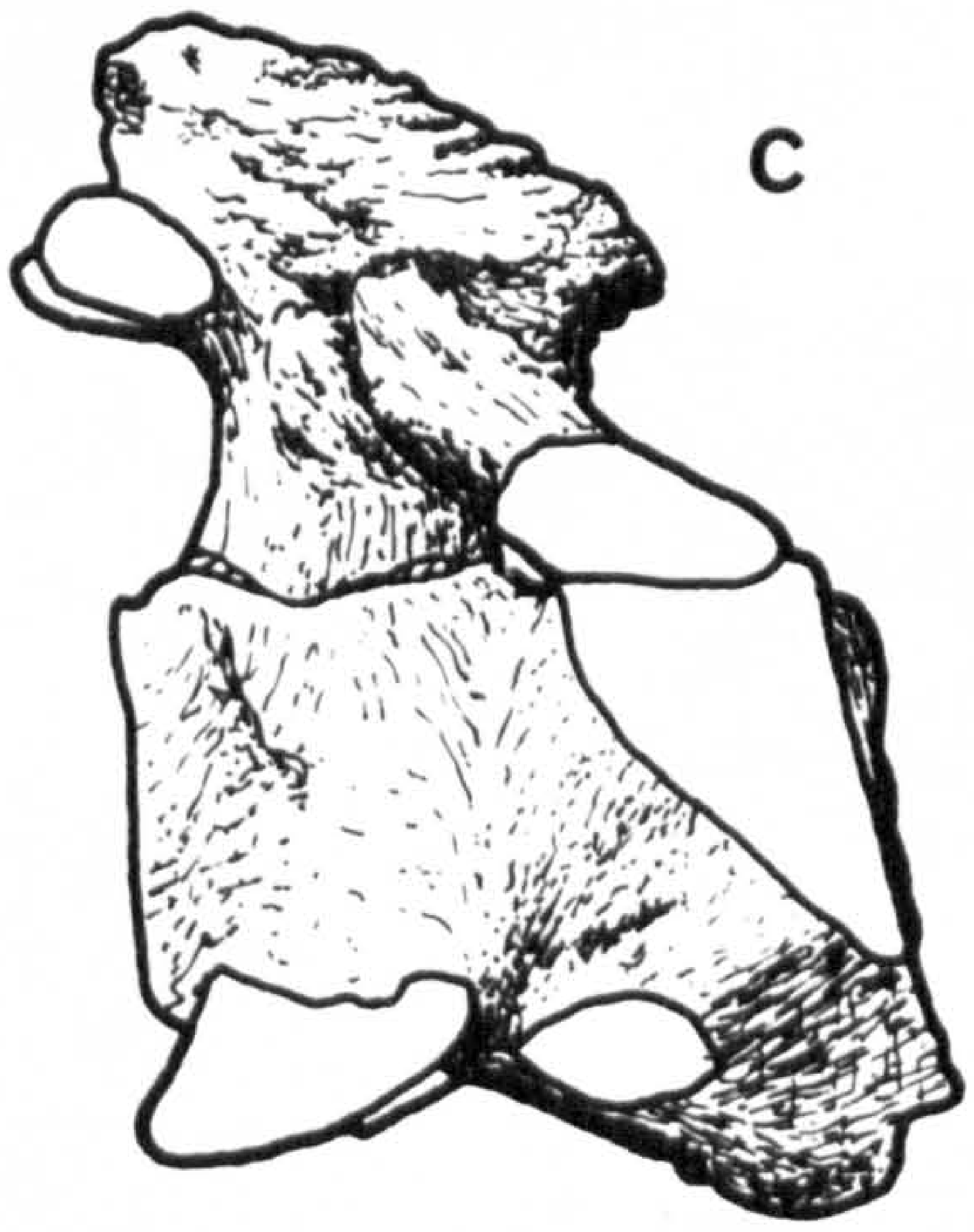
A



B



C



D

Figure 10

Cryptoclidus eurymerus: Cervical vertebrae of V.1104, x0.5.

A 5th cervical; B 13th cervical (reversed); C 25th cervical

a posterior views; b ventral views; c left lateral views

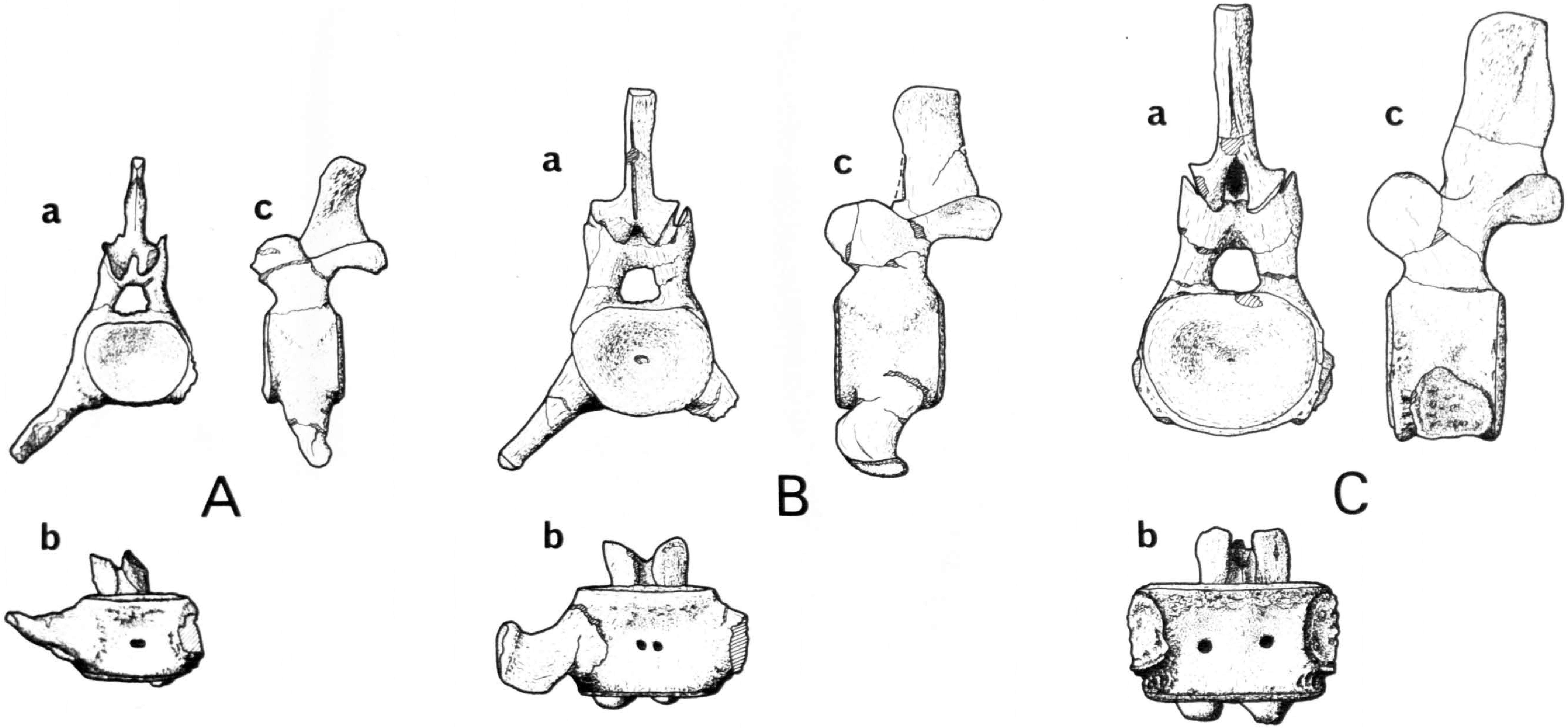

a
c
A
b
a
c
B
b
a
c
C
b

Figure 11

Cryptoclidus eurymerus: Pectoral and anterior dorsal vertebrae of V.1104, x0.5. Upper figure: left lateral view; Lower figure: posterior views; 1, 2 and 3: pectoral vertebrae; 4, 5 and 6: dorsal vertebrae (1st-3rd dorsals).


1
2
3
4
5
6
1
4
2
5
3
6

Figure 12

Cryptoclidus eurymerus: Dorsal vertebrae of V.1104, x0.5.

Upper figure: left lateral view; Lower figures: posterior views.

8, 15 and 20: 8th, 15th and 20th dorsal vertebrae.

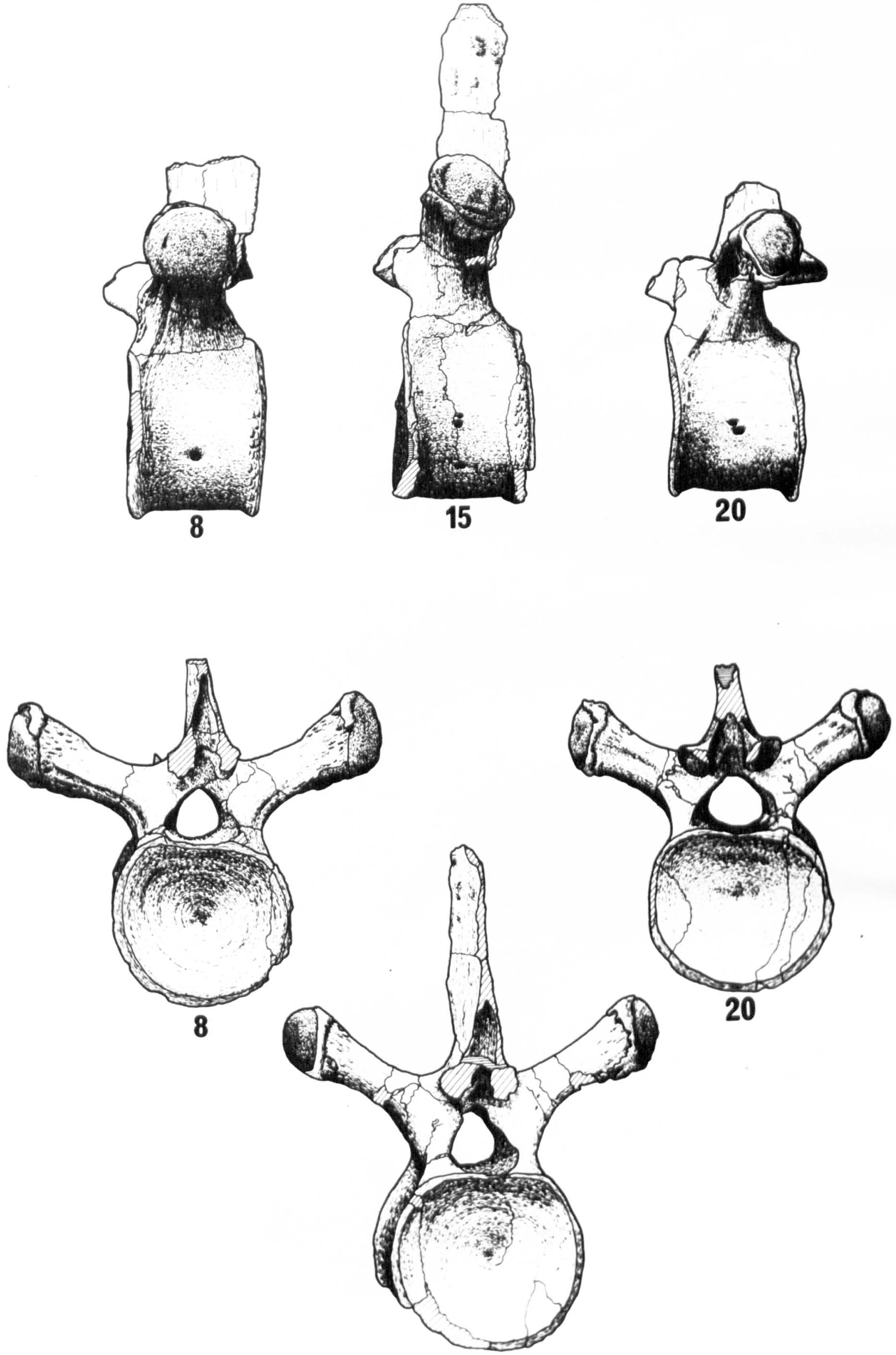

8
15
20
8
20
15

Figure 13

Cryptoclidus eurymerus: Sacrum of V.1104, x0.5. A left lateral view of vertebrae; B dorsal view of vertebrae and ribs. 1, 2 and 3: posterior dorsal vertebrae; 4, 5, 6 and 7: sacral vertebrae.

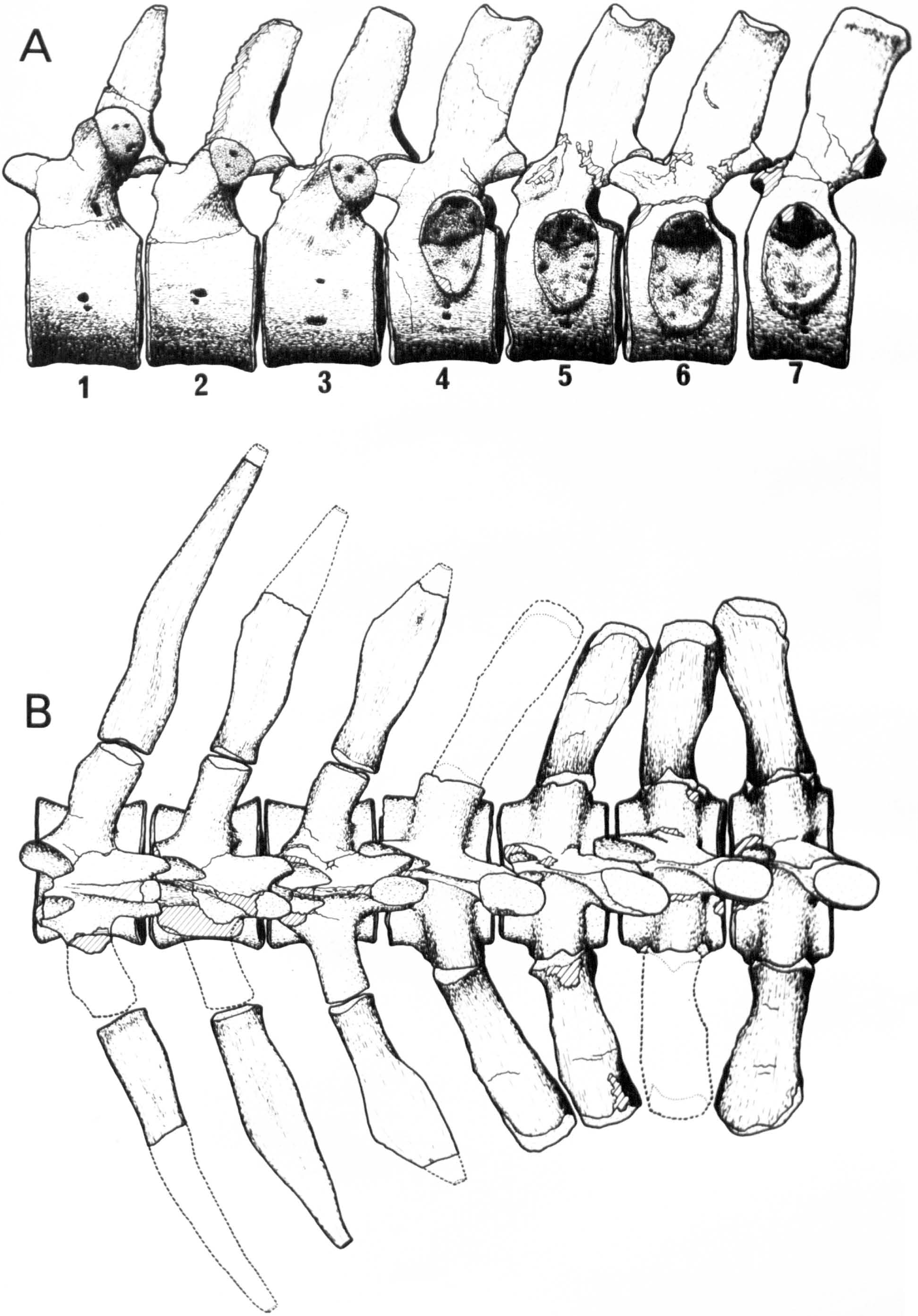

A
1
2
3
4
5
6
7
B

Figure 14

Cryptoclidus eurymerus: Graph of vertebral length index against vertebral number for three specimens of differing age. See text, pages 49-50 for explanation, and appendix, pages 257-259 for measurements and figures plotted.

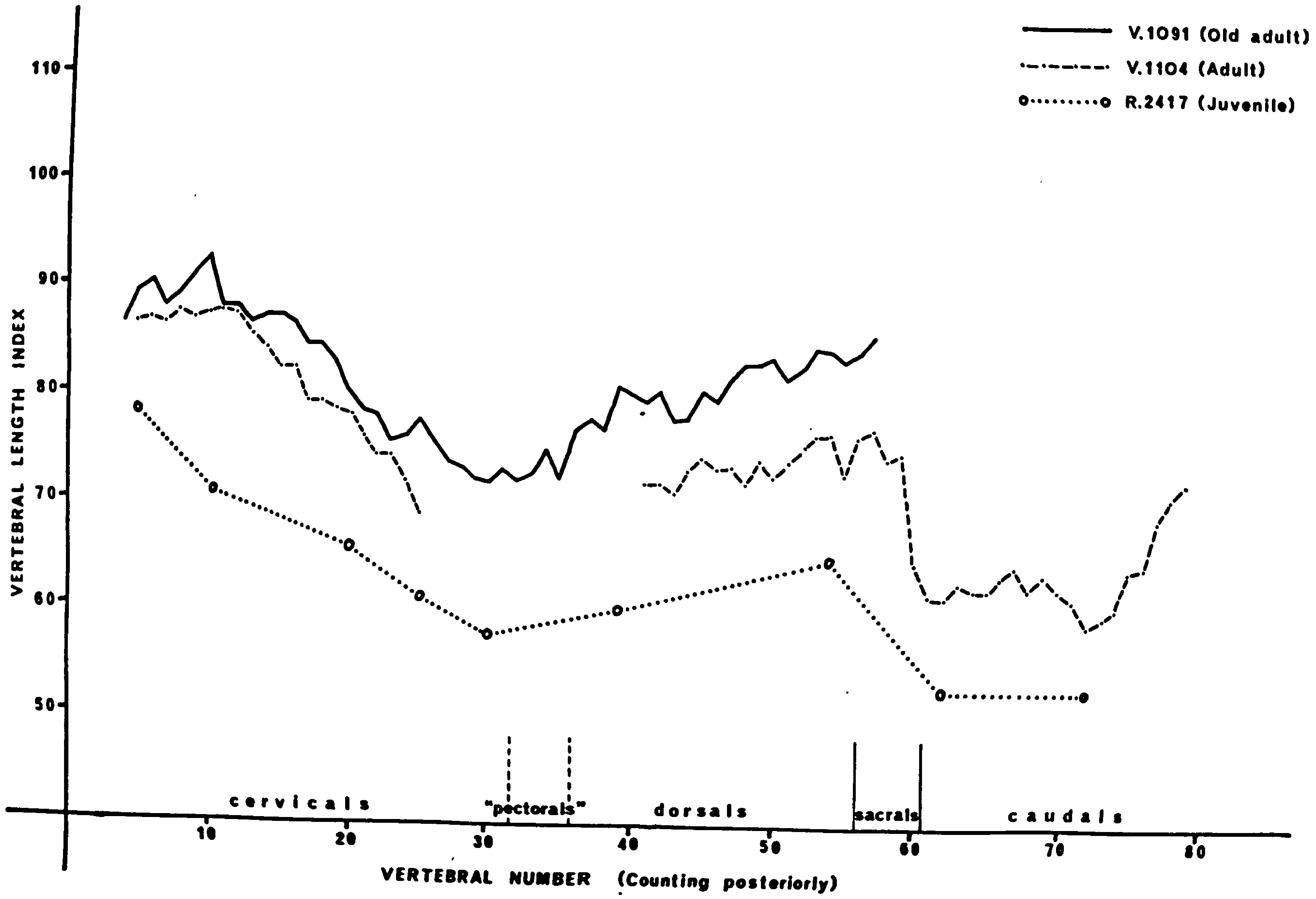

V.1091 (Old adult)
V.1104 (Adult)
R.2417 (Juvenile)
VERTEBRAL LENGTH INDEX
110
100
90
80
70
60
50
cervicals
"pectorals"
dorsals
sacrals
caudals
10
20
30
40
50
60
70
80
VERTEBRAL NUMBER (Counting posteriorly)

Figure 15

Cryptoclidus eurymerus: Left humerus of V.1104, x0.5

A posterior view; B ventral view; C anterior view.

