

**On Neusticosaurus pusillus (Fraas), an amphibious reptile having affinities with the terrestrial Nothosauria and with the marine Plesiosauria / by H.G. Seeley.**

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**Publication/Creation**

[London] : [publisher not identified], 1882.

**Persistent URL**

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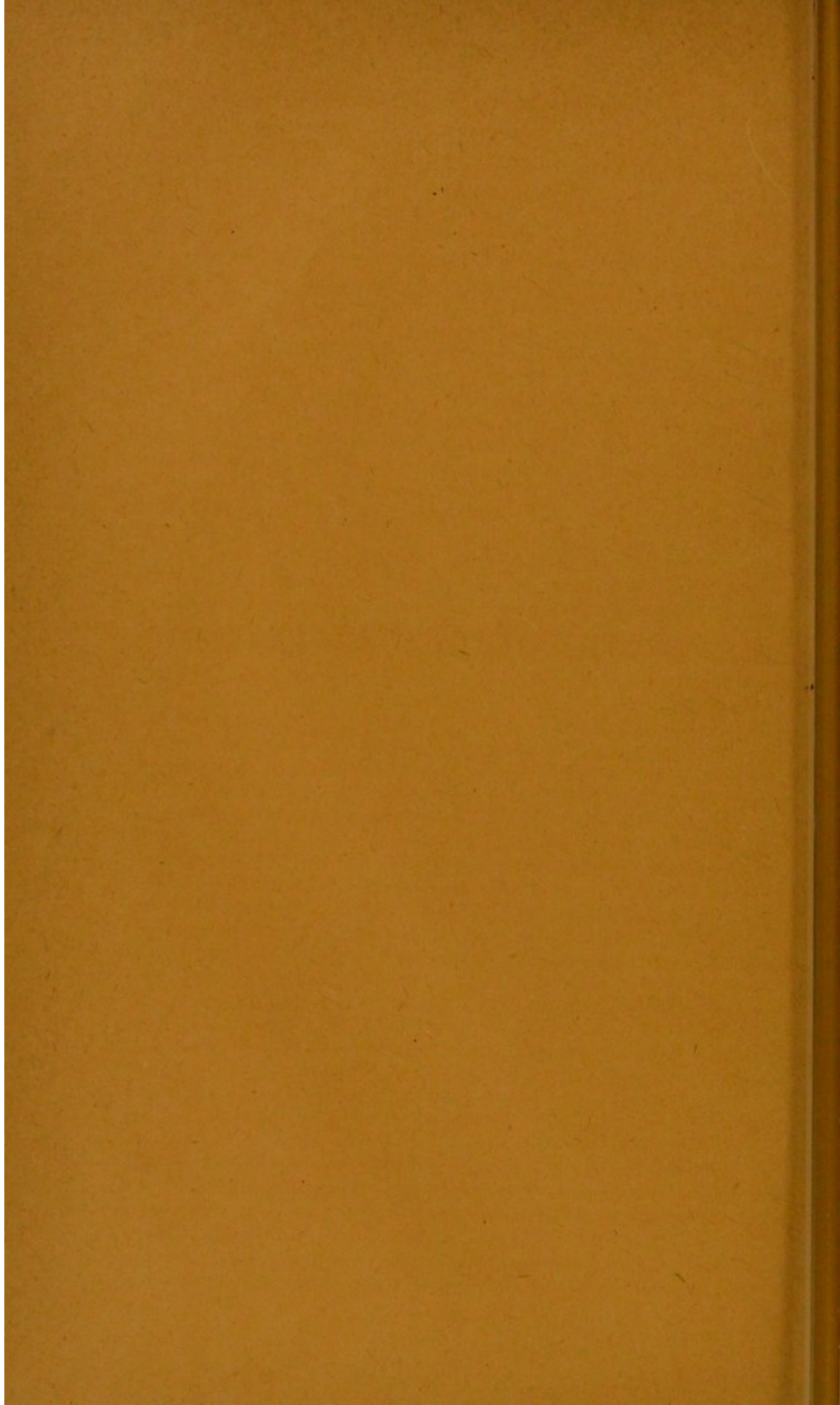
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1882

(7)





[From the QUARTERLY JOURNAL of the GEOLOGICAL SOCIETY for  
August 1882.]

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ON *NEUSTICOSAURUS PUSILLUS* (FRAAS).

On NEUSTICOSAURUS PUSILLUS (*Fraas*), an AMPHIBIOUS REPTILE having AFFINITIES with the TERRESTRIAL NOTHOSAURIA and with the MARINE PLESIOSAURIA. By H. G. SEELEY, Esq., F.R.S., F.G.S., &c., Professor of Geography in King's College.

[PLATE XIII.]

MR. JULIUS HOSER, of Stuttgart, submitted to me in June 1881 two of the most interesting Saurians ever discovered in the Trias. They were found in the Lettenkohle, which lies between the Upper Muschelkalk and the Keuper, in a quarry at Hoheneck, near Ludwigsburg, about nine miles north of Stuttgart. These fossils are the materials briefly noticed by Dr. Oscar Fraas in the 'Württembergische Jahreshefte,' 1881, and figured as *Simosaurus pusillus*. This animal is probably the smallest representative of the Plesiosauria yet exhumed; but it has a greater interest in exhibiting in the hind limbs all the characteristics of a land animal, while the fore limbs have become paddles, in which a more striking approximation is made to *Plesiosaurus* than was previously known in any Triassic representative of this order. Yet, in form of vertebræ and proportions of the vertebral column, in structure of the pectoral and pelvic girdles and conformation of their component bones, the Plesiosaurian common plan is so closely adhered to that no doubt can attach to the animal's systematic position. A photograph showing the condition of the principal slab when first discovered, which was taken as a record, in case of accident during its development from the matrix, satisfactorily attests that the bones are in their natural positions, and thus enables us to recognize in this animal a terrestrial Plesiosaurian in process of undergoing those structural modifications which would adapt it for aquatic life.

This is the first occurrence of a fairly complete Plesiosaurian skeleton in the Trias. None of the remains so admirably illustrated by von Meyer, and referred to *Nothosaurus*, *Pistosaurus*, *Conchiosaurus*, and *Simosaurus*, exhibit the skull in association with the vertebral column, or either with the limb-bones. The latter, indeed, have only been recovered in isolation from each other; and though the association of bones in certain quarries fully justified von Meyer in his cautious reference to *Nothosaurus* of the various elements of the skeleton, no restoration has been attempted. Even in the admirable analysis of the characters of this genus given by Prof. Owen in his 'Palæontology' (2nd edit.), the diagram (fig. 90, p. 230) of principal characters represents the fore limb as unknown\*. In studying this new fossil we need to remember that the genus *Simosaurus* is founded upon the skull, of which both superior and inferior aspects are well known †.

\* Von Meyer would have regarded the limb represented as a fore limb.

† Fauna der Vorwelt, Saurier des Muschelkalkes, pls. 16-20.



