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I.—On some remains of the Pycnodont fish, Mesturus, discovered by Alfred N. Leeds, Esq., in the Oxford Clay of Peterborough

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THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

"..... per litora spargite muscum,
Naiades, et circum vitreos considite fontes:
Pollice virgineo teneros hinc carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Dææ pelagi, et pingui conchylia succo."
N. Parthenii Giannettasii Ecl. 1.

No. 97. JANUARY 1896.

I.—*On some Remains of the Pycnodont Fish, Mesturus, discovered by Alfred N. Leeds, Esq., in the Oxford Clay of Peterborough.* By A. SMITH WOODWARD, F.L.S., of the British Museum (Natural History).

[Plates I.—III.]

THE systematic position of the Mesozoic fishes originally named Pycnodonts by Agassiz * has hitherto remained problematical. Notwithstanding the general descriptions in the 'Poissons Fossiles,' the later memoirs of Wagner †, Heckel ‡, Thiollière §, and Vetter ||, and the smaller contribu-

* L. Agassiz, 'Recherches sur les Poissons Fossiles' (1833-44), vols. i., ii.

† A. Wagner, "Beiträge zur Kenntniss der in den lithographischen Schiefer abgelagerten urweltlichen Fische: Die Pycnodonten," Abh. k. bay. Akad. Wiss., math.-phys. Cl. vol. vi. (1851) pp. 6-59, pls. i., iii., iv.

‡ J. J. Heckel, "Beiträge zur Kenntniss der fossilen Fische Oesterreichs: Die Pycnodonten, Agass., oder Pleurolepiden, Quenst.," Denkschr. k. Akad. Wiss., math.-naturw. Cl. vol. xi. (1856) pp. 187-242, pls. i.-xi.

§ V. Thiollière, 'Description des Poissons du Jura dans le Bugey,' pt. i. (1854).

|| B. Vetter, "Die Fische aus dem lithographischen Schiefer im Dresdener Museum," Mittheil. k. mineral.-geol. Mus. Dresden, pt. iv. (1881).

tions of Quenstedt*, Zittel†, and others, the osteology of these fishes is still very incompletely known; and a much fuller knowledge is required before the problem of their relationships can be solved. One disadvantage under which nearly all authors hitherto have laboured is the crushed nature of the specimens. With perhaps only two exceptions‡, all the important Pycnodont remains as yet described are flattened in the hard matrix of such formations as the Lithographic Stone of Bavaria and France, the English Purbeck Stone, and the fissile Cretaceous limestone of Mount Lebanon. Such specimens are admirable as displaying the trunk and fins, but rarely of much service in the matter of cranial osteology; and this must be thoroughly understood before there can be further progress in classification.

A new departure can now be made by the fortunate discovery of some beautiful skulls and other remains in the soft clay of Oxfordian age in the neighbourhood of Peterborough. Thanks to the skill and care of Mr. Alfred N. Leeds, F.G.S., who has already unearthed so many new Jurassic Vertebrata in this formation and locality, no less than five important specimens of the Pycnodont genus *Mesturus* are available for study. Though partly in concretionary clay, they are nearly all free from matrix, and can thus be examined almost as readily as the bones of a recent fish; the only difficulty consists in imperfections and fractures due to the circumstances of preservation. Except one specimen, which has been acquired by the British Museum, these fossils are in the private collection of Mr. Leeds, and will be referred to under their catalogue-numbers as follows:—

- No. 1 (Leeds Catalogue).—Greater portion of head and squamation of abdominal region, with remains of paired fins. (Pl. I.)
- No. 2 (Leeds Catalogue).—Hinder portion of head, with fragments of squamation and caudal fin, and detached mandible. (Pl. III. fig. 2.)
- No. 23 (Leeds Catalogue).—Imperfect head, with jaws and remains of anterior squamation.
- No. 24 (Leeds Catalogue).—Remains of head and pectoral arch, several elements being detached. (Pl. II.)
- No. P. 6834 (British Museum Catalogue).—Several isolated bones of one skull, comprising the parasphenoid,

* F. A. Quenstedt, 'Handbuch der Petrefaktenkunde' (ed. 1, 1852, ed. 2, 1867, ed. 3, 1883), and 'Der Jura' (1858).

† K. A. von Zittel, 'Handbuch der Palæontologie,' vol. iii. (1887).

