NO. IV.—ON *CLADODUS NEILSONI* (TRAQUAIR), FROM THE CARBONIFEROUS LIMESTONE OF EAST KILBRIDE. By R. H. TRAQUAIR, M.D., LL.D., F.R.S., Keeper of the Natural History Collections in the Museum of Science and Art, Edinburgh. With a Plate [No. IV.], by the Author.

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IN 1888 I published a brief account of this remarkable specimen, which has been since that time frequently referred to by writers on palæozoic Selachii. I regret that it is only now, after an interval of nearly nine years, that I send to the Secretary of the Society a detailed description, accompanied by drawings; but perhaps there is, after all, a counterbalancing advantage in having meanwhile been able to compare it with the descriptions and figures of other ancient Cladodont sharks given by American writers, namely, Newberry, Clappole, Bashford Dean, and Cope.

But as the main object of the present paper is to lay before ichthyologists the facts which are shown in this unique specimen, I shall for the present avoid as much as possible the discussion of those theoretical points which may be suggested by the structures therein displayed.

Description.—The specimen represented in Plate iv., fig. 1, as one half natural size, is in the collection of Mr. James Neilson of Glasgow, who obtained it from the late Mr. Andrew Patton of East Kilbride, by whom it was recovered from the quarry there. As the pieces of which it is composed came up separately from the workings, Mr. Patton did not, I understand, feel quite sure that they all belonged to the same specimen. They were, however, fitted together by Mr. Neilson, and after a most careful scrutiny of the whole, I came to the conclusion that the fragments did belong to the same specimen, and that they were rightly arranged.

We have here the greater part of the head, the branchial apparatus, the shoulder girdle, and the two pectoral fins—the parts exhibited covering a space 20 inches in length.

The head, crushed vertically, is in this figure seen from above. On the left side the cranium (*cr.*) is imperfect—a large portion, both laterally and anteriorly, being cut off by a line passing from a point to the right of the centre of the front of the rostrum obliquely backwards and outwards. On the right side it is easy

to distinguish the margin of the orbit (*o.*) with its preorbital process in front, and bounded posteriorly by a strong, pointed, nearly triangular postorbital projection, behind which the lateral cranial margin proceeds nearly straight backwards to join the transversely directed occipital one, the angle being however cut off.

As here exhibited the cranium is $5\frac{1}{2}$ inches in length, and one cannot fail to be struck with the resemblance which it bears in its contour to that of the Notidanidæ (*Notidanus*, *Chlamydoselache*).

On the side of the cranium, and behind the postorbital process, is the attachment of a strong, straight portion of cartilage, which passes backwards and slightly outwards for a distance of 5 inches. The only interpretation which can be placed on this cartilage is that it represents the *hyomandibular* element.

Behind the cranium, and extending back for a distance of 6 inches, and occupying a breadth of 4, is a confused mass (*br.*), consisting evidently of rod-like cartilages, all broken and crushed together. We see in this mass the remains of the branchial apparatus; and though there is no possibility of identifying individual branchial arches, the whole ends behind in a free pointed process (*c.*), which is plainly the posterior extremity of the last basibranchial piece, and which we find forming a similarly shaped and similarly placed pointed process in a large number of recent Selachii.

The anterior piece of the fossil can now be lifted up and turned over, as it is represented in fig. 2, in which we have a view of a large portion of the *under* surface of the head.

We are first struck by the two rami of the lower jaw (*mn*), which converge anteriorly to meet at a very acute angle; owing to vertical crushing the substance of these rami appears folded longitudinally. External to the margin of the lower jaw on each side, the whole space is covered with teeth, but these teeth are all in disorder, forming a confused mass in which nothing of their original arrangement can be seen. There can be no doubt that the cartilage upon which these teeth rest is the palato-quadrate, though the teeth themselves appertain to both jaws.

So far as can be seen in the specimen, all the teeth are similar in size and shape. Each consists of a base surmounted by pointed and striated cusps. The base equals (in the specimen figured in

Plate iv., fig. 4) $\frac{3}{8}$ inch in transverse and $\frac{1}{8}$ inch in antero-posterior diameter; it is flat below, oval in outline, but having the anterior contour flatter than the posterior, and it is also to be noted that at the anterior margin there is a small flattened button-like projection in the middle line.

From the upper surface of the base rise the pointed cusps, but it must be noted that *the front of the base forms a sharp margin* (fig. 3) *marked off from the cusps at their origin*, and by this feature the present specimen of *Cladodus* is distinguished from all others with which I am acquainted.