The superior aspect of the skull is remarkable for the large size of the temporal fossæ, orbits, and nostrils, the latter having a very forward position. The palate, on the other hand, is remarkable for its extensive ossification (pl. 17); and, as Professor Owen has observed, the pterygoids form a broad, expanded, unbroken, flat, imperforate expanse of bone, united by a median suture, and underlapping the sphenoid. The only large perforations on the palate are those beneath the anterior nares and those external to the pterygoids. If we now turn to the skull of the little animal figured by Dr. Fraas, the exposed surface, which he identifies as the palate, shows exactly that arrangement of vacuities which von Meyer figures (pl. 18) as distinctive of the superior surface of the head. There is, however, no reason to question the accuracy of Dr. Fraas's topographical identification, since the exposed surface is concave, as only the palate could be, shows alveoli, and has no trace of a parietal foramen, though the bones are too perfectly ossified and blended to permit of their individual definition in detail. But such a palate as the specimen exhibits makes reference of the species to *Simosaurus* impossible. Equally impossible is it to refer the type to any other genus hitherto instituted. The difference, indeed, is of a subordinal rather than a generic quality; for since all the allied Triassic genera hitherto known have the palate closed, in harmony with the Plesiosaurian plan (and it may be in relation to aquatic conditions of life), here we may have an indication of the kind of skull from which the Plesiosaurian type was originally derived. It has therefore appeared desirable to offer to the Society some further details of the anatomical structure of this animal, which I was enabled to study by the courtesy of Mr. Hoser, before the skeletons became finally deposited in the national collection at South Kensington.

The larger specimen (Pl. XIII. fig. 1) lies on the back in a slight sigmoid curve, and exposes the abdominal aspect of the skeleton, all the bones of which are *in situ* except some elements of the pectoral girdle, the abdominal ribs, and parts of the limbs, which are lost. The extreme length of this skeleton as it lies hardly exceeds 270 mm., though Mr. Hoser measuring the separate regions makes it 285 mm.

The second and somewhat smaller individual (Pl. XIII. fig. 3) exposes the dorsal aspect of the bones, but has lost the head and anterior part of the neck, the extremity of the tail, some of the smaller limb-bones, and the right hind limb. But though the conformation of the bones is slightly different in this animal, the differences are no more than may perhaps be attributed to sex or age.

#### *The Head.*

The head (Pl. XIII. fig. 2) is nearly 3 cm. long, and is 14 mm. wide in the posterior or quadrate region, where it is widest: the sides are at first nearly parallel, and then taper forward in a lanceolate shape. It lies flat, and has been carefully excavated so as to display the several regions of the palate. In front, resting close upon the maxillary bones, there appears to be a small fragment of the lower



jaw, still containing three teeth, two in one ramus and one in the other. These teeth are directed outward and upward; they are white, with a cylindrical fang, and a slightly expanded crown; but the fragment of lower jaw is very small and slender; it obscures the anterior termination of the snout so that the premaxillary bones are not seen. The maxillary bones extend backward to the region of the orbits, and appear to have been about 18 mm. long. The sockets for the teeth are circular, and about half a dozen can be counted on the left side of the specimen. The alveolar border is elevated on the inner margin of the sockets. The palatal plates of the maxillary bones are moderately developed in front of the palatal nares; they do not meet in the median line, but rest upon a vomer, which is either double or grooved in the middle. The palatal nares appear to have been ovate, but the posterior border is not clear; they approach to within 6 mm. of the anterior extremity of the head as preserved with the lower jaw. Posterior to the nares, the palate is deeply concave from side to side. This concavity is due, in part, to the mode of development of the palatine bones, though their limits are not clearly defined. They appear to be narrow in front, and to widen in a V-shape behind, and to have the posterior border concave. I am unable to recognize with certainty any suture between them. The posterior processes diverge towards the thickened part of the maxillary bone, where the teeth appear to terminate. There is a median ridge on the palatine, which dies away posteriorly; thus the palatines appear to form the posterior roof of the nares. They terminate backward in a sharp ridge. Posterior to this ridge, which is 13 mm. from the snout, the palate becomes concave from front to back, and appears to include two pairs of vacuities. The smaller pair is in about the middle of the skull, and probably just below the orbits, which are not seen. The two pairs of vacuities appear to be separated from each other by the transverse bone, which is only preserved on the left side, and unites with the hinder margin of the maxillary and with the pterygoid bones. The pterygoids divide the anterior pair of these vacuities from each other; they appear to show a median suture, are much constricted from side to side, but diverge posteriorly; they are short, and it is not possible to speak with certainty of their posterior limit, since no sutures can be accurately defined, and the large mass of bone between the hindermost pair of palatal vacuities has all the characters of the basisphenoid. This region is broadly channelled in length, its lateral margins are concave; and posterior to it is the basioccipital. It gives attachment to the quadrate bones posteriorly, which evidently send processes forward and inward so as to meet backward processes of the pterygoid. There is no articular condyle to the quadrate bone; but the articular surface appears to have been slightly concave. The palatal space between the condyles is concave; but the condyles themselves do not seem to have been prominently developed. The malar bar is preserved on the right side of the specimen only; but its condition does not show sutures, and therefore gives no evidence of the quadrato-jugal. The occipi-



tal condyle is small and globular. On each side of it there is a strong lateral bony mass as big as the condyle itself, but separated by an inferior groove, as is often seen in the basioccipital bone of Plesiosaurs.

The way in which this skull diverges from *Plesiosaurus* or *Nothosaurus*, suggests a distinct approximation to Lizards. And there are many lizards in which the palate might, by a median blending of the pterygoid bones, present a similar aspect.

An approximation to such a palate is offered by the common *Lacerta agilis*, though the superior surfaces of the two skulls are not likely to show any thing in common. The distinctive feature of the lizard palate consists in the presence of the vacuities which result from the pterygoid bones abutting against anterior angles of the sphenoid, so that they do not completely meet in the middle line. Even in *Amphisbæna* the structure of the palate, with the pterygoids external to the basisphenoid, is hardly an exception to the Lizard plan, though the pterygo-sphenoid vacuities are so far reduced as to make the palate essentially Chelonian. It is therefore probable that the Lizard-like conformation in this fossil, is not indicative of Lacertilian affinities, at least of affinity towards any surviving type of the group. It is at first sight as difficult to see any resemblance in it to the Plesiosaur as to distinguish it from the Lizard; for the backward position of the external nares towards the middle of the head in Plesiosaurs necessarily gives rise to a difference of proportion in the palatal regions, and causes the posterior nares to be carried backward so as to approximate to the Crocodilian plan (see Owen, Monog. iii. Rept. Kim. Clay, t. i. fig. 1, also Rept. of Lias, t. xvi.). But if the premaxillary bones had not extended their posterior margins backward so as to remove the external nares from the extremity of the snout, then probably the palate of *Plesiosaurus* would have compared better with our fossil; for the lateral vacuities in the palate might then have held a more forward position. But in any case *Plesiosaurus* has no representative of the vacuities which occupy the middle of the palate, and are margined posteriorly by the transverse bones, any more than has *Nothosaurus* or *Simosaurus*, in both of which the palatal nares are as far forward.