‡ *Mesodon rugulosus* (Ag.), A. S. Woodward, Proc. Geol. Assoc. vol. xii. (1892) p. 238, pl. iv. figs. 2-4. *Anomæodus Willetti*, A. S. Woodward, Geol. Mag. [3] vol. x. (1893) p. 489, pl. xvii. fig. 1.

supposed basisphenoid, right postfrontal, right and left squamosal, portion of right frontal, right and left operculum, and other fragments. (Pl. III. figs. 3-6.)

I. DESCRIPTION OF SPECIMENS.

Cranium.

The bones of the cranial roof form a continuous shield, much arched from side to side, and extend from the occiput to the rostrum without any fontanelle or loss of the tubercular ornamentation. The sutures between them can be readily recognized on close inspection, and the limits of some of the elements are remarkably inconstant. It is clear, indeed, that these are merely dermal bones, and there is so much difference between the cranial roof of the two best-preserved specimens, that it is necessary to describe them separately.

Specimen no. 1 *.—The hinder half of the skull in this fossil (Pl. I.) appears to exhibit its natural form; but from the middle of the orbits forwards it is much fractured and laterally compressed. The occipital crest is not much elevated, and the longitudinal median ridge of the roof is gently rather than sharply bent from side to side. A few fixed points can be definitely recognized, and it is necessary in the description to begin with these for the approximate determination of the more problematical bones. The occipital border of the cranium is exposed behind by the crushing of the numerous small supratemporal scales (Pl. I. figs. 1, 1 *a*, *s.t.*), and appears to have been directly transverse, with the exception of a short median peak formed by the supraoccipital element (*s.occ.*). The outer margin of the cranial roof is also well preserved on each side, and the exact limits both of the otic region and the orbits (*orb.*) are indicated. The margin of the supraoccipital plate (*s.occ.*) is distinct except in the hindermost part of its lateral sutures; it projects posteriorly to fit in a triangular notch of the median supratemporal, and is itself excavated in front for the reception of the pointed hinder extremity of another median plate (*p.eth.*), which partly separates the frontals. The latter elements are also readily recognized (*fr.*), and meet in the middle line anteriorly for nearly one quarter of their extreme length. Each frontal in this specimen is much crushed and fractured; but the sutures can be observed, and a detached fragment from another specimen (Brit. Mus. no. P. 6834) confirms the curious bifurcation of the hinder

* A diagram of the arrangement of the cranial roof-bones in this fossil is given in the recently published vol. iii. of the *Catal. Foss. Fishes B. M.* p. 192, fig. 30.

portion here indicated. The outer margin of the bone is excavated by the orbit (*orb.*), and exhibits a short and broad rounded process, extending downwards over the cheek near its anterior end, apparently covering the lateral ethmoidal (prefrontal) cartilage; posteriorly it first meets the squamosal (*sq.*), which also enters the border of the orbit, and then it is excavated by a deep re-entering angle, which divides it into an outer small, and inner large, posteriorly directed process; inwardly it is separated from its fellow of the opposite side by the supraoccipital (*s.occ.*) and another median element (*p.eth.*) behind, by the ordinary ethmoidal plates (*eth.*) in front, and only meets between these for the short length already mentioned; anteriorly the margin is not directly transverse, but inclined much forwards as it approaches the outer edge of the skull. The squamosal (*sq.*) is the last readily determinable element of the cranial roof, and in connexion with the specimen now being described it is interesting also to notice the detached examples of the same bone in the British Museum fossil no. P. 6834. Nearly one third of the outer margin of this bone enters the rim of the orbit, its hinder two thirds forming an almost straight edge above the opercular region; the posterior margin is at right angles to the latter, and the bone unites with adjoining elements in a very wavy suture. It is much broader behind than in front; and immediately behind the orbital rim there is a rugose facette on its inferior face for the articulation of the sphenotic (postfrontal). The smooth hyomandibular facette, which is not much extended, can also be observed; but the remainder of the attached surface of the bone exhibits no facettes. Of the problematical roof-bones, those between the frontal, squamosal, and supraoccipital (marked *x* in Pl. I. fig. 1 *a*) are the most difficult to understand. On the right side of the fossil, fitting into the posterior re-entering angle of the frontal, there is an irregularly triangular plate not extending so far as the occiput, and this element is apparently subdivided by a coalesced suture which obliquely crosses its middle. Another plate, not clearly exhibiting even coalesced sutures, completes the filling of the space between the last-described plate, the squamosal, frontal, and supraoccipital. On the left side of the fossil the same area is occupied by more numerous plates. One apparently equals the foremost triangular bone, but does not exhibit any trace of former subdivision. At least four elements correspond with the hinder bone, the two longitudinal sutures shown in Pl. I. fig. 1 *a* being open and the short transverse suture near the back apparently closed. The median plate (*p.eth.*) interposed between the posterior portion