The cusps are ordinarily five in number—one large median, with two smaller lateral ones on each side. The median cusp is conical and pointed, about as high as the transverse diameter of the base is long; it is slightly inflated below and very gently recurved, oval in transverse section, becoming two-edged upwards. The surface is covered with fine sub-parallel, nearly straight, vertical striæ, which increase towards the base by intercalation.

On each side there are two smaller cusps, of which the outer and larger is slightly divergent in its direction, while the inner and smaller has its axis more parallel with that of the central one. These two smaller cusps are conformed and striated like the central one.

If we now return to that portion of the fossil which lies behind the head and the remains of the branchial apparatus, we are at once struck by the presence of two largely-developed *pectoral fins*.

That of the right side is attached to a scapulo-coracoid cartilage (*s.c.*), whose postero-superior extremity is clearly exhibited, while its antero-inferior one is apparently concealed by the crushed mass of branchial cartilage. It is expanded anteriorly, and gently curved—the anterior margin being regularly concave, but the posterior one shows a bluntly angular projection to which the fin is attached.

The elements of this fin are seen to fall into two sets, proximal and distal, separated by a longitudinal line of joints. These correspond respectively with the “basals” and “radials” of the ordinary shark pectoral.

The proximal or basal set consists first of some eight or nine staff-shaped pieces (*pt.*), each about $\frac{3}{4}$ inch in length, placed close together, and having their proximal extremities attached to the

above-mentioned projection of the posterior margin of the shoulder-girdle. These are immediately followed posteriorly by a flat oblong trapezoidal piece (*mt.*) $1\frac{3}{4}$ inch in length, and broader in front than behind. Its anterior portion shows some slight appearance of having been formed by the fusion of staff-like bars similar to those in front. The rest of the surface is flat, while its narrow posterior margin articulates with the first of a series of nine flattened rectangular pieces, forming a posteriorly-directed narrow jointed stem which attains a length of five and a half inches.

The distal elements consist of slender cylindrical rays (*r.*) articulated to the shorter staff-like proximal pieces (*pt.*), and to the oblong piece behind these (*mt.*). Closely placed, they rapidly increase in length in front and fall off more gradually behind, the longest being cut off by the edge of the stone. But it is also to be noticed that behind these closely set rays attached to the pieces marked *pt.* and *mt.*, there are three which are shorter, more slender, and more distantly placed. One of these arises from the junction between the oblong plate (*mt.*) and the first small rectangular joint of the longitudinal chain; the second from the junction between the first and second of these pieces; the third from the middle of the second piece of that chain. On the inner or post-axial side of the chain no rays whatever are seen.

The fin of the left side is much less perfectly preserved. Only a small portion of the scapulo-coracoid cartilage is seen, but the rest of the elements are clearly indicated, though no small rays appear on the outer aspect of the chain. The two chains, right and left, cross each other near the hinder edge of the stone, but that this is obviously a *post mortem* distortion it is hardly necessary to remark.

Observations.—I hardly think that, so far as the configuration of the teeth is concerned, anyone will deny to the present specimen a position in the genus *Cladodus* of Agassiz, though it differs markedly from the type species *C. mirabilis* (Ag.) in the front of the base of the tooth, which shows, below the origin of the median cusp, a prominent rim instead of a shallow excavation. And although there can be no doubt that the *Cladodont* shape of tooth was also present in form generically distinct from the typical *Cladodus*, it will certainly be convenient to retain the

East Kilbride specimen, provisionally at least, in the genus in question.

As to species, it is certainly not referable to any of those which are ordinarily known, the only form resembling it being *Cladodus Hibberti* of Agassiz, from Burdiehouse—at least judging from the figure given by Agassiz in the "Poissons Fossiles." But neither that figure nor the description in the text is adequate to determine the species in the absence of the type specimen, which seems unfortunately to be lost. Feeling therefore under the necessity of devising a new specific name for the above-described fish, I have pleasure in adopting for it the name of my friend Mr. Neilson, to whose kindness I am indebted for the loan of the specimen and permission to publish it.

The next point to be noticed is the great resemblance which the skull of *C. Neilsoni* bears to the skull in the living Notidanidæ, and especially to that of *Chlamydoselache*, Garman. It will be remembered that Garman, in his description of that remarkable genus, specially insisted on its relation to the extinct Cladodonts, on account of the configuration of the teeth of which those at least which are situated towards the angle of the mouth are very Cladodont in appearance. But the skeleton of the pectoral fin has in *Chlamydoselache*, as in *Notidanus*, already assumed the structure of the ordinary shark pectoral, its basal elements showing the three characteristic pieces named by Gegenbaur propterygium, mesopterygium, and metapterygium; and though the latter has more than one segment, it does not run back in the form of a long many-jointed chain, as in the fish now before us. It is, however, of great interest to see that there is a bond between *Cladodus* and *Chlamydoselache*, though the alliance is perhaps not quite so close as Mr. Garman supposed.