#### *Vertebral Column.*

The neck (Pl. XIII. fig. 1) is twice or twice and a half as long as the head. It includes about 20 vertebræ; but the state of preservation is such as to present considerable difficulty in determining which should be taken as the last cervical; and it may be that some would prefer to count only 17 vertebræ. The length of the cervical vertebræ appears to vary but little, though the centrums increase in size as they recede from the head and approach the back. The cervical region, however, is not so well preserved as to show the exact form of the bones. There is no clear evidence of the form and characters of the articular face of the centrum; in the lower part of the neck the base of the centrum appears to be grooved. I am unable to recognize any cervical ribs



such as are found in the anterior part of the neck in *Plesiosaurus*; but after the 17th, where the vertebræ became wider, ribs are preserved. Each vertebra is about 3 mm. long. The rib is about 5 or 6 mm. long, and tapers to a point. It is impossible to adopt the same mode of classifying the regions of the vertebral column as is in use with Plesiosaurs; for although the first four or five vertebræ with ribs probably have the stout expanded head of the rib supported partly on the centrum and partly on the neural arch, there is no evidence that this is the case; and therefore, though I should be disposed to regard these vertebræ as pectoral, other writers might group them with the neck, because they are anterior to the scapular region, or with the back, because they bear ribs.

The cervical vertebræ do not lie quite undisturbed; the atlas and axis appear to be broken; the third vertebra exposes the articular end, showing the neural canal to be higher than wide, with the posterior articular face of the centrum flattened, but slightly convex from above downward. The upper table of the neural arch extends back a little beyond the neurapophyses, and extends outward a little beyond them. The sixth vertebra, which lies on its side, has a distinct tubercle for the rib, on the lower part of the centrum; and the fifth shows a median ridge on the base of the centrum, with a groove on each side of it. The middle cervical vertebræ have lost their neural arches, and there only remain the facets to which arches were attached. These facets are ovate, placed towards the anterior part of the centrum, and separated from each other by a considerable interval, so that the spinal cord rested upon the centrum. The neural arches are better seen in the second specimen (Pl. XIII. fig. 3), in which, however, only seven cervical and three or four pectoral vertebræ appear to be indicated with certainty. Only the dorsal aspect of the neural arch is there shown. It is remarkable in character, because there is no neural spine, the neural spine being only represented by a slight ridge, unless, indeed, it should have been broken away in excavating the specimen, of which I am unable to detect any certain evidence under the magnifying-glass. This slight ridge is, moreover, prolonged forward as a blunt conical spine, which overlaps and apparently articulates with the neural arch of the vertebra in front. On each side of this ridge the upper surface of the neural arch is rounded, somewhat oblique, and forms remarkable zygapophyses, the zygapophysial facets being unusually large both in front and behind. In front they are completely divided by the median ridge; they are directed horizontally, and form an unusually compact connexion in the neck.

In the principal slab (Pl. XIII. fig. 1) the dorsal vertebræ all lie on their sides. In the lower part of the dorsal region they are covered by the thin bones of the pelvic girdle, so that it is difficult to count the exact number. Including the pectoral vertebræ, there are, however, 29 vertebræ in the back, reckoning the last dorsal to be in a line with the ischio-pubic suture.

The second specimen, however, cannot count more than 26 vertebræ in the same limits; there is therefore some reason for



supposing that we may have here to do with a second species, a suggestion which is supported by some characters of the tail and the smaller bones of the limbs. If distinct, however, the specimens are so closely allied that I feel justified in quoting the characters of one as illustrative of the other.

In nearly all Plesiosaurs the dorsal rib is supported upon a more or less developed tubercle or transverse process. This type, however, shows *no trace of any such character*. Each centrum is 4 mm. long; the body of the centrum is rounded; and instead of there being a constriction between the two articular ends, the centrum is slightly inflated in the middle so as to approximate to a barrel-like form. Above the centrum is the neural arch, generally to be recognized by its suture; and at the base of the neural arch, where it expands a little, is the articulation for the rib. And while the rib is single-headed as in *Plesiosaurus*, the ribs themselves have a Crocodilian aspect, because, articulating at the base of the neural arch, the slight transverse tubercle indents or notches them out above. The neural arch is less high than the centrum; it is oblong, and nearly as long as the centrum. Where there is a slight displacement in the series the articular end of the centrum appears to be flat. In the region of the shoulder-girdle several centrams appear united together (Pl. XIII. fig. 1). The second and smaller animal only exhibits the neural aspects of the vertebræ (Pl. XIII. fig. 3). The sides are divided by the median longitudinal ridge indicative of the neural spine, which may be a trifle broader than in the neck. The lateral parts of the neural arch are transversely expanded and somewhat rounded; each neural surface is once and a half as wide as long, has its anterior margin slightly convex, its posterior margin concave, its lateral margins straight. The ridge of the neural spine appears to be prolonged between the zygapophyses, though to a less extent than in the neck. There is no sacrum formed by union of vertebræ, and no vertebra that can be recognized as sacral from any modification of structure that it presents. The vertebra, however, immediately behind the ischio-pubic suture should be counted sacral; and then in the larger specimen there would seem to be 15 caudal vertebræ. At least 13 caudal vertebræ are preserved in the smaller specimen; but they correspond in form and size to the first 8 in the larger specimen, and obviously are only a portion of the tail. This, with some differences in the length of the vertebræ, would again suggest that the specimens may belong to two species.

In the larger individual the tail is only presented on one side, and it has been developed so as to show the transverse processes. The second centrum behind the ischiac bones is 7 mm. long. The transverse process arises from the front part of the centrum, and is broad, compressed, and strong; but these processes become rapidly smaller and soon disappear.

The length of the tail, as preserved, reckoning to the back of the sacral vertebra, is only 45 mm.; and although it may have extended further there is no proof or, indeed, reason to suspect that the length would have exceeded 5 cm. In the second specimen the



tail, as preserved, is 5 cm. long, but shows no indication of being near the end where it terminates. In this length the vertebræ are compressed from side to side, and have the transverse processes less robust than in the larger specimen. The processes become shorter, and in the last 3 or 4 vertebræ are only indicated by tubercles. Hence in the larger or type specimen the vertebral formula appears to be 17 cervical, 29 dorsal, 1 sacral, and 15 caudal.

#### *The Ribs.*

The large specimen (Pl. XIII. fig. 1) has the ribs spread out on each side of the vertebral column symmetrically and in natural position, except for a slight displacement on the right side of the body in the pectoral region. Seven vertebræ anterior to the humerus have ribs; the first of these may belong to the cervical region. The next four may also belong to the neck, but the two immediately in front of the humerus are probably to be counted as dorsal. Reckoning in this way, there are 22 or 23 pairs of ribs with corresponding vertebræ anterior to the pubis, all of which must be reckoned as dorsal. The length of this region is about 98 mm. The width across the ribs and vertebral column as they lie is 34 mm. in the middle, narrowing a little towards the anterior and posterior ends, owing to the ribs becoming somewhat shorter. The ribs are curved; measured from end to end without regarding the curve, they are about 2 cm. long. Cylindrical in the abdominal two thirds, they are expanded, thickened, and enlarged towards the articulation with the vertebra. The thickening appears to have been greatest from above downward; and, as already remarked, there is a sort of notch at the articular end, different from what is observed in any Plesiosaur, and highly suggestive of a double articulation, though not inconsistent with the Lizard type. No specimen shows the articular facet, but the corresponding facet on the neural arch always exhibits a pit.