of the frontals and filling the re-entering angle in the anterior margin of the supraoccipital is bilaterally symmetrical, acutely pointed behind, and widest in front. Some of its median tuberculations are relatively very small. The ethmoidal and facial region in advance of the frontals is apparently completely covered with irregular polygonal plates (*eth.*), more finely tuberculated than the hinder portion of the cranial roof. Some of the posterior median ethmoidal plates are fused together, but indications of the original sutures are distinct. The vomerine region (*v.*), as usual in Pycnodonts, is shown to be very robust and provided with a regularly arranged pavement of teeth. Remains of an external tuberculated plate on the right side may perhaps represent the maxilla (Pl. I. fig. 1, *y*). The stout smooth premaxillæ (*pmæ.*), each exhibiting the bases of three large teeth, are preserved at the end of the snout.

Specimen no. 24 (Leeds Catalogue).—The second well-preserved specimen (Pl. II.) wants the ethmoidal region, but displays the greater part of the cranial roof behind, especially on the right side. The supraoccipital plate (*s.occ.*) extends, as described before, in a short pointed process fitting into the large median supratemporal; but it differs in being much further produced forwards, and may, indeed, be regarded as the supraoccipital proper fused completely with the problematical median plate (*p.eth.*), which is a separate element in the above-described fossil. The frontals (*fr.*) are apparently similar in general form and proportions to those already described; but there is a marked difference in the circumstance that they do not meet at any point in the middle line. The supposed compound supraoccipital plate gradually contracts in width in its anterior half, but is prevented by truncation from ending quite in a point. Its contracting lateral margins articulate with the frontals; but its short front border is apposed to another median plate (*eth.*), which extends as far forwards as the ethmoidal tesseræ. This element is also antero-posteriorly elongated, but gradually widens to the foremost point of its suture with the frontals, and is then quickly narrowed again at its irregular articulation in front. It is doubtless equivalent to the triangular portion of the ethmoidal shield, which only extends into the frontal region for a very short distance in specimen no. 1. The outlines of two of the polygonal ethmoidal plates can be distinguished on the right side of the fossil immediately in advance of the frontal. Among inner bones the crushed ossified mesethmoid can be seen supporting the single denticulous vomer, while a portion of the parasphenoid splint is

exposed from its inferior aspect. The main part of this bone (fig. 1 *a*) is short, stout, and broad, produced below into a median longitudinal keel, and its basiptyergoid processes (*bpt.*) are short, with a very coarsely dentated articular end. At the front extremity of the otic region the parasphenoid is abruptly truncated, the keel terminates in a roughened pointed knob (*k.*), and the element continues merely as a narrow slender median bar across the region of the orbit. A detached example of the same bone in specimen no. P. 6834 (Pl. III. figs. 3, 3 *a*) may be described in almost similar terms; but here the basiptyergoid processes (*bpt.*) are turned a little more outwards and the median keel is partly broken away. The inner face (fig. 3 *a*) shows that this keel was hollow in its deepest portion; and there is a long median scar for articulation probably with the most anterior elements of the brain-case. A pair of foramina, one on either side of the posterior part of the median keel, seem to pierce the bone and open directly on its inner face.

Other Specimens.—The three more fragmentary specimens only remain for consideration, and may be dismissed with brief remarks. No. 2 (Leeds Catal.) is interesting as exhibiting the squamosals with the clearly defined straight occipital border of the skull; and in this fossil the supraoccipital has a less prominent hinder peak than is observed in the specimens described above. No. 23 (Leeds Catal.) is very much crushed and fractured, but the outline of the left frontal is distinct, and, if appearances be not deceptive, its connexions are different from those in both types described above. Here the frontal seems to meet its fellow of the opposite side for some distance, and the ethmoidal shield is disposed as in no. 1; but the hinder part of its inner suture is shaped as in no. 24, and was thus presumably articulated with a median plate much resembling the anterior end of the supraoccipital in the last-named fossil. The third and last specimen is the small group of isolated bones (Brit. Mus. no. P. 6834) of which the squamosal and parasphenoid have been incidentally described above. Among these the right postfrontal (sphenotic) is specially worthy of notice as being well preserved. It is small and meets the squamosal in a triangular rugose facette; its smooth outer face is triangular, while its equally smooth anterior face is gently concave, to form part of the hinder wall of the orbital cavity; inwardly it is roughened for articulation with another otic element; its posterior aspect takes part in the facette for the upper end of the hyomandibular; and its lower extremity shows a coarsely interdigitating articular surface. A problematical bone from the

