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29.

THE NATURE OF THE SHOULDER GIRDLE AND CLAVICULAR ARCH IN SAUROPTERYGIA.

BY

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I. THE NOMENCLATURE OF THE BONES OF THE SHOULDER GIRDLE.

§ 1. *In Ichthyosauria.*

The Sauropterygia and Ichthyosauria having formerly been combined in the group termed Nexipoda or Enaliosauria, it has been rather assumed than proved that the bones which form the shoulder girdle in those orders are homologous. The Ichthyosaurian shoulder girdle was well figured by Sir E. Home ('Phil. Trans.,' 1818, Part I) and Cuvier ('Oss. Foss.,' Pl. 258). Figures by other authors agree substantially (Huxley, 'Anatomy of Vertebrates,' p. 244) in showing (1) that the coracoids meet ventrally in the median line; (2) that there is a notch on the anterior margin of the coracoid between the median anterior cartilaginous border of the bone and the scapula, and this notch varies in depth and width with the species; (3) the scapula is directed outward, upward, and forward; (4) its articular end has a posterior part which contributes with the coracoid to form the glenoid cavity for the head of the humerus, a median part, which articulates with the anterior articular edge of the coracoid, and an anterior surface, which does not differ in its cartilaginous articular aspect or thickness from the middle portion, but which looks inward without any bony element of the shoulder girdle to articulate with it. This condition has not been explained. At one time I doubted the existence of such a surface in the undisturbed skeleton ("Pectoral Arch, &c., of *Ophthalmosaurus*," 'Geol. Soc. Quart. Journ.,' December, 1874, p. 698), and some subsequent writers have restored the shoulder girdle as though no such surface existed (J. W. Hulke, "Presidential Address, Geol. Soc., 1883," p. 19, copied by R. Lydekker, 'Cat. Foss. Rept. and Amph. Brit. Mus.,' Part II, 1889); (5) the scapula carries the rod-like clavicle upon the anterior margin of the bone, and from the posterior or ventral surface of the clavicles the median bar of the interclavicle is prolonged backward ventrally upon the coracoid bones.

Since 1874 I have examined most of the Ichthyosaurian skeletons from English and German strata without finding a specimen which

leads me to doubt the substantial accuracy of the early interpretations of Home, Buckland, and Cuvier, in regarding the scapula as extending an articular surface inward and forward towards the pre-articular portion of the coracoid. Various circumstances lead me to suggest that the notch on the anterior margin of the coracoid is a portion of the precoracoid foramen; that the precoracoid element of the shoulder girdle was cartilaginous in *Ichthyosaurus;* and that this cartilage usually articulated with the part of the scapula anterior to the external articulation of the coracoid, and also with the anterior inner processes of the coracoids, so as to complete the precoracoid foramen anteriorly. Among the reasons which suggest this interpretation are: (1) It accounts for the structure of the shoulder girdle, and explains its homology; (2) it brings the shoulder girdle of *Ichthyosaurus* into harmony with *Nothosaurus*, in which there is a similarly incomplete (precoracoid) foramen and similar cartilaginous surfaces of coracoid and scapula in close juxtaposition; (3) it brings the shoulder girdle of *Ichthyosaurus* into harmony with that of the Anomodontia, because they correspond in the form of the scapulæ, the positions and forms of the clavicles, interclavicles, and coracoids; so that, if the Anomodont precoracoid were unossified, the differences from *Ichthyosaurus* would be small, except that some of the Anomodonts (*Pareiasaurus*) develop an epiclavicle of Labyrinthodont type. On this evidence a cartilaginous precoracoid is shown in the restoration now given.

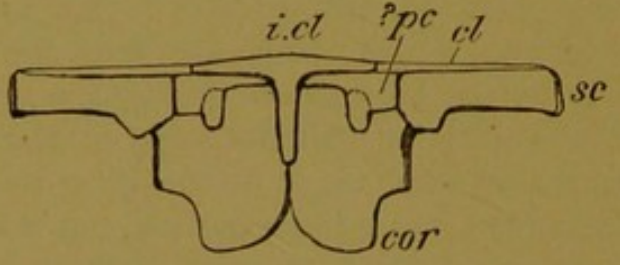


Fig. 1.—Shoulder girdle of *Ichthyosaurus*. *cor.*, coracoid; *sc*, scapula; *? pc*, precoracoid, supposed to have been cartilaginous; *cl*, clavicle; *i.cl*, interclavicle.

Before the Enaliosauria were subdivided, the bone which is here named interclavicle was regarded by Sir E. Home as homologous with the interclavicle of *Ornithorhynchus*, but it is named episternum by Cuvier, Sir R. Owen, and some recent writers like K. von Zittel. To the best of my belief the episternum was identified as being the interclavicle by Professor Huxley. My own earliest use of the term in relation to *Ichthyosaurus* is in 1869 ('Index to Fossil Remains, &c., Woodw. Museum'). If the ossifications are membrane bones, they are rightly classed as clavicles; if they are cartilage bones, they may be connected with the sternum, and take a sternal name. Each of

these three bones terminates in a sharp edge or point, and no one of them shows a terminal surface which has the aspect of being cartilaginous; there is therefore no evidence of a cartilaginous origin, while the mutual relations of the bones and their forms closely parallel the clavicles in Chelonians and some Lacertilians; they are therefore identified with those elements,* because there is no ground for regarding them as parts of the sternum.

§ 2. *In Sauropterygia.*

The nomenclature of the bones of the shoulder girdle in the Sauropterygia has given rise to greater differences of opinion.† The Amphibian mode of ossification of the long bones by long conical epiphyses‡ connected by a dice-box shaped shaft, coupled with a general resemblance of the pelvis and shoulder girdle to those of Chelonians, led to the conclusion that, while the scapula, precoracoid, and coracoid are all separate from each other in some existing Amphibians, the Amphibian plan had been modified in the Chelonia by the scapula and precoracoid remaining undivided, while in the Sauropterygia the coracoid and precoracoid remained in primitive undivided condition. The strongest argument against this is the absence of a recognisable coracoid foramen in Sauropterygia in the coracoid bone,§ which, when present, may be supposed always to occur at the junction of the coracoid and precoracoid elements. At the same time the clavicles were recognised in the Sauropterygia as distinct lateral ossifications, placed at the sides of the interclavicle, and closely united with it by suture in some species of *Plesiosaurus*.

The difficulty with the scapular arch is in the theoretical postulates concerning the elements of which its several parts consist. Sir R. Owen ('Brit. Assoc. Rep.,' 1839, p. 56) used the Chelonian hypothesis to explain the scapula in *Plesiosaurus*. And E. D. Cope ('Amer. Phil. Soc. Trans.,' 1870, p. 51), in *Elasmosaurus*, regarded the ventral plate of the bone anterior to the coracoid as clavicles or procoracoids, assuming a scapula external to it, as in Chelonians. And in 1883 Mr. Hulke (*loc. cit.*) also urged that the Plesiosaurian bone, usually named scapula, is a compound bone formed of scapula and precoracoid, as in Chelonians.

In support of this interpretation, it might be urged that the bones

* Hulke, *loc. cit.*

† 'Those which prevailed prior to 1874 were summarised in the 'Quart. Journ. Geol. Soc.,' for that year.

‡ 'Index to Fossil Rept. Woodw. Mus.,' pp. 98, 120, 1869.

§ The specimen figured 'Quart. Journ. Geol. Soc.,' 1874, p. 446, is suggestive, but not conclusive, for the bone is very thin, and no portion of the margin of the perforation is seen, so that its existence as a normal character is unproved.

are similarly situate in both ordinal types, and similar in having a scapular portion which extends vertically, and a precoracoid portion which extends inward horizontally to the median line. On the other hand, there is no close resemblance between these Orders in the bones in question. (1.) The coracoids are dissimilar in form, and are differently conditioned, for they do not meet in the median line in any Chelonian, while there is no Sauropterygian in which they have not a mesial union. (2.) In Mr. Hulke's figures it is only the anterior portion of the ventral plate of the scapula which is lettered as precoracoid. Thus the precoracoid does not enter into the humeral articulation, or hold any position which theoretically can be compared with the bone in Chelonia; while the clavicular arch is anterior to the supposed precoracoid in Sauropterygians, but holds no comparable relation in Chelonians. This latter difficulty apparently led Mr. Hulke to regard the bones termed clavicular as omosternal in Sauropterygia. But no Chelonian possesses an omosternum; so that, if the identification were demonstrated, it does not support the Chelonian hypothesis of the shoulder girdle.

First, it may be observed that it is only in Anura that the precoracoid enters the anterior margin of the glenoid cavity; but in Urodela the precoracoid appears to be excluded, so that it is not theoretically impossible on an Amphibian hypothesis for the precoracoid to be anterior to the acetabulum; but the bone is always wedged between the scapula and coracoid, and on the coracoid border the coracoid foramen is always persistent, so that there is no analogy between Urodele and Sauropterygian to sustain the identification of the precoracoid which has been offered. Whenever two divergent bones form the scapular arch those two bones are the coracoid and scapula; but there is no analogy to support the hypothesis that the precoracoid might form the free extremity of the scapula, as in Mr. Hulke's figure (*loc. cit.*). There is no conclusive evidence of the mutual relations of the scapulo-precoracoid to the glenoid cavity in the Chelonia, but, unless it could be shown that the relations of these bones to the shoulder girdle were the same in both types, Chelonian analogy with Sauropterygia in this part of the skeleton rests upon an inconclusive basis of fact. In Chelonians the ascending process of the scapula extends dorsally towards the vertebræ, while in Sauropterygia it extends backward above the glenoid articulation for the humerus, and there is no evidence that these structures are homologous.

If the evidence is insufficient to sustain the interpretation discussed, it is found that the precoracoid has disappeared as a separate element from the skeleton in Lacertilia, and in most existing Ornithomorpha ('Roy. Soc. Proc.,' vol. 49, p. 520). It is recognised in association with the coracoid in certain Birds; and the persistence of the coracoid foramen gives some evidence that the precoracoid is not unrepre-

sented on the scapular side of the foramen in all members of that class except the Ornithosauria. Its individuality is retained in some of the Sauromorpha; and, although they have no distinct osseous representative of the bone, the nearest analogy to the shoulder girdle in Sauropterygia is found among Nothosauria; and there is no doubt that these resemblances and those with Anomodonts are closer than with existing orders of animals.

The Nothosaurian shoulder girdle contains the same number of constituent elements as in Sauropterygians, and the same nomenclature has been applied to them. There are some slight differences in the coracoid. In the Nothosauria it lies more obviously behind the glenoid cavity, while in many Plesiosaurs, especially the typical forms from the Lias, it also has a considerable median anterior extension. Further, in Nothosaurs there is a notch in the anterior margin of the coracoid, already contrasted with the similar notch in the coracoid of Ichthyosaurs, anterior to which are rough cartilaginous surfaces of scapula and coracoid, which have the aspect of having supported a cartilage which completed the coracoid foramen. There is no anterior prolongation of the scapula in *Nothosaurus* such as is seen in *Plesiosaurus*, but the clavicles are much elongated. They form a squamous overlap on the visceral surface of the scapula, according to von Meyer, and their length, and prolongation forward, removes the interclavicle from contact with the coracoids. If the suggested precoracoid cartilage in *Nothosaurus* existed, it makes the nature of both coracoid and scapula clearer in *Plesiosaurus*, and shows that the precoracoid need not be displaced into the position here assigned to the clavicle.