In the smaller specimen (Pl. XIII. fig. 3) the ribs are more nearly in natural position, but their distal ends are crushed together so as to be absolutely in contact. The principal bones of the pelvis and of the scapular arch are hidden; but I do not think more than 22 pairs of ribs could properly be reckoned as dorsal. The proximal ends of the ribs appear to be relatively larger and more cylindrical than in the other specimen, and the interspaces between the ribs appear to be less, though in no case is the interspace equal to the width of the rib itself, as they lie. The transverse width across the ribs in the small specimen is little more than 2 cm.

In the remarkable elongation of the neck and proportions of the vertebral column, the characters are entirely Plesiosaurian; but, for a member of this group, the intercentral surfaces are remarkably flat; and unless the apparent blending of the early dorsal centrums in the region of the coracoids is an accidental character, it makes a marked difference from known Plesiosaurians. The appearance of pegging together in the neural arch has, at first sight, a suggestion of the mode of union of the neural arches of certain Lizards and



Ophidians; but there is no reason to regard it as an evidence of affinity. Similarly the long neck recalls the lizard from the Chalk named *Dolichosaurus*, which also has the arches joined by zygosphene and zygantrum. And in the rib rising directly from the side of the vertebra in our fossil, without transverse processes to support it, the character is more Lacertian than in *Plesiosaurus*. But it should also be remembered, that *Pliosaurus*, and *Rhomaleosaurus* from the Lias, like *Nothosaurus*, have the cervical ribs articulated by double heads, as in Crocodiles; so that much weight cannot be attached to characters in which the vertebral column shows Lacertilian analogies.

#### *The Pectoral Arch*

is imperfectly preserved (Pl. XIII. fig. 1). The coracoid on the left side is entirely removed; on the right side it is complete. It has very much the form of an ischium of *Plesiosaurus*, and is as unlike the coracoid of Plesiosaurs as could be while still formed on the same plan. The bones were directed backward, and met in the median line by a suture which was not more than 7 mm. long. The oblique position of the coracoid will be best understood by stating that the median suture is entirely posterior to the glenoid cavity for the humerus. The transverse width of the bone is about 12 mm. Its extreme length, measured obliquely, is about 14 mm. It is constricted in the middle; but the anterior concavity is shorter and deeper than the posterior concavity. The width at the scapular end is less than 7 mm., and the corresponding antero-posterior measurement at the median suture is more than 8 mm. At the suture with the other coracoid there is a small wedge-shaped interval at the posterior margin, such as is usually seen in Plesiosaurs. The scapular end has a small anterior surface for union with the scapula, and a wider, thicker antero-lateral surface for union with the humerus. In transverse measurement the bone is concave, while from front to back it is flattened. The scapulæ are imperfect; but that on the left side is the better preserved. It has somewhat of a chopper-like shape, the part which would correspond to the handle of the chopper being directed above the head of the humerus, much like the supra-humeral process of the scapula in *Plesiosaurus*. The blade of the bone is subobovate, with a slight median ridge dividing the surface into two nearly equal portions. This ridge terminates posteriorly in a thickened, rounded articulation, which contributed with the coracoid to form the glenoid cavity for the humerus. Interior to this, though not well seen, is the articular surface which unites the bone with the coracoid. The ridge on the bone not improbably indicates the area which was overlapped by the clavicle. The length of the blade of the scapula is just over 1 cm.; its breadth is 6 mm.; the length of the posterior process cannot be given with certainty, since it is partly covered by the head of the humerus; but it could not have been less than 3 mm. This process ascends at a considerable angle above the plane of the base of the bone. As already remarked, the



bone is convex from side to side, owing to the ridge; it is slightly concave in length.

In the second specimen the coracoids are not seen, and the scapulæ, looked at from above, present no resemblance to the bones just described. How far this apparent difference may be due to position, and how far to their being covered by the clavicular bones, I am unable to determine. The posterior processes are parallel to each other; and the transverse external width across them is 2 cm. The length of the scapula appears to be about  $13\frac{1}{2}$  mm.; but the posterior process is not quite complete behind, where it extends over the head of the humerus and the articular part of the coracoid. The scapulæ appear to converge forward in a convex curve.

The coracoid is essentially the same in type as that so well figured by von Meyer as pertaining to *Nothosaurus*. The scapula only differs in specific characters and smaller size from some small bones (Muschelkalksaurier, t. 33. fig. 40-44) found near Jena, which von Meyer did not name. It has a general resemblance to the scapula of *Nothosaurus* (t. 34). The fragment of a left clavicle which adjoins the corresponding scapula is broad, but too imperfect to give any idea of the nature of the clavicular elements of the arch. Thus the pectoral bones, as a whole, are much more like those of *Nothosaurus* than *Plesiosaurus*. The Nothosaurian coracoid is essentially a modified crocodilian coracoid, differing chiefly in having the median margin rather more elongated; and instead of having the articular end of the bone pierced by a foramen, there is a notch between it and the scapula, as in many Dinosaurs and Ichthyosaurs; but this notch is not developed in our fossil. It only needs that the antero-posterior elongation of the coracoid of *Neusticosaurus* should be carried further to make it comparable with that of *Plesiosaurus*. Thus the form of that bone in *Plesiosaurus* becomes a modification of a crocodilian type.

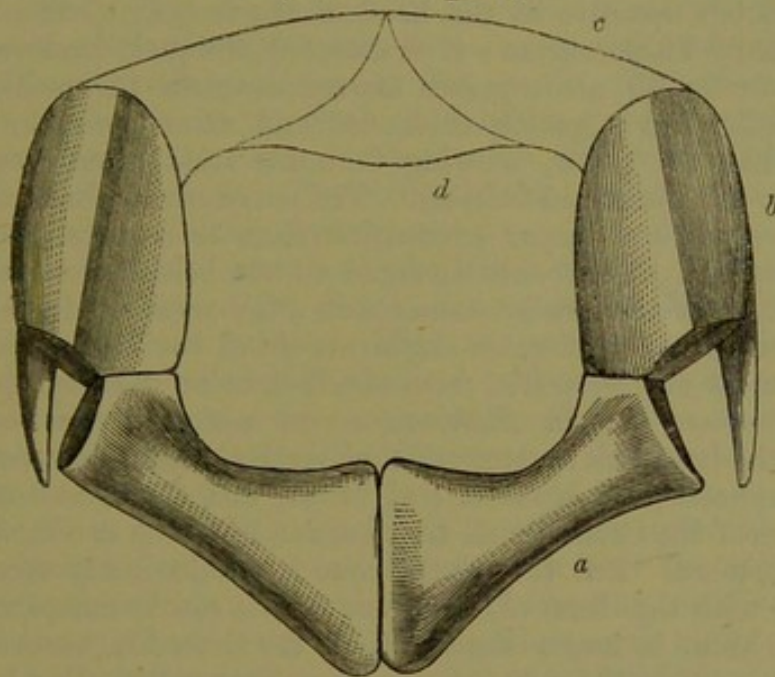
The scapula is at first sight more difficult to understand; but when that bone in *Nothosaurus* is compared with the scapula of the Crocodile, the blade of the bone is similarly directed upward and backward, but is not so expanded as in the Crocodile, while the anterior or preacetabular part of the bone is more developed. The resemblance is not so close as in the coracoid; but the difference is one of proportion, not of plan, and therefore may be classed as functional. In our fossil the blade of the bone becomes directed more backward and assumes a form closely approaching the supraacetabular process of the scapula in some Plesiosaurs, which I am thus led to identify with the blade of the scapula in the Crocodile. The preacetabular part of the scapula in *Nothosaurus*, or even in this fossil, diverges much less from the crocodilian type than does the scapula of such a genus as *Colymbosaurus* from that of *Nothosaurus*.