base of the skull (Pl. III. figs. 4, 4 a) is also interesting. It is bilaterally symmetrical and seems to have been formed in cartilage; and the only suggestion the present writer can make is that it represents a basisphenoid immediately behind the parasphenoid. It is longer than broad, and its presumably inferior face (fig. 4) exhibits a longitudinal keel which is partly broken away; it is narrowest at what appears to be its hinder extremity, while the lateral margins form sharp edges, each apparently notched near its anterior end. There is an oblique roughened articular surface behind, shown on the lower aspect (fig. 4, *p.f.*), and another similar surface, sloped in the opposite way, appears from the inferior aspect in front (*a.f.*), this fitting very well upon the parasphenoid if it happens to have been placed as here supposed. The inner face of this problematical bone (fig. 4 a) is comparatively flat, exhibiting only a possible articular surface at its narrowed posterior end. A pair of large foramina pierce the bone obliquely near its middle, the inferior opening being situated further forwards than its superior exit.

Jaws and Facial Bones.

The mandibular suspensorium is unknown and the pterygoquadrate arcade is exhibited only in one specimen (no. 1). Like that of *Anomæodus Willeti*, this arcade is in the form of a delicate toothless plate (Pl. I. fig. 1, *ptq.*), but it is unfortunately only preserved and exposed in its most posterior portion, where the concavely arched front margin of the ectopterygoid passes into that of the quadrate (*qu.*). The latter element is comparatively robust, and it seems to exhibit a surface of attachment for the symplectic along nearly the whole of its hinder margin; at least an apparently articular surface may be observed in this position on both sides of the only known specimen. Its articular face for the mandible is irregularly oval, much deeper than broad, and slightly concave. The premaxillæ (*pmx.*) are robust, deep, and narrow, meeting in the middle line and each showing the bases of three teeth. They are smooth and overlapped by the tuberculated ethmoidal plates, and each is notched on its outer lateral margin. Whether or not any facial element can be identified with the maxilla is uncertain; but one large tuberculated cheek-plate (*y*), deeper behind than in front, extends down to the border of the upper jaw. This plate is very thin and toothless. A small cheek-plate (*z*) covers the outer face of the postfrontal bone, and there is evidence of equally small irregular suborbitals (*s.o.*). The mandible is sometimes

partly obscured by the crushing of facial bones upon it; but the four specimens in the Leeds Collection suffice to exhibit all its elements. The dentary bone (Pl. I. fig. 1, *d.*; Pl. II. fig. 4; Pl. III. fig. 2, *d.*) is comparatively insignificant, thin, deep, and narrow, meeting its fellow in the middle line and bearing a row of four large teeth. The greater portion of its external surface is ornamented with tubercles, and it sends a postero-inferior process underneath the large angular plate. The latter plate (Pl. II. fig. 5; Pl. III. fig. 2, *ang.*) does not extend upwards so far as the oral margin, but it completes the hinder portion of the outer face of the mandibular ramus, and its hinder ascending portion meets a small coronoid bone (*cor.*) in a very wavy suture, which is frequently closed. The upper portion of the coronoid bone is very thin and quite smooth, and does not reach the tip of the great coronoid process of the splenial. Indeed, the splenial element (Pl. I. fig. 1, *spl.*; Pl. II. fig. 3; Pl. III. fig. 2, *spl.*) is exposed on the outer aspect of the entire margin of the mandibular ramus behind the short oral border of the dentary. It is much the largest and stoutest bone in the jaw, meeting its fellow of the opposite side at the symphysis and completely covered to the base of its coronoid elevation with a pavement of teeth. The articular bone (Pl. I. fig. 1, *art.*), on the inner face of the angular and apparently distinct, is always distorted by crushing, though considerably ossified.

Dentition.