First, the foramen which appears to be indicated in the anterior margin of the coracoid in some species of *Ichthyosaurus* as a deep narrow notch, in other species widens to a concave anterior border to the bone; and similarly, in the specimen figured by Deecke as *Lariosaurus Balsami*, there is no trace of the anterior notch in the coracoid such as characterises *Nothosaurus*, but that bone has a smooth sharp anterior concave border such as the bone shows in *Plesiosaurus*. It would therefore seem to follow that the precoracoid foramen of *Nothosaurus* becomes the coraco-scapular foramen of *Plesiosaurus*, and that the precoracoid in Elasmosaurs ceases to exist as a distinct cartilage. It cannot be inferred to be lost by connation with the coracoid, because the foramen might then be supposed to persist, but, as there is no foramen in either the scapula or coracoid,* there is no evidence of the composite nature of either bone in *Plesiosaurus*. Nevertheless, since the precoracoids meet in the median line in many Amphibians, and in Chelonians, and the scapulæ never have a median ventral union, there is an *a priori* probability that bones formed from cartilage, placed

* Always subject to the doubtful evidence of the Brit. Mus. fossil 2041*.

anterior to the coracoids, meeting in the median line, should rather be precoracoids than scapulæ in such Sauropterygia as show these characters. It has already been shown to be probable that the foramen anterior to the coracoid is the precoracoid foramen, having undergone such an enlargement in transition from *Nothosaurus* to *Plesiosaurus* as does the obturator foramen between the pubis and ischium in transition from the pelvis of *Dicynodon* to the pelvis of a Mammal. Therefore the precoracoids may have ceased to be differentiated, even as separate cartilages, and the coracoids may have grown forward at the expense of this cartilage, just as the scapulæ extended inward and backward at its expense; so that, while the scapulæ are conveniently so named, it may be recognised that in *Elasmosaurus*, *Colymbosaurus*, *Muræenosaurus*, and their allies, the parts of the bone which meet in the median line, and are in median contact with the clavicular arch, are theoretically in the position of precoracoid elements, which connect the scapulæ with the coracoids. But since the Plesiosauridæ show no such median union of scapular elements, or ossifications in front of the coracoids, it follows that there is no evidence that the precoracoid was ossified at all, while the cartilage representing it, if present, must have been a slender bar, comparable to the suggested precoracoid cartilage in *Ichthyosaurus*, as shown by the absence of a thick cartilaginous truncation of the anterior median termination of the coracoids in *Plesiosaurus*.

In the Anomodontia the plan of development of the shoulder girdle has been modified by the great extension of the clavicular arch outward and upward, so that the scapulæ are rather on the type of the Ichthyosauria than of the Sauropterygia. But the position and relations of the Anomodont precoracoid furnish some support to the interpretation given to the element in Ichthyosauria and Sauropterygia; because, if the precoracoid foramen in Anomodonts were theoretically enlarged to the dimensions seen in *Colymbosaurus*, *Plesiosaurus*, or *Lariosaurus*, it would be manifest that for so long as it connected the scapula and coracoid it was Elasmosaurian; so long as it remained attached to the extremity of the scapula only it would be Plesiosaurian; and so long as a remnant remained of cartilage in contact with the inner border of the clavicle the condition would be Lariosaurian.

There is thus a fundamental difference of plan between the imperforate coracoid of Sauromorpha and the perforate coracoid of Ornithomorpha, which depends upon the way in which the precoracoid bone loses its individuality.

§ 3. *Nomenclature of the Bones in the Clavicular Arch.*

Early writers regarded the median bone anterior to the coracoids in *Plesiosaurus* as the sternum. Sir R. Owen named it episternum. Pro-

fessor Huxley regarded it as interclavicle and clavicles ('Anatomy of Vertebrated Animals,' 1874, p. 210). In 1874 I figured the clavicles as posterior to the interclavicle in *Plesiosaurus Hawkinsi*, and drew attention to the similar condition in *Pl. laticeps* ('Geol. Soc. Quart. Journ.,' 1874, p. 444, since figured by Zittel). Mr. Hulke, in 1883 ("Presidential Address, Geol. Soc.," p. 20), regards these ossifications as indivisible, and names the mass omosternum, thus reverting to the hypothesis that the ossifications have a cartilaginous origin, and are episternal. It follows from Mr. Hulke's views that the reputed clavicles of *Nothosaurus* are precoracoid, and the median bone between them is the omosternum.

The late Professor W. K. Parker fully discussed the omosternum in the Vertebrata. It is found in Mammals and in Anura, but is not present in all Anura, and is not always ossified. In the genus *Calamites* it appears to extend slightly on the visceral surface of the precoracoids. In the Amphibian group which it characterises clavicles are probably not found, so that it is in place of an interclavicle, if it does not represent it. It is sometimes single, sometimes paired, but never tripartite, as the median bone among Sauropterygians. Among Mammals Mr. Parker found the omosternum (paired) uniting with the sternum, while laterally it is continued by the clavicles, though there is a pair of small cartilages, termed precoracoids, between it and those elements of the skeleton. In the Monotremata the interclavicle is in the position of the omosternum. In *Anguis fragilis* Mr. W. K. Parker figures both interclavicle and clavicles, but there is no omosternum. The omosternum behaves as though it were the name given to the interclavicle when that element ossifies from cartilage.

A sternum is developed in every existing animal in which the omosternum is present, but in no Sauropterygian is there ever any trace of a sternum, so that there is nothing to suggest an omosternum. The omosternum has not been recognised in any existing order of Reptiles, and the Sauropterygia is the only fossil type except the Nothosauria in which it has been supposed to be found. That suggestion appears to rest upon the fact that the omosternum is found anterior to the precoracoids in certain existing Amphibia. There is the circumstance that the bones in *Plesiosaurus* extend on the visceral surfaces of the scapulæ and coracoids, while the clavicles in *Ichthyosaurus* are on the anterior and ventral surfaces of the same bones; but no animal is known in which the omosternum is developed in the position of the bone which has been so named in *Plesiosaurus*, and, so far as position goes, there is no evidence known to me which suggests that the bones in question should be omosternal rather than clavicular.

The omosternum has never been shown to consist of a T- or V-

shaped median piece flanked by separate lateral ossifications as in *Plesiosaurus*, while this condition parallels the interclavicle and clavicles in all animals in which they are found.

It has never been shown that any one of the bones in question in *Plesiosaurus* retains a surface which has the aspect of having been cartilaginous. On the contrary, every specimen which I have examined is more or less thin and squamous, with contours completely ossified to sharp edges, even in the most immature specimens; while the interclavicle, when preserved, unites with the clavicles either by a thin squamous overlap or by sagittal sutures. This condition seems to me to demonstrate that the bones are membrane bones. I submit it follows that they are clavicles, and therefore that the visceral position of the clavicular arch, although anomalous, is not inconsistent with clavicular homology. Bone for bone, the three clavicles in *Plesiosaurus* seem to me to correspond to those of *Ichthyosaurus* and *Nothosaurus*. In the former their union is usually squamous, in the latter it is sutural. In Sauropterygia both conditions are found. The proposal made to identify the three anterior bones in the shoulder girdle in *Nothosaurus* as omosternum and precoracoids introduces the precoracoid as a distinct bone,* which is not known to be paralleled in any allied group of animals except the Anodomontia, in which there is no omosternum, and where the precoracoids are differently conditioned, being in the closest union with the coracoids, with a well-developed clavicular arch. But when the supposed precoracoids of *Nothosaurus* are recognised as clavicles, which rest by squamous overlap on the visceral surfaces of the scapulæ, like the clavicles of *Plesiosaurus*, the clavicular arch is in harmony with that of the Sauropterygia, and the supposed differences in its composition disappear.

There are two family types in the Sauropterygia defined by differences in the shoulder girdle and other characters, known as Plesiosauridæ and Elasmosauridæ, though the organic differences which characterise them have not been fully set forth.

II. Further Evidence of the Nature of the Clavicular Arch in the Plesiosauridæ.

§ 1. *Nature and Limits of the Family.*

There are four principal genera of Plesiosauridæ, which are named *Plesiosaurus*, *Eretmosaurus*, *Rhomaleosaurus*, and *Pliosaurus*. The family is characterised by the cervical ribs being attached to the vertebræ by more or less completely-defined double facets and by the scapulæ being separated in the median line by the clavicular arch, by

* Hulke, *loc. cit.*

which they are braced to the coracoids. In the British Museum Catalogue ('Fossil Rept. and Amph.,' Part II), the Plesiosauridæ is made to also include the Elasmosauridæ, and the genera are enumerated in the following order:—*Pliosaurus*, *Peloneustes*, *Thaumatosaurus*, *Polyptychodon*, *Cimoliosaurus*, *Eretmosaurus*, *Plesiosaurus*. I should restrict the family to the fossils indicated by the names *Pliosaurus*, *Peloneustes*, *Thaumatosaurus*, *Eretmosaurus*, and *Plesiosaurus*. Good skeletons of these genera are known with the exception of *Thaumatosaurus*, which was founded by von Meyer ('Palaeontographica,' vol. 6) upon remains which closely resemble those of *Pliosaurus*. And, after examining the type specimens, which are imperfect cervical vertebræ, dorsal vertebræ, teeth, and portions of the hinder region of the maxillary bone, I was unable to discover any character inconsistent with reference of the species to *Pliosaurus*. The head was evidently as large as in *Pliosaurus;* the teeth are circular in the crown, and show no trace of the area more or less flattened and free from carination defined by a lateral ridge on each side which characterises the anterior teeth of *Pliosaurus grandis*, resembling in this respect the posterior teeth. In the late cervical vertebra figured by von Meyer, the centrum has the same form and relative shortness from front to back as in *Pliosaurus;* the articular facet for the rib is similarly elevated, has a like transverse division forming a superior subtriangular part and an inferior transversely ovate part. The only characters in which there is not absolute agreement with the English species are that the articular faces of the centrums are more circular and more concave. These differences may be of specific value; and von Meyer's species may be classed as *Pliosaurus oolithicus*, till it is fully known. For similar reasons I am unable to separate *Peloneustes* from *Pliosaurus*. And if the type species was originally referred to *Plesiosaurus*,* it was because I then regarded the subtriangular crowns of anterior teeth in *Pliosaurus* as a generic character, and that character now seems less important. It has been necessary thus to explain differences of nomenclature, because the genus *Thaumatosaurus* ('Brit. Mus. Cat. Foss. Rept.,' Part II) has been made to include six species in addition to the type, which, with one exception, are all from the Lias. They were previously named *Rhomaleosaurus Cramptoni*, *Plesiosaurus arcuatus*, *P. megacephalus*, *P. carinatus*, *P. propinquus*, *P. indicus*. I am unable to place any of these species in *Pliosaurus* or *Thaumatosaurus*, nor is there evidence that all are referable to one genus; and it does not appear that a genus based on characters drawn from this assemblage of species can displace the definite conception of von Meyer indicated in the type of *Thaumatosaurus*. Most of these species not included in *Rhomaleosaurus* appear to belong to *Eretmosaurus*.