The striking and distinctive feature of these Triassic Saurians consists in the great development of the clavicular bones, which form an arch in front of the preacetabular elements of the scapulæ. Nothing corresponding to these elements, except the interclavicular



bone, is known to exist in any Crocodile. In Plesiosaurs, however, the clavicles have become small or absent, and blended with the greatly enlarged interclavicle in those species in which they have been observed; so that in this respect the clavicular region in *Plesiosaurus* is rather more like that of the Crocodile than is that of *Nothosaurus*. The resemblance, however, cannot be pressed, because in *Plesiosaurus* the interclavicle connects the scapulæ together, and braces both of those bones to the coracoids. But we are justified in inferring that, with the diminution of the anterior expansion of the scapula in Crocodiles, the clavicle became lost.

Fig. 1.—*Restoration of the Pectoral Arch of Neusticosaurus (external aspect).*



a. Coracoid.                      b. Scapula.  
c. Clavicle.                        d. Interclavicle.

#### *The Pelvic Arch.*

The pelvis consists, as usual, of ilium, pubis, and ischium. In the principal specimen (Pl. XIII. fig. 1) the articular head of the ilium is seen *in situ*, contributing to form the upper and major portion of the tripartite articulation; but on the right side the acetabulum is broken away; so that I can only mention that the head of the ilium is rhomboid, 4 mm. wide, and 5 mm. deep. The pubic and ischiac bones meet by suture in the median line, and extend over 4 or 5 vertebræ. The length of the pelvic region, formed by these two bones is about 2 cm. The bones are expanded and thin, and closely resemble the corresponding elements in *Plesiosaurus*. The transverse measurement across the pubic bones, as preserved, is 23 mm.; but there seems to have been a slight displacement on the left side, by which the antero-posterior measurement of the bone has become less than on the right side. Each bone is subqua-



drate; it met its fellow in the median line, though the suture cannot be distinguished; it also met the ischium behind in the median line, and on each side of this union the posterior margin is concavely excavated to contribute to the formation of the transversely ovate ischio-pubic vacuity. In front there appears to have been a concave notch between the united pubic bones, about as wide as the base of the centrum; and then each sent forward a short anterior process or prepubic element. External to this, the anterior margin has a deep semiovate concavity. The external margin consists of two nearly equal parts, an anterior oblique area, directed outward and forward, with the margin sharp, and a posterior thickened articulation. The length of this external side of the pubis is about 8 mm. Just behind the articulation is a slight narrow notch opposite to the head of the ischium. The ischium is even more Plesiosaurian; it is directed obliquely backward, and extends in length as it passes inward towards the median line. The articular end is greatly thickened and extends outward rather further than the pubis, showing that the acetabulum was chiefly formed by the ilium and ischium. The anterior margin of the bone is concave, with a deeper excavation than is seen on the longer lateral margin. The bones diverged a little behind from imperfect ossification, like the ischial elements in *Plesiosaurus*. In the pelvic bones there is a considerable departure from the crocodilian type. The ilium is not separated from the matrix in these specimens of *Neusticosaurus*; but in *Nothosaurus*, in which it was evidently similar, the bone has no trace of that vertical elongation seen in all true Plesiosaurs, but is short, and broad, and thick, and as much suggestive of the Crocodile as an ilium can be which is only attached to one vertebra. But though the bone is not distinctly crocodilian, it is only with the ilium of Crocodiles that it can be compared.

The ischium is larger than that of the Crocodile, and especially more elongated in the antero-posterior median suture; but in its not possessing the preacetabular process which supports the pubis, there is a fundamental difference. This process, however, does not appear to have existed in the Triassic Crocodiles; and according to Huxley (*Stagonolepis*, p. 32) the acetabulum was formed by union of all three pelvic elements; so that there is no divergence from the crocodilian plan in such a difference from existing Crocodiles as *Neusticosaurus* exhibits.

The pubis is not crocodilian in form, and differs in having a far greater antero-posterior development of the postpubic portion, by which the prepubic process becomes dwarfed. But if von Meyer was right in some of his identifications, it would seem that there is scarcely any difference between the plan of the pubis of *Nothosaurus* and that of the Crocodile, both being expanded towards the median suture, and both constricted near the articular end. As a whole, the pelvis of *Neusticosaurus* is less like the Crocodile pelvis than that of *Nothosaurus*; and as it diverges from *Nothosaurus* it makes an approximation to *Plesiosaurus*.



*Fore Limb.*

On the left side the fore limb is fairly well preserved (Pl. XIII. fig. 1), though the carpal bones are but slightly indicated, and the phalanges appear to be somewhat scattered. On the right side the humerus is gone, apparently through bad collecting, since there is the cavity in which the bone rested. Ulna and radius are well preserved; but there is only one phalange. On the left side the fore limb is 5 cm. long. The humerus has the shape usual with that bone in *Plesiosaurus*. It is 21 mm. long, 4 mm. wide at the proximal end,  $3\frac{1}{2}$  mm. wide in the middle of the shaft, and  $7\frac{1}{2}$  mm. wide at the distal end. The proximal part of the shaft is cylindrical, with the articular end rounded, and some muscular roughnesses on the shaft near the proximal end. The lower part of the shaft is more flattened and compressed; near the distal end there is a groove or foramen for a vessel towards the posterior border, as in *Nothosaurus*. The anterior border, in its upper third, exhibits a slight angular bend, such as occurs in some Liassic Plesiosaurs, and is paralleled in the humerus of *Nothosaurus*. The outline of the bone between this angle and the distal end is very slightly concave. The posterior outline is much more concave, owing to the distal end of the bone being expanded posteriorly. The distal articulation is without facets, and is convex from front to back. The ulna and radius are longer and more slender than those of Plesiosaurs, and present a marked transition towards these bones in a Crocodile, though in shortness the forearm rather suggests the Chelonian type. There can be no doubt about the nomenclature of the bones, since they are *in situ*; but from the form alone it might well have been inferred that the anterior bone was the ulna, and the posterior bone the radius. The radius is 12 mm. long. It is imperfect proximally, on the left side; but on the right side the proximal end is seen to be somewhat enlarged and bent inward, with an oblique articular facet to articulate with the humerus; its distal end is more slender; and the bone all together resembles a crocodilian ulna. The ulna on the right side, where best preserved, is 11 mm. long. It is also wider proximally than distally, with nearly parallel sides; the proximal end has an oblique facet. Below the ulna are two small carpal bones; but there appear to be two or three more displaced among the digits, so that the structure of the carpus is unknown; but it had a Plesiosaurian character.