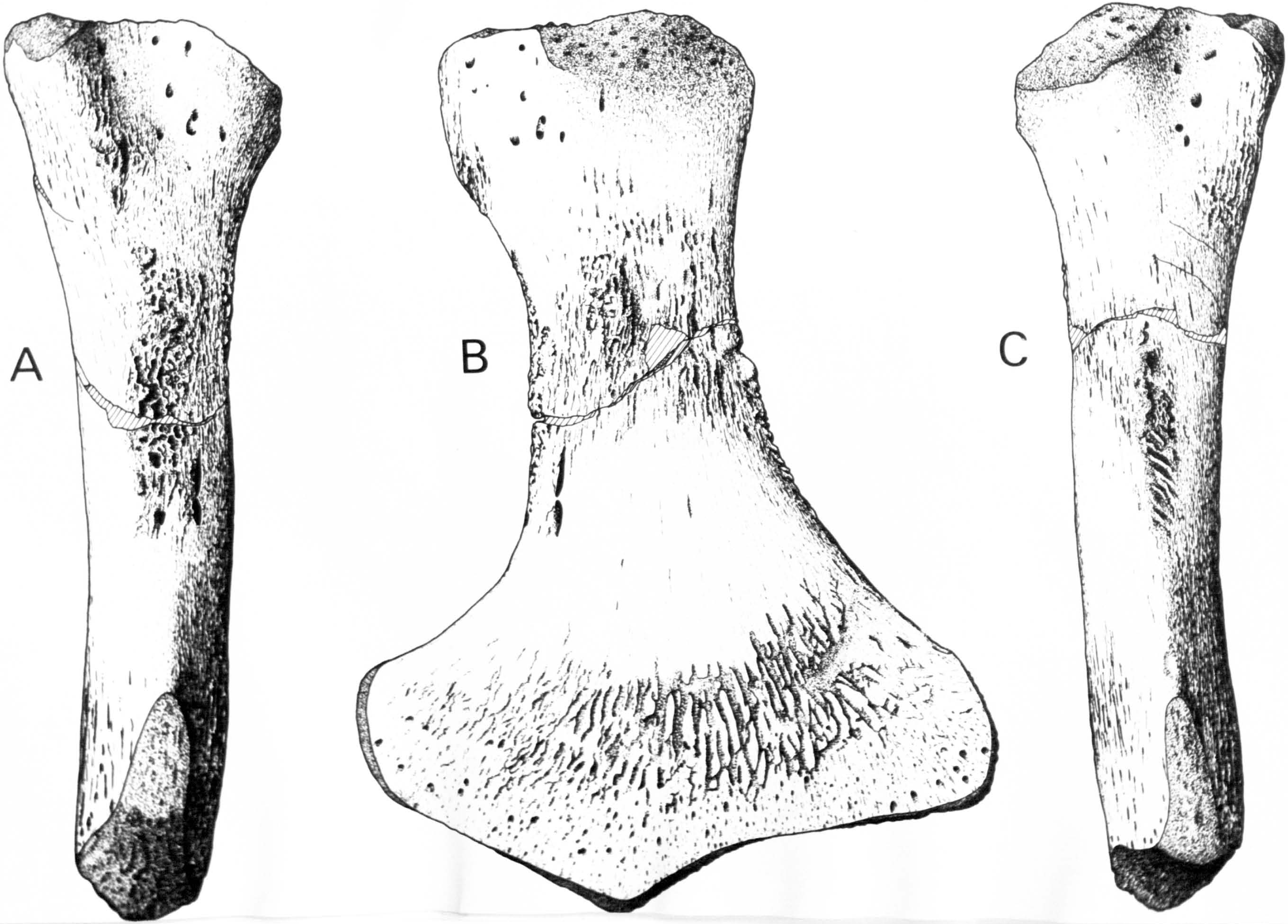

A
B
C

Figure 16

Cryptoclidus eurymerus: Left humerus and femur of V.1104, x0.5

A humerus, dorsal view; B femur, dorsal view.

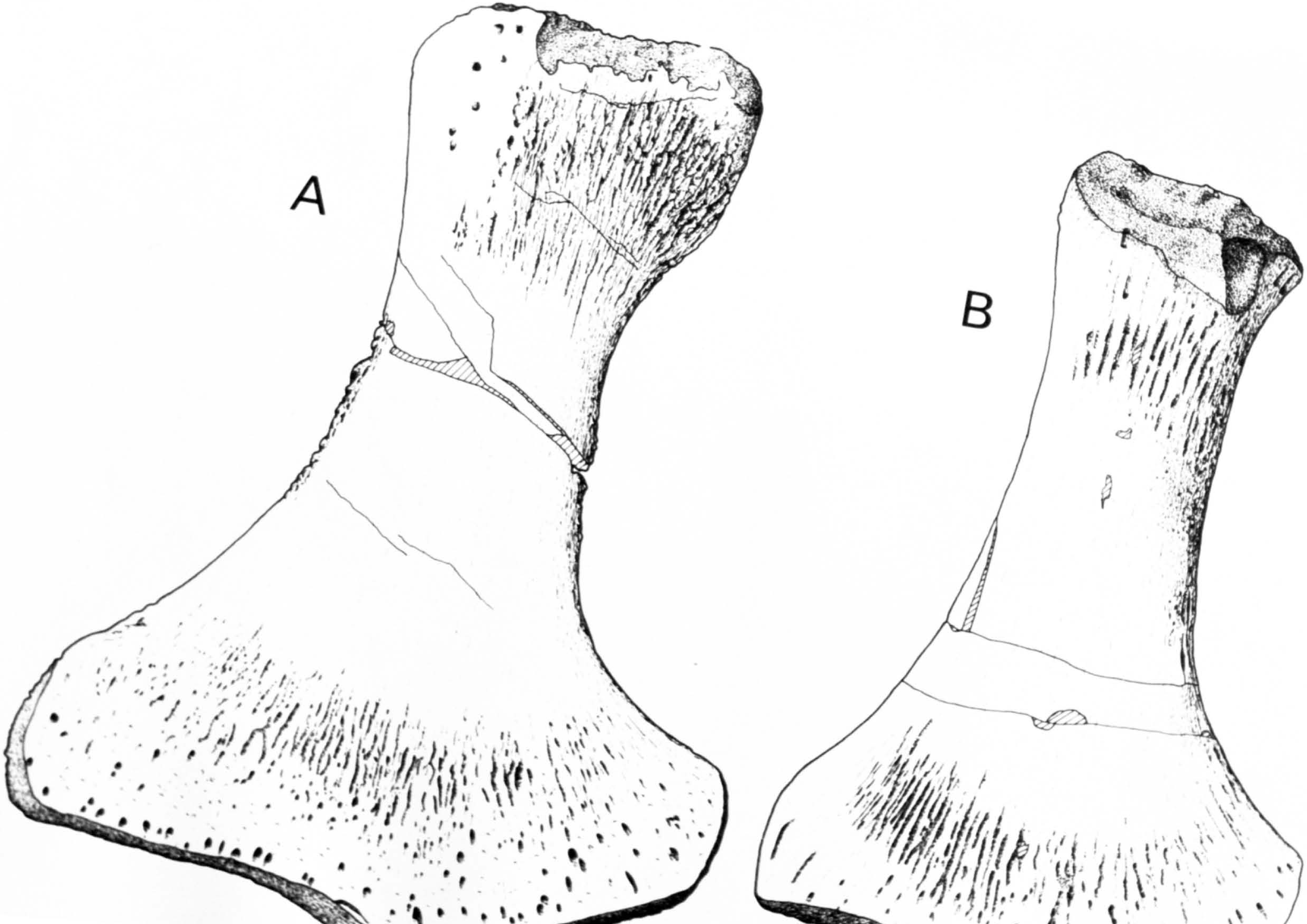

A
B

Figure 17

Cryptoclidus eurymerus: Left humerus and femur of V.1104, x0.5

A humerus, proximal view; B humerus, distal view;

C femur, proximal view; D femur, distal view.

tub. tuberosity of humerus
tr. trochanter of femur

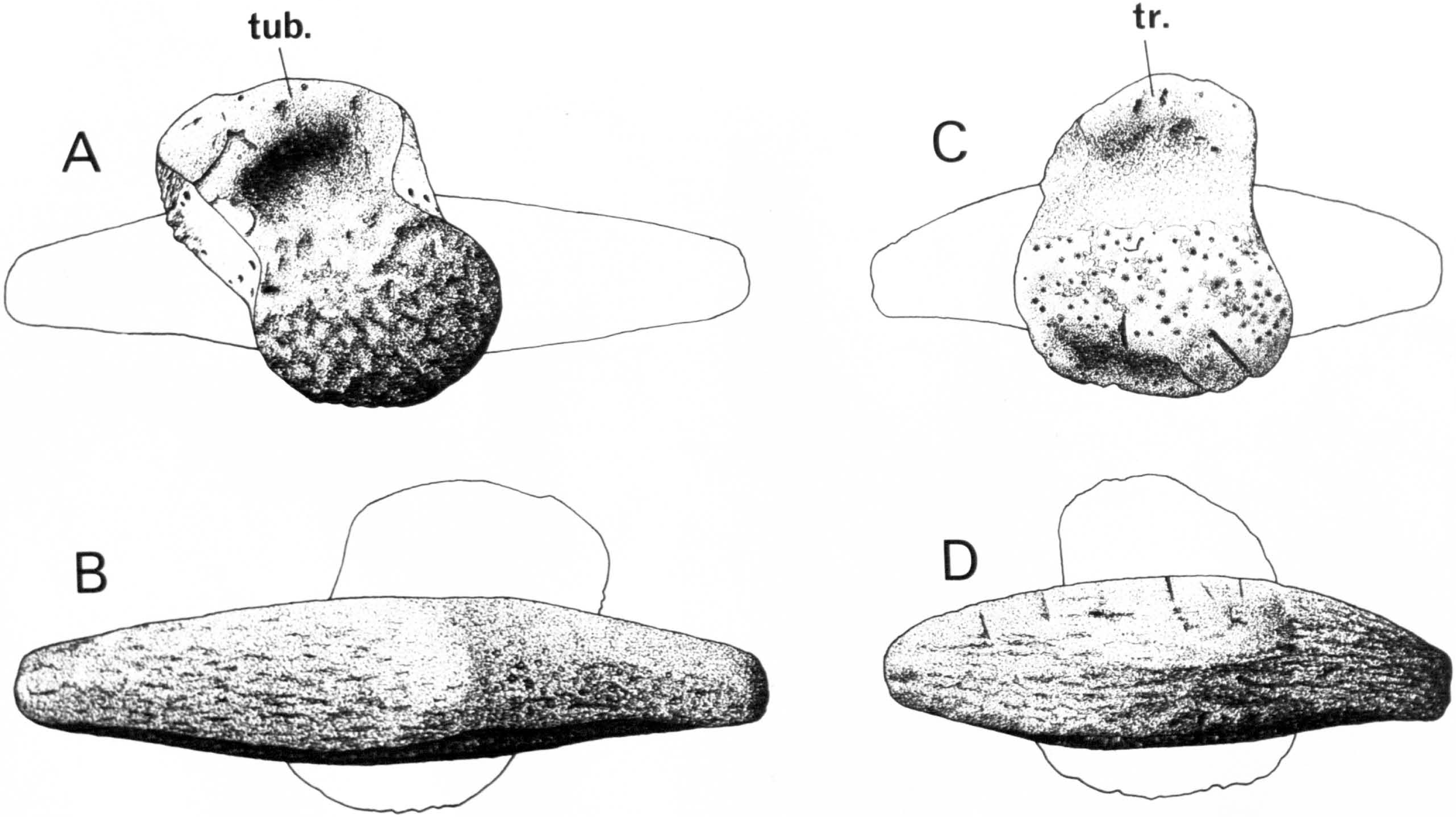

tub.
A
tr.
C
B
D

Figure 18

Cryptoclidus eurymerus: Left femur of V.1104, x0.5

A posterior view; B ventral view; C anterior view.

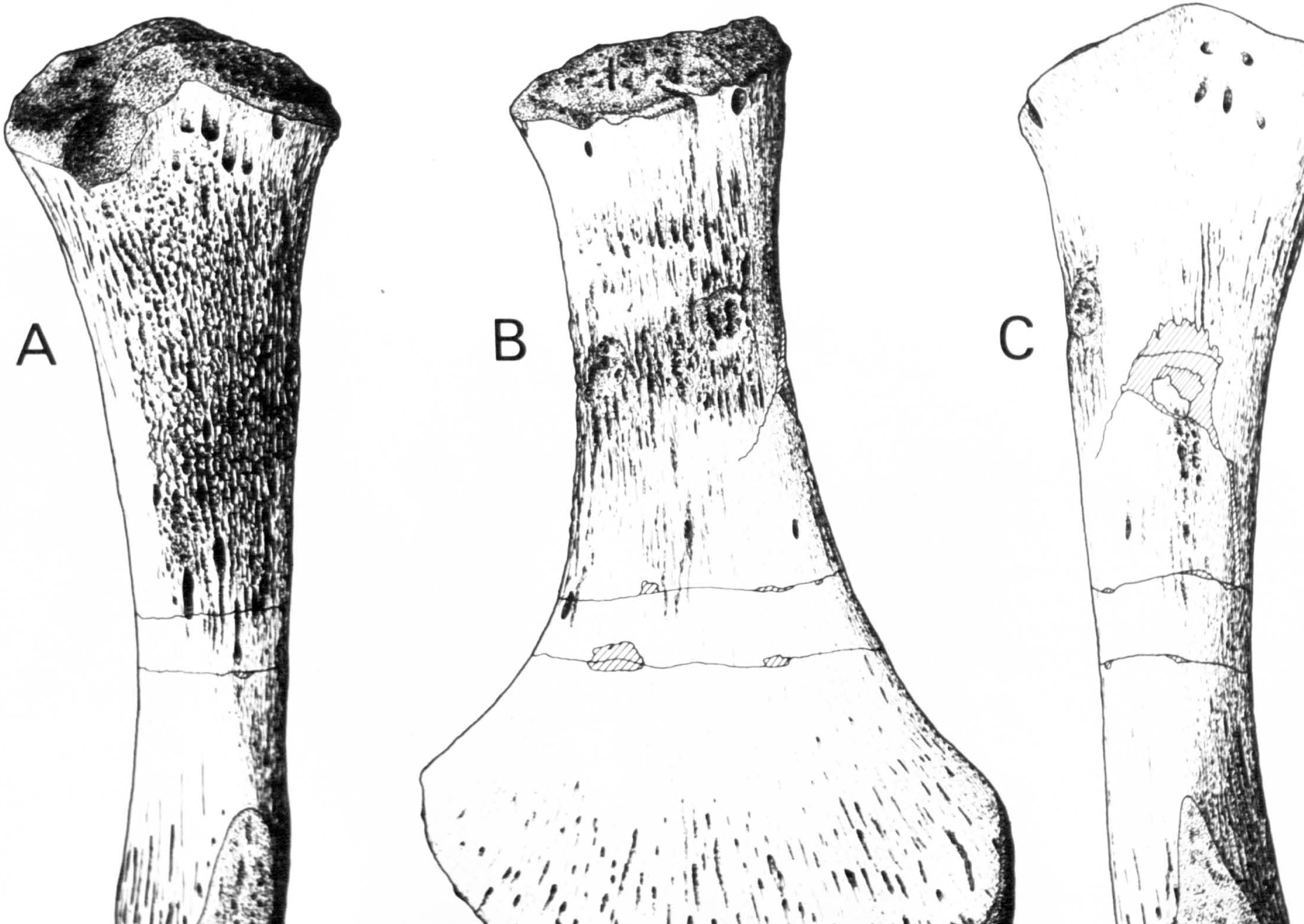

A
B
C

Figure 19

Muraenosaurus leedsii: Tooth, showing ornamental ridges.

a axial view (i); b lingual view; c axial view (ii); d buccal view.

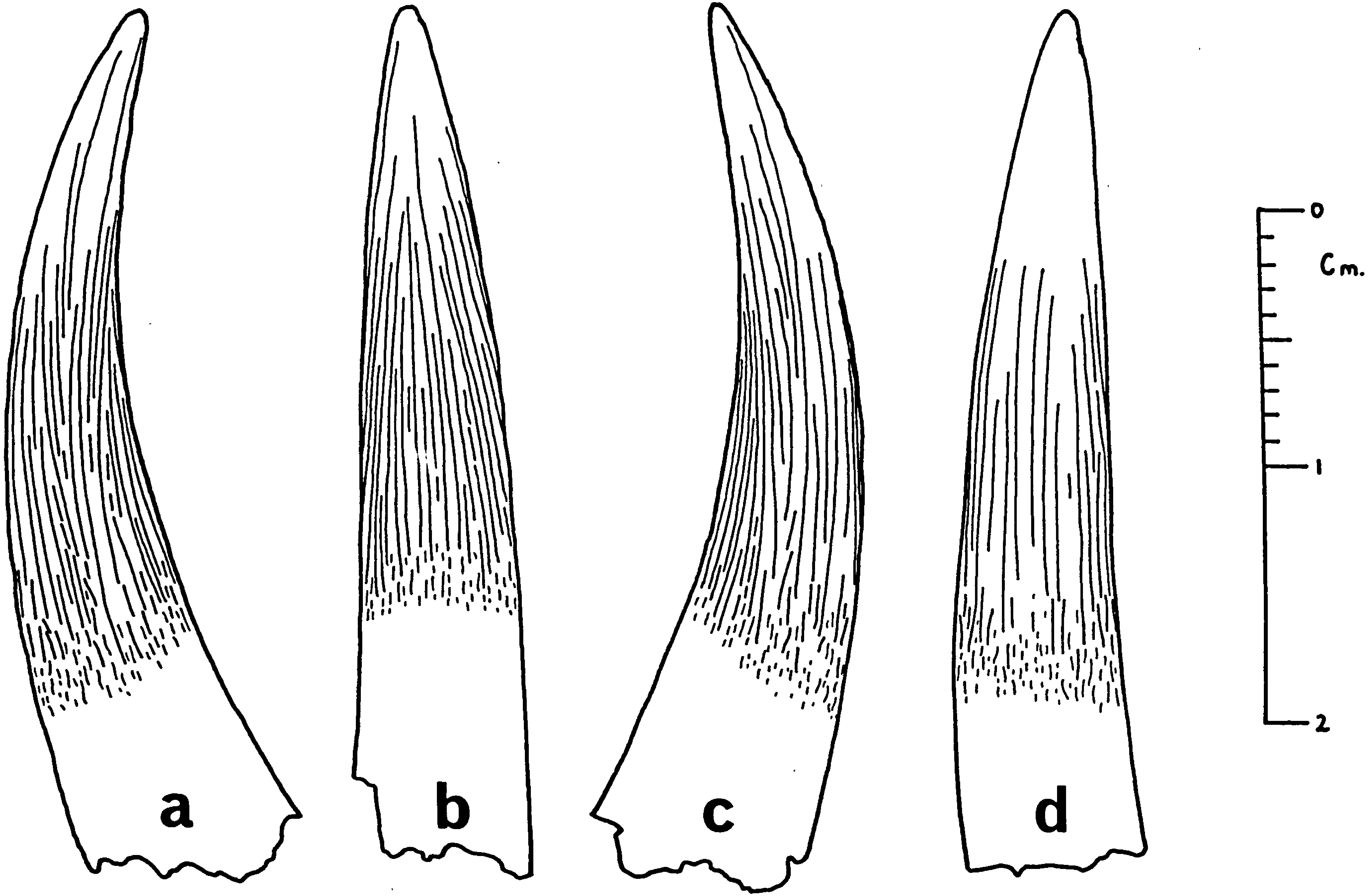

a
b
c
d
0
Cm.
1
2

Figure 20

Muraenosaurus leedsii: Interclavicles and clavicles, x0.5.

A R.2678; B R.3704; C R.2426; D R.2428.

Missing outlines of interclavicles approximately restored with broken lines.