Teeth are confined to the vomer, splenial, premaxilla, and dentary. They are all hollow, with a short base firmly ankylosed to the supporting bone. Certain displaced and unusually coloured dental crowns are more suggestive of the existence of successional teeth than any evidence the present writer has hitherto observed; but there is still no conclusive proof of such displacement of the worn teeth. Of the prehensile front teeth only one is preserved in the right dentary of no. 24 (Pl. II. fig. 4); its base is elevated, while the crown is transversely elongated and chisel-shaped, convex on the outer face, concave within. As already mentioned, each premaxilla bears three of these teeth, while each dentary has four, all about of equal size. The oral surface of the vomer (Pl. I. fig. 1 *b*; Pl. II. fig. 2) is flat and bears three principal longitudinal series of teeth, one median and a symmetrical pair on the lateral margins. The lateral teeth are not much inferior in size to those of the median series, but in the anterior half of the bone there is an intermediate pair of rows of teeth scarcely

half as large as the others; and as these pass backwards they become more and more irregular, are supplemented with more intermediate teeth, the majority still smaller and all very irregularly arranged. The dentition on the splenial bone (Pl. I. figs. 1, 1 c; Pl. II. fig. 3) extends to its outer margin as far as the base of the coronoid process. There is one principal longitudinal series of oval teeth, about as large as the median vomerine series, but the long axis of each tooth oblique. The outermost row of teeth (wanting in the original of Pl. I.) is not much inferior in size, and, as in the vomer, the external end of each tooth is produced into a slight peak for grasping. Within the principal series one regular row of round teeth about half as large and an innermost irregular row of still smaller teeth can be observed. Between the principal and outermost series the same small teeth, disposed almost symmetrically with those on the inner side of the principal series, are also seen; but, except in the anterior third of the bone, these two rows are supplemented and partly disturbed by the interposition of other small teeth. All these tritoral teeth in both jaws are smooth and exhibit a shallow apical indentation, with a crimped margin, very rarely also with a slight median tubercle. The shape of the indentation varies with that of the tooth, and the hinder portion of its crimped border is not infrequently wanting.

Opercular and Branchiostegal Apparatus.

The opercular apparatus is well displayed, and the operculum and preoperculum can be readily identified. On the left side of no. 2 these bones are crushed a little downwards and the upper end of the hyomandibular is thus partly exposed, showing the short and deep process for the suspension of the operculum. The last-mentioned plate is also preserved among the isolated bones in Brit. Mus. no. P. 6834 (Pl. III. figs. 5, 6). It is comparatively small, deep and narrow, its truncated upper end twice as broad as the supratemporals (shown in Pl. I. fig. 1), its straight anterior border placed vertically at the line of the occiput, and its lower half tapering to a point. In front it is overlapped, as usual, by the preoperculum (*p.op.*), and there is a large hollowed articular facette (Pl. III. fig. 5 *a, f.*), well within on its anterior border near the upper extremity, for its suspension on the hyomandibular process. The preoperculum is the large irregularly triangular plate always conspicuous in *Pycnodont* skulls, and in no. 2 its hinder margin distinctly corresponds with that of the hyomandibular. On the right side of no. 1

(Pl. I. fig. 1, *p.op.*) it is shattered by fracture in front, but it is well preserved at the upper end; and in this fossil, as also in no. 2, there is shown interposed between it and the squamosal a small apparently nearly square plate (*z*), which is tuberculated as usual. The preoperculum thus does not extend upwards quite so far as the operculum, which seems to touch the hinder angle of the cranial roof; but its great expanded inferior portion reaches considerably further downwards on the cheek than the tapering lower end of the latter element. Below the preoperculum in no. 1 there are remains of two slender plates having the appearance of branchiostegal rays, the upper of considerable size, the lower very small and delicate. The first is also seen in nos. 2 and 23, and on the external face it is always in part tuberculated. The space between the mandibular rami (Pl. III. fig. 2) is completely covered with very small and delicate polygonal tessellated plates (*t.*), marked with a tubercular ornament as coarse as that of the other bones.

Appendicular Skeleton.