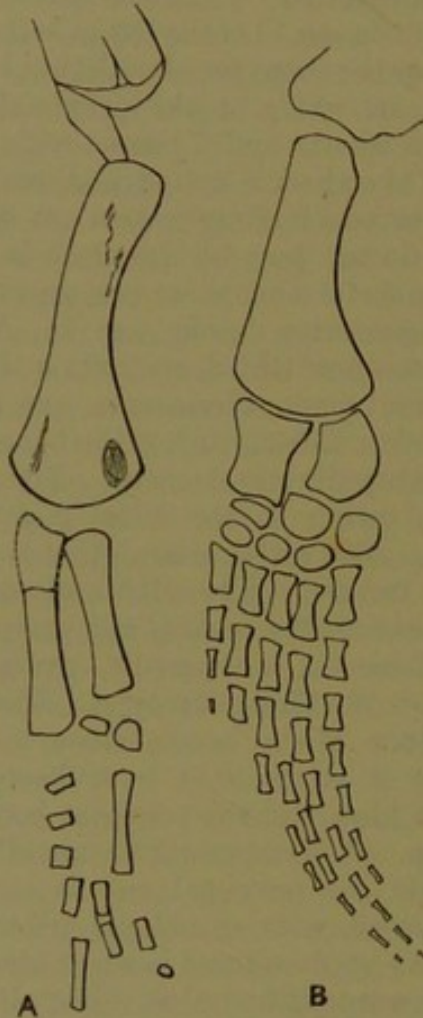
The number of digits is uncertain, and there may not have been more than three. Only one metacarpal (5 mm. long) is preserved; and there are two short conical terminal phalanges.

In the second specimen the humeri are exposed, so that the right shows the dorsal, and the left the posterior lateral aspect. The left bone is not quite perfect distally, and is fractured in three places. The right humerus is fully 18 mm. long; its proximal end is narrower above than below, and is thicker than wide; the distal end is  $6\frac{1}{2}$  mm. wide; the anterior margin is convex in outline proximally, concave distally; the distal end does not appear to be quite so much



expanded as in the other specimen; and there is a distinct thickening of the shaft in a blunt ridge near the distal articulation, towards its middle. The radius is 11 mm. long. No digits are preserved.

Fig. 2.—*Comparison of Fore Limbs of Neusticosaurus and Plesiosaurus.*



A. *Neusticosaurus pusillus.*  
B. *Plesiosaurus Hawkinsii.*

The fore limb at first sight suggests nothing but a modified Plesiosaurian, in which the forearm is relatively more elongated, and the digital bones are fewer than in known forms. These are differences such as are well known in certain genera among the Cetacea. But when we compare the bones of the fore limb with those which von Meyer has referred to *Nothosaurus*, a marked difference is observed in the humerus; for that bone in *Nothosaurus* has no trace of the Plesiosaurian form, and is essentially the humerus of a land animal. The difference consists chiefly in expansion of the anterior part of the bone towards the distal end. There is the same slight proximal curvature of the head of the bone backward, the same curvature of the posterior margin, the same distal foramen on the hinder margin of the bone. And seeing how growth



is everywhere developed by intermittent pressure and tension, it seems to me that the difference between these two is precisely such as might be expected to result from conditions of existence such as would result from increased leverage of the body being thrown upon the anterior distal end of the humerus, in consequence of the bone being used as a chief organ in progression, in an animal which was adapting itself to aquatic conditions. Further, on the posterior margin of the humerus of *Nothosaurus*, in the upper third, is a process like a trochanter, which is often seen in certain species of *Plesiosaurus*, in the same position though less developed; and this process I regard as a representative of the radial crest, less developed than in the Crocodile, and rotated further backward. We shall seek in vain among existing reptiles for any near analogue of the Nothosaurian humerus; and if the character were isolated in the skeleton, it would be impossible to say whether the slight crocodilian character were an analogy or an affinity.

In Crocodiles and Chelonians, even more than in Lizards, the humerus is more elongated than the forearm; but in *Neusticosaurus* the forearm is relatively shorter even than in the Crocodiles; for while in the Alligator these regions are in the proportion of about 7 to 5, in the fossil the proportion is 10 to 6. But while the segment of the limb is shortened, the bones have the aspect of those of a land animal: the radius is broad at the proximal end, like the radius of *Plesiosaurus*; and the ulna is broad and curved a little, so as to foreshadow the way these bones in *Plesiosaurus* became shortened as they ceased to support the weight of the body, and at the same time increased in width with the increased tension under new conditions of use.

The proportions of the bones of the hand and their number show no striking departure from the terrestrial type, except in the form of the terminal phalanges, which, as being conical, seem to preclude the idea of functional terminal claws, and approximate towards the condition seen in *Plesiosaurus*, though the phalanges were few, and did not give the limb a Plesiosaurian elongation. (See Fig. 2.)

Unfortunately, the limb-bones of *Nothosaurus* have not yet been found in natural association.

#### *The Hind Limb.*

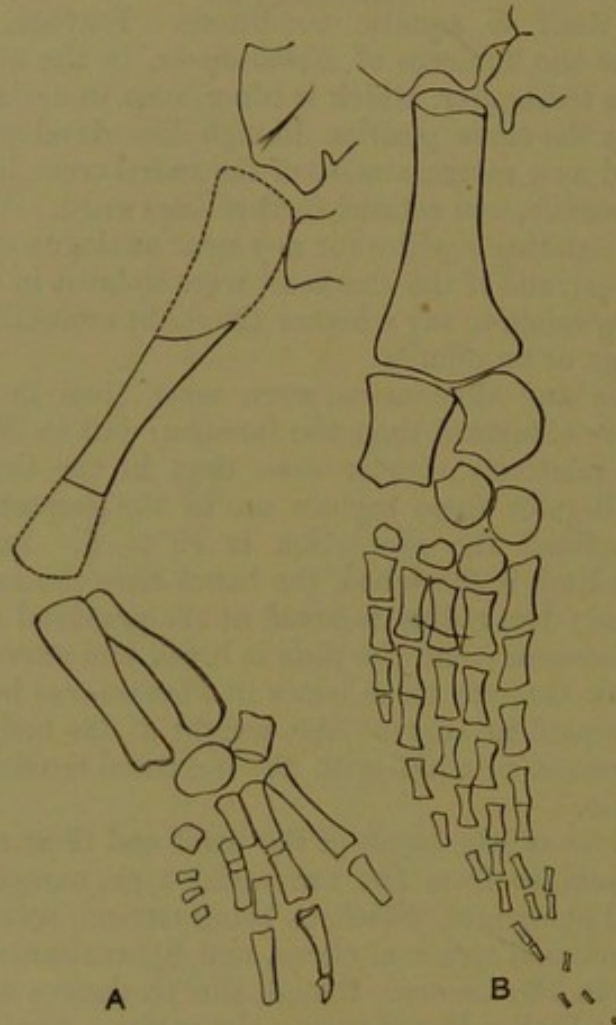
The hind limb is no longer than the fore limb, but of an altogether different character; for while the latter suggests a swimming type, the former is the hind limb of a land animal.