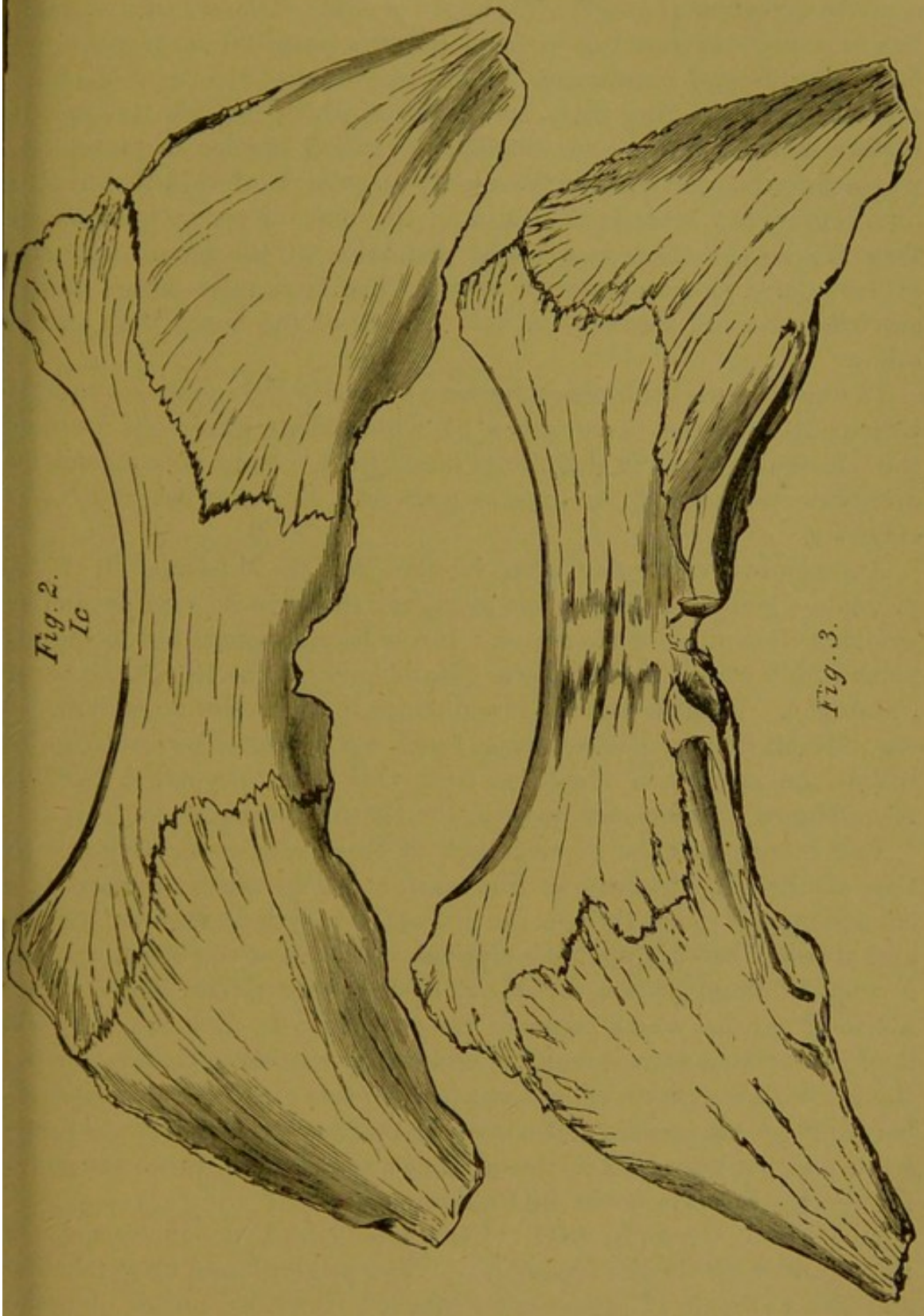
* 'Index to Aves, Ornith., and Rept. in Woodw. Mus.,' 1869, p. 139.

§ 2. *The Clavicular Arch.*

(i.) Since the clavicular arch was figured in *Pl. Hawkinsi* ('Geol. Soc. Quart. Journ.,' 1874, p. 444), v. Zittel has figured the clavicular bones in *Pl. laticeps* ('Handbuch der Paläontologie,' vol. 3, p. 489); but, while the clavicles are clearly shown, the interclavicle is named episternum. The most important evidence of this structure in Plesiosauridæ, however, is to be seen in *Plesiosaurus arcuatus* ('Brit. Assoc. Rep.,' 1839, p. 76; and 'Cat. Foss. Rept. and Amph.,' Part II, p. 163), preserved in the British Museum. From that specimen, No. 2028*, the character has been attributed to *Thaumatosaurus* (*loc. cit.*, p. 159): "Omosternum consisting of a large single plate, much expanded transversely, with a wide and shallow anterior notch."† The anterior margin of the interclavicle in this specimen resembles in contour that attributed to *Eretmosaurus* ('Geol. Soc. Quart. Journ.,' 1874, p. 445) in its wide open curvature; but there is no evidence to show whether the shoulder girdle, pelvis, and limbs in *Plesiosaurus arcuatus* were constructed on the same plan as in *Pl. rugosus*. There is no doubt that the bone consists of three distinct elements united by sutures. These are a median interclavicle and two lateral bones which I regard as clavicles. On the visceral aspect the triangular clavicles are separated from each other by the wide short posterior median bar of the interclavicle, but the clavicles extend forward so that only a narrow transverse bar of the T-shaped interclavicle is exposed in front of them, extending across the entire width of the bone. The interclavicle is $10\frac{1}{4}$ inches wide, concave on its anterior margin, $1\frac{1}{2}$ inch from front to back at the widened extremities of the cross-bar, and $\frac{8}{10}$ inch in the same measurement towards the oblong middle portion of the bone. The right anterior transverse limb of the cross-bar is 4 inches wide; the left limb is 3 inches wide. The middle portion of the bone is $3\frac{1}{4}$ inches wide and $2\frac{1}{2}$ inches in antero-posterior measurement. The sutural line which defines the interclavicle is sagittal, and consequently irregular. On each side of this T-shaped interclavicle (fig. 2), in contact with the posterior margin of its transverse bar and the lateral margin of its short wide median stem, is a large triangular clavicle which is directed backward and outward. In harmony with the dimensions of the transverse bar, the right clavicle is the wider. Anteriorly it is $4\frac{3}{4}$ inches wide; it is nearly 6 inches long. The external border, which is slightly convex, is continuous with the truncated lateral termination of the interclavicle in front of it. These external margins diverge outward as they extend backward, so that the transverse measurement over the posterior extremities of the clavicles is $14\frac{3}{4}$ inches. The postero-internal

† Compare Sollas, 'Geol. Soc. Quart. Journ.,' vol. 37, 1881, p. 457.

contours of the clavicle are irregularly concave, and as they extend inward are continuous with the posterior border of the interclavicle,



FIGS. 2 and 3.—Ventral and visceral aspects of clavicular arch of *Plesiosaurus arcuatus*, showing the median interclavicle and lateral clavicles. *Ic* is placed on the anterior margin.

and as they extend outward approximate toward the external contour of the bone without meeting it posteriorly in a point.

The ventral aspect of the clavicular arch is different (fig. 3) owing to variation in the positions of the sutures between the bones. The interclavicle no longer shows the T-shaped contour of the visceral surface, but is a wide curved bar with an irregular sagittal termination on its postero-lateral extremities. This is owing to the method of its squamous interlocking with the clavicles, which overlap its visceral surface more in front, and overlap its ventral surface more behind, where their pointed extremities nearly meet each other in the median line behind the interclavicle, and in the inch of space from which they are absent there is a slight distortion of the bone, and some evidence of a median posterior notch. The triangular forms of the clavicles are more marked on this aspect of the bones than on the other.

The most remarkable character here shown is the squamous sutural interlocking of the three bones by which their shares in forming the clavicular arch is definitely established. It is also shown by different directions of the lines of growth in the clavicles and interclavicles.

An isolated clavicular arch in the British Museum, R. 1322, presents a similar character and form, and shows in its sutures similar evidence of composite character. It has been assigned to the species named *Plesiosaurus megacephalus* (Stutchbury) in the British Museum Catalogue. It has a similar resemblance to the anterior contour of the interclavicle in *Eretmosaurus*, but I am aware of no evidence by which the species is identified from this bone, beyond a general resemblance to some specimens in the Bristol Museum.

The correspondence of structure in these clavicular arches with that figured in *Plesiosaurus Hawkinsi* and *Plesiosaurus laticeps* is a coincidence of plan, though the difference may indicate a sub-genus, and shows, I submit, that the original definition of the bones was not a conjectural suggestion, as stated by Professor Sollas, but a recognition of sutures which separate the interclavicle from the clavicles. And it seems to me a sound induction that whenever the margins of the clavicular arch are concave in front and behind, those concavities border the interclavicle, and whenever there are wings produced outward and backward, as in the specimen now figured, those wings are formed by the clavicles in all Plesiosauridæ.

(ii.) Sir R. Owen, in 1841 ('Brit. Assoc. Rep.,' p. 64), remarks on the shoulder girdle of *Pliosaurus*:—"The pectoral arch owes its chief strength to a pair of immensely expanded coracoids, having a broad and short entosternal bone on their anterior interspace, and supporting the clavicles or acromion productions of the scapulæ."* Subse-

* I have examined the specimens in the Museum of the University of Oxford

quently ('Geol. Soc. Quart. Journ.,' 1883, p. 135) a diagram of the shoulder girdle in this genus was given by that author, which represents the scapula and coracoid as meeting each other on the Elasmosaurian plan; but, unlike Elasmosaurians, the scapulæ are divided from each other on the visceral aspect by a long triangular interclavicle (named episternum) which shows a mesial notch in front. I have not seen this specimen, which is not assigned to any species, locality, or collection. It would appear to show an intermediate condition between Plesiosaurs and Elasmosaurs, but it is impossible for me at present to affirm this. No specimen is known to me which shows that in *Pliosaurus* the scapula and coracoid completely enclose the coracoid foramina. The evidence is imperfect, but it leads to the conclusion that the shoulder girdle was Plesiosaurian in plan.

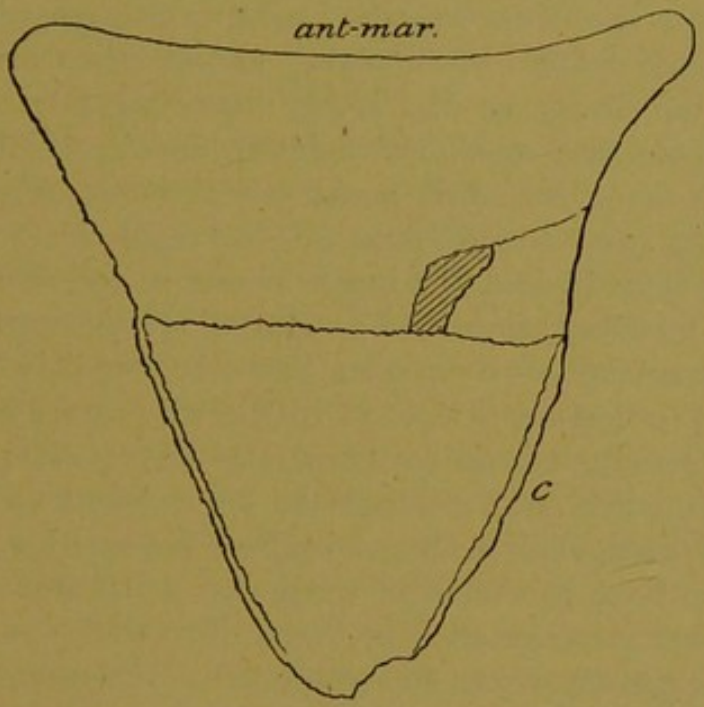


Fig. 4.—Interclavicle, *Pliosaurus philarchus*. *ant-mar*, anterior border; *c*, a lateral surface which may have been a clavicular attachment.