The post-temporal bone and supraclavicle are not recognizable. There is reason to believe that neither of them was exposed on the tuberculated exterior of the fish, for in no. 1 the expanded upper end of the first dorso-ventral series of flank-scales is shown to curve forwards and to be directly overlapped by the small supratemporals. The same arrangement is also suggested by no. 2, where the foremost scales are displaced and exhibit the comparatively fine tubercles of their hidden front margin. The clavicle is relatively small, and this element of the left side is detached in no. 24. Its exposed portion (Pl. II. fig. 6) is restricted and narrow, ornamented with tubercles only on its short inferior limb, while its long fibrous upper limb is considerably thickened. There is no laminar expansion of the bone bent inwards at its anterior border. The coraco-scapular attachment is shown on the inner face (Pl. II. fig. 6 *a*), but neither coracoid, scapula, nor basals are preserved, only the unjointed bases of the fin-rays in one specimen.

The pelvic fins are present, but quite small and insignificant. The best-preserved example in no. 1 exhibits only five rays, which are rather stout and soon become very closely divided and articulated at a short distance above the base. Nothing is known of the basal pelvic elements.

Of the median fins only a fragment at the origin of the caudal is preserved in no. 2. This is identifiable on com-

parison with the corresponding fin in a specimen of *Mesturus verrucosus* in the British Museum (no. 37023). The rays at the anterior border gradually increase in length. The two foremost rays are practically only elongated ridge-scales, the right and left halves of each being fused together at the apex; the next two rays are also unjointed, but exhibiting the two halves completely separated; the fifth ray shows three articulations, two being close together and the third a long distance further up; the succeeding rays are all closely jointed distally. Between the extremities of the second to the fifth rays on the anterior border there are four short and delicate regularly alternating intercalary rays, which may perhaps be termed fulcra.

Squamation.

The trunk is very incomplete in all the specimens, but considerable portions of the squamation of the abdominal region are preserved. The scales (Pl. III. fig. 1) are all thick and quadrangular, not strengthened within by any well-defined rib, but deeply imbricating, and united above and below both by the peg-and-socket articulation and by a jagged suture. This remarkable suture is most pronounced on the middle of the flank, reduced to a slight waviness towards the ventral border of the fish, while in one specimen (no. 23) it is comparatively feebly marked. The external face of each scale is ornamented with large and rounded closely arranged tubercles; but these are wanting towards the smooth hinder border, which is not denticulated. The very regular flank-series become less regular towards the ventral margin, and in no. 1 one series terminates in a wedge-shaped scale slightly above and in advance of the pelvic fins. Some of the flank-scales are about twice as deep as broad, while those of the ventral region are mostly about as broad as deep. The azygous ventral ridge-scales are very narrow, ornamented as the others, but having some of the tubercles pointed and delicately striated; they are destitute of any inwardly directed process, and merely unite with the adjoining scales by a jagged suture.

II. SYSTEMATIC DETERMINATION.

The generic determination of the fossils thus described is rendered easy by the nature of the scales. The typical species of *Mesturus*, *M. verrucosus**, as represented in the British

* A. Wagner, Abh. k. bay. Akad. Wiss., math.-phys. Cl. vol. ix. p. 338, pl. iii. fig. 1 (1862).

Museum by a fine specimen from the Bavarian Lithographic Stone (no. 37023), shows that most of the scales in this genus are united above and below by jagged sutures—a feature, so far as the present writer is aware, unique among fishes. The new Oxfordian specimens from Peterborough not only agree in exhibiting this peculiarity, but also in the general aspect of all the other parts which can be compared. Although the caudal fin is wanting in all these fossils, there can therefore be no doubt that they belong to the fan-shape-tailed *Mesturus* rather than to the fork-tailed *Gyrodus*, which is the only other genus displaying much resemblance.

With regard to specific characters, it may be remarked that these are usually sought among Pycnodonts in the tritoral dentition. The precise characters of the teeth of *M. verrucosus*, however, are unknown, and the dentition in three of the Oxfordian specimens now described is so remarkably similar, notwithstanding the striking differences in the arrangement of the bones of the cranial roof and the variation in the tubercular ornament, that it is difficult to form any judgment as to nomenclature. The specimen of *M. verrucosus*, however, in the British Museum is characterized by an irregular enlargement of the tubercles along the anterior half of the course of the “lateral line,” while many of its scales display radiating structural lines; and both these features are wanting in the new fossils from the Oxford Clay. We therefore appear to be dealing with a new species, of which the dental characters are described in detail on p. 8, and it may be appropriately named *Mesturus Leedsi*, in compliment to its discoverer. The fossil no. 1 (Leeds Catalogue) must be regarded as the type specimen, and the others are provisionally associated with it until complete examples of each of these varieties are discovered.