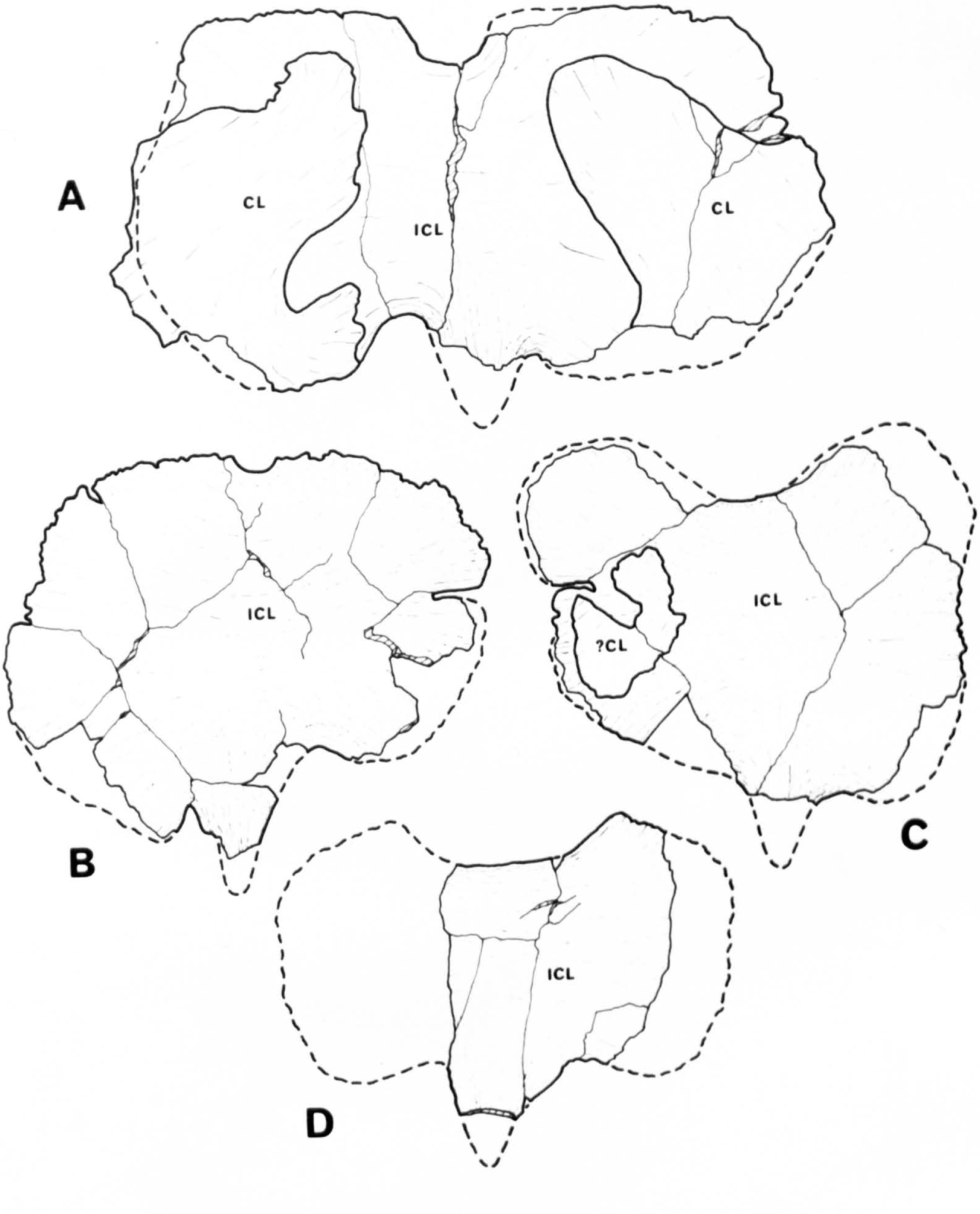

A
CL
ICL
CL
B
ICL
C
ICL
?CL
D
ICL

Figure 21

Tricleidus seeleyi: Skull reconstruction, x1. Lateral view.

A	angular	po.b.	postorbital bar (postorbital and/or postfrontal)
D	dentary		
F	frontal	PT	pterygoid
J	jugal	Q	quadrate
MX	maxilla	SA-ART	fused surangular-articular
P	parietal	SO	supraoccipital
PMX	premaxilla	SQ	squamosal

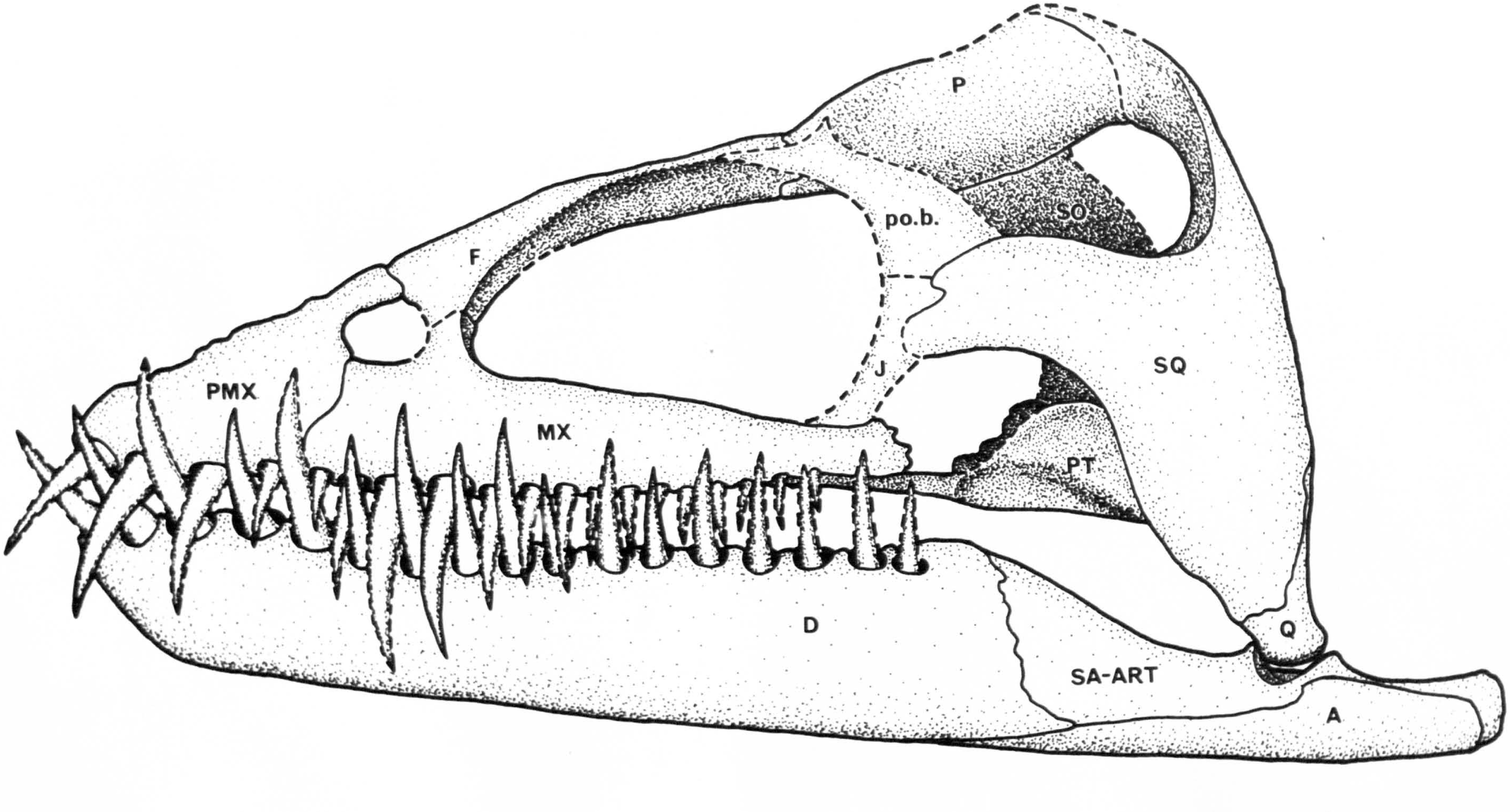

P
SO
po.b.
F
SQ
J
PMX
MX
PT
D
Q
SA-ART
A

Figure 22

Tricleidus seeleyi: Skull reconstruction, x1. Occipital view.

A	angular	Q	quadrate
BO	basioccipital	SA-ART	fused surangular-articular
EO-OP	exoccipital-opisthotic	SO	supraoccipital
P	parietal	SQ	squamosal
PT	pterygoid		

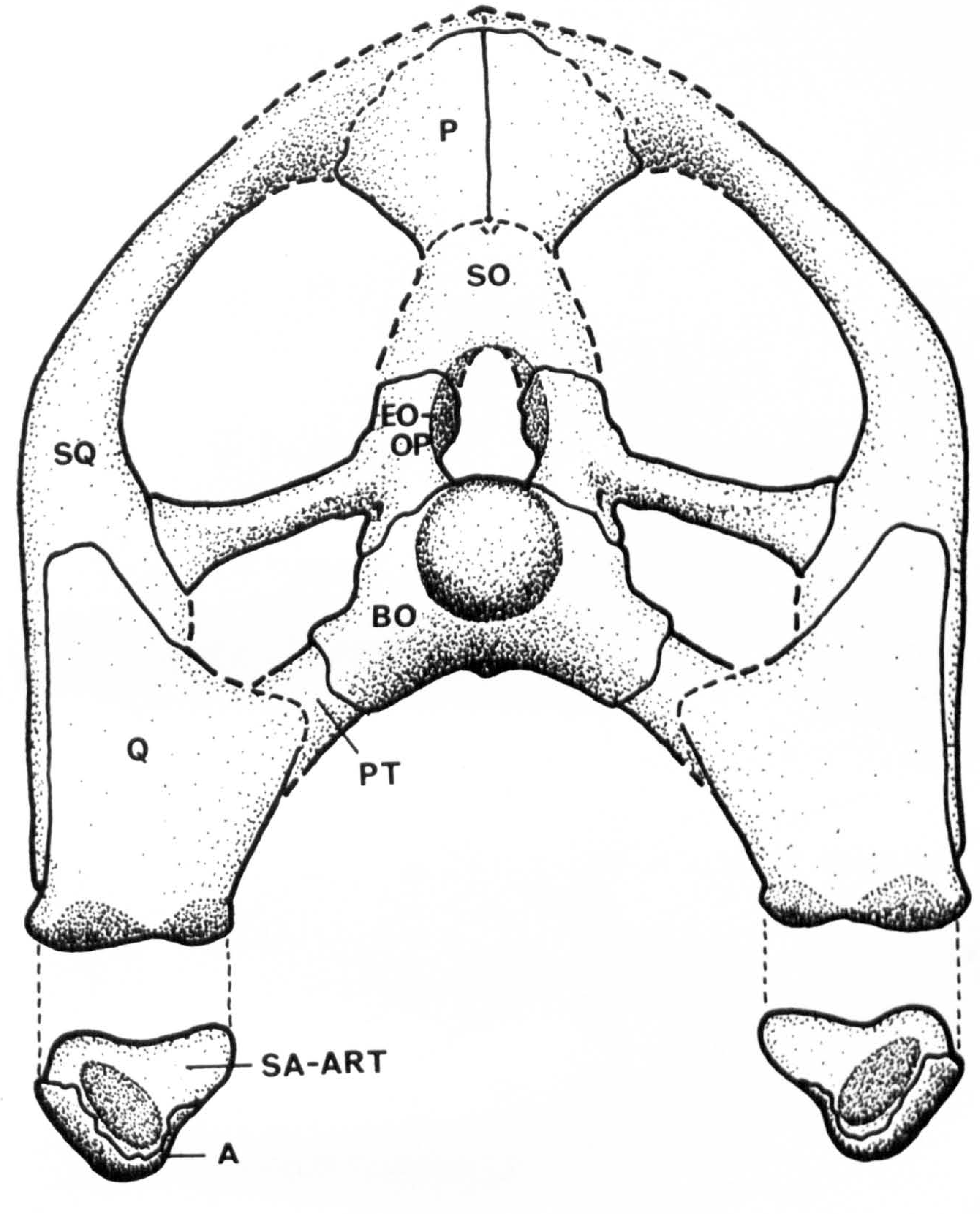

P
SO
EO
OP
SQ
BO
Q
PT
SA-ART
A

Figure 23

Tricleidus seeleyi: Interclavicles and clavicles, x1

a interclavicle of R.3539, dorsal view; b interclavicle of 19.96.G7, ventral view; c left clavicle of R.3539, dorsal view; d left clavicle of 19.96.G7, ventral view.

Missing outlines reconstructed in broken lines.

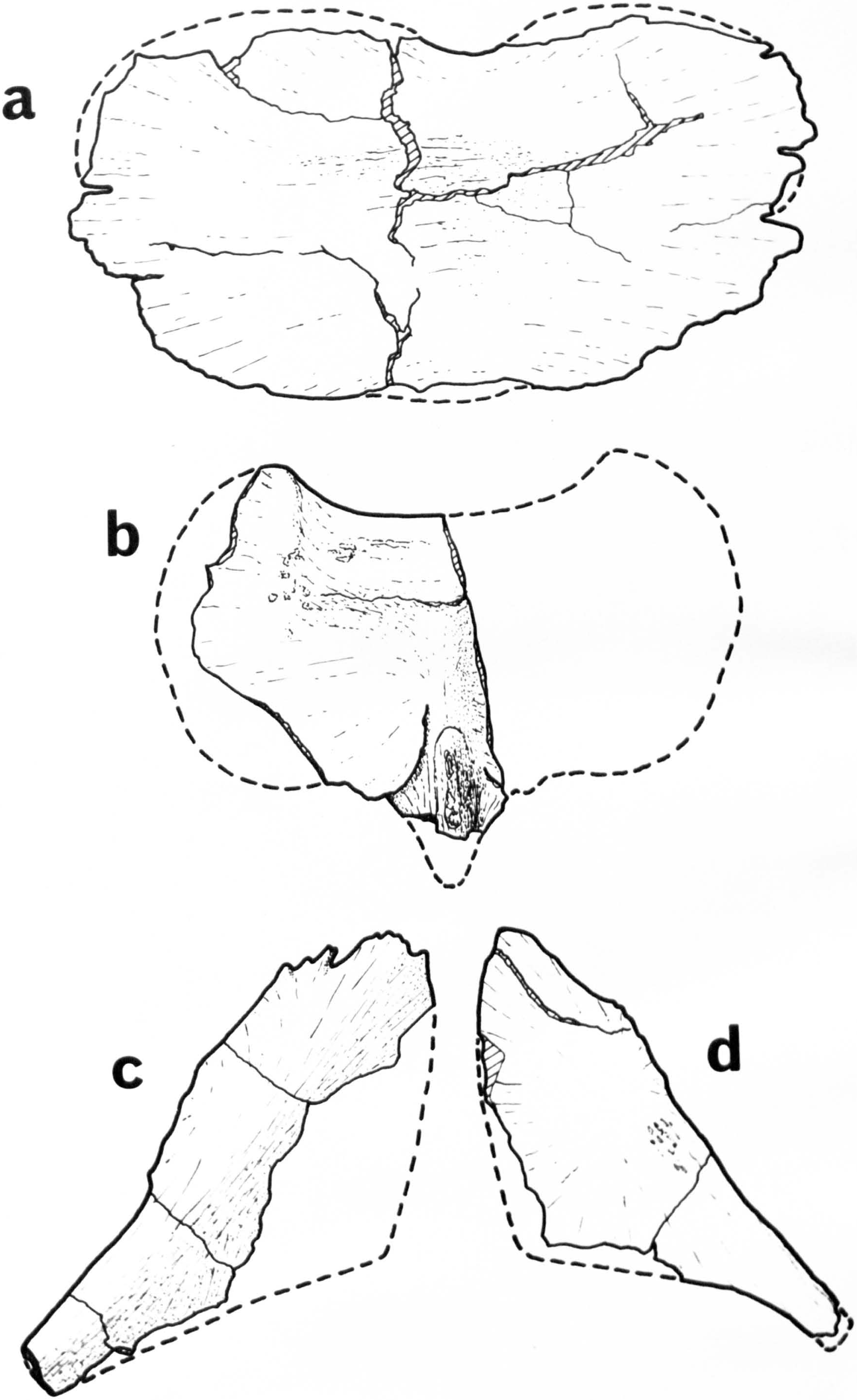

a
b
c
d

Figure 24

Kimmerosaurus oweni: Skull reconstruction, x0.9. Lateral view.

A	angular	po.b.	postorbital bar (postorbital and/or postfrontal)
D	dentary		
F	frontal	PT	pterygoid
J	jugal	Q	quadrate
MX	maxilla	SA-ART	fused surangular-articular
P	parietal	SO	supraoccipital
PMX	premaxilla	SQ	squamosal


P
SO
po.b
F
PMX
MX
J
SQ
PT
D
SA-ART
Q
A

Figure 25

Kimmerosaurus oweni: Skull reconstruction, x0.9. Occipital view.

A	angular	Q	quadrate
BO	basioccipital	SA-ART	fused surangular-articular
EO-OP	exoccipital-opisthotic	SO	supraoccipital
P	parietal	SQ	squamosal
PT	pterygoid		

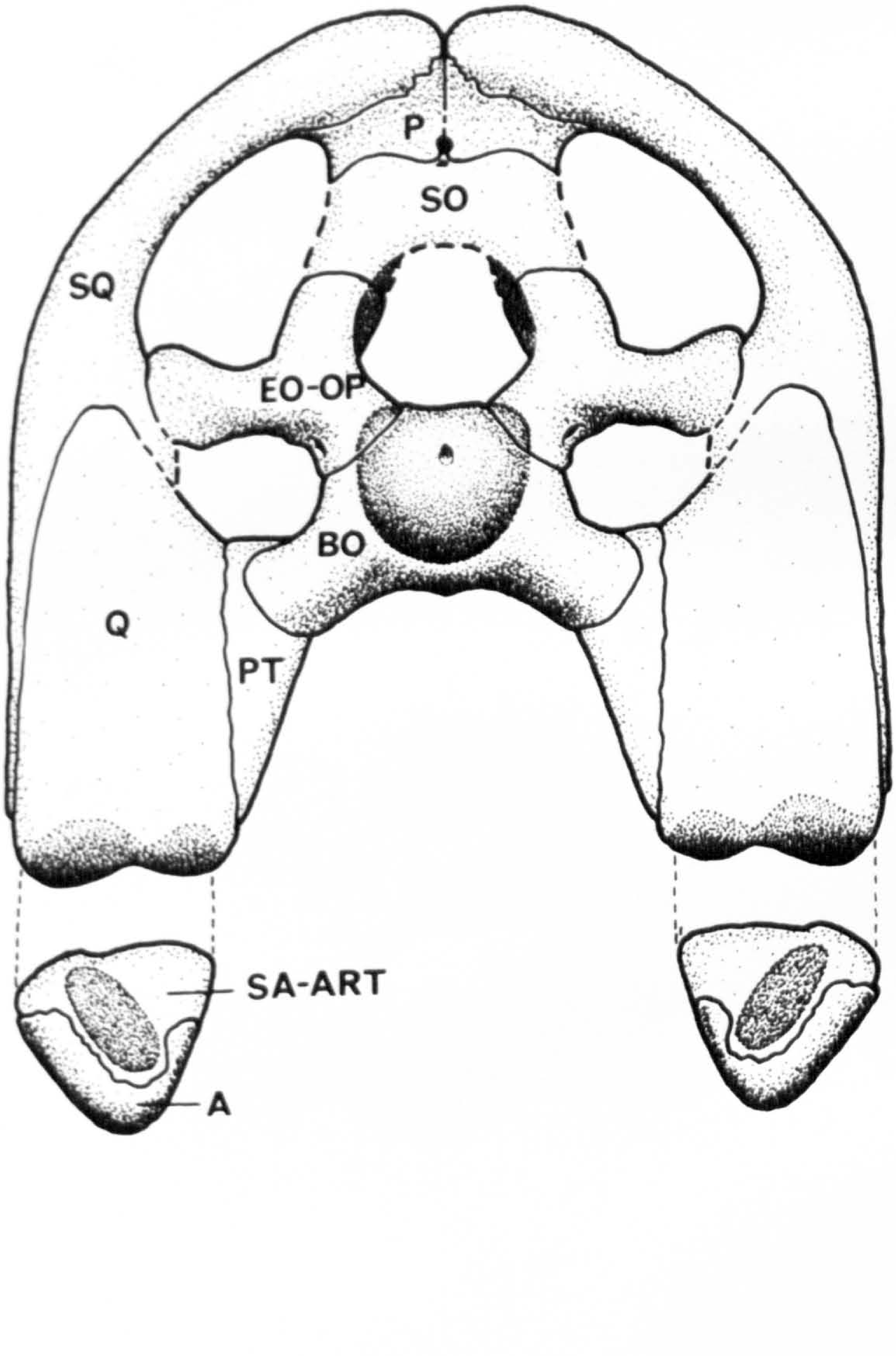

P
SO
SQ
EO-OP
BO
Q
PT
SA-ART
A

Figure 26

Kimmerosaurus oweni: Dentary of R.8431, x0.9

D dentary PMX fragment of premaxilla

Outline of posterior of lower jaw rami taken from fig. 27B.


PMX
D

Figure 27

Kimmerosaurus oweni: Posterior portion of lower jaw (right ramus) of R.8431, x0.9. A mesial view; B dorsal view; C lateral view.