In the type specimen, only the middle of the shaft of the femur is preserved; but the impressions of its extremities in the matrix show it to have been 21 mm. long (Pl. XIII. fig. 1). In the smaller specimen the length is a little less than 20 mm., and the bone appears to be of slightly different form; for in the larger example the impression of the distal end indicates an appreciable widening of the bone, of which there is no trace in the small specimen, which has the distal end more slender than the difference in length would have suggested. But this difference may result from the bone being exposed laterally in the case of the small animal, since in section the shaft of the



larger animal's femur is ovate. The distal end,  $1\frac{1}{2}$  mm. thick, is compressed from front to back, flattened inferiorly, with a sharp

Fig. 3.—*Comparison of Hind Limbs of Neusticosaurus and Plesiosaurus.*



A. *Neusticosaurus pusillus*.  
B. *Plesiosaurus Hawkinsii*.

ridge margining the inferior external border in its distal half; the external side is oblique and rounded distally, and separated by a ridge from the superior aspect of the bone. Proximally the lateral aspect of the bone widens in a wedge shape to 4 mm.; its inferior aspect is flat and forms nearly a right angle with the lateral surface, which is slightly convex; the superior aspect appears to be flattened. There is no indication exposed of an articular condyle to the proximal end, such as might have been expected from a longitudinal ridge running down the underside of the shaft. The tibia and fibula are about 11 mm. long in the larger individual, and 1 mm. less in the small one; and, in harmony with the positions of the skeletons, one exhibits the anterior, the other the posterior aspect of the bones; but both bones are unduly slender in the small specimen. In the larger animal the tibia has a massive appearance: its



proximal end is more than 3 mm. wide; the distal end is fully 2 mm. wide. As the specimen lies, the head of the fibula extends in front of the tibia. The fibula is a characteristic bone, with the external margin straight and the internal margin concave, so that the bone is constricted in the middle and expanded at the two ends.

There are only two tarsal bones—first, a large transversely ovate tarsal placed between the tibia and fibula, and a similar smaller one adjacent to it, and below the fibula. These bones differ in proportions somewhat in the two specimens, but have a close general resemblance to the tarsals of *Plesiosaurus*, in having the lateral surfaces concave, with an elevated margin round the articular edge. The transverse measurement of the large tarsal is 4 mm.

The metatarsal bones and phalanges of the hind limb, like the corresponding bones of the fore limb, in the larger specimen, are badly preserved. The foot was short; but there is no certain evidence whether it included four or five digits. Besides the metatarsal there may not have been more than two phalanges in each digit, though the number probably varied and augmented.

The metatarsals are compressed from side to side, and somewhat enlarged at both ends; in the larger specimen the first is 6 mm. long. Three terminal phalanges are preserved: they are claws of the Lizard pattern, relatively long, compressed from side to side, well hooked, and quite unlike the small terminal conical bones in the fore limb.

In the smaller specimen the metatarsal bones are better preserved. There are four bones placed side by side, and the fractured proximal end of a fifth. There is no divergence between the bones, which increase slightly in length from the first to the fourth. The transverse measurement over these four bones, as preserved, is 6 mm.; the length of the longest is somewhat more. Only one or two fragments of phalanges are preserved, but too imperfect for measurement.

The point of greatest interest in this animal is probably to be found in the diversity of type exhibited by the fore and hind limbs. I am disposed to regard the femur as best comparable to that of the Triassic Crocodilia, in which the bone is straighter than in existing types, and more widened at the proximal end. The divergence, however, is so great that intervening types would be required to justify a detailed comparison; and in this matter *Nothosaurus* gives but little help. The remarkable compressed claws are not crocodilian, but suggest certain Lizards and various extinct animals.

#### Conclusion.

In endeavouring to estimate the value of the various resemblances to Crocodiles which I have attempted to indicate, it must be remembered that in discussing an animal which lived in the beginning of the Secondary period, comparison has had to be made with a type which still exists, and which, therefore, can scarcely give much clue to the actual modifications which its ancestral forms presented in Triassic times. But as the Crocodiles are traced back through the



Teleosaurs and Belodonts there is a nearer approximation of structure towards Plesiosaurs, which may especially be seen in the conformation of the skull, form of the vertebræ, articulation of cervical ribs, and development of transverse processes from the neural arch in the dorsal region, no less than in the conformation of the elements of the pectoral and pelvic girdles. The proportions of the limbs, too, become more those of a Crocodile in such a genus as *Neusticosaurus*; and this genus demonstrates, I think, that the Plesiosauria must have had ancestors which lived entirely upon land, before the limbs came to be used for natation. That those animals were more nearly allied to Crocodiles than to any existing reptilian order, seems to me highly probable.

In such a group, I fancy, we are reaching the parent type of the great subclass of reptiles which von Meyer named PALÆOSAURIA, which I would enlarge, to include Crocodilia, Rhynchocephalia, Chelonia, Ichthyosauria, Plesiosauria, Anomodontia, and Dinosauria, and especially distinguish from the subclass CAINOSAURIA, in which should be comprised the Lacertilia and Ophidia.

While this genus is closely affiliated to the Nothosaurs and their allies, we see in those animals a type rather terrestrial than marine, which, in the bones of the extremities, diverges widely from the true Plesiosaurs. This osteological modification amounts to a subordinal difference; and for this group it may be convenient to use the name Nothosauria, or to adopt von Meyer's name Macrotrachelia, though that term, being equally applicable to *Plesiosaurs*, is not so distinctive.

#### EXPLANATION OF PLATE XIII.

Fig. 1. Type of *Neusticosaurus pusillus* (Fraas) showing ventral aspect, natural size.

2. Skull of the same specimen, twice natural size.

3. Dorsal aspect of a second specimen of *Neusticosaurus*, natural size.

Both examples are in the Natural-History Museum, South Kensington.

#### DISCUSSION.

Mr. W. A. FORBES pointed out that a similar modification of the anterior and posterior limbs was to be seen in the Penguins. Possibly the anterior and posterior limbs of *Neusticosaurus* may have been used in the same restricted manner as in those birds.