III. CONCLUSIONS.

Two most important results are obtained from the new specimens of *Mesturus* now described. The arrangement of the cranial roof-bones of a Pycnodont fish is discovered for the first time, and the true nature of the opercular apparatus is determined. It is also interesting to observe a partial confirmation of the facts in regard to the arrangement of the jaws, which were revealed two years ago by the study of the Cretaceous genus *Anomæodus**.

* A. S. Woodward, “On the Genus *Anomæodus*, with Remarks on the Structure of the Pycnodont Skull,” *Geol. Mag.* [3] vol. x. (1893) p. 487, pl. xvii. fig. 1.

The bony shield of the cranial roof is remarkable for its close resemblance to the corresponding shield in *Acipenser* and certain Siluroids. It is, in fact, the first instance of this arrangement of plates recorded among fishes which exhibit a trunk and fin-skeleton on the same biological level as the Pycnodont type. Moreover, the disposition of the sutures is evidently as capricious as that in *Acipenser*; for not only do the parietal plates of no. 1 lack bilateral symmetry, but two specimens so closely similar in other respects as nos. 1 and 24 differ completely in the arrangement of the median roof-elements. It is also to be noted that in the allied genera *Mesodon*, *Microdon*, and *Gyrodus* there is only one parietal plate on each side, while from this in the two first-mentioned genera there arises a large posteriorly directed process with digitate extremity, which extends immediately beneath the dorsal scales of the trunk. In the Cretaceous *Coccodus* all the elements of the cranial roof are fused together. The external bones of the Pycnodont skull are thus of an anomalous and variable character.

The opercular apparatus is equally remarkable, and only paralleled among deep-bodied Teleostean fishes in which the jaws are displaced far forwards (e. g. *Lampris* and the Gymnodonts). The small operculum has hitherto been described as "supraclavicle;" but if any evidence of its identity is required beyond that described above, it is only necessary to examine a specimen of *Gyrodus* in the British Museum (no. 37108), where the element may be seen suspended by the opercular process of the hyomandibular*. The identification of the preoperculum ("operculum" of previous authors) is confirmed by its demonstrated relationships in *Anomæodus Willetti*. The two branchiostegal rays and the tesseræ of the gular region have previously been noticed in *Gyrodus*.

In estimating the taxonomic value of these and the generally-known characters of Pycnodonts it is necessary to remember two facts:—Firstly, that *Acipenser* and its living allies are proved by palæontology to be the degenerate descendants of ganoid fishes which had the cranial roof-bones arranged in a normal manner (cf. *Chondrosteus*); secondly, that the disposition of the opercular apparatus, as also the firm fixation of the pterygo-palatine arcade, observed in the Pycnodonts, is likewise met with in more than one group of the bony fishes—is, in fact, merely a physiological correlation (1) with the reduction in size of the outlet of the gill-cavity, (2) with the forward displacement of the mouth, and (3) with

* This fossil is described and figured in the recently published vol. iii. of the Catal. Foss. Fishes B. M. p. 235, pl. xvi. fig. 3.

the powerful development of the dentition. Thus the Pycnodonts *may* be closely related to other ganoid fishes with normal skulls, and their nearest allies *may* exhibit a quite ordinary opercular and branchiostegal apparatus if the mouth be less displaced or the dentition less powerful.

Having premised so much, it only remains to emphasize again the contention of Traquair * that the Pycnodont skeleton, considered apart from the head, is completely "Lepidosteoid" in character. This emphasis is all the more necessary since, even in a modern handbook, which is authoritative in most respects, the exploded errors of thirty years ago are allowed undue influence, and the "special" difference between Pycnodonts and the Palæozoic Platysomidæ is said to consist in "the dentition and arrangement of the jaws" †. As a matter of fact, all the fundamental differences are in the trunk. In Pycnodonts the tail is atrophied-heterocercal, the rays of the dorsal and anal fins are supported by a single series of endoskeletal elements of equal number, and there are no infraclavicles. Even the most specialized of known Platysomidæ never exhibit the faintest approach to this combination of characters; the heterocercal tail and multiple-rayed median fins are as pronounced in the most specialized as in the most generalized types. The summit of Platysomid evolution seems to have been attained by the anomalous Permian genus *Dorypterus*. The only known link between the grade of fish to which *Platysomus* belongs and the higher grade in which the Pycnodonts must be placed is the Triassic family of Catopteridæ, where the upper caudal lobe is hemiheterocercal, while the rays of the dorsal and anal fins are nearly as few as their supports, which are ranged in only one series. Present knowledge is therefore in favour of the supposition that the Pycnodonts are a secondary modification of the higher or "Lepidosteoid" grade, which was first reached through comparatively generalized types of fishes resembling the Catopteridæ.