A	angular	fr.	unidentifiable fragments of skull and two teeth
ART	articular	SA	surangular

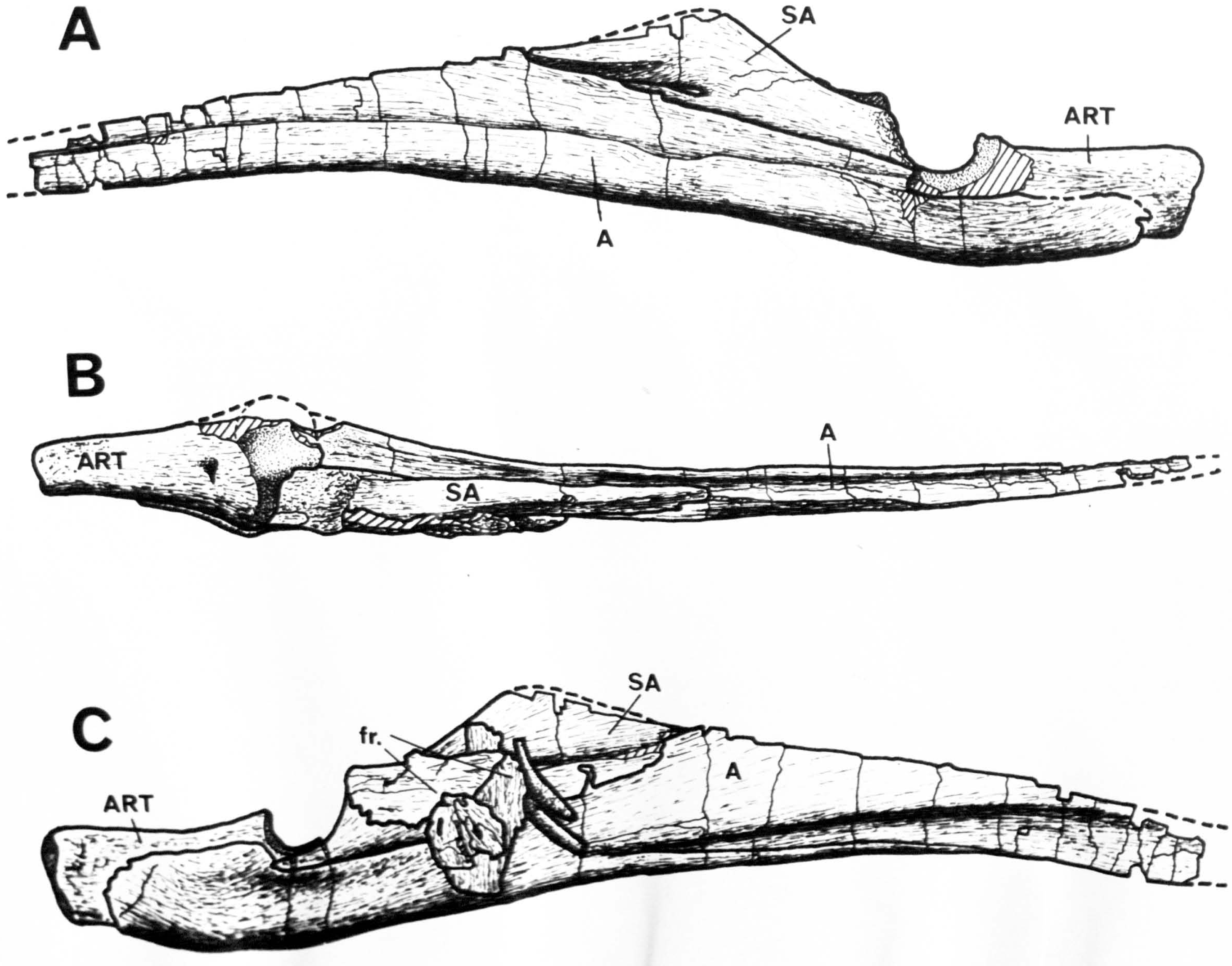

A
SA
ART
A
B
ART
SA
A
C
SA
fr.
A
ART

Figure 28

<u>Kimmerosaurus oweni</u>: Isolated tooth of R.8431. a anterior axial view; b lingual view; c posterior axial view; d buccal view.

f facet in root of tooth formed by the lateral advancement of a developing replacement tooth.

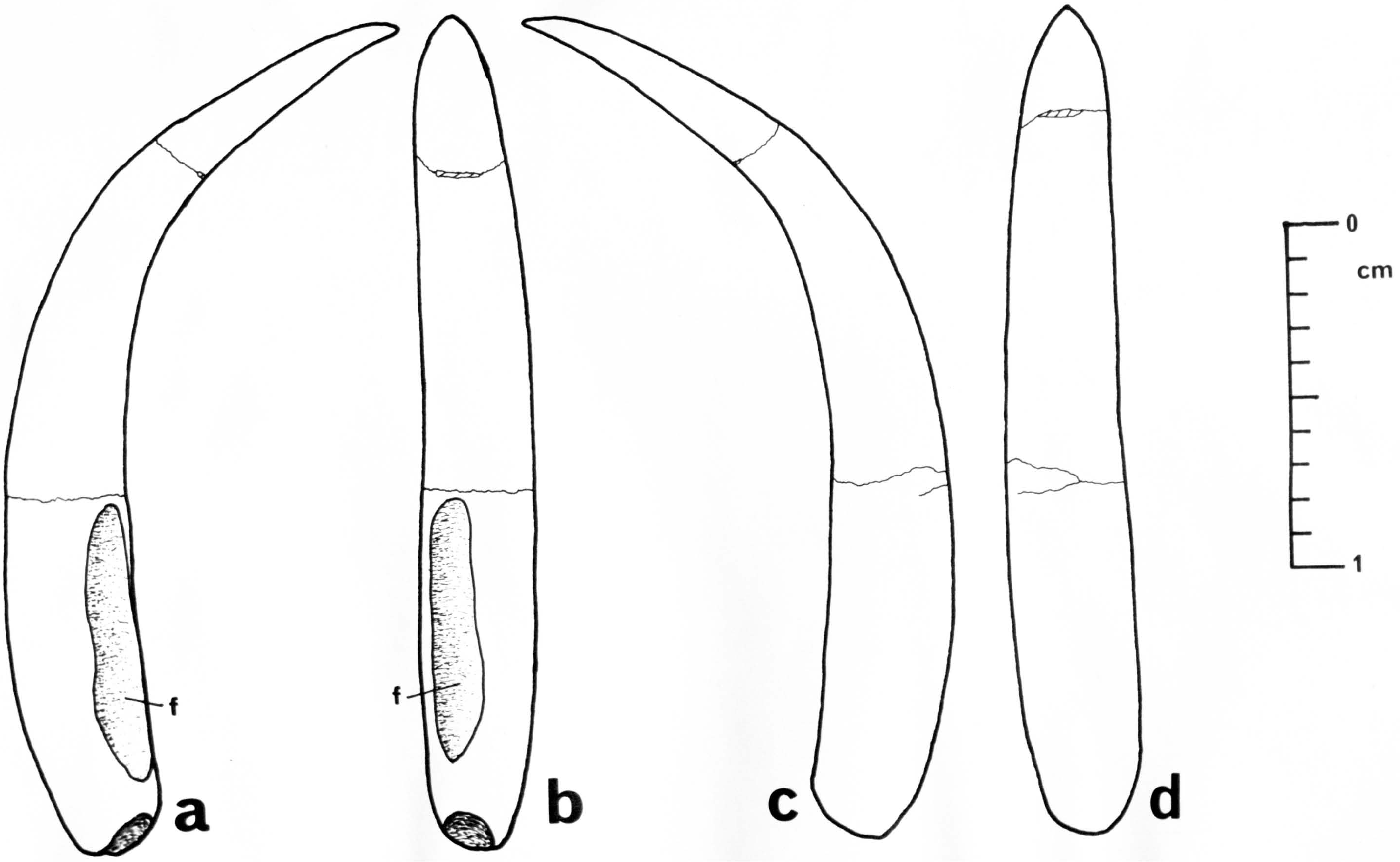

a
b
c
d
f
f
0
cm
1

Figure 29

Kimmerosaurus oweni: Skull roof of R.8431, x1. Dorsal view.

F	frontal
P	parietal
PF	postfrontal
PO	postorbital
SQ	squamosal

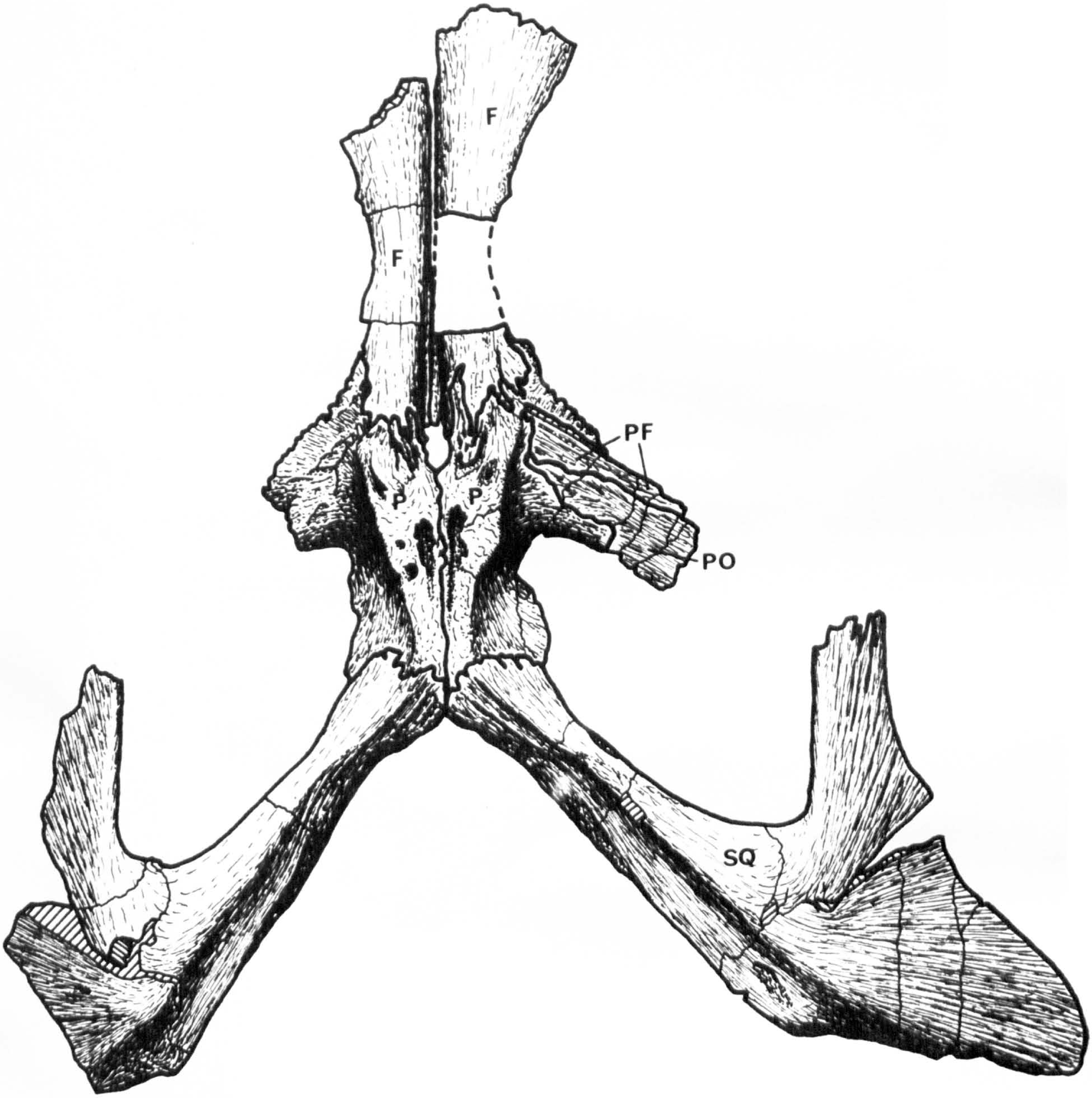

F
F
PF
P
P
PO
SQ

Figure 30

Kimmerosaurus oweni: Skull roof of R.8431, x1. Ventral view.

F	frontal
f.eo-op	facet for paroccipital process of exoccipital-opisthotic
f.q.	facet for quadrate
f.so	facet for supraoccipital

P	parietal
PF	postfrontal
PO	postorbital
SQ	squamosal

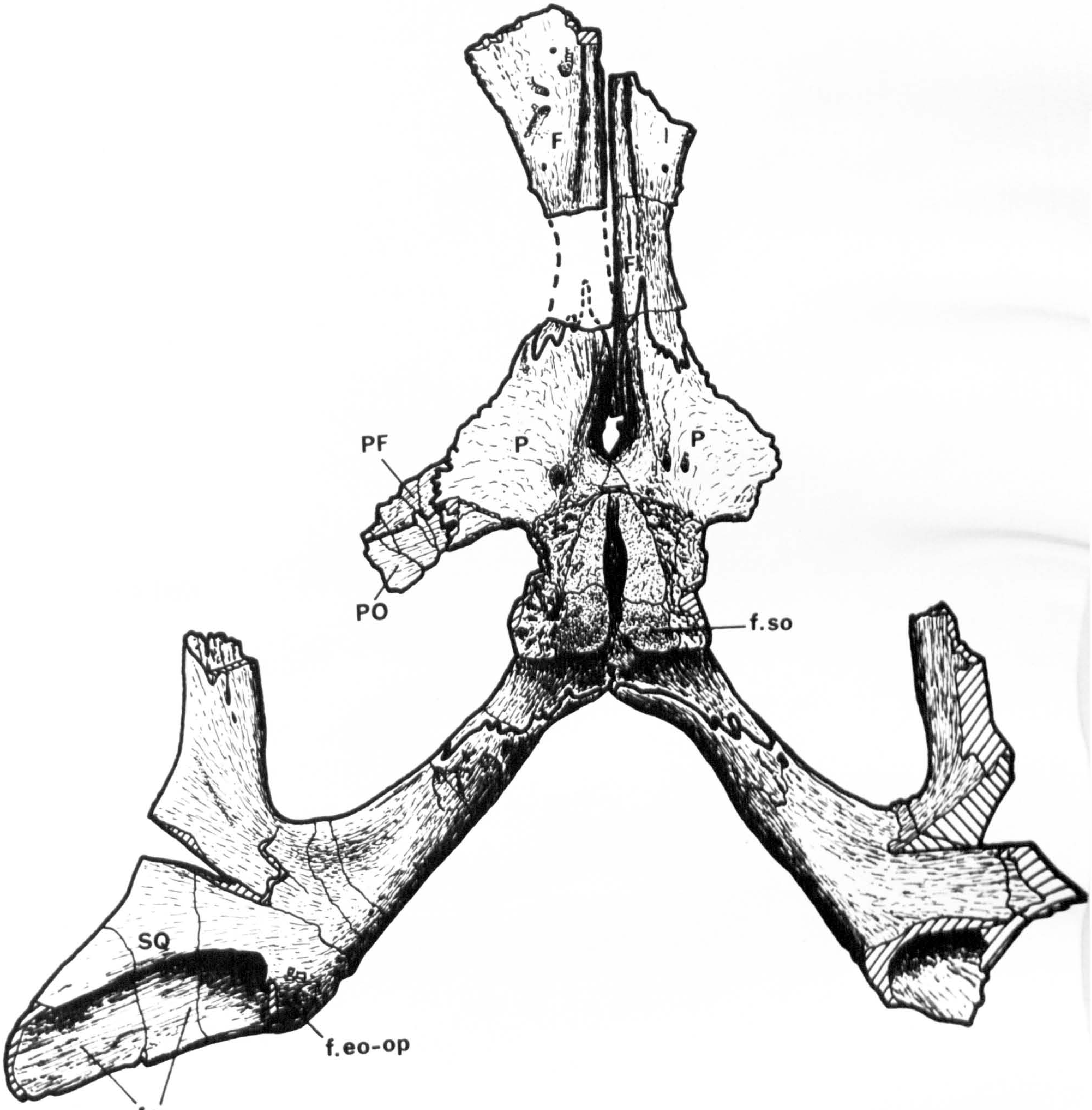

F
F
P
P
PF
PO
f.so
SQ
f.eo-op
f.q

Figure 31

Kimmerosaurus oweni: Left quadrate of R.8431, x1.

a lateral view; b posterior view; c dorsal view; d mesial view.

con.	condyles for articulation with lower jaw
f.pt.	facet for pterygoid
f.sq.	facet for squamosal
hd.	primary head

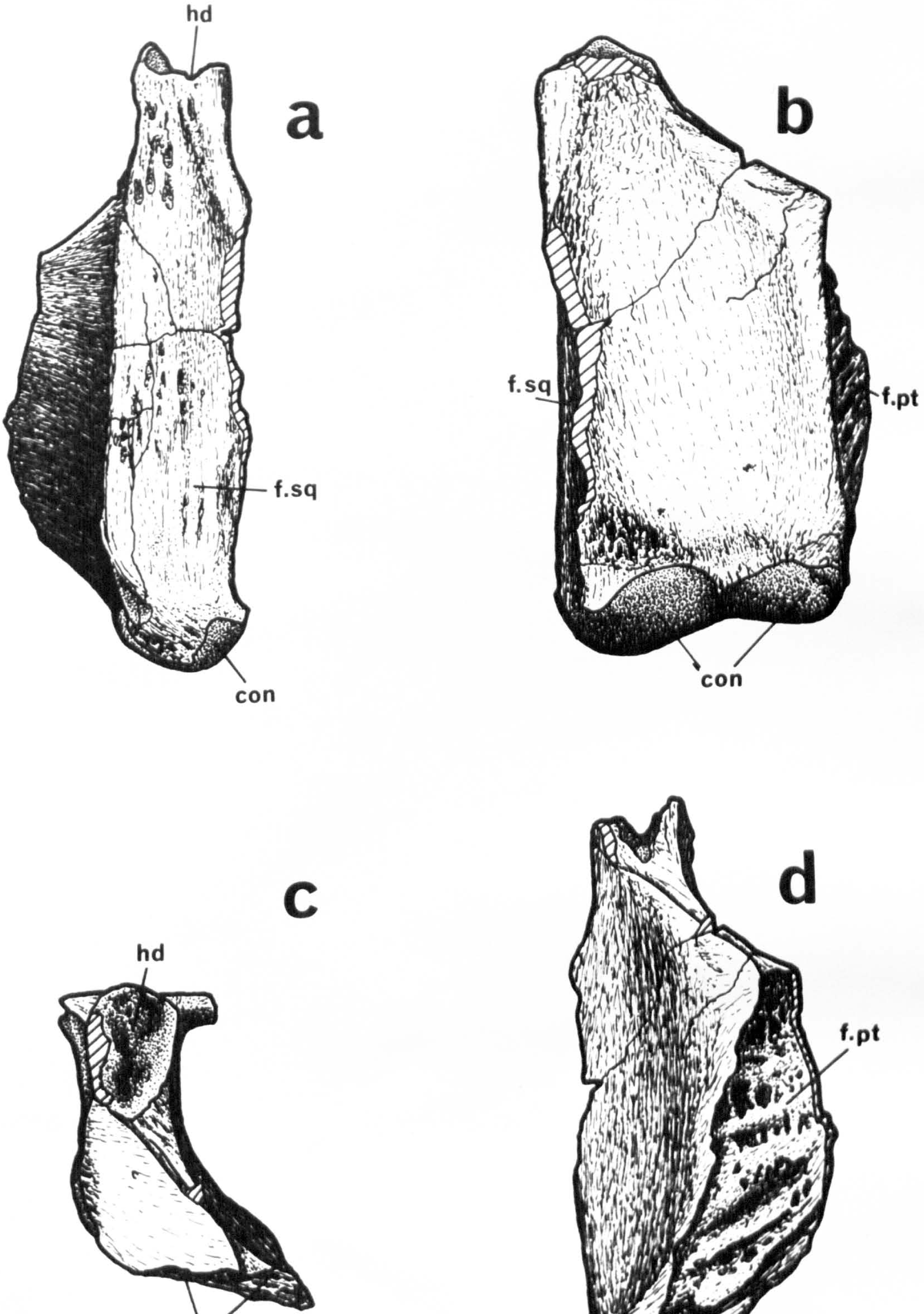

hd
a
b
f.sq
f.sq
f.pt
con
con
c
hd
f.pt
d
f.pt

Figure 32

Kimmerosaurus oweni: Right pterygoid of R.8431, x1

a lateral view; b dorsal view; c mesial view.

f.bo	facet for basioccipital
f.bs	facet for basisphenoid
f.q	facet for quadrate

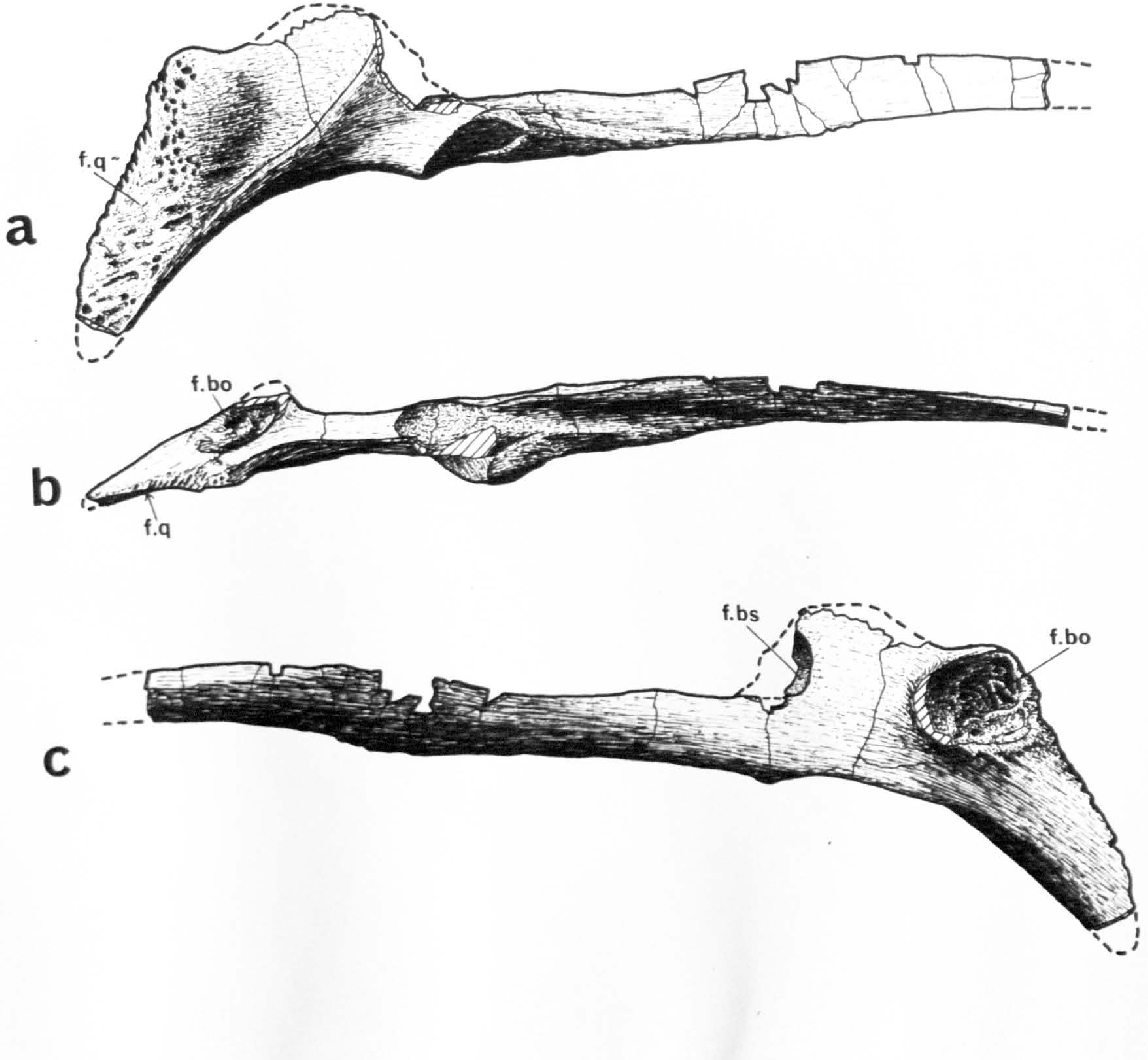

f.q
a
f.bo
b
f.q
f.bs
f.bo
c

Figure 33

Kimmerosaurus oweni: Basioccipital of R.8431, x1.