Pliosaurus philarchus, on which the genus *Peloneustes* has been founded ('Cat. Foss. Rept. and Amph.,' Part II), in form of the scapula closely resembles Pliosaurian remains in the British Museum. Their approximating margins are convex, and between those margins Mr. Lydekker has inserted the interclavicle (termed omosternum),

with Professor A. H. Green, F.R.S., without finding evidence of this entosternal part of the skeleton. What appear to be scapulæ of *Pliosaurus brachydeirus* have the inner and outer borders of the bones sub-parallel, with the anterior extremity but slightly widened. Zittel has interchanged the names to Owen's figures of the shoulder girdles of *Pliosaurus* and *Plesiosaurus*. I have not seen the originals of those figures.

which is triangular, flat, very thin, and has perfectly straight sides, which, in their hinder approximating two-thirds, are slighly bevelled. There is no evidence given that the bone occupied the position which has been figured, and I see no reason for believing that it was not placed, as in other Sauropterygians, on the visceral surface of the slightly inclined scapulæ, where there is a doubtful indication of what may be an imperfectly preserved right clavicle. If the straight lateral border of the interclavicle was in contact with the flat visceral surface of the scapula, the bones would be in harmonious relation. The bevelled margin appears to look inward, and is therefore inferred to have given attachment to a lateral ossification which was still more delicately thin. This condition is shown in the following figure of the bone.

(iii.) A third modification of the Plesiosaurian type may be* indicated by the specimen in the Leeds Collection in the British Museum numbered 36. It is small, and the bones are not sharply ossified and immature, as Mr. Leeds has always believed. But I have not observed any specimen in his collection which would, with certainty, represent its adult state. The bones of the shoulder girdle are thick, and the scapula and coracoid are formed on the Plesiosaurian type, in that the inner border of the scapula gives no evidence of a median precoracoid prolongation backward to meet the coracoid. There is no indication that the coracoids and scapulæ ever met in the median line, even in the supposed adult condition, since there is no anterior median process to the coracoid; but there is a cartilaginous interval between them in front like that attributed to *Pliosaurus*. The scapula is a stout triradiate bone with a wide external process, and in form it resembles the bones attributed to *Pliosaurus*. But the cervical vertebræ have no trace of the Pliosaurian modification, and have the aspect of the vertebræ of *Plesiosaurus*, except that the articulation for the rib is not divided in the cervical region. Some Plesiosaurs from the Lias have shown the closest possible approximation of those surfaces, but the divided condition of the rib facet did not terminate with the Lias species, since some specimens from the Wealden (which are referred to *Cimoliosaurus*, 'Brit. Mus. Cat. Foss. Rept.,' Part II, p. 227, No. 2,444, No. 26,000) retain the character in a condition similar to that attributed to *Thaumatosaurus carinatus* (*loc. cit.*, p. 168, fig. 57). It may be that the imperfect ossification causes the facet of bone to appear single in this Oxford Clay fossil, while its cartilaginous terminations during life may have been divided; but so far as the evidence goes it rather suggests a sub-generic modification of the genus *Plesiosaurus* as indicated by the scapular arch, distinguished by undivided articular heads to the cervical ribs, if the adult preserved

* I am not sure that this immature Plesiosaurian type did not, on attaining maturity, become the Elasmosaurian genus *Cryptoclidus*.

the characters of the young animal. This inference is supported by the evidence of the clavicular arch, and by the large size of the radius and tibia as compared with the small size of the ulna and fibula. These bones are not in natural association, being free from matrix; but I see no reason to doubt that Mr. Leeds has arranged them in positions which are correct. The characters of the skeleton lead to the conclusion that the species is new, and could not become transformed by growth and perfected ossification into any other known species.

The following are measurements which help to define the species:— Lower jaw, 9 inches. Vertebral column, as preserved and arranged, 64 inches. Thirty cervical vertebræ, 23 inches; two pectoral vertebræ supporting ribs on the neural arch and centrum, $1\frac{3}{4}$ inch. Twenty-two dorsal vertebræ measure 22 inches; three vertebræ in the sacral region, which support ribs, partly on the neural arch and partly on the centrum, $2\frac{3}{4}$ inches. Twenty-two caudal vertebræ measure 15 inches, but the extremity of the tail is not preserved. The height of the dorsal vetebræ and neural arch is about $2\frac{3}{4}$ inches. The transverse measurement over the transverse processes of the dorsal vertebræ is $4\frac{1}{4}$ inches. The longest dorsal ribs measure about 9 inches. The ilium is 4 inches long. The transverse width over the pelvic articulation is $7\frac{1}{2}$ inches. The antero-posterior extent of the pelvis is 9 inches. The pubis measures $4\frac{1}{2}$ inches from front to back. The ischium is $3\frac{1}{2}$ inches in the same measurement toward the median line. The pelvic foramina were separated from each other by cartilage. The femur is 8 inches long and 4 inches wide. The coracoid is 7 inches long by $4\frac{1}{4}$ inches wide; the scapula is $4\frac{1}{4}$ inches in length and width. These shoulder girdle bones are exceptionally thick. The transverse width over the two clavicles is $7\frac{1}{4}$ inches.

The clavicles are thin triangular bones, perfectly ossified, with sharp well-defined margins and no signs of immaturity, probably because they are membrane bones. If they met each other in the

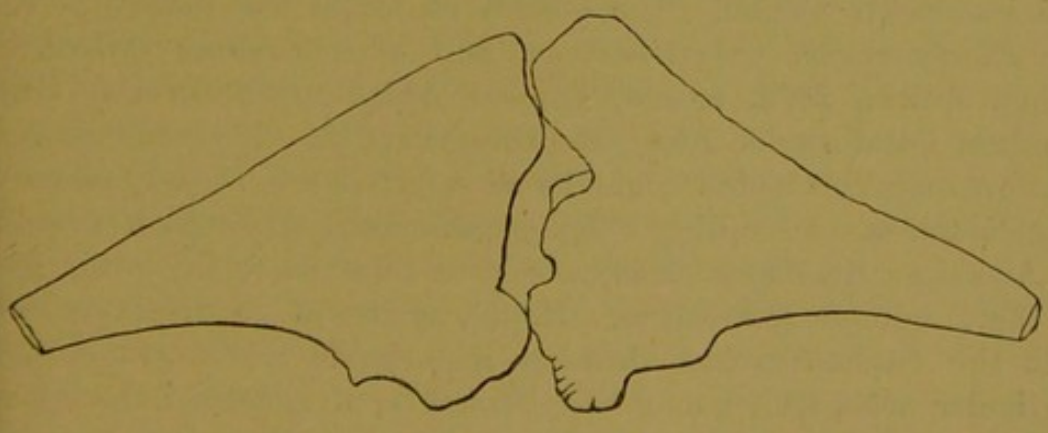


Fig. 5.—Clavicles of a young individual *Plesiosaurus durobrivensis*.

median line it can only have been by squamous approximation. Thus arranged they would be inclined to each other. As preserved, each clavicle is about 4 inches wide; and on its inner border measures $2\frac{3}{4}$ inches from front to back, and at the external angle the corresponding measurement is $\frac{3}{8}$ of an inch. The anterior border is straight; the inner border is sinuous and unsymmetrical on the opposite sides; the posterior border is $3\frac{1}{2}$ inches long and concave, with the concavity broken on the inner third by a sharp prominence which separates a slight inner concavity from the longer external concavity.

The external extremities of the bones are truncated and striated.

The only specimen which distantly approximates to this in the large size of the radius as compared with the small ulua is an Elasmosaurian indicated in the Leeds Collection by the number 31. In that also there is no trace of an interclavicle, but the shoulder girdle is not perfectly preserved, and its clavicles are of dissimilar form. If the scapulæ in mature individuals of this species united in the median line and extended back to the coracoids, then the fossil would be Elasmosaurian, and possibly a species of *Cryptoclidus*.

III. The Clavicular Arch in the Elasmosauridæ.

§ 1. *The Nature and Limits of the Family.*

When the Elasmosauridæ was defined in 1874 its clavicular arch was unknown and supposed to be wanting, and the family was based upon the circumstance that the bones named scapulæ met each other in the median line, and were prolonged backward to unite with the median processes of the coracoids in *Elasmosaurus* and *Colymbosaurus*. I owe a knowledge of the clavicular arch in this family to A. N. Leeds, Esq., of Eyebury, who for twenty years has collected the fossil Vertebrata from the Oxford Clay near Peterborough. In this family the cervical vertebræ have the ribs attached by undivided articular heads. The carpal and tarsal bones are polygonal and well ossified. The genera on which the family is based are *Elasmosaurus*, *Colymbosaurus*, and *Muræosaurus* ('Geol. Soc. Quart. Journ.,' 1874, p. 436), none of which appear in the 'British Museum Catalogue of Fossil Reptiles,' Part II. The only genera in that enumeration which could be so referred are *Polyptychodon* and *Cimoliosaurus*. Excepting *Polyptychodon* only, all English as well as all American Elasmosaurians have been referred to the latter genus in the Catalogue referred to. Hence, as it will be presently shown that the Elasmosauridæ develop remarkable modifications of the clavicular arch, which may be regarded as of generic importance, it is convenient to determine as far as possible the synonymy of the genera comprised in the family.

The genus *Cimoliosaurus* figured by the late Dr. Leidy in 1865 ('Smithsonian Contributions to Knowledge') rests upon thirteen centrums of vertebræ without arches or processes, noticeable chiefly for their transverse width. Fourteen other vertebræ from the Greensand of New Jersey are described; but there is no evidence of any other part of the skeleton. Leidy expressed doubt whether his genus *Discosaurus* might not prove to be founded on vertebræ of *Cimoliosaurus*. This view was adopted by Professor Cope ('Amer. Phil. Soc. Trans.,' vol. 14), but that identification only contributed a knowledge of the carpal and metacarpal bones. Hence the characters by which the genus is defined in the 'British Museum Catalogue' are not drawn from Leidy's type.

The generic characters of *Cimoliosaurus* which may be obtained from Leidy's figures are: Articular face of the centrum flat or flattened, short from front to back, transversely extended in the cervical region. The neural arch is small, with compressed lamellar neurapophyses, which appear to be anchylosed to the centrum. The facet for the cervical rib is single, at first compressed from above downward, afterwards becoming ovate; the facets are on short pedicles. The chevron articulations impress both the anterior and posterior margins of the short centrums in the middle of the caudal series. The carpals are transversely oblong. The metacarpals and phalanges are compressed from above downward.