And if this species *Neilsoni* be rightly referred by me to the genus *Cladodus* of Agassiz, then Bashford Dean is also right in separating, under the new generic name of *Cladoselache*, those remarkable fishes with Cladodont teeth, flap-like paired fins, and sclerotic ring, from the Upper Devonian of Ohio, which had been referred to *Cladodus* by the late Professor Newberry. For so far as Dr. Dean's researches go, the basal arrangement in the paired fins of *Cladoselache* are of a simple character, and there is no trace of the long-jointed stem which is so prominent a feature in the pectoral of *C. Neilsoni*.

And what is, in point of fact, the real significance of that remarkable arrangement of cartilages exhibited in the pectoral fin of *Cladodus Neilsoni*?—that is the question which gives the specimen its chief interest.

The skeleton of the pectoral fin of the recent sharks, with its three basal cartilages, *propterygium*, *mesopterygium*, and *metapterygium*, which intervene between the shoulder girdle and the radials, is maintained by Gegenbaur to have been probably derived from an arrangement like that in the recent *Ceratodus*, where we have a median segmental stem, fringed with radials on each side, postaxial as well as preaxial. To this type of paired fin-structure which occurs not only in both pectoral and ventral limbs in Dipnoi, *e.g.*, in the recent *Ceratodus* and the fossil *Dipterus*, *Phaneropleuron*, &c., but also in the pectoral of the fossil Crossopterygian *Holoptychius* and of the fossil Selachian *Pleuracanthus*, Gegenbaur applies the term *Archapterygium* as embodying the idea of its primitive character in relation to the paired fin-structure seen in more modern sharks and other fishes. And the mode in which he supposes the Archapterygium to have evolved into the usual Selachian arrangement is briefly as follows:—The median stem simplified, shortened up, and losing all its radials on the postaxial side, except in some cases, a few near the tip, becomes the metapterygium, while the mesopterygium and propterygium are formed by the fusion into two pieces of the basal joints of a number of preaxial radials which have reached and become attached to the shoulder girdle in front of the metapterygium.

Now, the specimen of *Cladodus Neilsoni* before us gives what seems to be a remarkable corroboration of the truth of the general correspondence of the parts. The oblong trapezoidal piece (marked *mt.* in Plate iv., fig. 1), with its succeeding chain or stem of narrow joints, is unquestionably the metapterygium, while the mesopterygium and propterygium are equally clearly represented by the still separate staff-shaped cartilages (*pt.*) in front, which, according to Gegenbaur's view, may be the basal joints of the more anteriorly-situated preaxial radials, to whose extremities they are articulated distally, while proximally they have reached the shoulder girdle. As there are no radials on the postaxial side of the metapterygial stem, I stated in my first description of the

specimen that the arrangement was "capable of bearing the interpretation that we have here a veritable uniserial archipterygium intermediate between the truly biserial one of *Xenacanthus* (*Pleuracanthus*) and the pectoral fin of ordinary sharks." Furthermore, I added that "if this interpretation is correct, then along with *Xenacanthus* this specimen is a witness against the lateral fold theory of the paired fins at present so popular with anatomists and embryologists."

A fragment of a Cladodont fish from the Coal Measures near Galesburg, Ohio, has, however, been recently described by Professor Cope under the name of *Symmorium reniforme*, in which, while the pectoral fin bears some resemblance to that of my *Cladodus Neilsoni*, the metapterygium is not divided into transverse segments. Remarking on this form, Professor Cope observes that "the fin-structure discovered by Traquair, contrary to his supposition, supports the ptychopterygium theory, and the modern fin is derived not from the archipterygium but from the ptychopterygium."

To enter here into a discussion of the archipterygium and lateral fold theories of the paired limbs would carry us far beyond the scope of the present paper, which is simply to give an accurate figure and description of the specimen of *Cladodus Neilsoni* from East Kilbride. It will suffice for the present if I point out the way in which the supporters of the lateral fold theory, in the form advocated by Cope and Bashford Dean, will naturally explain the pectoral fin-structure which is exhibited in that specimen.

According to that theory the pectoral and ventral members represent portions now isolated of an original hypothetical lateral fin-fold, from which they have been evolved while the intermediate portion of the fold has disappeared. The earliest stage in the development of skeletal structures will then be seen in the paired fins of *Cladoseleache*, figured and described by Newberry, Bashford Dean, and Smith Woodward, in which these organs appear to form fold-like rounded-triangular projections from the side of the body, supported by rod-like "radial" cartilages jointed to shorter "basals" placed in the body-wall. This is the "*Ptychopterygium*" of Cope.