a posterior view; b left lateral view; c anterior view.

bpt.pr	basipterygoid process	not.pit	notochordal pit
f.bs	facet for basisphenoid	nut.for	nutritive foramina
f.eo-op	facet for paroccipital process of exoccipital-opisthotic	oc.con	basioccipital portion of occipital condyle
f.pt	facet for pterygoid		

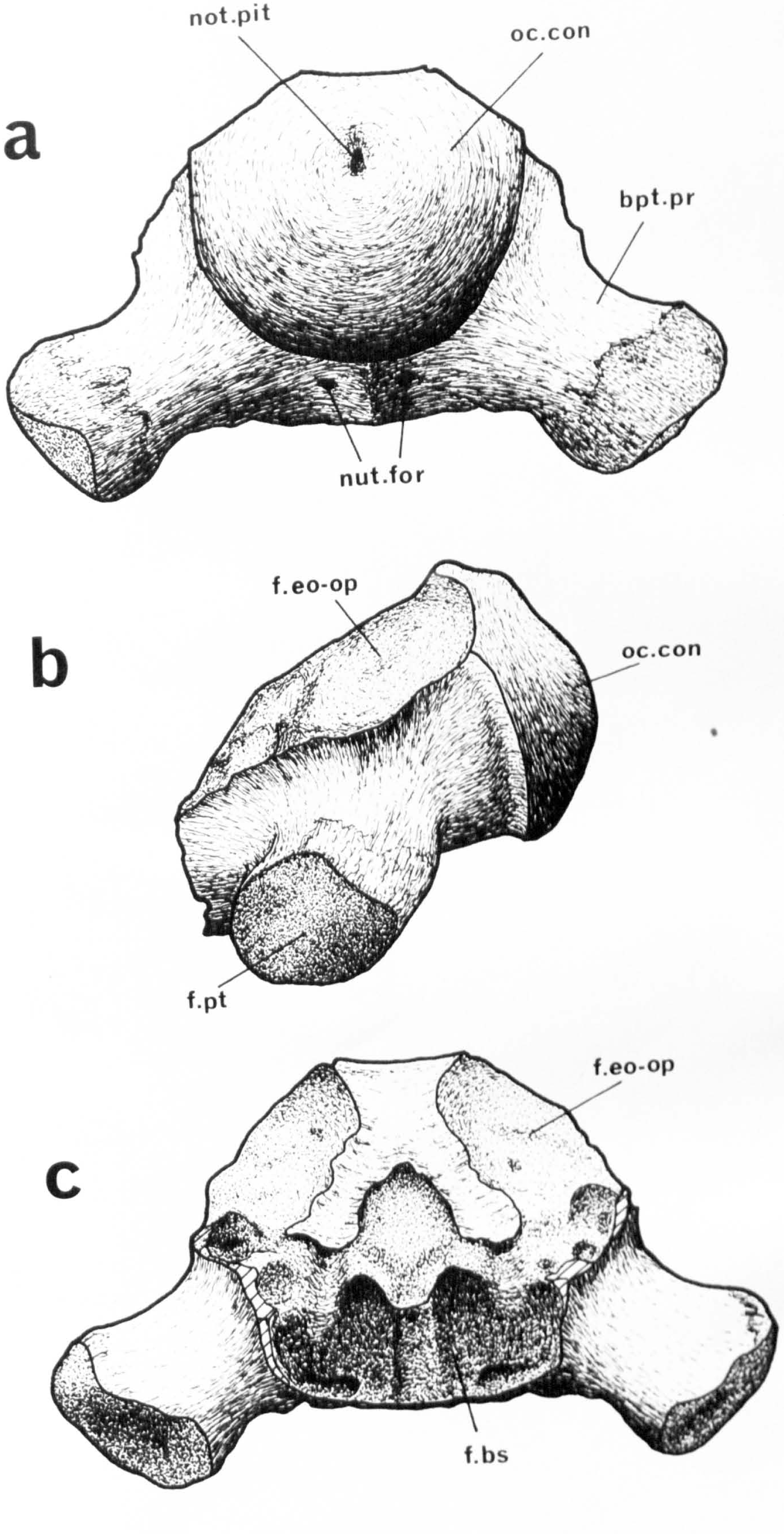

a
not.pit
oc.con
bpt.pr
nut.for
b
f.eo-op
oc.con
f.pt
c
f.eo-op
f.bs

Figure 34

Kimmerosaurus oweni: Right exoccipital-opisthotic of R.8431, x2.

a posterior view; b lateral view; c anterior view; d mesial view.

EO	exoccipital portion of fused element
f.bo	facet for basioccipital
f.pro	facet for prootic
f.so	facet for supraoccipital
f.sq	facet for squamosal
fen.ov	fenestra ovalis
h.c	horizontal semicircular canal
oc.con	exoccipital portion of occipital condyle
OP	opisthotic portion of fused element
par.pr	paroccipital process
post.v.c.	posterior vertical semicircular canal
sut	line of fused suture between exoccipital and opisthotic
ut	utriculus
X	jugular foramen for vagus nerve
XII	foramina for branches of hypoglossal nerve

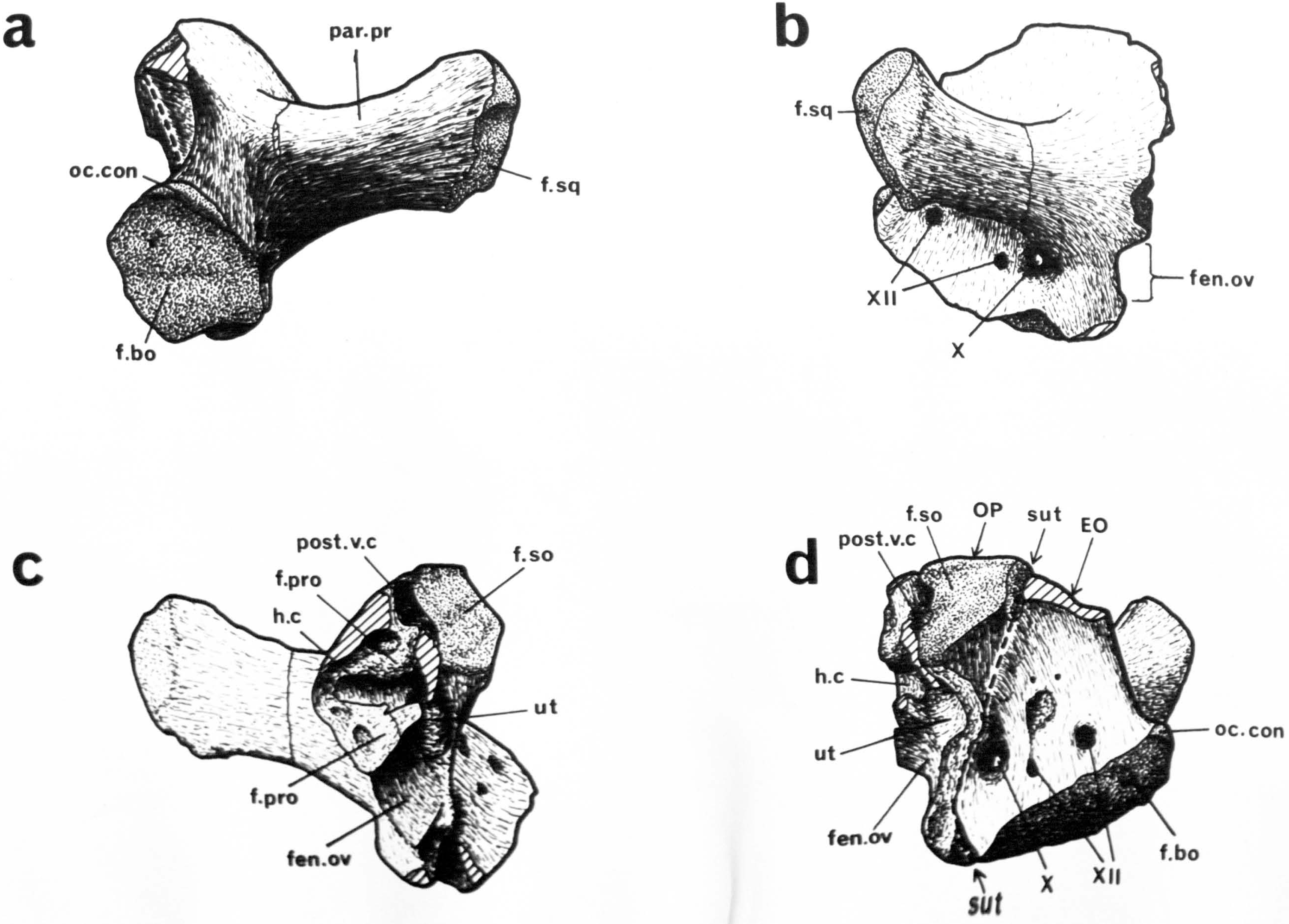

a
par.pr
oc.con
f.sq
f.bo
b
f.sq
XII
fen.ov
X
c
post.v.c
f.so
f.pro
h.c
ut
f.pro
fen.ov
d
post.v.c
f.so
OP
sut
EO
h.c
ut
oc.con
fen.ov
f.bo
X
XII
sut

Figure 35

Colymbosaurus trochanterius: Left femur and epipodials of the specimen in the Castle Museum, Norwich (not numbered), x$\frac{1}{3}$. Ventral view.

FEM	femur	PIS	pisiform
FIB	fibula	TIB	tibia

Outline of pisiform reconstructed from B.M.(N.H.) 40640.

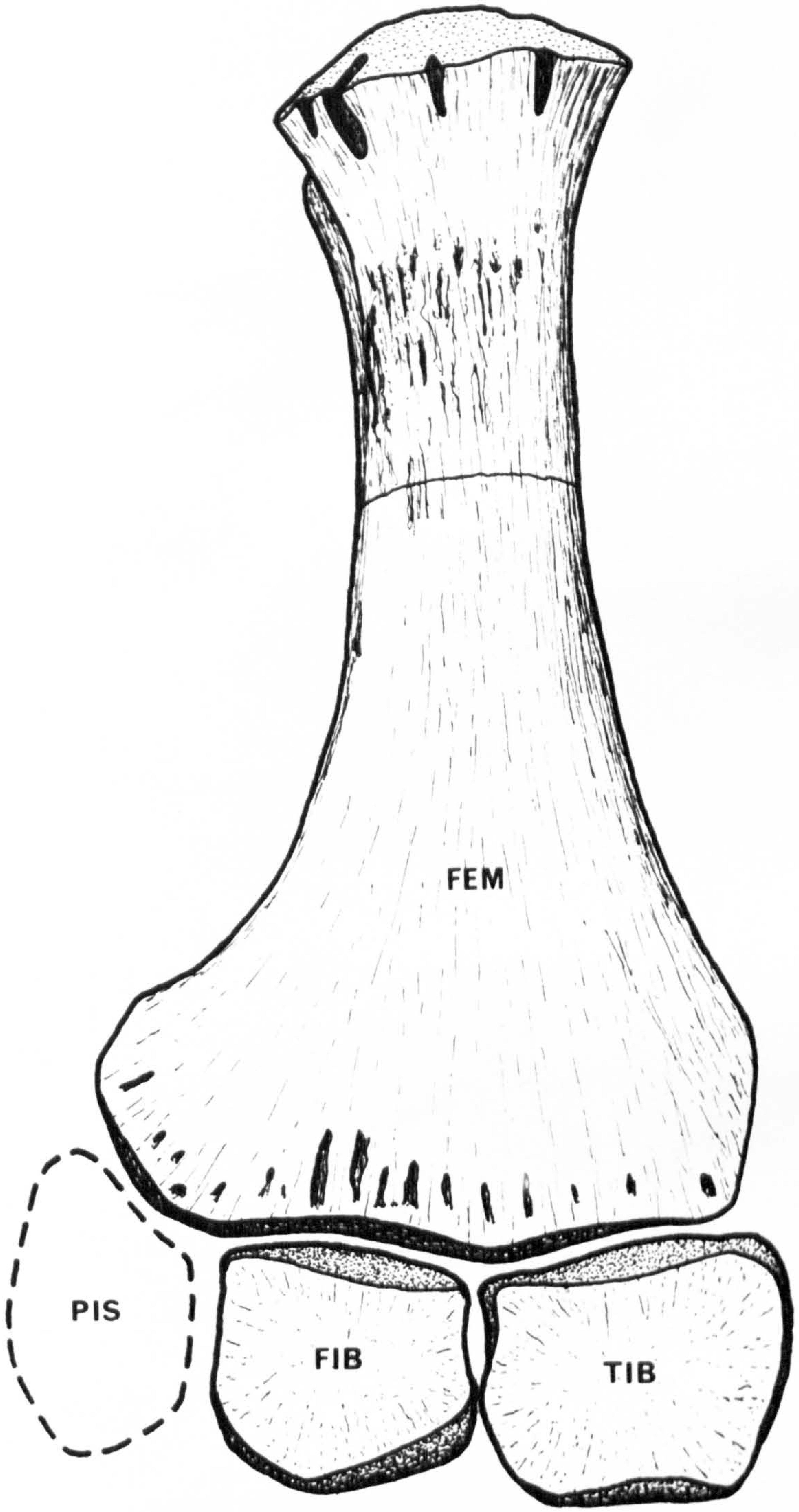

FEM
PIS
FIB
TIB

Figure 36

Isolated tooth from the Kimmeridge Clay, J.30070. Indeterminate.

a axial view (i); b lingual view; c axial view (ii); d buccal view

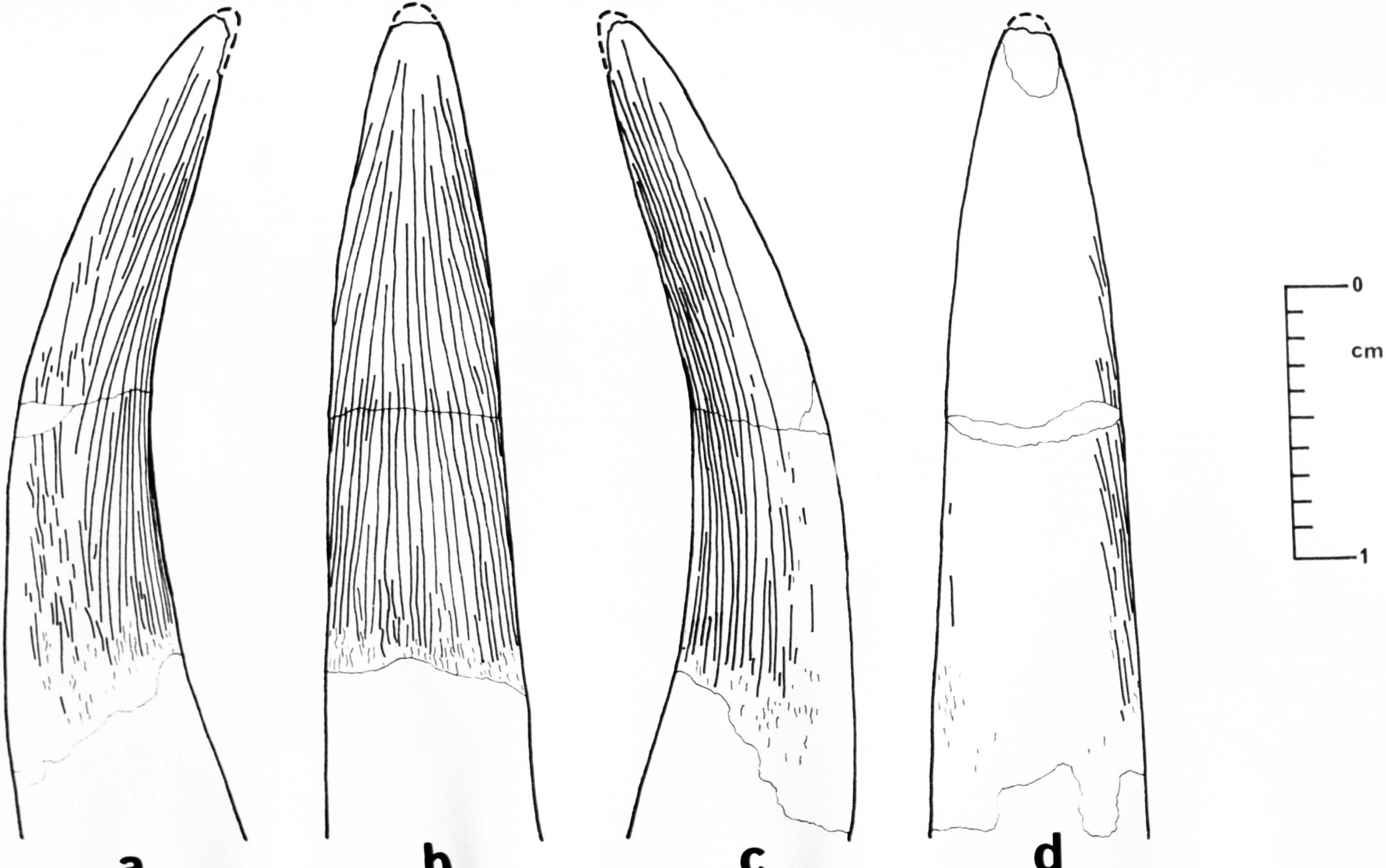

a
b
c
d
0
cm
1

Figure 37

Isolated tooth from the Portland Stone, J.14270a. Indeterminate.