The name *Brimosaurus* (Leidy, 'Philadelphia Acad. Nat. Sci. Proc.,' 1854, Pl. 2, p. 72), was proposed for Plesiosaurian vertebræ which have the ventral surface flat instead of concave, as in *Cimoliosaurus;* but, as the genus is not mentioned in that author's 'Cretaceous Reptiles of the United States,' 1865, it may be regarded as probably abandoned and included in *Cimoliosaurus*.

Dr. Leidy also proposed a genus *Oligosimus* ('Philad. Acad. Nat. Sci. Proc.,' 1872, p. 39). It is unfigured and based upon an early caudal vertebra. It has the neural arch anchylosed to the centrum. A groove defines the limit of the articular face of the centrum. The chevron facets only impress the posterior border of the centrum. Its measurements are: length, 1 inch; width, 2·3 inches; depth, 1·9 inch. These characters seem insufficient at present to distinguish the type as a genus.

Professor E. D. Cope has decribed five other genera which he regards as distinct from *Cimoliosaurus;* they are named *Elasmosaurus*, *Polycotylus*, *Orophosaurus*, *Uronautes*, and *Piptomerus*.

Polycotylus from Cretaceous Limestone, near Fort Wallace, Kansas ('Amer. Phil. Soc. Trans.,' vol. 14, Part 1, p. 35, Pl. 1, 1870), s founded upon dorsal and caudal vertebræ. It is characterised by the very short dorsal vertebral centra, which are deeply biconcave. The tibia is broader than long. The neural arch is anchylosed to the

centrum, as are the caudal ribs. To these characters may be added from Professor Cope's figures; neural arch depressed, with massive neurapophyses, and small neural canal. These characters help to define the genus from *Uronautes*. Phalanges remarkably short. The author subsequently states ('Amer. Naturalist,' 1887, p. 564) that in *Polycotylus* the neurapophyses and all diapophyses and parapophyses are co-ossified with the centra.

In *Piptomerus* ('Amer. Naturalist,' 1887) the neurapophyses and all other processes of the vertebræ articulate freely with the centra. The cervical vertebræ are short, twice as wide as long, and deeper than long. The dorsal vertebræ are two-thirds as long as the cervicals, deeper, and rather narrower.

In *Orophosaurus* the neural arches are co-ossified, and the parapophyses free. The centrum is a little wider than deep.

In *Uronautes* both neural arches and parapophyses are co-ossified. All vertebræ are short, nearly twice as wide as long, as deep as wide, centrum biconcave, neurapophyses lamellar, neural canal large.

In the American specimens referred to *Plesiosaurus* Professor Cope states that the neural arches of the vertebræ are loosely articulated.

Until the American types are fully figured it will not be possible to judge whether these genera are all founded on characters which will enable them to be recognised in adult individuals.

In *Elasmosaurus* the characters given for the genus are: Neural arch anchylosed with the centrum; cervical centrum longer than deep, deeper than wide; ribs articulated to oval pits. Vertebræ numerous. The dorsal vertebræ have strong transverse processes. In the caudal vertebræ the articular chevron facets are said to be on the inferior face, near its posterior articular aspect. This condition is not unknown in early caudal vertebræ in English Sauropterygians from the Pelolithic strata, but no evidence has been given that it extends throughout the caudal series in any Sauropterygian species. The scapular arch has the well-known form, with the scapulæ meeting in the median line, and continuous posteriorly with the coracoids, so as to enclose two large foramina between the bones. The scapulo-precoracoid appears to form about two-thirds of the wall of the glenoid cavity. No clavicle was found. The ilium appears to articulate with the pubis only. No limb bone was found, nor any abdominal ribs.

Professor Cope states that this genus is distinguished from *Cimoliosaurus* by the shortness of the neck in the latter, and its elongation in *Elasmosaurus*. In *Elasmosaurus* the cervical centrum is transversely compressed, and comparatively long; while in *Cimoliosaurus* it is short, broad, and vertically depressed.

Finally, Mr. F. W. Cragin has described *Trinacromerum* ('Amer. Geol.,' vol. 2, p. 405, 1888, and vol. 7, September, 1891, p. 171) from the Cretaceous rocks of Kansas, but no figures of it have yet been

given. In it the ilium articulates with the ischium only, as in some species of *Muræenosaurus* from the English Oxford Clay (Leeds Collection, Brit. Mus.). The shoulder girdle is on the Elasmosaurian plan, enclosing two vacuities, but the structure of the glenoid cavity is distinctive. There are three bones in linear succession at the distal end of the humerus and femur. The tibia and fibula are transversely extended, and of oblong form, apparently resembling *Colymbosaurus*. The phalanges are unusually numerous. The neural arch is anchylosed to the centrum. The neural canal is large. The cervical vertebræ are sub-quadrate, depressed, and transversely wide. The dorsal centrum is sub-circular. The articular faces are shallow concavities.

The characters assigned to *Polycotylus*, *Cimoliosaurus*, *Elasmosaurus*, and *Trinacromerum* are such as enable the types to be recognised; and, therefore, pending fuller information, it is convenient to adopt them as genera limited, so far as is at present known, to the Cretaceous period. It is probable that all belong to the Elasmosauridæ, but *Elasmosaurus* and *Trinacromerum* are the only types in which the shoulder girdle is known. The oblong form of the tibia in *Trinacromerum* and *Polycotylus*, and the transverse elongation of a carpal in *Cimoliosaurus*, make it probable that the middle segments of the limbs had the bones transversely elongated in all these genera. In none of them have clavicles as yet been recognised.

Polyptychodon is probably to be included with these genera; but it is only known from teeth, cranial fragments, and vertebral centra, which do not differentiate the genus; though the cervical vertebræ ('Quart. Journ. Geol. Soc.,' vol. 32, p. 433) are relatively short and deep.

The Elasmosauridæ are well represented in the Cretaceous rocks of this country. Two genera, *Muræenosaurus* and *Colymbosaurus*, have also been regarded as peculiar to the Oxford and Kimeridge Clays. These genera are best defined by the bones of the extremities. In both the bones of the shoulder girdle are essentially the same.

In *Muræenosaurus* the cervical region is long. The zygapophysial facets have a cylindroid curve. The articular faces of the centra are rather wider than deep, though nearly circular and biconcave. The ulna and radius are sub-quadrate. There is no third bone in the fore-arm. The phalanges are stout and but little compressed. The shoulder-girdle is on the Elasmosaurian type, with clavicles. The type species is *M. Leedsii*.*

In *Colymbosaurus* the neck is equally long. The neural arch and ribs are anchylosed to the centrum. The neurapophyses are lamellar and compressed from side to side. The centrum is biconcave, but the concavity decreases posteriorly. The articular surface is transversely,

* 'Geol. Soc. Quart. Journ.,' 1874, p. 197.

ovate at first, but afterwards deeper. The centrum is always wider than long, and has an oblique margin, which is absent in *Cimoliosaurus*. The humerus and femur are deeper than wide proximally. In the fore-arm there are three bones in a row, of which ulna and radius, like the tibia and fibula, are broader than long. There may sometimes be a fourth bone in this row (*C. Manselli*, Hulke sp.). The phalanges are not compressed. The types are from the Kimeridge Clay, and include *P. megadeirus* and *P. Manselli*.

These genera are distinguished by the extremities, though the vertebral articulation of the zygapophyses and many parts of the skeleton furnish differential characters.

Both genera are defined from *Polycotylus* and *Piptomerus* by the length of the dorsal centrum. The bevelled or rounded margin to the articular face of the centrum separates them from *Cimoliosaurus*. The absence of side-to-side compression of the centrum distinguishes them from *Elasmosaurus*. And they are separated from *Trinacromerum* by the structure of the glenoid cavity for the humerus, and the small number of uncompressed phalanges in the digits. Hence, without disregard of generic characters, and the facts of stratigraphical distribution, it seems impossible to follow the British Museum Catalogue, which enlarges the genus *Cimoliosaurus* to make it comprise all these Elasmosauridæ. And it will presently become evident that in *Muræno-saurus* the diversity of modification found in the clavicular arch is such as may define sub-genera within its present limits.

Notwithstanding the diverse aspects of the shoulder girdle in the Elasmosauridæ and Plesiosauridæ, and the circumstance that intermediate types are at present unknown, the difference between them is essentially in the fact that in all Elasmosaurians the supposed precoracoid region is ossified so as to come into median union with the coracoid by suture, and co-ossified with the scapula so as apparently to be an inseparable part of that bone; and it is these precoracoid portions of the scapulæ which alone meet each other in the median line, as do the precoracoid bones in *Procolophon* ('Phil. Trans.,' 1889, B, Pl. 9, fig. 9). In all Plesiosaurians, on the other hand, the precoracoid, if developed, remains cartilaginous; but I infer that a cartilage always extended from the anterior margin of the coracoid to the anterior extremity of the scapula, and by ossification of such cartilage the Plesiosaurian shoulder girdle would become Elasmosaurian.

§ 2. *The Clavicular Arch in the Elasmosaurians discovered by Mr. A. N. Leeds in the Oxford Clay.*

The clavicular bones may be placed anterior to the scapulo-precoracoids, partly under them on their visceral surface, but they never extend back to meet the coracoid bones, as in *Plesiosaurus*. Or they

may be wedged in the fork between the anterior termination of the scapulo-precoracoid elements. Or they may be entirely hidden from view, and lie upon the visceral aspect of the scapulo-precoracoid bones. These specimens are all in the Leeds Collection in the British Museum, or in that of Mr. A. N. Leeds at Eyebury.

They appear to me to show three types of structure:—

First, a clavicular arch formed of a large interclavicle with two clavicles forming its lateral wings, joined by squamous overlap, and not by suture.

Secondly, species in which the interclavicle is a V-shaped triangle, and clavicles are doubtfully present.

Thirdly, species in which two clavicles meet by median suture, without any indication of an interclavicle.

These modifications are such as might be expected to characterise genera rather than species, and they are accompanied by diversities in other parts of the skeleton.

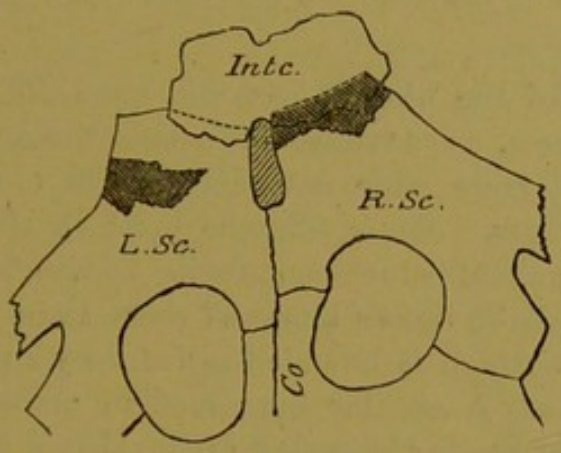


FIG. 6.—Part of the shoulder girdle and clavicular arch of *Muræosaurus platyclis* from a drawing by Mr. A. N. Leeds, showing the position of the clavicular arch when found. *Co*, coracoid; *Sc*, scapula; *Intc.*, interclavicle and clavicles. The dark parts are missing. The light shading is a foramen.