From these basal cartilages the propterygium, mesopterygium, and metapterygium of ordinary sharks will be evolved by a process

of fusion, the metapterygium having also a tendency to rotate outwards and so become *external* to the body-wall.

What then, according to this scheme, is the central-jointed axis of the *Pleuracanthus* or *Ceratodus* fin? It will still remain the equivalent of the metapterygium, but the process of evolution will have proceeded precisely in the opposite direction to that conceived of in the theory of Gegenbaur. The metapterygium will have to be looked upon not as formed from the fusion of the joints of an original central axis, but from the fusion of basals whose original position was in the body-wall; not as having originally had radials on both sides (biserial), but as having had them originally only on the preaxial side (uniserial); not as having been originally a projection from the outline of the body, but to have been originally *in* the body-wall, and then, *turning outwards*, to have *subsequently* acquired radials also on the postaxial side, so as to form the central axis of such a fin as is seen in *Pleuracanthus* and in the Dipnoi.

Turning now to our *Cladodus* from East Kilbride, it is easy to see how the supporters of this view will find in it a corroboration of their ideas. A line of articulations separates the slender cartilages (*r.*) (Plate iv., fig. 1), both from the staff-like elements (*pt.*) (= propterygium and mesopterygium) and from the oblong piece (*mpt.*) which, with its appended chain of little rectangular pieces, represents the metapterygium. The staff-like bodies (*pt.*) will then not be, as Gegenbaur's theory requires, the proximal joints of archypterygeal radials which have reached the shoulder-girdle, but *basals* which still remain ununited, while in the first oblong piece of the metapterygium (*mpt.*) they are fused—the succeeding rectangular segments of the chain being also formed, each from a certain number of united basals. Thus, instead of this *Cladodus* fin being a transition from the *Pleuracanthus* form to that of the ordinary shark, it will, from this point of view, be a transition from the "ptychopterygium" of *Cladoselache* to the *Pleuracanth* and Dipnoian limb.

It will also, however, have to be noted that, while Cope and Bashford Dean would derive the tri-basal pectoral of ordinary sharks direct from the ptychopterygium, Fritsch and Smith Woodward would look upon it as being again in its turn derived from the *Ceratodus*-like fin of *Pleuracanthus*.

As I have said previously, it would be out of place for me in the present paper to enter into a discussion of the enormous subject of the evolution of the skeleton of the paired fins in fishes. More especially as practically a new aspect has been given to the matter by Dollo in his recent valuable paper on the "Phylogeny of the Dipnoi"—his views demanding most careful thought and study before we can venture either to accept or reject them. It is, however, plain that if Dollo's theory as to the origin of the Dipnoi from the Crossopterygian "ganoids" is correct, then the "archipterygium" of the Selachian *Pleuracanthus* must have had a distinct origin from those of the Dipnoan *Dipterus* and *Ceratodus*.

Literature.—The literature of the fin-question is enormous. It is, however, only necessary here to note such works as more especially bear upon the subject of the above paper:—

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3. Dean, Bashford.—"A New Cladodont from the Ohio Waverley." *Trans. New York Acad. Sci.*, vol. xiii., 1894, pp. 115-119.
4. Dean, Bashford.—"The Fin-fold Origin of the Paired Limbs, in the light of the Ptychopterygia of Palæozoic Sharks." *Anatomischer Anzeiger*, vol. xi., 1896, pp. 674-679.
5. Fritsch, A.—"Fauna der Gaskohle, &c., der Permformation Böhmens," vol. iii., pt. 2, 1893.
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8. Woodward, A. S.—"Catalogue of Fossil Fishes in the British Museum," pt. ii., 1891.
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Fig. 3.

Fig. 4.

CLADODUS NEILSONI, Traquair.
East Kilbride.

EXPLANATION OF PLATE IV.

Fig. 1.—Head and pectoral fins of *Cladodus Neilsoni*, Traq., Lower Carboniferous, East Kilbride, in the collection of Mr. James Neilson, Glasgow. One-half natural size; *o.*, orbit; *h.m.*, hyomandibular; *br.*, branchial cartilages; *c.*, pointed posterior extremity of the last median basibranchial piece; *s.c.*, scapulo-coracoid cartilage; *r.*, radials; *pt.*, cartilages equivalent to the propterygium and mesopterygium; *mt.*, cartilage equivalent to the metapterygium of ordinary sharks, and to the median-jointed stem in the pectoral of *Pleuracanthus*.

Fig. 2.—Head of the same specimen turned round, and seen from the under surface. *mn*, rami of mandible.

Fig. 3.—Tooth magnified.

Fig. 4.—Base of tooth seen from below, and magnified.