a axial view (i); b lingual view; c axial view (ii); d buccal view


a
b
c
d
0
cm
1

Figure 38

Humeri of British Upper Jurassic plesiosaurs: left humeri, dorsal profiles

a *Cryptoclidus eurymerus*: V.1104

b *Cryptoclidus richardsoni*: R.6696

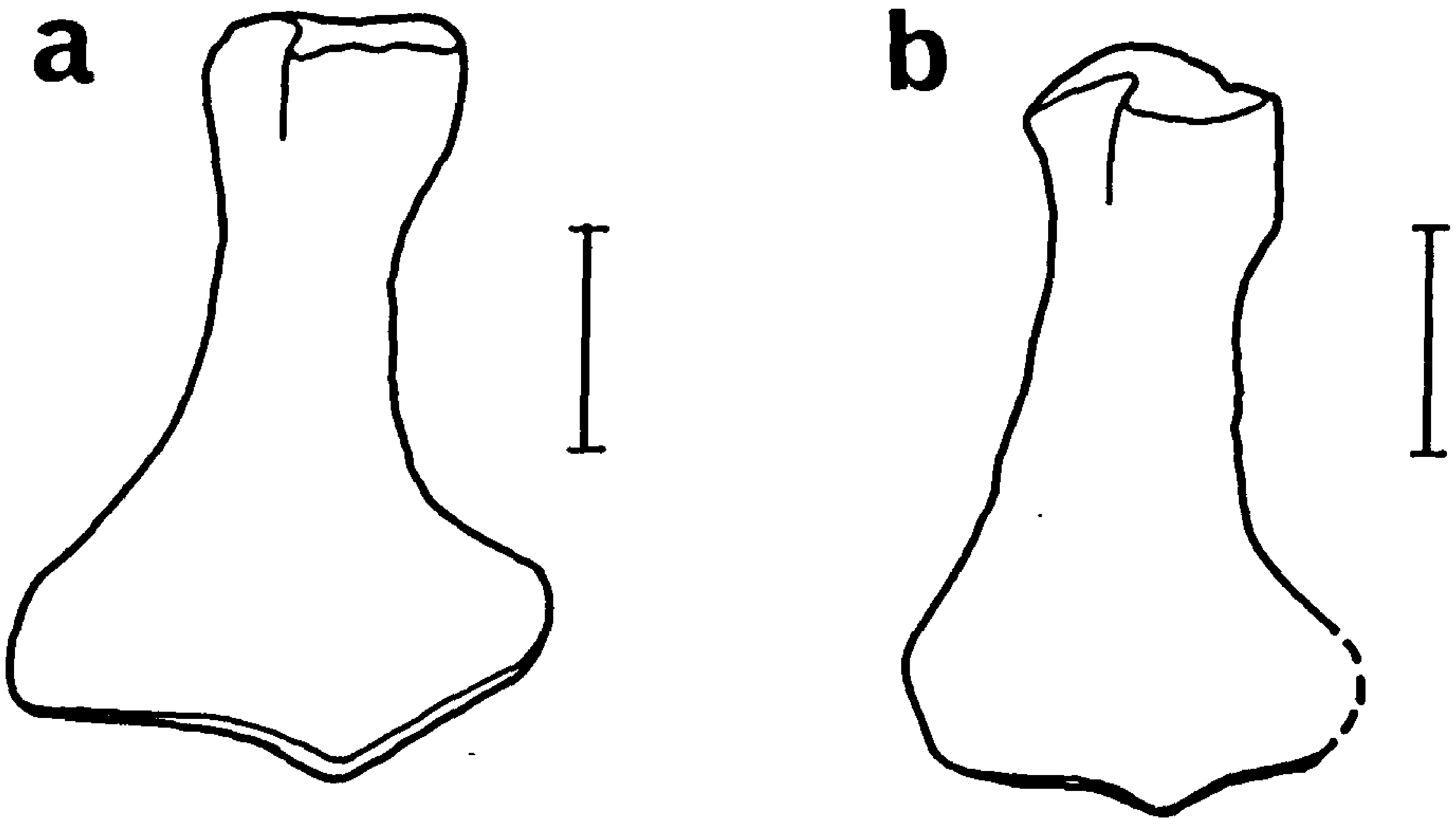
c *Muraenosaurus leedsii*: R.2426

d *Muraenosaurus beloclis*: R.1965

e *Tricleidus seeleyi*: R.3539

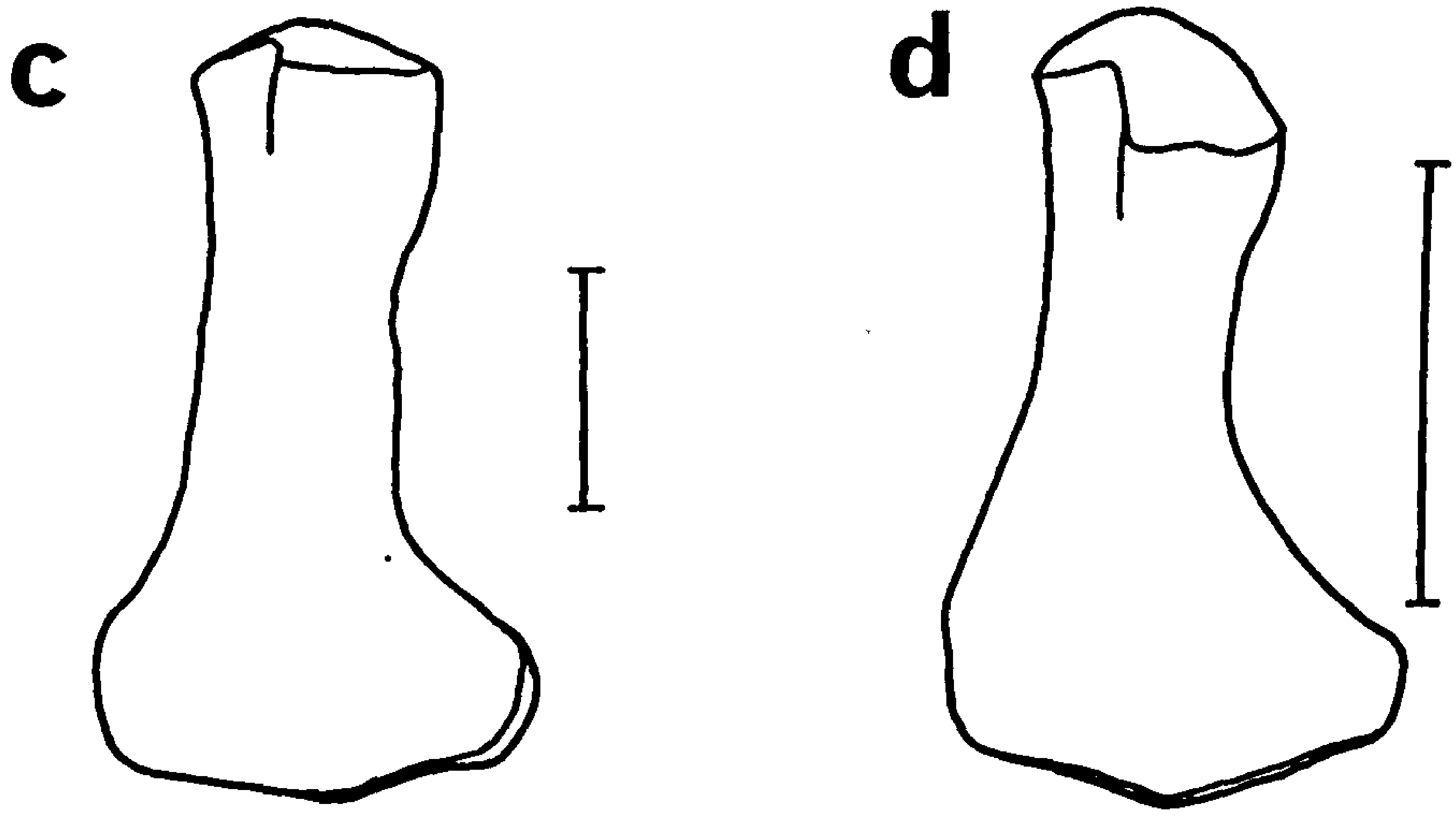
f *Colymbosaurus trochanterius*: L.3166

Scale lines represent 10 cm.



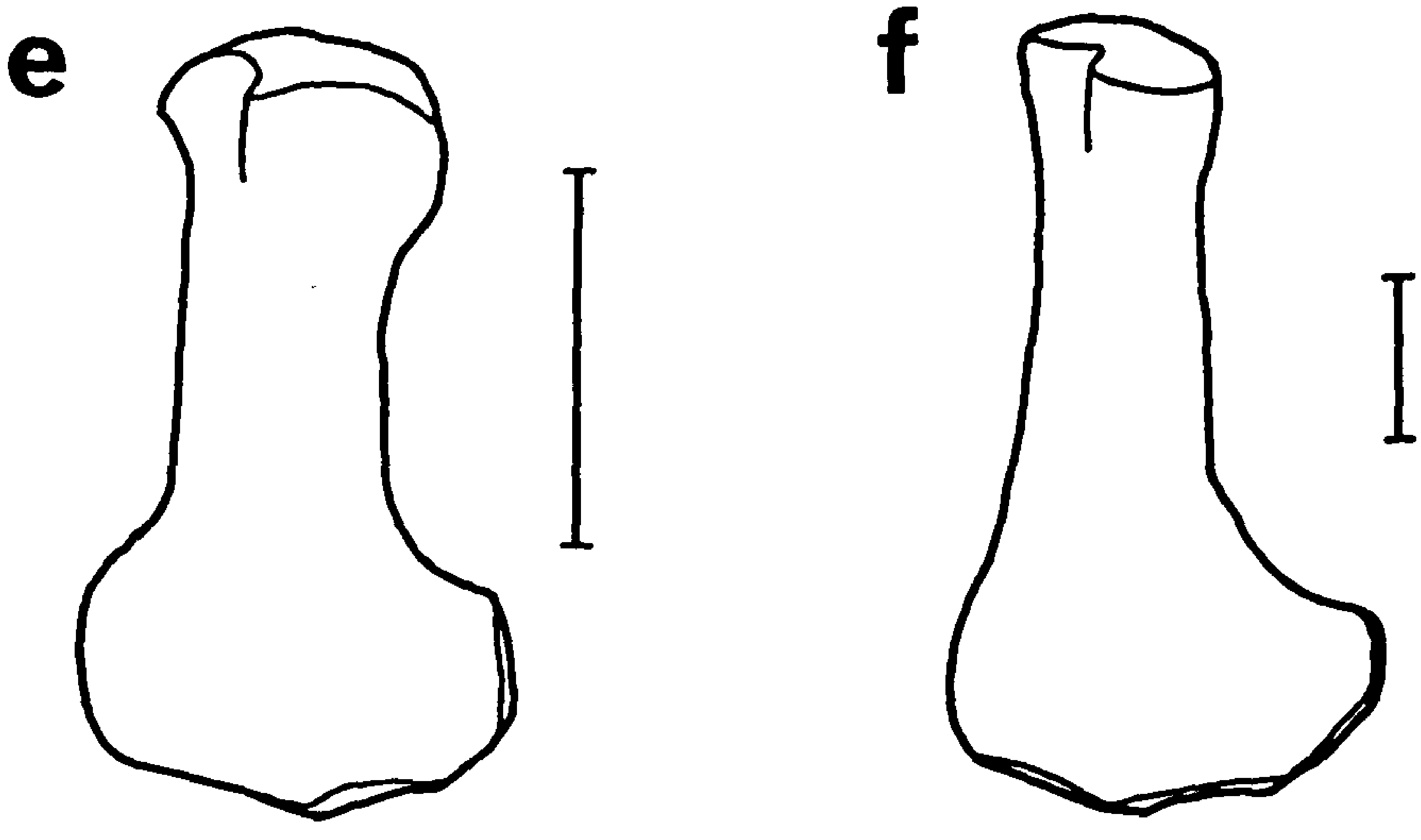
Cryptoclidus eurymerus

Cryptoclidus richardsoni



Muraenosaurus leedsii

Muraenosaurus beloclis



Tricleidus seeleyi

Colymbosaurus trochanterius

Figure 39

Pectoral girdles of British Upper Jurassic plesiosaurs: dorsal profiles

a *Cryptoclidus eurymerus*: R.2616 b *Muraenosaurus leedsii*: R.3704

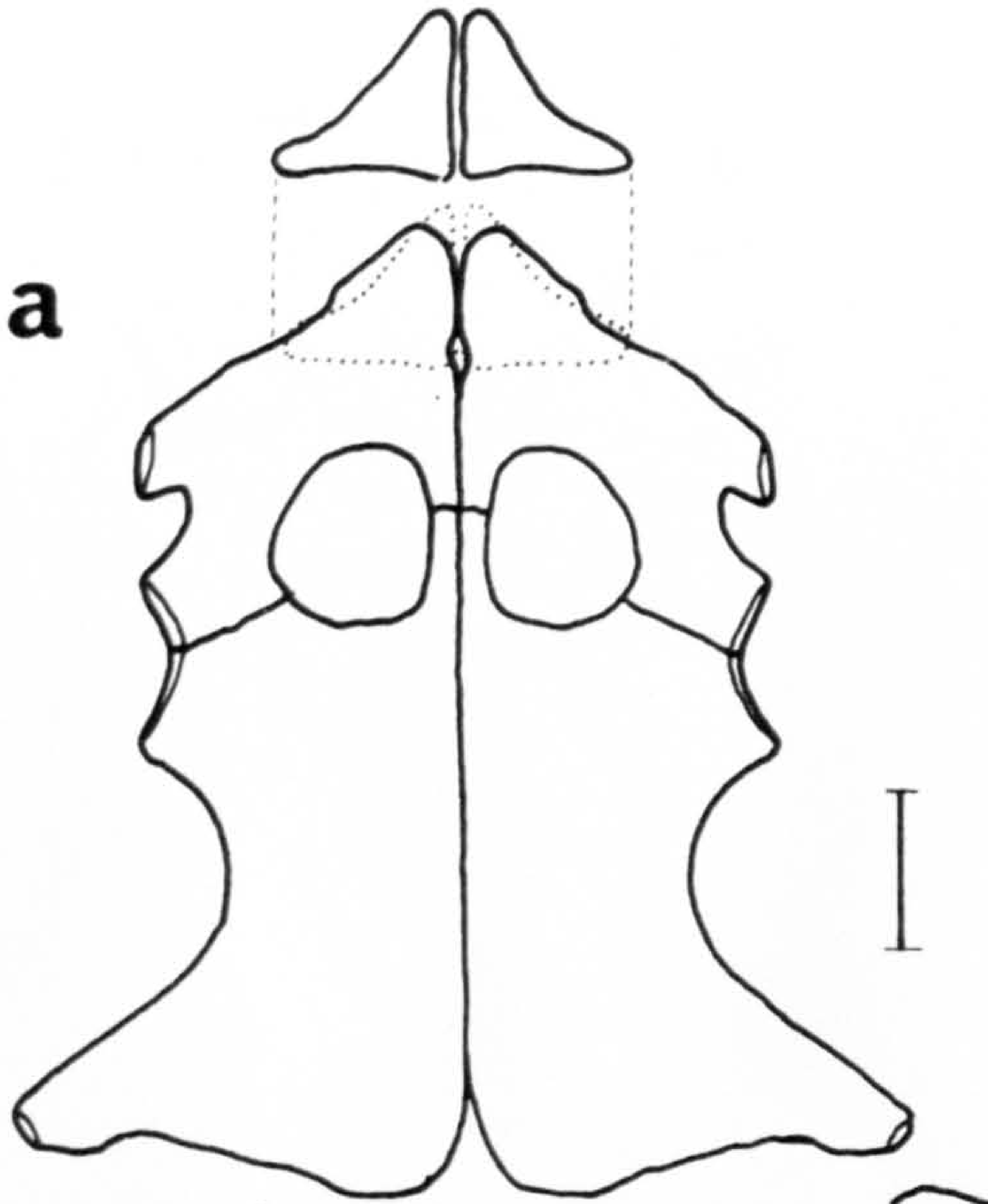
c *Muraenosaurus beloclis*: R.1965 d *Tricleidus seeleyi*: R.3539

e *Colymbosaurus trochanterius*: specimen in the Manchester Museum (no number)

Dermal elements moved forwards to show ventral rami of scapulae.

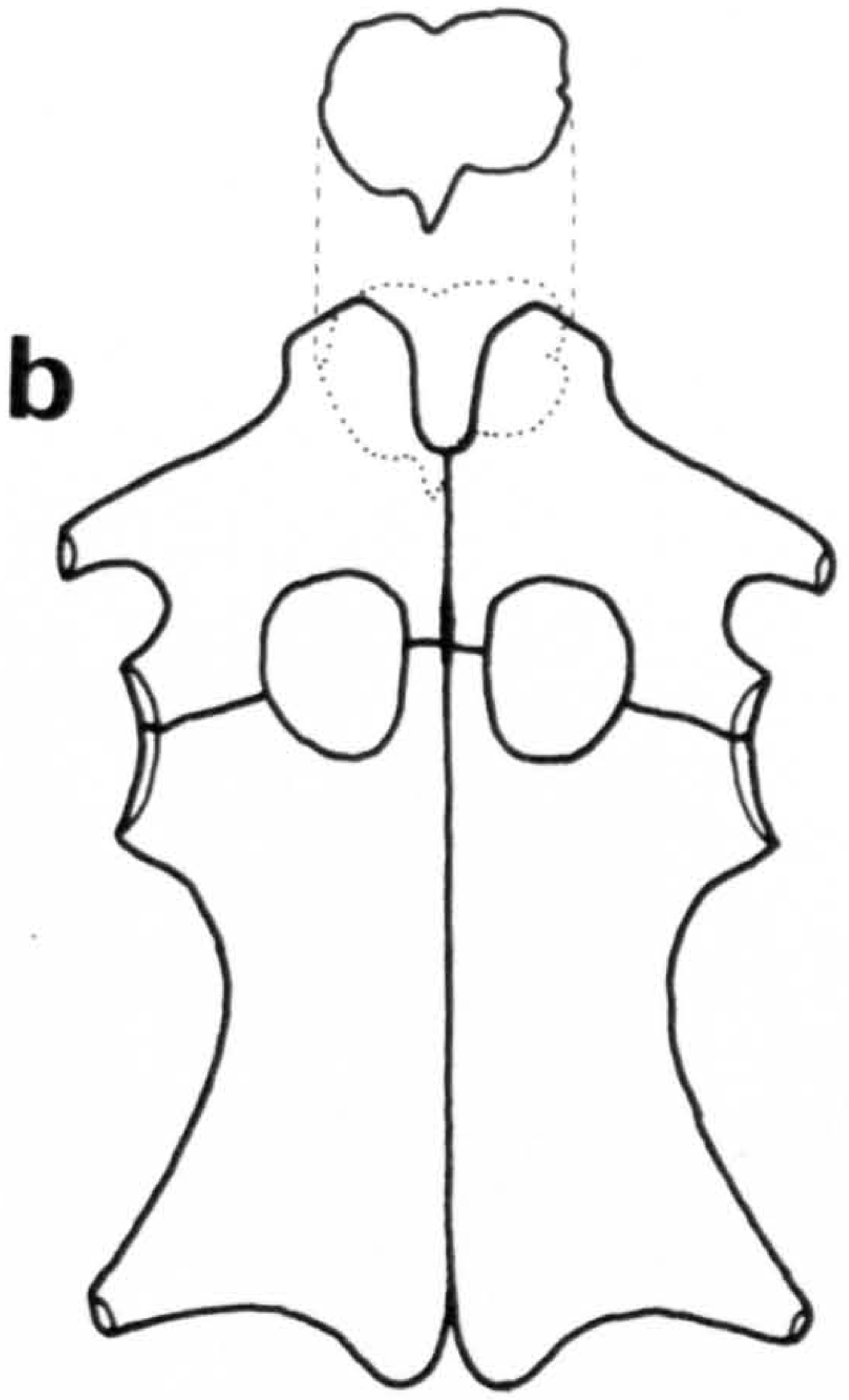
Scale lines represent 10 cm.