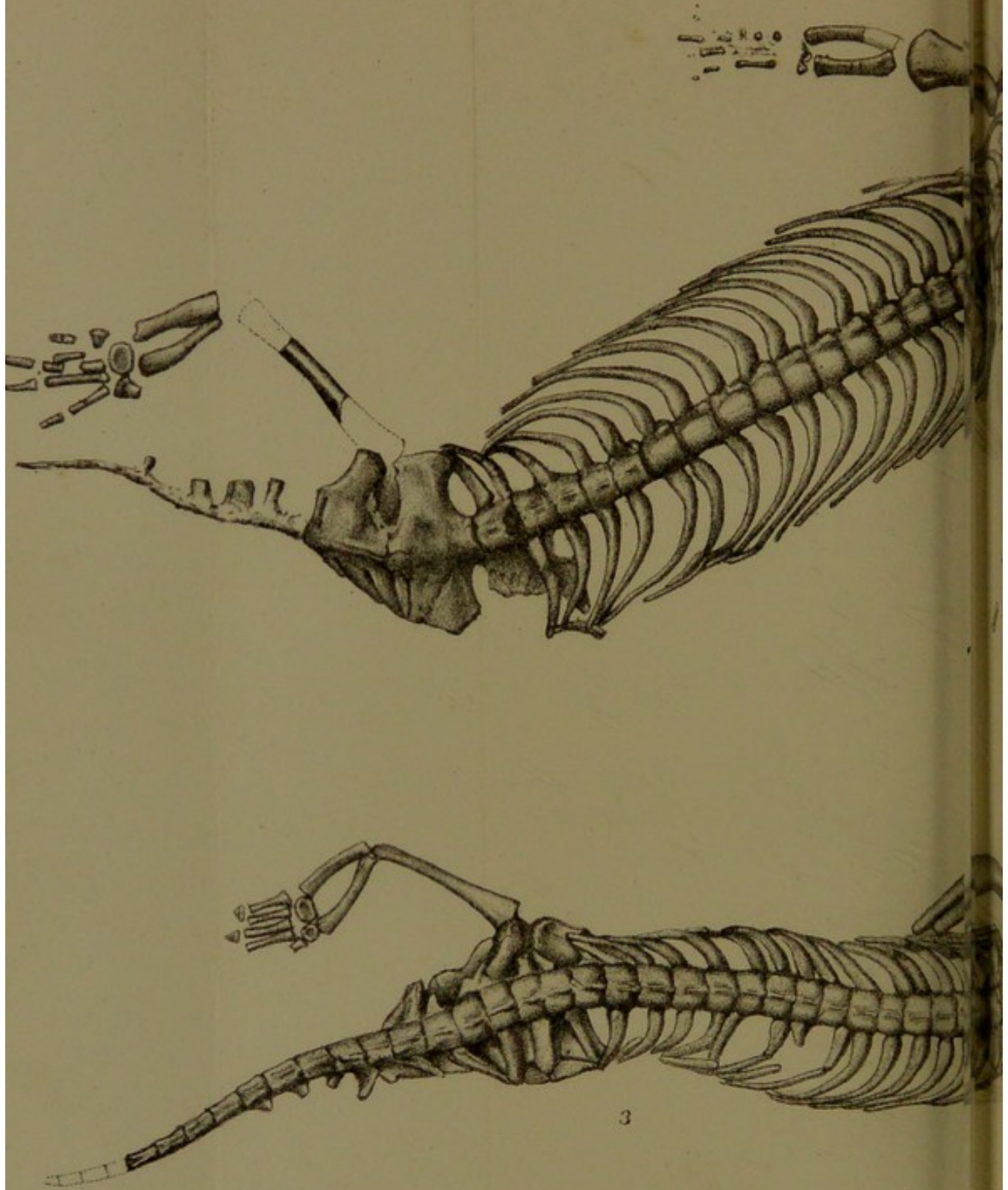
Mr. HULKE spoke highly of the value of the paper; the subject of it was a most remarkable Saurian. The modification described of the fore and hind limbs was very singular; it was very remarkable to find combined in one animal characters which were found in animals so widely separated at the present day.

The AUTHOR agreed with Mr. Forbes that the Penguins presented a parallel instance in some respects.





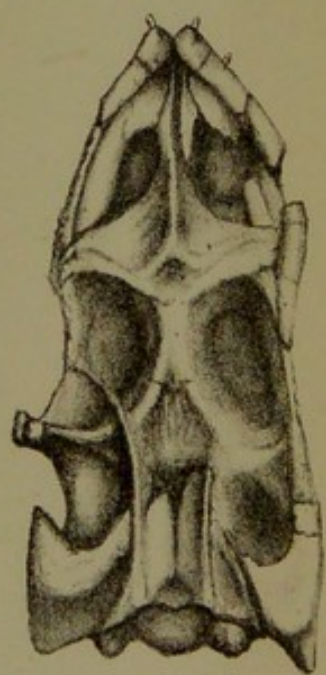
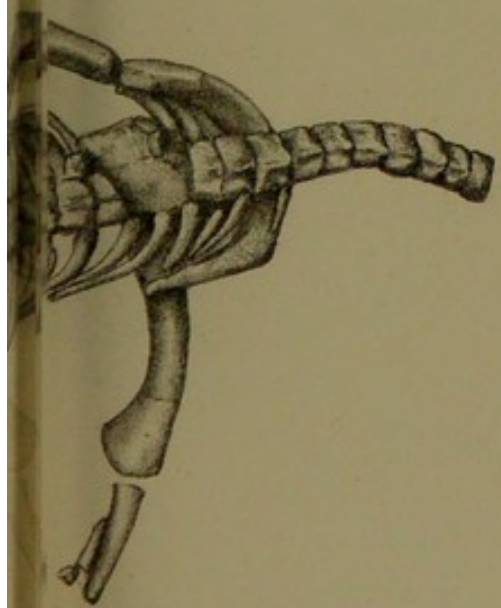
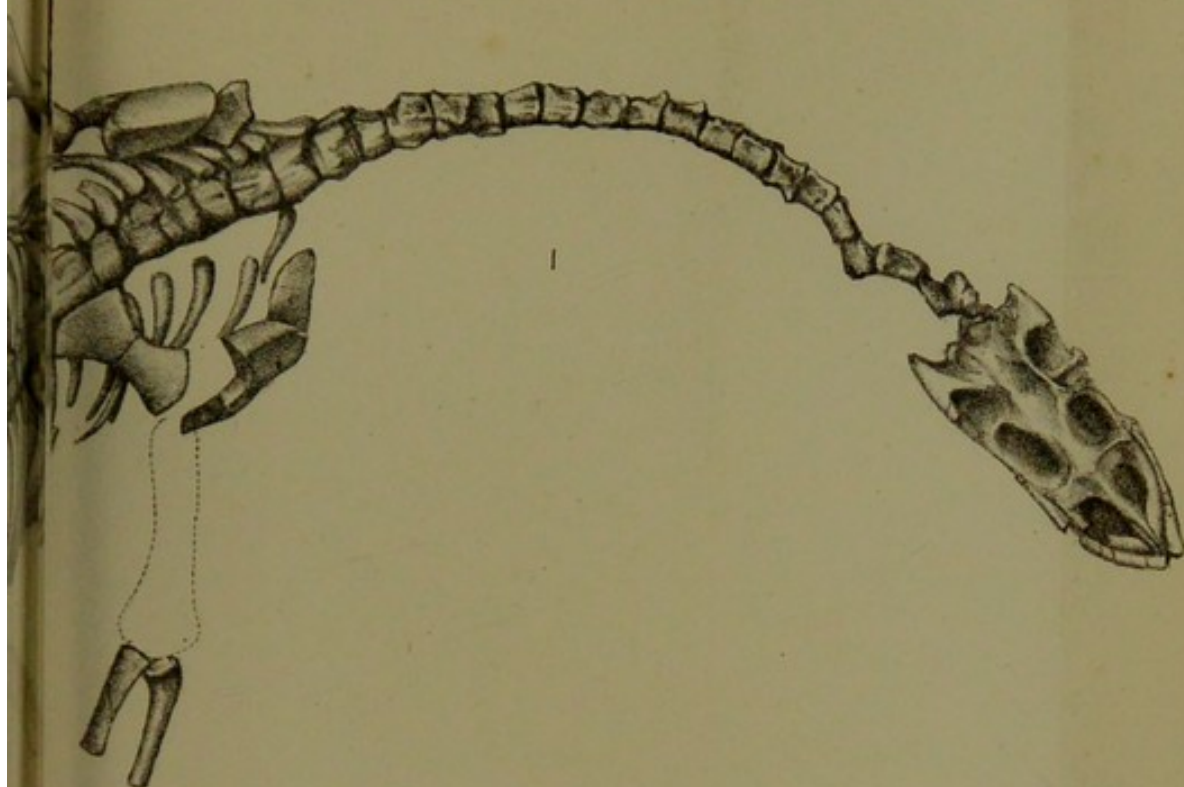




C Berjeau del et lith.

NEUSTIUS





2

Hanhart imp.

URUS.