(i.) In the first type the clavicular arch is formed substantially on the same plan as in the Lias genus *Plesiosaurus*, except that the clavicles rest upon the interclavicle by squamous overlap on its visceral surface, and their posterior-lateral prolongation is broken away. Yet when this surface is compared with that of *Plesiosaurus arcuatus* an almost identical T-shaped configuration of the interclavicle is exposed, while on the slightly convex ventral surface the clavicles are not seen at all in the specimen as preserved.

In the skeleton to which this specimen belongs the shoulder girdle is perfectly ossified. The transverse measurement over the humeral articulations is about 16 inches. The median processes of the coracoids are prolonged far forward, so as to make more than half

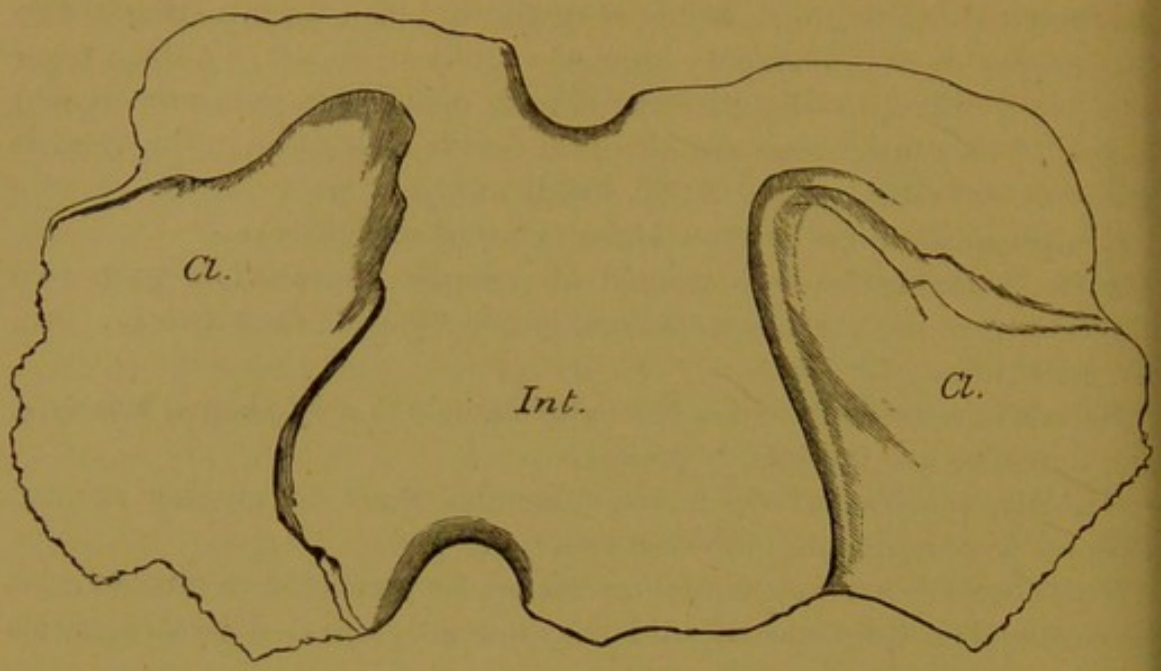


FIG. 7.—Clavicular arch of *Muræosaurus platyclis*, showing *Cl*, the clavicles, resting upon *Int.*, the interclavicle.

the inner borders of the scapulo-coracoid vacuities. They terminate in transverse sutures, in advance of which the scapulæ extend for 8 inches, forming large wide flat plates, with oblique slightly concave anterior borders. These scapulæ meet in the usual way by a median suture for about 4 inches, anterior to which is a long median vacuity or foramen, $3\frac{1}{2}$ inches long and more than 1 inch wide, with sub-parallel sides, which is bounded in front by a posterior concavity in the interclavicle. A similar long median notch is seen between the scapulæ in the Leeds Collection (Brit. Mus.), No. 27, and in that specimen there is a similar, though smaller, interclavicle, more imperfectly preserved.

The anterior transverse bar of the interclavicle now described is defined by the clavicles which rest upon the bone. It is 7 inches wide. Owing to the contour of the clavicles, its lateral halves increase in depth to about an inch as they extend outward. The concave median notch in the anterior border is less than an inch wide. It corresponds in form and size with the notch on the posterior border of the bone, but is rather shallower. Between these opposite concavities which indent the interclavicle the antero-posterior measurement is $2\frac{3}{4}$ inches. This median part of the bone, which forms the wide longitudinal bar between the clavicles, is $2\frac{1}{2}$ inches in transverse measurement anteriorly, but widens posteriorly to 4 inches. Owing to the way in which the lateral margins are concavely defined by the overlapping clavicles, all the contours are somewhat unsymmetrical from distortion.

The right and left bones are unequal in length as preserved: one

measures 3 inches from front to back, and the other an inch more. Their internal borders are concave and sinuous, recalling the clavicles of *Plesiosaurus durobrivensis* already described. It is probable that the external processes of the clavicles now broken away were directed outward and backward, and in form similar to that species.

(ii.) A second Elasmosaurian clavicle, of different shape apparently, is preserved in the skeleton No. 23, in which 77 vertebræ were found. It has the vertebræ nearly flat at the articular ends, with the transverse measurement and depth of the centrum similar. Neither the neural arches nor cervical ribs are anchylosed, but both have relatively deep attachments.

In this species only one clavicle is preserved, but its form is perfect. One half of the other clavicle was found, but no trace of an interclavicle, though I suppose both of these bones to have rested upon the interclavicle, much as in the species just described. The bone is triradiate, 4 inches long and as wide. Its inner margin is the shortest, and is concave and slightly irregular. The superior and

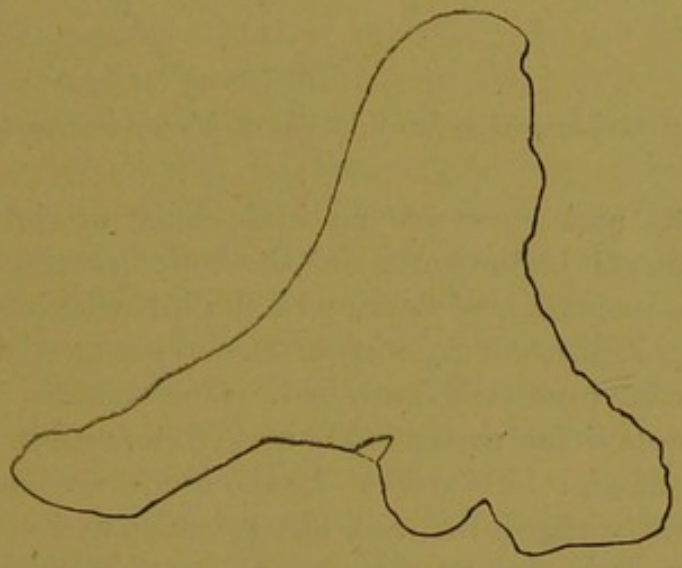


Fig. 8.—Clavicle of *Murænosaurus* (sp.).

inferior processes are about twice as wide as the external process, which is relatively long and slender. The anterior margin is concave. What I suppose to be the posterior margin is also concave, but a rounded prominence occurs on its inner third, and breaks the contour into a long external curve and a small inner notch.

The external termination is slightly widened and obliquely truncated, as though for attachment.

(iii.) A third form of clavicular arch, which appears to be probably of the same type, is represented by the imperfectly preserved interclavicle in the skeleton No. 26 in the Leeds Collection (Brit. Mus.). The scapulæ in this specimen are badly preserved, but they

have the external ascending process elongated rather more than in other specimens.

The interclavicle appears to have been sub-reniform, but its margin is imperfect all round. Its thin condition is more like that of a clavicle. It is $4\frac{1}{2}$ inches wide, and $3\frac{1}{2}$ inches deep. It shows radiating

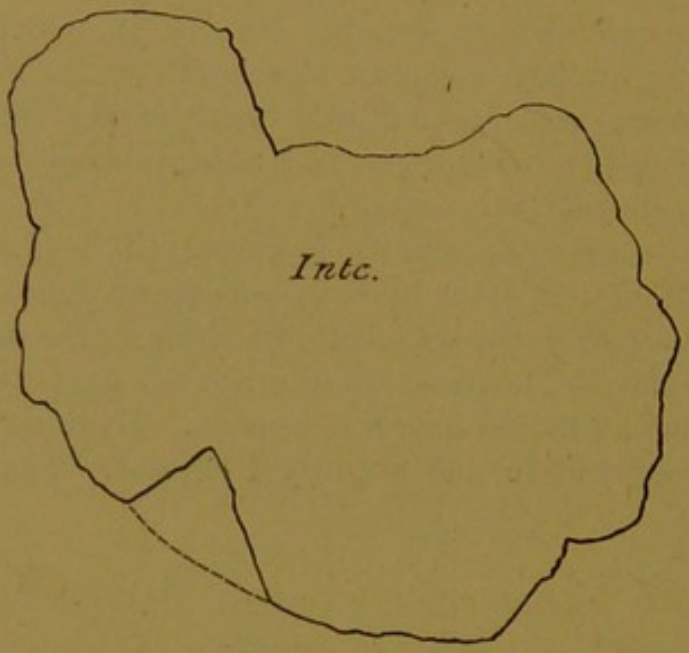


Fig. 9.—Imperfect interclavicle of *Murænosaurus* (sp.).

lines of growth, and there are no indications of contact with other elements of the clavicular arch. If the bone is correctly determined, it shows an interesting modification of the interclavicle.

Oxford Clay Elasmosaurians show two types of variation from the kind of clavicular arch now described. One consists in the approximation of the clavicles, so that they articulate, and in this type there is no evidence of an interclavicle. In the other modification the interclavicle persists, wedged between the scapulæ, and the clavicles are probably not represented, or present as delicate films which have not been perfectly preserved.

(iv.) The type in which the clavicular arch reaches the smallest dimensions known to me is in the private collection of Mr. A. N. Leeds. Its remains comprise the shoulder girdle, bones of the fore limb, and some cervical vertebræ. A vertebra which is from the middle of the neck, and believed by Mr. Leeds to be about the 15th, has the centrum transversely ovate, $1\frac{3}{4}$ inch wide, $1\frac{1}{8}$ inch deep, and $1\frac{1}{4}$ inch long. The articular face is slightly concave, and margined by a narrow border. The ribs and neural arch are anchylosed to the centrum. The neural spine is compressed and somewhat elongated, rising $4\frac{1}{2}$ inches above the base of the centrum.