In fact, making allowance for the morphological changes necessitated by a reduced branchial outlet and a forwardly displaced mouth—further, admitting that the anomalous arrangement of the cranial roof-bones is the result of degeneration—there is little to distinguish the Pycnodonts from *Lepidotus*, *Dapedius*, and their allies. It is certainly noteworthy that *Lepidotus* itself, which has the most highly developed tritoral dentition, exhibits very few branchiostegal

* R. H. Traquair, "On the Structure and Affinities of the Platysomidæ," Trans. Roy. Soc. Edinb. vol. xxix. (1879), pp. 382-386.

† K. A. von Zittel, 'Grundzüge der Palæontologie' (1895), p. 574.

rays and no gular plate, while the cheek-plates are very irregularly subdivided. It is also curious that the allies of this genus and *Dapedius* (e. g., *Tetragonolepis* and *Aetheolepis*) are the only known "Lepidosteoids" in which the caudal squamation degenerates behind a definite straight line, as it does in so many Pycnodonts. On the whole, therefore, it is reasonable to refer the fishes under discussion to a place among the "Lepidosteoids" corresponding with that occupied by *Acipenser* among the "Acipenseroids" and by the Siluridae among ordinary Physostomi.

EXPLANATION OF THE PLATES.

Mesturus Leedsi, sp. n.—Oxford Clay, Peterborough. All the figures natural size unless otherwise stated.

PLATE I.

- Fig. 1.* Head &c., right lateral aspect, with right mandibular ramus removed, one-half nat. size. [Leeds Collection, no. 1.]
Fig. 1 a. Ditto, superior aspect, one-half nat. size. *art.*, articular; *d*, dentary; *eth.*, ethmoidal plates; *fr.*, frontal; *op.*, operculum; *orb.*, orbit; *p.eth.*, posterior ethmoidal; *p.op.*, preoperculum; *pct.*, pectoral fin; *pma.*, premaxilla; *ptq.*, pterygo-quadrate arcade; *qu.*, quadrate; *s.o.*, suborbitals; *s.occ.*, supraoccipital; *s.t.*, supratemporals; *spl.*, splenial; *sq.*, squamosal; *v.*, vomer; *x*, parietals; *y*, maxilla (?); *z*, undetermined dermal plate.
Fig. 1 b. Ditto, vomerine dentition.
Fig. 1 c. Ditto, left splenial dentition, wanting outermost series.

PLATE II.

- Fig. 1.* Imperfect head, superior aspect, two-thirds nat. size. [Leeds Collection, no. 24.] Letters as in Pl. I.
Fig. 1 a. Ditto, parasphenoid, inferior aspect, two-thirds nat. size. *bpt.*, basiptyergoid process; *k.*, knob; *pas.*, main part of bone; *pt.f.*, postfrontal (sphenotic).
Fig. 2. Ditto, vomerine dentition.
Fig. 3. Ditto, left splenial with dentition.
Fig. 4. Ditto, right dentary, outer aspect.
Fig. 5. Ditto, right angular, outer aspect.
Fig. 6. Ditto, left clavicle, outer and inner (6*a*) aspects.

PLATE III.

- Fig. 1.* Portion of squamation. [Leeds Collection, no. 1.]
Fig. 2. Mandible. [Leeds Collection, no. 2.] *ang.*, angular; *cor.*, coronoid; *d.*, dentary; *spl.*, splenial; *t.*, tesserae.
Fig. 3. Parasphenoid, inferior and superior (3*a*) aspects. [British Museum, no. P. 6834.] *bpt.*, basiptyergoid process.
Fig. 4. Supposed basisphenoid, inferior and superior (4*a*) aspects. [Ditto.] *a.f.*, anterior facette; *p.f.*, posterior facette.
Fig. 5. Right operculum, outer and inner (5*a*) aspects. [Ditto.] *f.*, facette for hyomandibular suspension.
Fig. 6. Left operculum, imperfect below, outer aspect. [Ditto.]