a



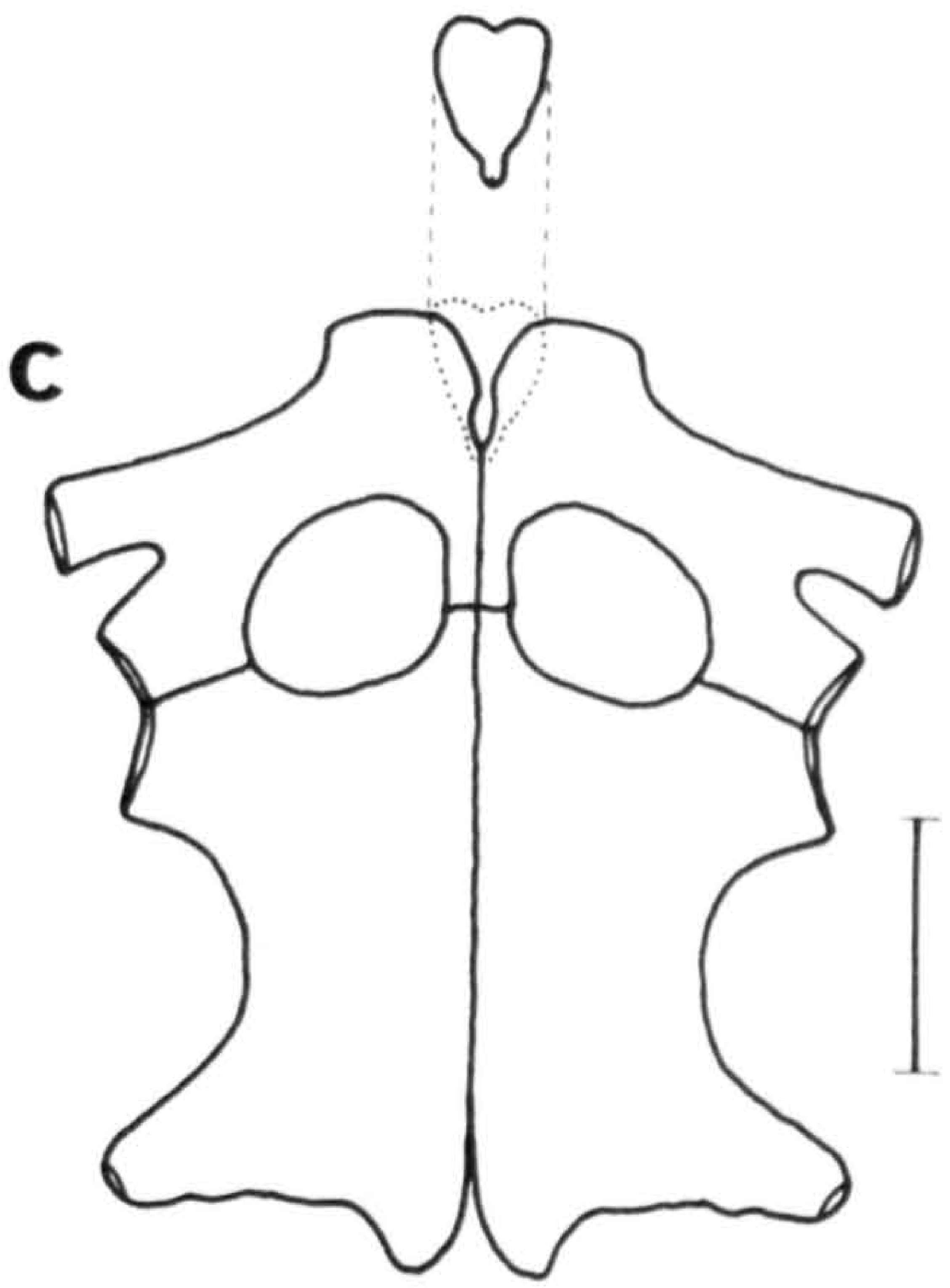
Cryptoclidus eurymerus

b



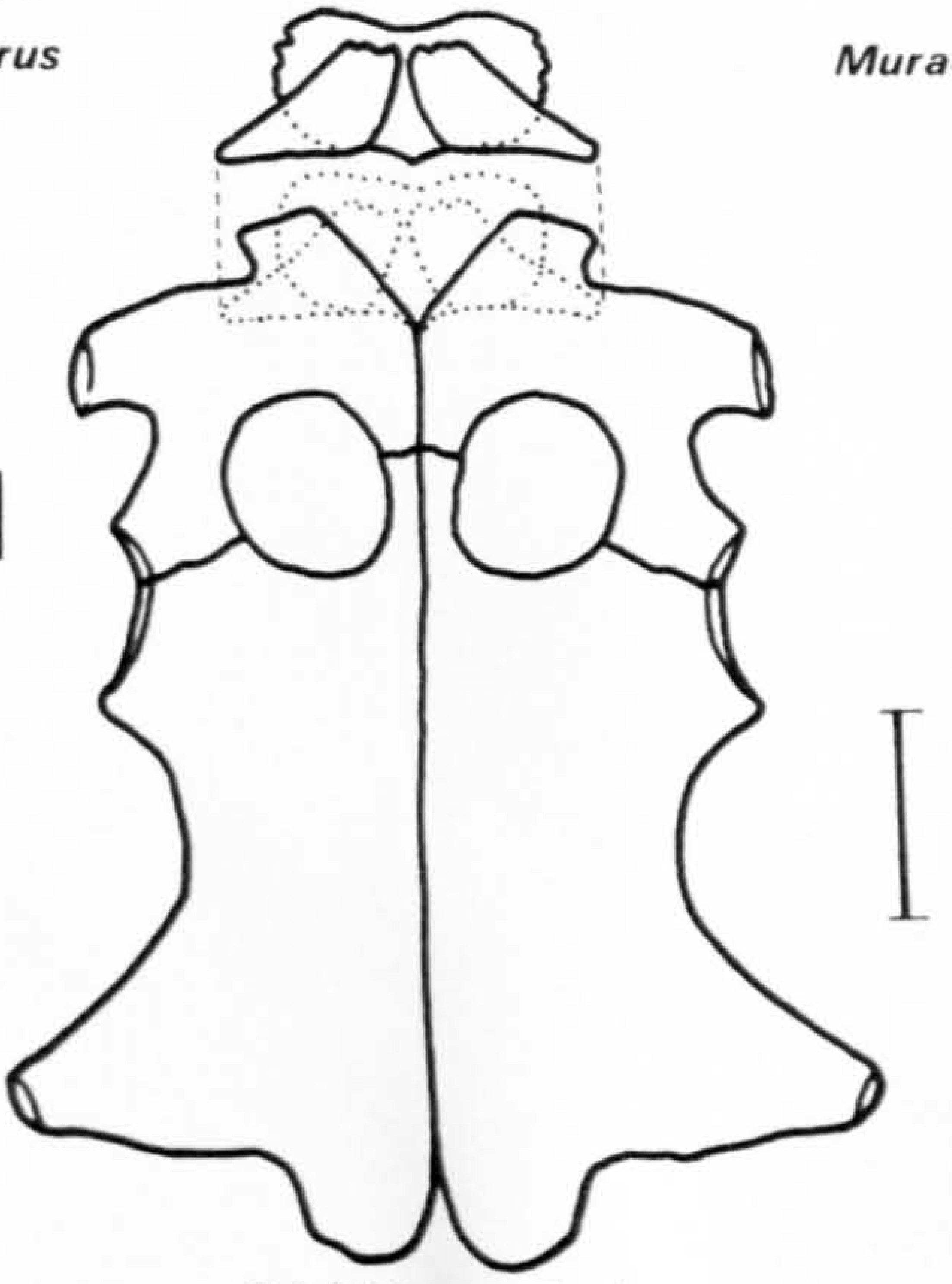
Muraenosaurus leedsi

c



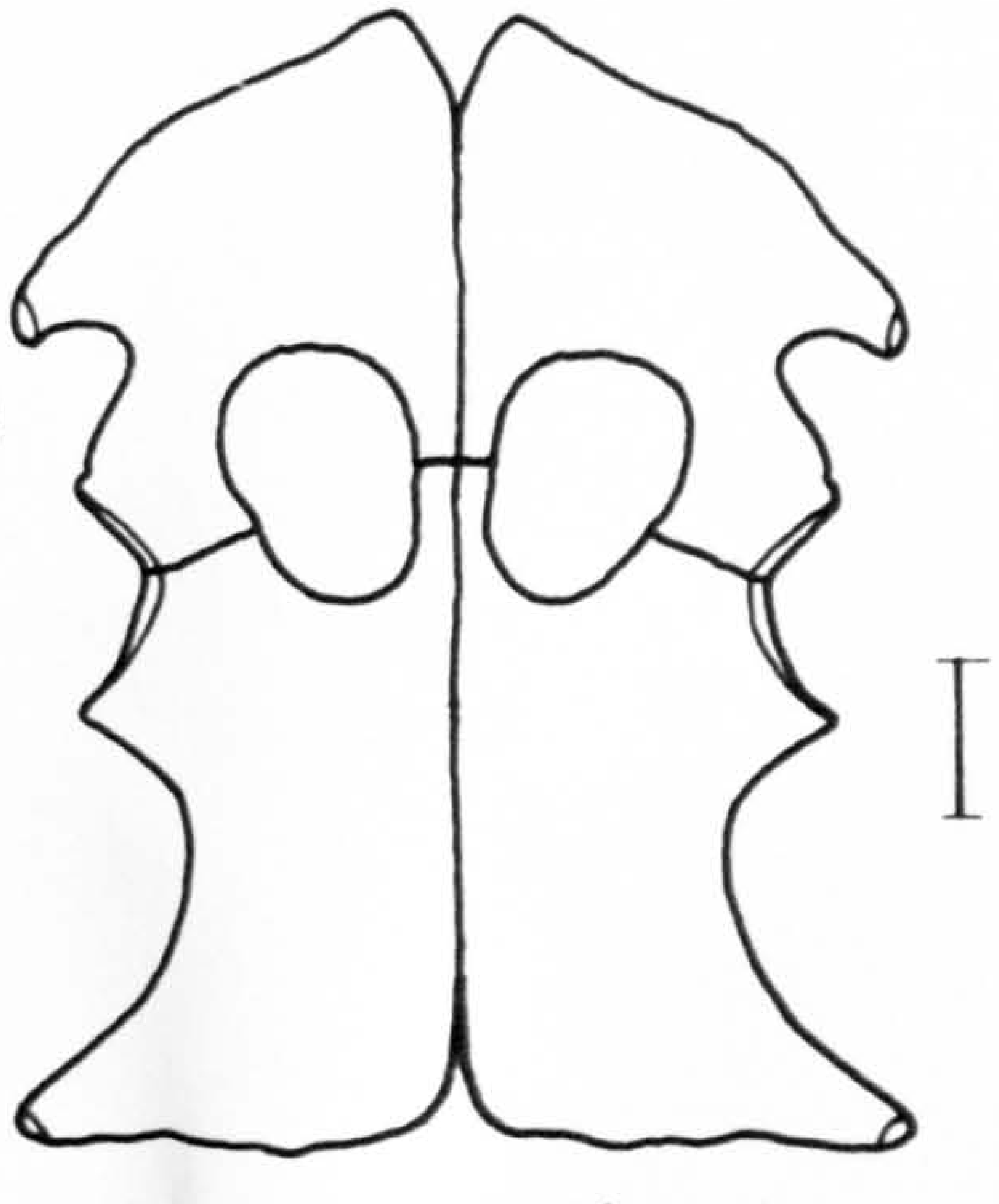
Muraenosaurus beloclis

d



Tricleidus seeleyi

e



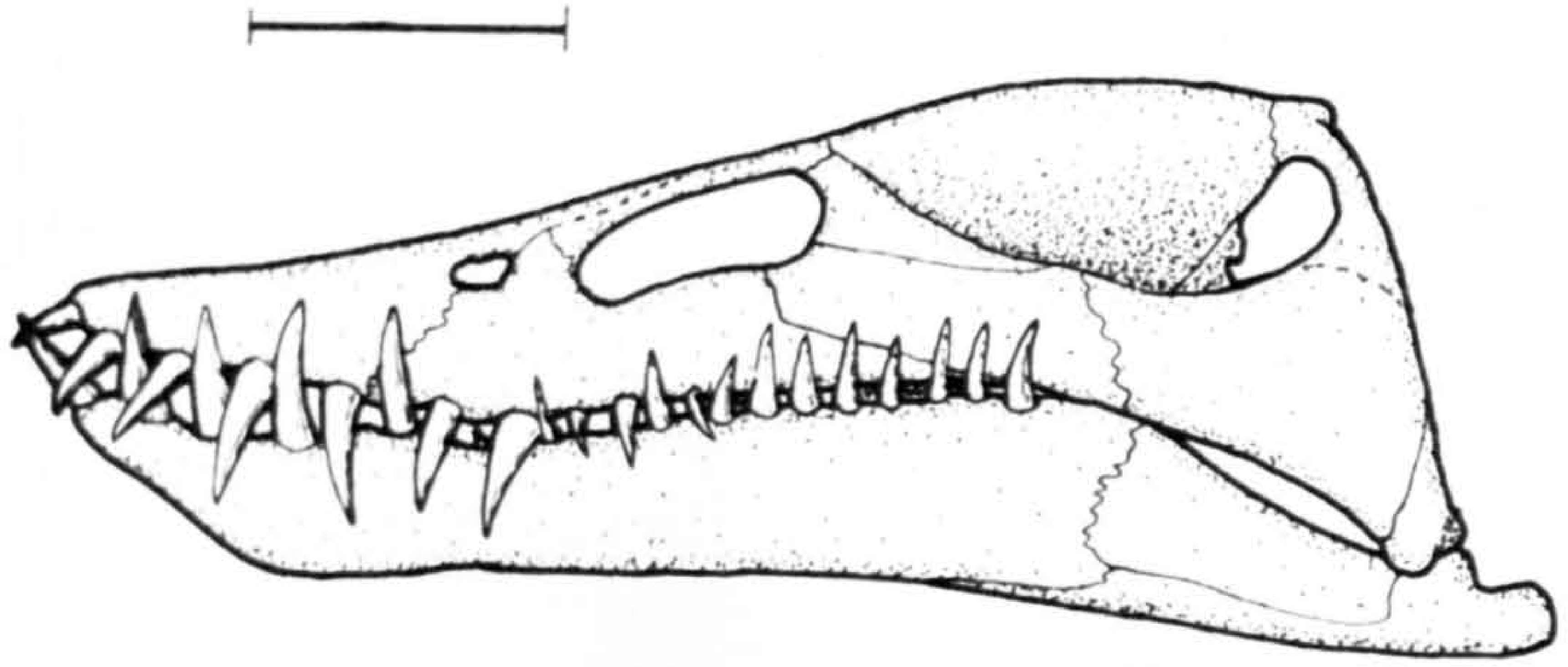
Colymbosaurus trochanterius

Figure 40

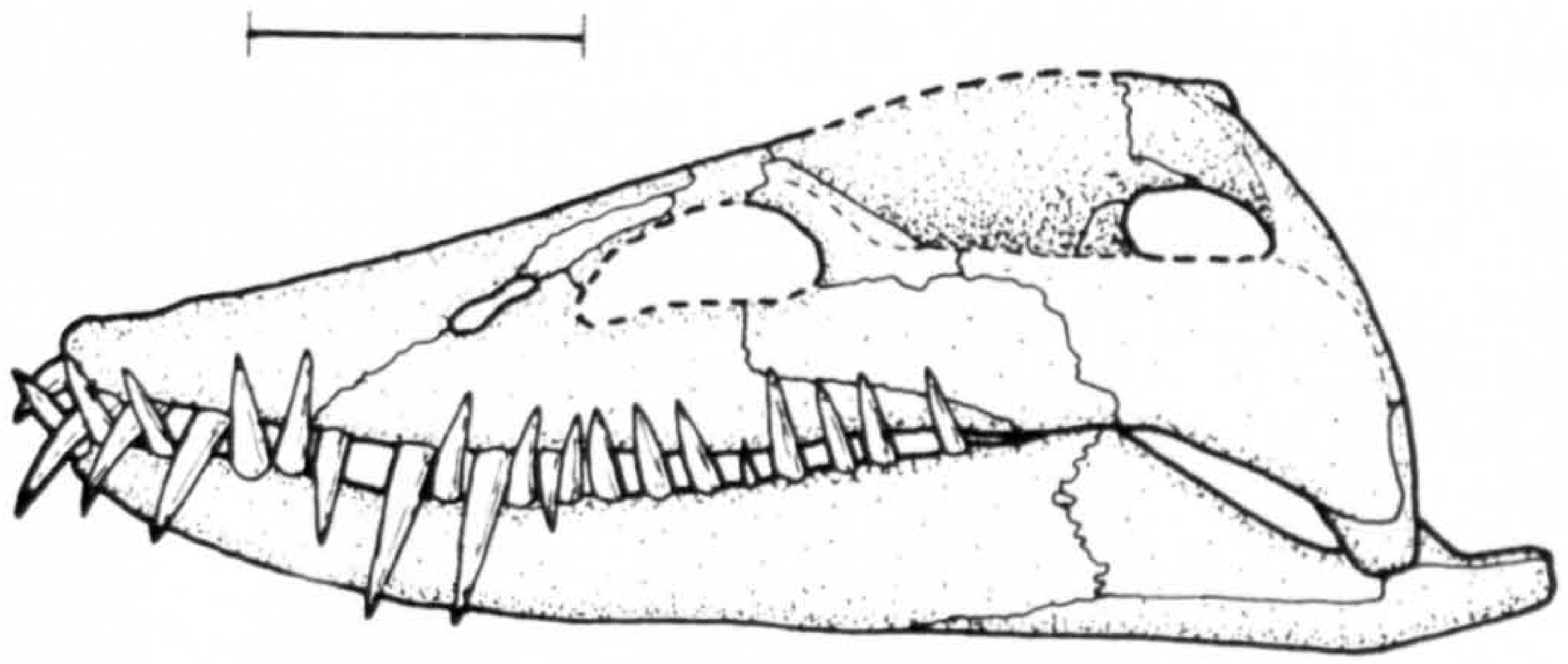
Comparison of plesiosaurian skulls.

Styxosaurus snowi and *Thalassomedon haningtoni* (Elasmosauridae, Upper Cretaceous of U.S.A.) redrawn from Welles, 1952. *Elasmosaurus morgani* (Elasmosauridae, Upper Cretaceous of U.S.A) redrawn from Welles, 1949. *Tricleidus seeleyi* (Elasmosauridae, British Upper Jurassic), *Cryptoclidus eurymerus* and *Kimmerosaurus oweni* (Cryptoclididae, British Upper Jurassic) redrawn from figures 21, 1 and 24.

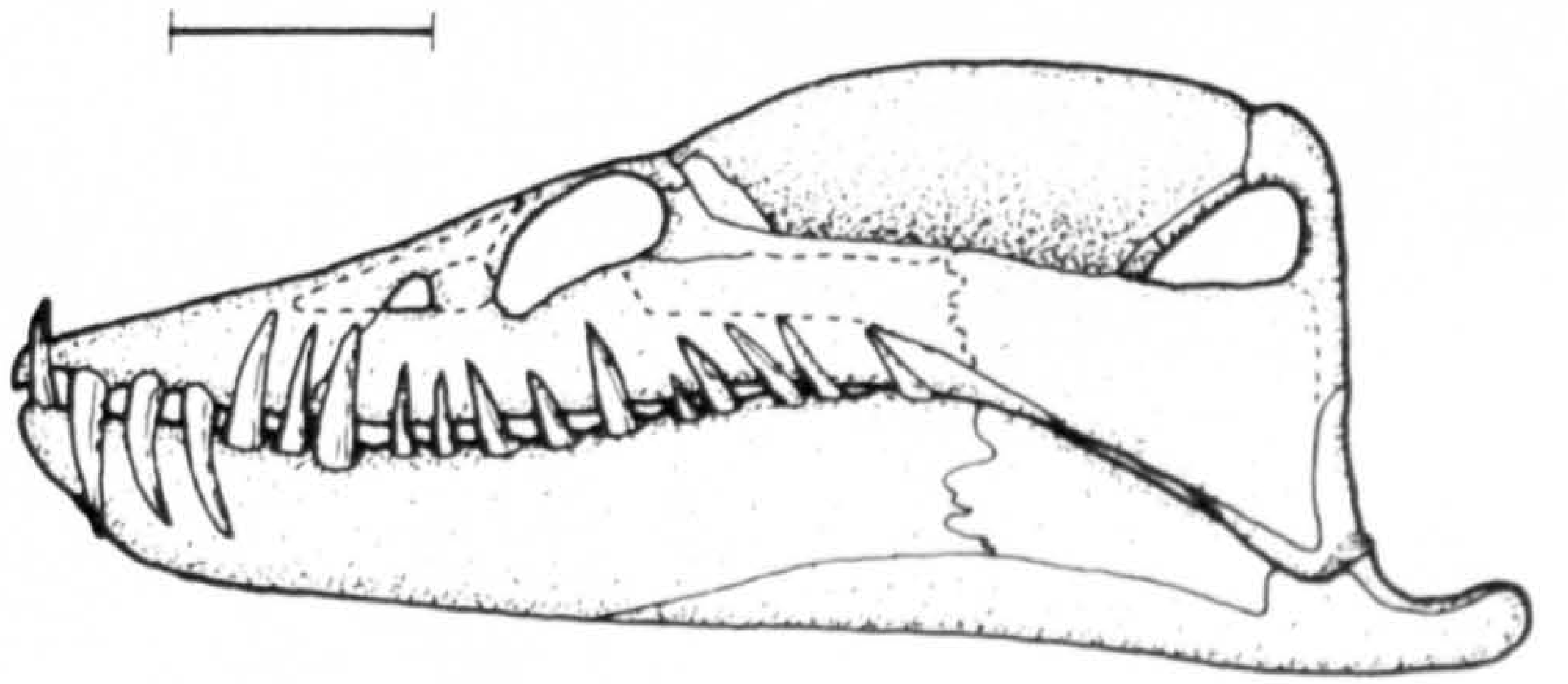
Scale lines represent 10 cm.