The shoulder girdle is perfectly preserved. The least transverse measurement over the articular surfaces for the humerus is under

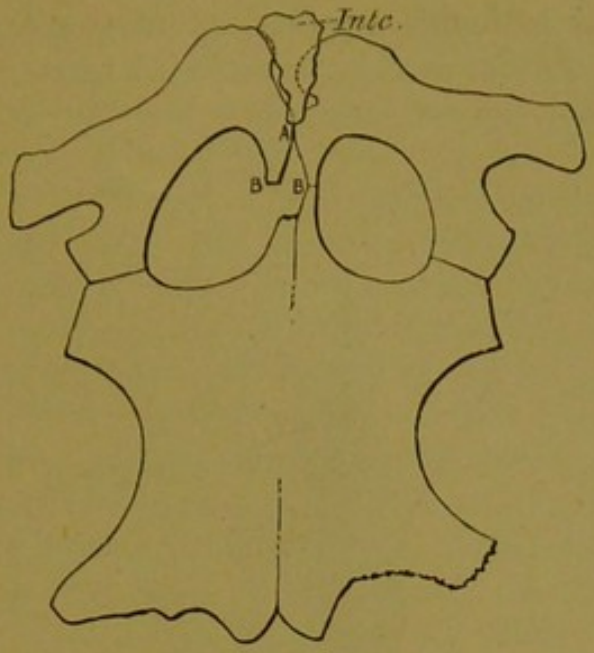


FIG. 10.—Shoulder girdle and interclavicle of *Muræosaurus beloclis*. *Intc.*, Interclavicle. Scapulæ slightly distorted at their union with anterior processes of the coracoids.

10 inches. The antero-posterior measurement of the coracoids is 11 inches in the median line, and that of the scapulæ in the median line is $3\frac{3}{4}$ inches. The scapulæ are exceptionally slender, since the least width from the concave lateral border to the foramen is $1\frac{1}{2}$ inch. The least transverse width of the coracoids in the middle of their concave sides is $6\frac{1}{2}$ inches. The transverse measurement of the scapulæ behind the ascending process is $9\frac{1}{4}$ inches. The ossification between the anterior median margins of the scapulæ is not complete, and as they extend outward they are convexly rounded.

The interclavicle was found *in situ*, resting on the visceral surface in a depression between the anterior margins of the scapulæ and not projecting in advance of those bones. It is lanceolate in contour, $2\frac{3}{4}$ inches long, $1\frac{3}{4}$ inches wide towards the slightly concave anterior margin, and half as wide at the rounded posterior extremity. It is a little distorted, like the other bones of the shoulder girdle, has a flat visceral surface, and an angular ventral surface, due to the bone being traversed by an elevated median ridge, which dies away anteriorly, and from this ridge the lateral surfaces are inclined. On the left side of the ventral surface its middle part is covered by a thin film of bone, which I suppose may be part of the clavicle. It corresponds in texture and thickness with a detached film of bone which rests upon the right scapula. That ossification is triangular, about $1\frac{1}{4}$ inch in each measurement, and has nearly straight sides. It is quite separate from the interclavicle, and lies towards the external border of the scapula; there is no surface for its articulation, for all the margins of the interclavicle are sharp, thin, and perfectly ossified, like its

median crest. It is therefore probable that the clavicles were either loosely articulated to its margin, or extended between the interclavicle and scapula.

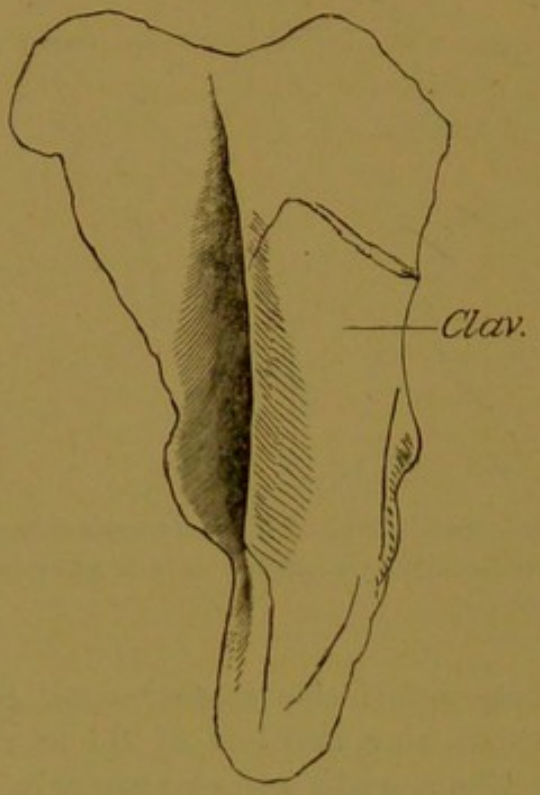


Fig. 11.—Ventral aspect of interclavicle, *Muræosaurus beloclis*; *Clav.* may be a portion of the thin left clavicle upon its ventral surface.

There is no other example of an interclavicle received between the scapulo-precoracoids as in this species, for the anterior notch between these bones in advance of their sutural surfaces is not unlike the notch already described under the heading (i), except that it is less well defined and more irregular and narrower, and it is into this notch that the base of the interclavicle is articulated. In its posterior part the surrounding bone is thick, forming a concave channel on each side, which is limited in front on the visceral surface by a tubercle, anterior to which is a small transverse notch on each side in the scapular bone, which becomes thin as it extends forward, thus making the clavicular cavity +-shaped. There is every appearance of cartilage having extended between the opposite scapular margins, so that the interclavicle may have been hidden upon the ventral surface, and the anterior part of that bone may not have been in actual contact with the thin scapular plate in front of it. The position of the interclavicle appears to show that it ossified prior to the bones between which it is placed.

In this series of Elasmosaurians there is seen a remarkable change in the condition of the clavicular arch. In the first species described it is large and much broader than long, and placed behind the

scapular bones. But in this species it has become small, is much longer than wide, and placed between the scapulæ in a way which shows that it might by further decrease entirely disappear, or when ossification obliterates the median suture it may become embedded between the lateral ossifications of the precoracoid region, and cease to be recognisable. But the clavicles might still persist on the visceral surface of the scapulæ if such a change took place.

I refer all these types in which clavicles and interclavicle are developed, and connected in the way described, to the genus *Muræno-saurus*, of which the type has been already described.* In all these species the ulna and radius, and tibia and fibula, are approximately equal and sub-quadrate bones, usually with the radius and tibia slightly the larger, meeting each other in both limbs, and enclosing a foramen between what were in *Plesiosaurus* the long concave sides of the bones. In the species last described there is an interesting tendency, though a slight one, to vertical elongation of the radius and transverse elongation of the ulna, both bones being about 2 inches wide, while the radius is $2\frac{1}{4}$ inches long and the ulna $1\frac{7}{8}$ inch long. The humerus in this type is 7 inches long and 4 inches wide, with well-ossified facets for the radius and ulna, which are mutually inclined, and meet at a sharp angle.

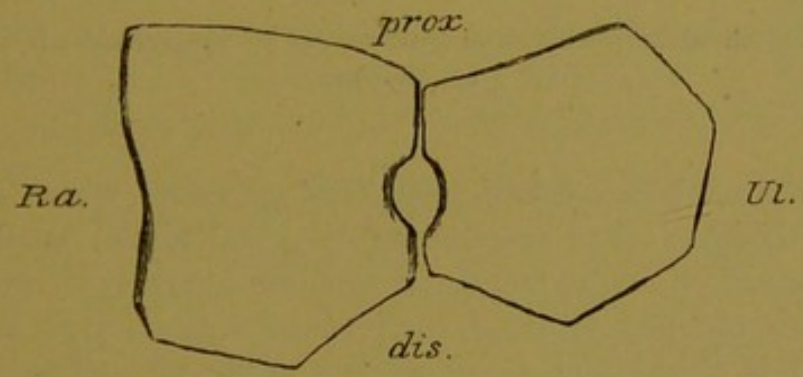


Fig. 12.—Radius and ulna of the same specimen. *Ra.*, radius; *Ul.*, ulna; *prox.*, proximal margin; *dis.*, distal border.

(v.) The specimen in the Leeds Collection (Brit. Mus.) numbered 31 has been referred to *Cimoliosaurus eumerus* (Phillips species), ('Cat. Foss. Rept. and Amph., Brit. Mus.,' Part II, p. 205); but the different forms and proportions of all the limb bones justify its separation, and as a sub-genus of *Muræosaurus* it is named *Cryptoclidus platymerus*. As compared with *Muræosaurus Leedsii* (No. 25, Leeds Coll., Brit. Mus.), it has the centrum broader, shorter, and more

* 'Geol. Soc. Quart. Journ.,' 1874, p. 197. At that time the shoulder girdle was only known from fragments; and the account now given of the scapulæ corrects the conjectural restoration which was based on that imperfect evidence.

concave. The cervical and caudal ribs and neural arch are anchylosed to the centrum. The cervical neural spine is short. The zygapophyses are rather less cylindroid. The scapulæ are unfortunately imperfect; enough is preserved to show that they were wide anterior to the scapulo-coracoid foramina, but not enough to show how they terminated in front. The coracoids are large, and have the postero-lateral prolongation of the bone well developed, as in *Colymbosaurus*.

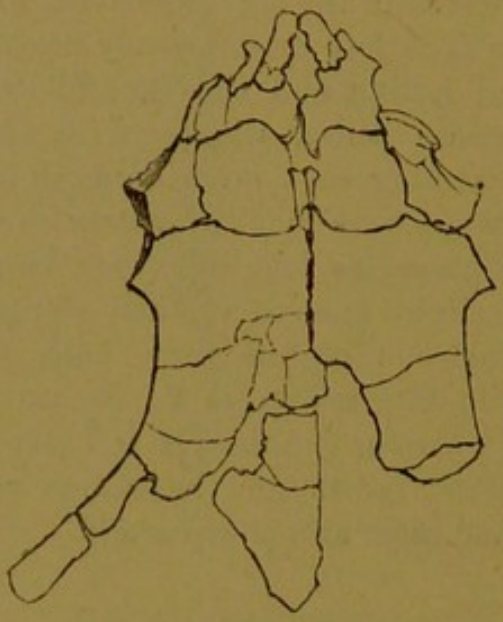


Fig. 13.—Shoulder girdle of *Muræosaurus* (*Cryptoclidus*) *platymerus*.
c, clavicles.

There are two bones found with this specimen which I regard as clavicles. Unlike other specimens,* they unite with each other by an ovate suture, which is from half to three-quarters of an inch long, and they are inclined to meet each other anteriorly at an angle of 45°, which is about the same as the angle of inclination of the scapulæ. The left clavicle is an oblong plate $4\frac{1}{4}$ inches long as preserved, but imperfect on both the posterior and internal margins. The right fragment is $3\frac{1}{4}$ inches long. The anterior end is truncated, and hardly extends beyond the articulation, where the transverse measurement of the bone is $1\frac{1}{2}$ inch. Just behind the articulation, the inner border has a concavity more than half an inch long, notching out the border in both specimens; but behind the notch the bone is broken away. Its smooth external border is slightly concave in length, and is prolonged diagonally outward and backward. The width of the left plate at the posterior fracture is about 2 inches.

* Mr. Leeds informs me that he has since obtained another type in which the two triangular clavicles meet in the median line, without trace of an interclavicle.