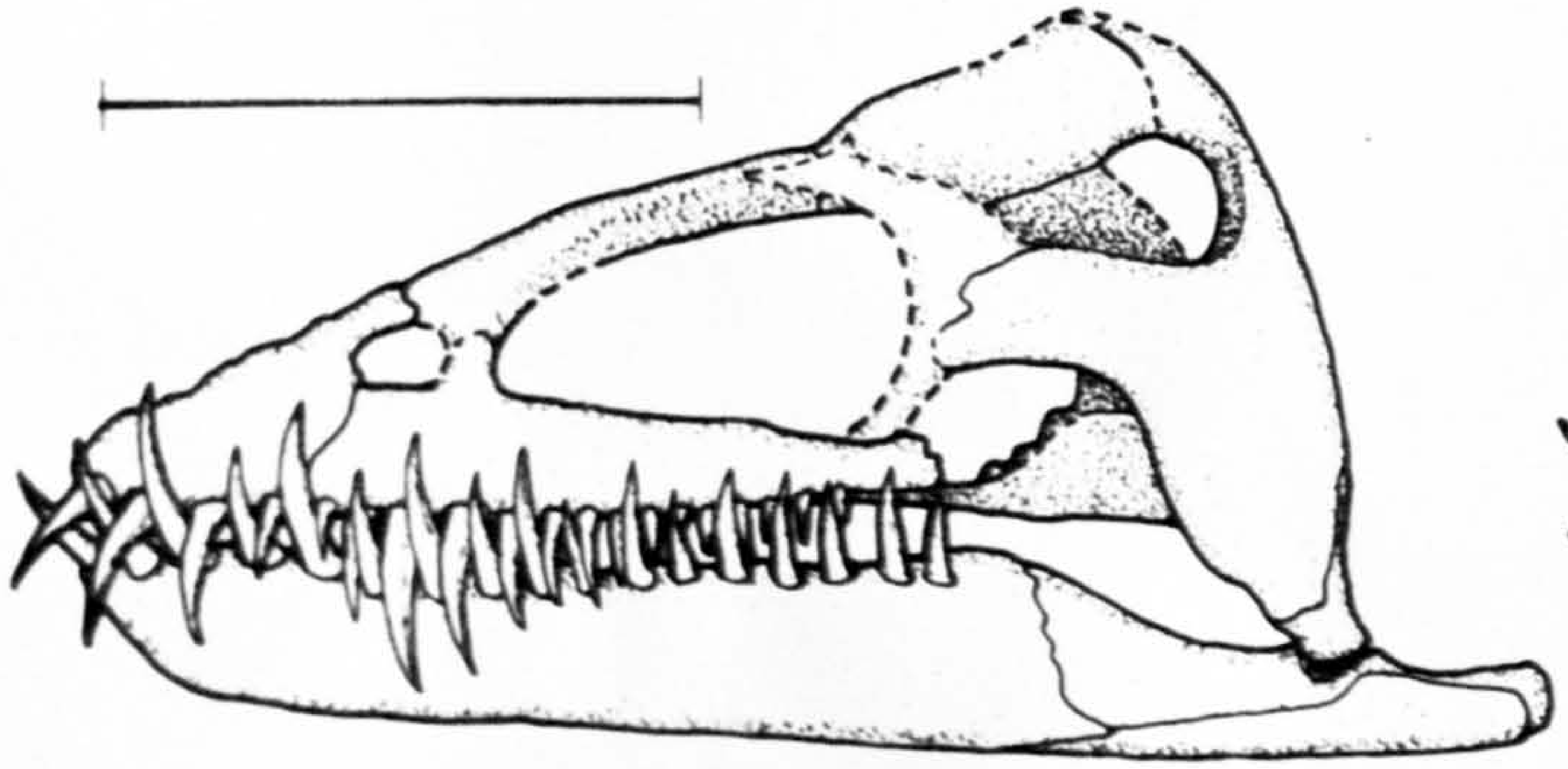
Styxosaurus snowi



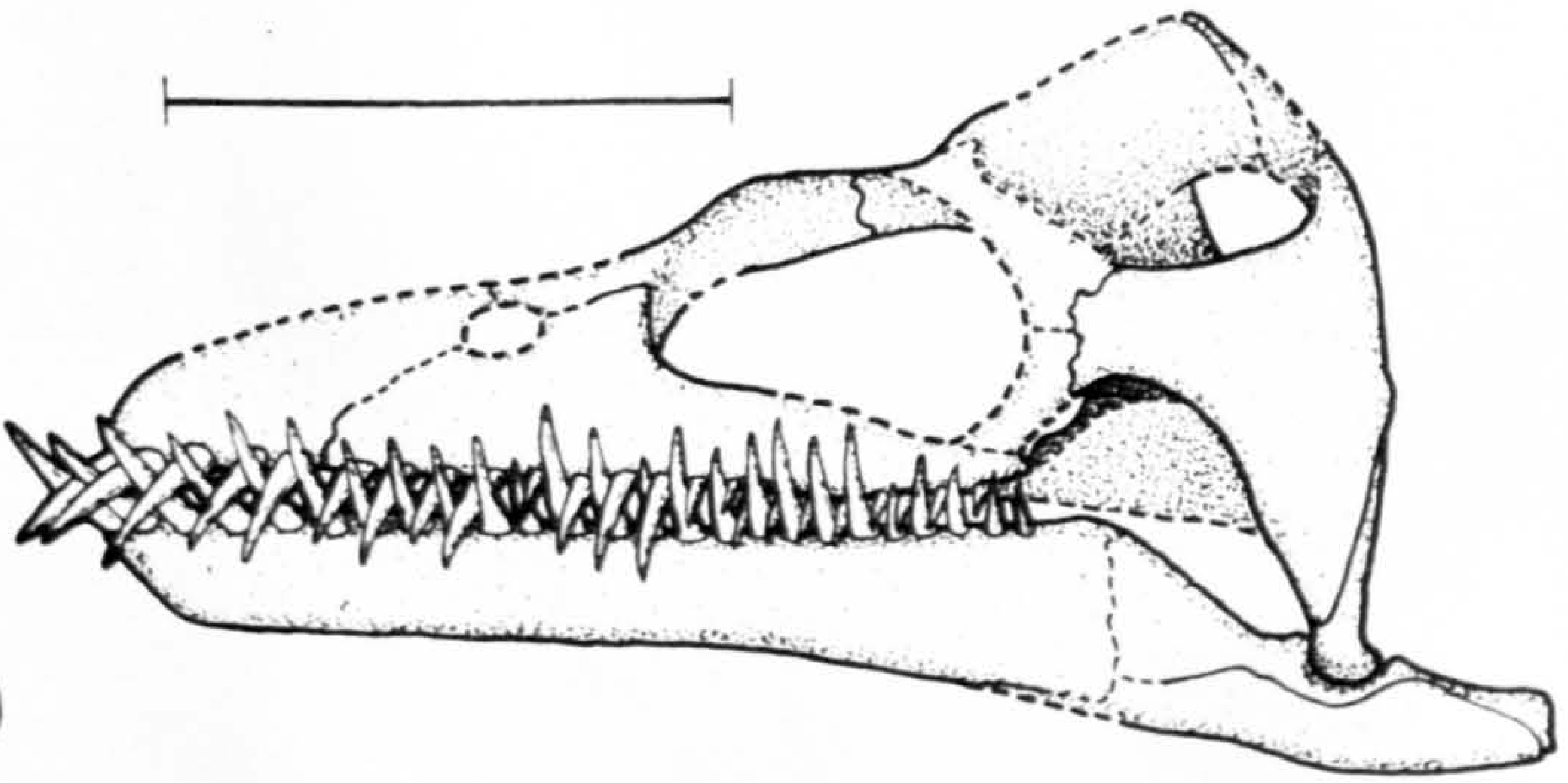
Elasmosaurus morgani



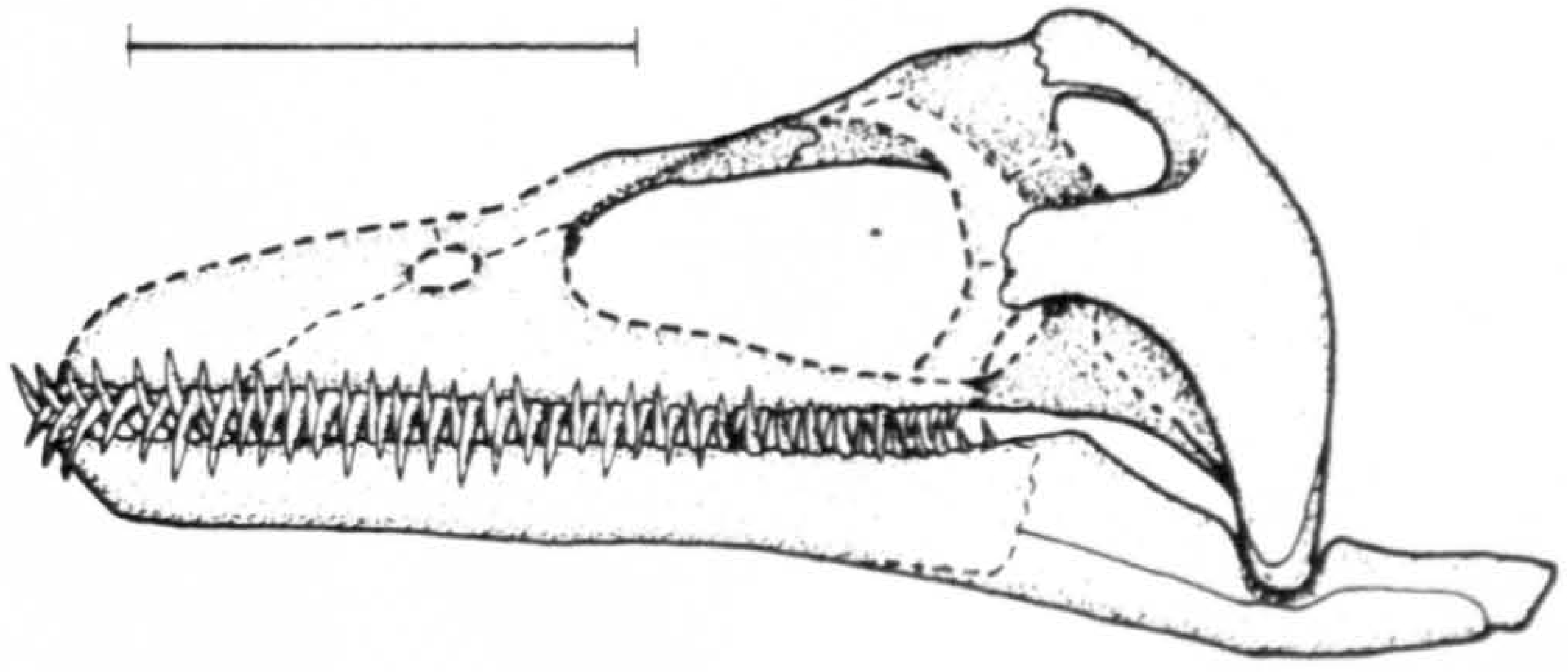
Thalassomedon haningtoni



Tricleidus seeleyi



Cryptoclidus eurymerus



Kimmerosaurus oweni

Figure 41

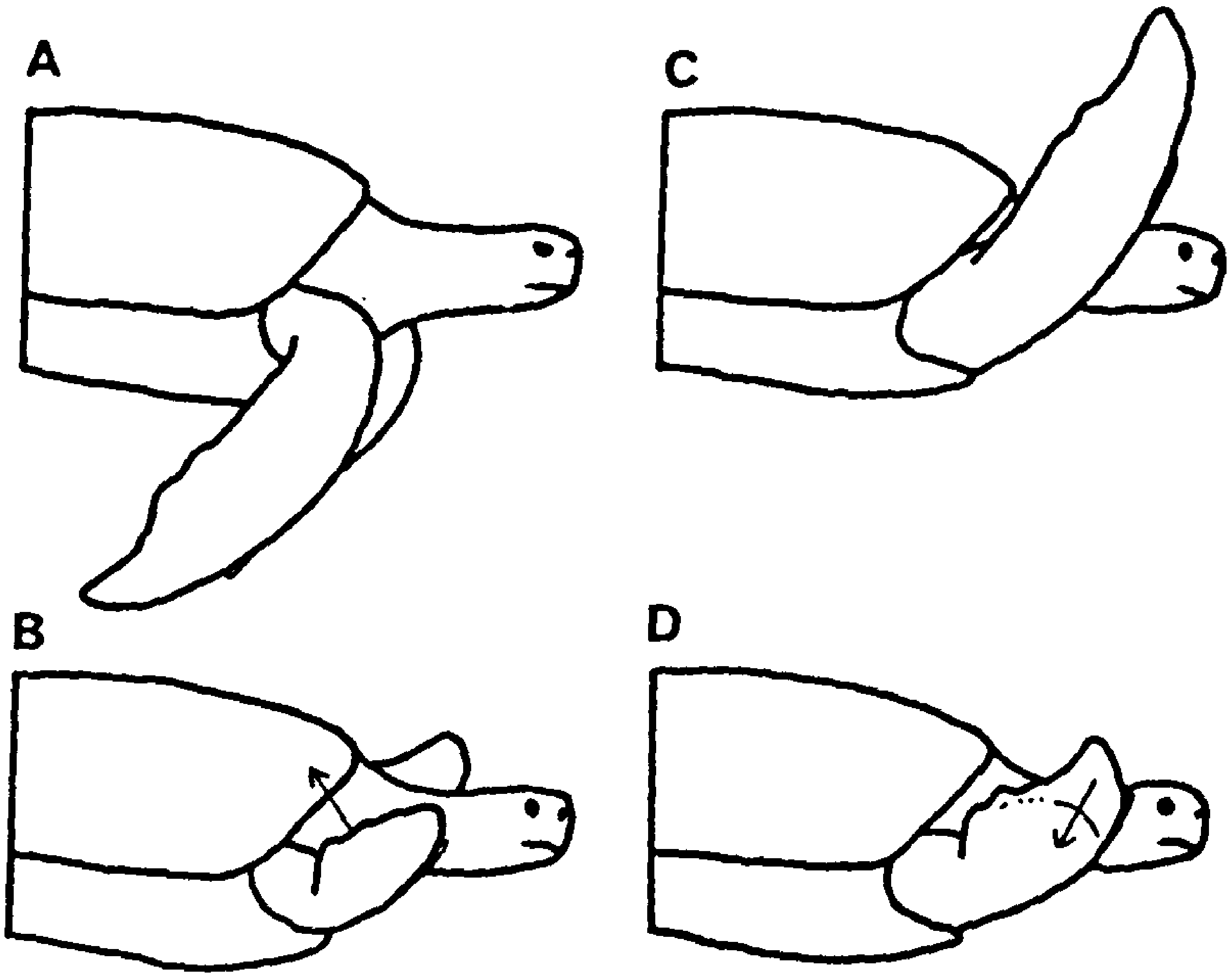
Locomotion of cheloniid turtles: the fore paddle.

Figures redrawn from Walker, 1971 (figs. 1 and 2).

i "Drawings made from enlargements of motion picture frames of four successive stages in a limb cycle of Chelonia m. mydas. A, pectoral limb at bottom of cycle; B, on the way up; C, at top of cycle; D, on way down. The fine line on the blade in D suggests curvature of distal part of blade". Arrows indicate direction of thrust.

ii "Composite drawings of pectoral limbs of Chelonia m. mydas during a representative cycle. A, line of excursion of blade; B, movements of blade tip and its angles of attack with turtle in a fixed position. The dashed lines in A and B show the overall axis of blade movement".

i



ii

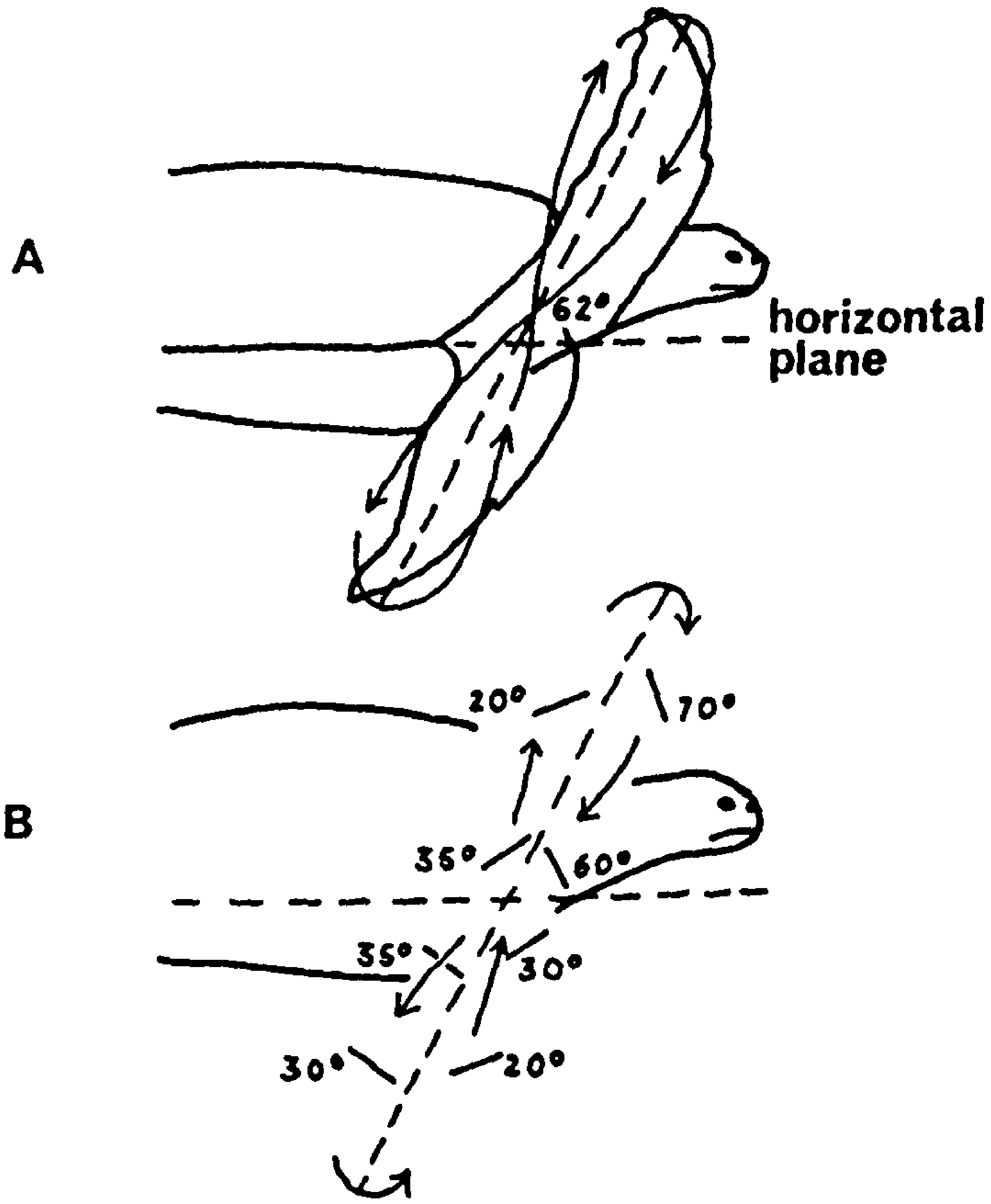
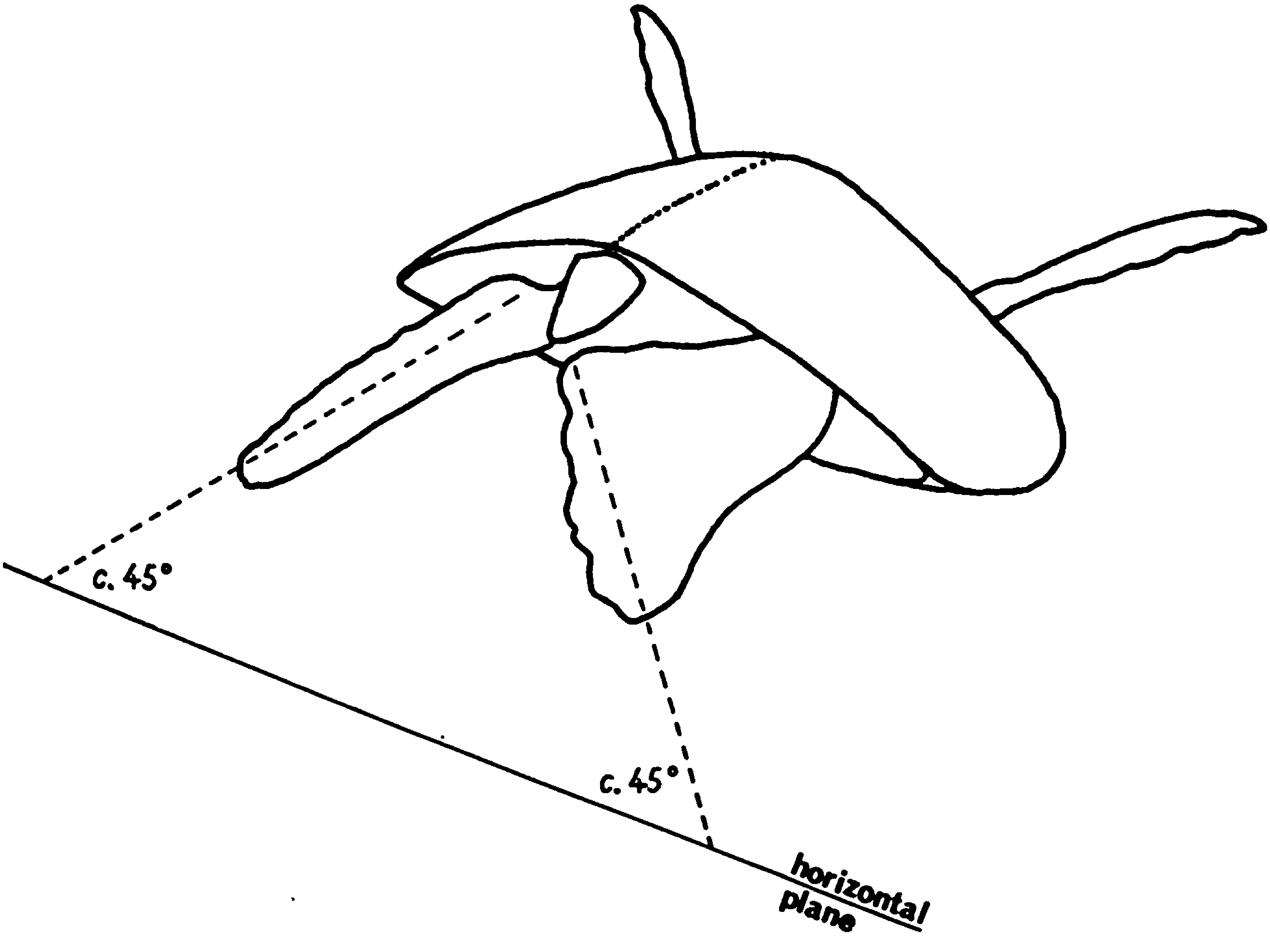


Figure 42

Locomotion of cheloniid turtles: the hind paddle

Drawing traced from a frame of the film "Search in the Deep", a volume in the series "The undersea world of Jacques Cousteau" (B.B.C. copyright), showing natural attitude of hind paddles of Chelonia m. mydas during normal straight swimming. The paddles are held behind the animal and inclined at about 45° to the horizontal plane.


c. 45°
c. 45°
horizontal plane