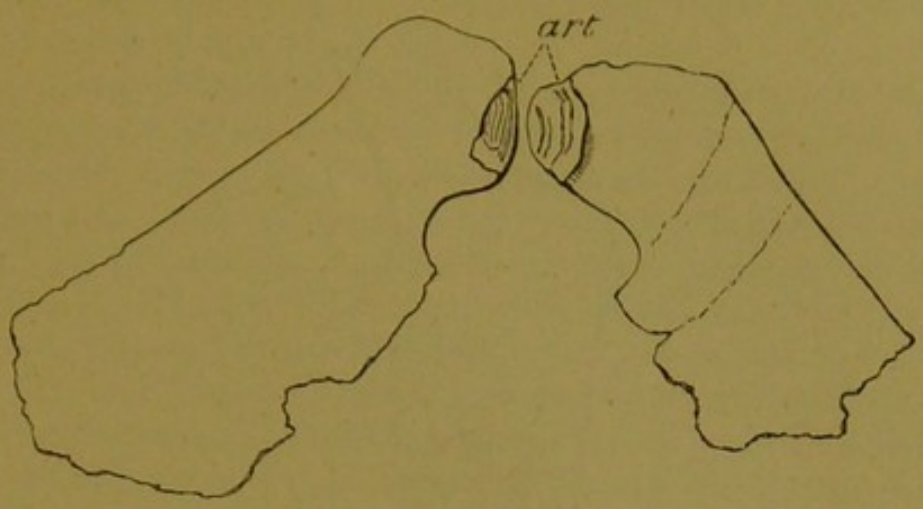


FIG. 14.—Clavicles of *Cryptoclidus platymerus*. *art*, median articular surface.

On the visceral surfaces of the scapulæ are shallow depressions terminating outward in a sharp angle such as might have received the external processes of clavicles like those found with the Leeds Collection specimen No. 36. These impressions are symmetrical and seen in both scapulæ, and so far they support the interpretation of this clavicular arch now offered. No evidence of an interclavicle was met with, and there is no evidence of its existence.

If the clavicles are correctly identified, their mode of occurrence may account for the circumstance that they have not been observed in *Colymbosaurus*. And their sutural union as in a Chelonian may be regarded as a generic character, separating this type from *Muræosaurus*.

An important generic character is found in great vertical depth of the radius and transverse elongation of the ulna. It has been stated that the ulna in another specimen consists of two separate bones* ('Cat. Foss. Rep. Brit. Mus.,' Part II, p. 206), but I have been unable to detect evidence of a suture between them, and regard the division as a fracture. Extreme as is the divergence in proportion, these bones are better compared with those of *Muræosaurus* than any other type. The separation of the ulna from the olecranon characterises the genus *Colymbosaurus*, and is seen in *C. Manselli* (Hulke sp.), in which the bones are in close union, in *C. megadeirus* apparently, and in *C. Portlandicus* (Owen sp.), in which the bones are ovate, less perfectly ossified, and separate. This species, No. 31, may be a precursor of *Colymbosaurus*, but there is no reason for referring it to that genus, which has the humerus long and narrow. The first row of the carpus appears to have originally comprised five bones, as in the Mesosauria; but the small inner and outer elements are now blended with the carpals next them, reducing the number of

* The fragments, which had been mended, have been separated.

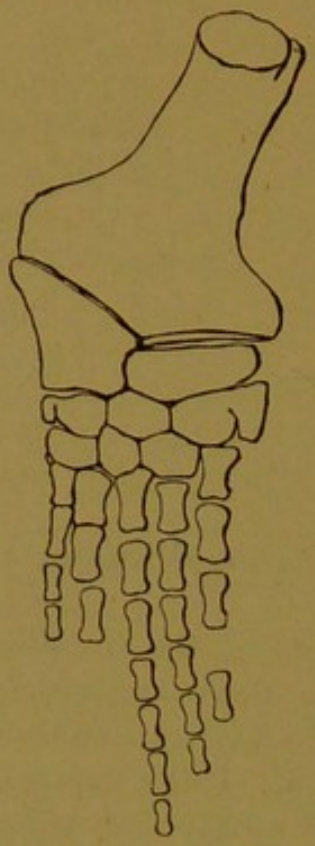


FIG. 15.—Fore limb of *Muræosaurus* (*Cryptoclidus*) *platymerus*.

separate bones to three. There are only three carpals in the second row, though there may be a rudimentary fourth bone on the anterior margin.

The first digit is slender and short in this species, and all the phalangeal bones are sub-cylindrical, showing, as in other species of *Muræosaurus* no trace of the compression which characterised *Cimoliosaurus*.

It is not improbable that, with fuller knowledge, the conceptions of genera here indicated may, in some cases, be modified; but, till better examples of the American genera are found and figured, it will be difficult to contrast them with those now described, and make the definitions exact.

IV. CLASSIFICATION.

Characters of value in classification show gradations of development in the Sauropterygia. This is conspicuous in the size and form of the head, the relative length of the neck, the mode of articulation of the cervical ribs by two heads or by one, or by anchylosis, the length of the centrum in relation to its breadth in the several regions of the vertebral column, the form and mode of attachment of the neurapophyses, the form of the zygapophyses, the structure of the shoulder girdle, the forms and conditions of the mesopodial

bones, and the arrest or development of the process of ossification in the various elements of the skeleton.

Of all these characters the last is the most difficult to value, for there is some evidence tending to the inference that ossification became better developed with the progress of geological time, and surfaces which in Liassic types had always retained the cartilaginous condition of immaturity, in Cretaceous types show the completed ossification of old age. This condition is not, however, universal, since *Eretmosaurus rugosus* has ossification perfected in a way not known in other Liassic genera, and *Stereosaurus platyomus* of the Cambridge Greensand has the vertebræ crowded together irregularly, while the extremities of the short, wide, thick propodial bones remain unossified.

And it is remarkable that many Liassic species have the articular faces of the vertebral centra deeply biconcave, while in many Cretaceous species those surfaces are nearly or quite flat; in the shoulder girdle nothing but continued ossification apparently is needed to convert the Liassic Plesiosaurian into the Oolitic and Cretaceous Elasmosaurian type. *Eretmosaurus* is the nearest approach to this type, known from the Lias.

It thus appears as though some animals complete their embryology early in life, others at intervals during life, while in most types the embryonic development takes place gradually during successive epochs of geological time, giving rise to classification of its stages, indicated as genera, families, orders; and therefore that the young individuals of a late period of time simulate genera of an earlier age.

The character which appears to be most important in Sauropterygia as a ground for primary classification is the presence of two facets, or one facet, on the side of the centrum for the articulation of the cervical rib. If two are present, both facets are upon the centrum, and exhibit many degrees of approximation, seen in *Rhomaleosaurus*, *Pliosaurus*, *Plesiosaurus*, before the division becomes obliterated in *Murænosaurus*, *Colymbosaurus*, and the Cretaceous types. This condition is of further interest, from the fact that among existing Vertebrates a similarly divided articulation for the rib upon the centrum is only known in the existing Urodele Amphibia. Most, if not all, of the Plesiosauridæ have the rib facet transversely cleft; while no Elasmosaurian is at present known in which the same condition is found. So that a division may be made into groups with ribs of the Y-type and I-type. The former sub-division includes two extreme modifications, one with a long neck, which is well represented in the Lias by *Plesiosaurus homalospondylus* and *P. dolichodeirus;* and a type in which the head becomes larger and the neck shorter, represented by *Rhomaleosaurus Cramptoni* in the Lias and *Pliosaurus* in the Oxford and Kimeridge Clays.

The short-necked genera are distinguished as a group by having the two articular costal facets placed chiefly at the sides of the centrum, and not at its infero-lateral angle. This circumstance appears to indicate that the neck is elongated chiefly by the addition of vertebræ to its anterior portion. The mesopodial bones are two in number, and more or less quadrate, with a tendency to transverse extension in the ulna. The dorsal vertebræ are relatively long compared with those of the neck. In *Rhomaleosaurus* the average length of the cervical centrum is 2·66 inches, while the average length of the dorsal vertebræ is 3·2 inches. In *Rhomaleosaurus* the facets remain separated to the end of the series, but in some species of *Pliosaurus* there is an approximation of the facets in the posterior cervical vertebræ which is not seen further forward. The relatively small size of the head in *Rhomaleosaurus* as compared with *Pliosaurus* shows that the head is not necessarily long in all the short-necked genera. The shoulder girdle in the Rhomaleosaur being unknown at present, there is no means of comparing it with that attributed to *Pliosaurus*.

The long-necked genera have the cervical vertebræ in greater number, and relatively longer, and, except the earliest, they are usually as long as the dorsal vertebræ. The articulations for the cervical ribs are elongated from front to back, longitudinally divided, but usually so compressed from above downward that the division is only a narrow shallow channel, always placed at the infero-posterior angle of the centrum. The two facets are obvious in species like *P. dolichodeirus*; in many others they are only to be recognised by careful examination. In this genus the radius is elongated, with its lateral borders concave and ossified, and the distal end narrower than the proximal end.

The scapulæ and coracoids never meet in the median line, unless in the genus *Eretmosaurus*. This condition has been figured in the British Museum specimen 2041 ('Geol. Soc. Quart. Journ.,' 1874, p. 446), where a wide interspace is left between the coracoids and scapulæ in the median line in front, and there is a roughness upon the scapula as though the interclavicle or clavicle had extended upon it. The interclavicle usually completes the inner border of the coracoid foramen in *Plesiosaurus*; but in this fossil the relations of the bones are like those attributed to *Pliosaurus* by Sir R. Owen. According to Mr. Lydekker, what I regard as the pre-articular part of the scapula is the humerus of *P. Hawkinsi* ('Cat. Foss. Rept. Brit. Mus.,' Part II, p. 277). This is a matter that may be definitely determined by examination of the specimen, which comprises the scapula only, closely united by suture to the coracoid.

In the second division of the Sauropterygia or Elasmosauridæ the cervical ribs articulate by a single head with the centrum, the scapulæ, as well as the coracoids, meet each other in the median line, the clavicles, so far as they are known, are usually slender, the meso-

podial bones are quadrate or transversely elongated, and the carpals and tarsals are transversely oblong. There is a certain parallelism between this group and the Plesiosauridæ, as though it had been modified from it, and the genus *Polycotylus* in the shortness of its centrum has some resemblance to *Rhomaleosaurus*, just as in length of neck and vertebræ *Muræosaurus* resembles *Plesiosaurus*.

This scheme of classification is summarised in the following table :—

SAUROPTERYGIA.

Aquatic Sauromorpha, with the extremities modified for swimming only. They are divided into two groups :—

Dicranopleura comprise all genera with fork-headed cervical ribs. They are divided into two groups :—

Dolichodeira (or Plesiosauridæ) comprise the long-necked genera—

Plesiosaurus, in which the carpus is weakly ossified.

Eretmosaurus, in which the carpus is strongly ossified and the scapula appears to have an inner and an outer union with the coracoid.

Brachydeira (or Pliosauridæ), the genera with short necks—

Rhomaleosaurus, in which the cervical vertebræ are shorter than the dorsals. Articular face concave.

Pliosaurus, in which the cervical vertebræ are shorter, and flat on the articular face.

Cercidopleura comprise all genera with single-headed, or skewer-like, cervical ribs. They are not yet divided into groups, and are all included in the Elasmosauridæ—

Polyptychodon.
Polycotylus.
Cimoliosaurus.
Stereosaurus.
Mauisaurus.
Elasmosaurus.
Trinacromerum.
Colymbosaurus.
Muræosaurus.
Cryptoclidus.

HARRISON AND SONS, PRINTERS IN ORDINARY TO HER MAJESTY, ST. MARTIN'S LANE.