NOTICES OF MEMOIRS.

BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE, BRADFORD, 1900.

ADDRESS TO THE ZOOLOGICAL SECTION. By RAMSAY H. TRAQUAIR, M.D., LL.D., F.R.S., President of the Section. (Slightly abridged.)

(*Concluded from the October Number, p.* 470.)[1]

COMING now to say a word regarding the Elasmobranchii, it is plain from the fin-spines found in Upper Silurian rocks that they are of very ancient origin, and that if we only knew them properly they would have a wonderful tale of evolution to tell. But their internal skeleton is from its nature not calculated for preservation, and for the most part we only know those creatures from scattered teeth, fin-spines, and shagreen, specimens showing either external configuration or internal structure being rare, especially in Palæozoic strata. But from what we do know, there is no doubt that the ancient sharks were less specialized than those of the present day, and that the recent Notidanids still preserve peculiarities which were common in the Selachii of past ages.

If we ask whether the fossil sharks throw any light on the disputed origin of the paired limbs, whether from the specialization of right and left lateral folds, or whether that type of limb called 'archipterygium' by Gegenbaur, consisting of a central jointed axis with pre- and post-axial radial cartilage attached, was the original form, I fear we get no very definite answer from Elasmobranch palæontology. The paired fins of the Upper Devonian shark, *Cladoselache*, as described by Bashford Dean, Smith Woodward, and others, seem to favour the lateral fold theory, and Cope pointed to the right and left series of small intermediate spines which in some Lower Devonian Acanthodei (*Parexus* and *Climatius*) extend between the pectorals and ventrals as evidence of a former continuous lateral fin. So also, if I am right in looking on the lateral flaps of the Cœlolepidæ as fins, the evidence of these ancient Ostracodermi would be in the same direction.

But, on the other hand, we have the remarkable group of Pleuracanthidæ, extending from the Lower Permian back to the Upper Devonian, in which the paired fins are represented by an 'archipterygium' which in the pectoral at least is biserial.

From this biserial 'archipterygium' in the Pleuracanthidæ, Professor A. Fritsch, ten years ago,[2] derived the tribasal arrangement of modern sharks, much according to the Gegenbaurian method, effecting, however, a compromise with the lateral fold theory by assuming that the Pleuracanth form originated from one, consisting of simple parallel rods, like that described in *Cladoselache*.

[1] The reader is requested to note the following errata in the part of this Address published in our last number, namely, at p. 465, line 30, for "Under" read "Unless," and in line 31 delete the semicolon after "pectorals."

[2] "Fauna der Gaskohle und der Kalksteine der Permformation Böhmens," vol. iii, pt. 1 (Prague, 1890), pp. 44–45.

In my description of the pectoral fin of the Carboniferous *Cladodus Neilsoni*,[1] I have shown that the cartilaginous structures apparently present an uniserial archipterygium intermediate between the arrangement in *Pleuracanthus* and that in the modern sharks, but I felt compelled to acknowledge that the specimen might also be interpreted in exactly the opposite way, namely, as an example of a transition from the 'ptychopterygium' of *Cladoselache* to the Pleuracanth and Dipnoan limb. And so, in fact, this fin of *Cladodus* is claimed in support of their views by both parties in the dispute.

When we add that Semon emphatically denies that there is any proof for considering that the pectoral fin of *Cladoselache* is primitive in its type,[2] and that Campbell Brown, in his recent paper on the Mesozoic genus *Hybodus*,[3] supports Gegenbaur's theory, it will be seen that Elasmobranch palæontology has not as yet uttered any very clear or decided voice on the question as to whether the so-called archipterygium is the primary form of paired fin in the fish, or only a secondary modification. We shall now inquire if we can obtain any more light on the subject from the Crossopterygii and Dipnoi.

The Crossopterygii are a group of Teleostomous fishes characterized externally by their jugular plates and lobate paired fins, and represented in the present day only by the African genera *Polypterus* and *Calamoichthys*, which together form the peculiar family Polypteridæ. The Crossopterygii appear suddenly in the middle of the Devonian period, their previous ancestry being unknown to us.

Four families[4] are known to us in Palæozoic times—the Osteolepidæ, Rhizodontidæ, Holoptychiidæ, and Cœlacanthidæ—but it is only with the first three that we have at present to deal. The Osteolepidæ and Rhizodontidæ, which appear together in Middle and die out together in Upper Palæozoic times, resemble each other very closely. In both we have the paired fins, more especially the pectoral, obtusely or subacutely lobate; there are two separate dorsal fins, one anal, and the caudal, which is usually heterocercal, though in some genera it is more or less diphycercal. In both the teeth are conical and have the same complex structure, the dentine being towards the base thrown into vertical labyrinthic folds, exactly as in the Stegocephalian Labyrinthodonts, and this along with the lung-like development of the double air-bladder in the recent Polypteridæ has given rise to the view that from these forms the Stegocephalia have originated. The nasal openings must have been on the under surface of the snout, as in the Dipnoi.

Of these two so closely allied families we must conclude that the Osteolepidæ are the more primitive, as in them the scales are acutely rhombic and usually covered with a thick layer of ganoine, while

[1] Trans. Geol. Soc. Glasgow, vol. xi, pt. 1 (1897), pp. 41–50.

[2] "Die Entwickelung der paarigen Flossen des *Ceratodus Forsteri*"; Jena, 1898.

[3] "Ueber das Genus *Hybodus* und seine systematische Stellung": Palæontographica, vol. xlvi (1900).

[4] *Five*, if we include the singular and still imperfectly known Tarrasiidæ of the Lower Carboniferous.

in the Rhizodontidæ they are rounded, deeply imbricating, and normally devoid of the ganoine layer, which, however, occasionally recurs on the scales of *Rhizodopsis* and the fin-rays of *Gyroptychius*.

What, then, of the structure of the paired fins? Fortunately, in the Rhizodont genera *Tristichopterus* and *Eusthenopteron* the internal skeleton of the lobe was ossified, and what we see clearly exhibited in the pectoral of some specimens is striking enough. We have a basal piece attached to the shoulder-girdle and followed by a median axis of four ossicles placed end to end. The first of these shows on its postaxial margin a strong projecting process, while to its preaxial side, close to its distal extremity, a small radial piece is obliquely articulated, and a similar one is joined also to the second and third segments of the axis. The arrangement in the ventral fin is essentially similar.

In fact, we have in the Rhizodontidæ a short uniserial 'archipterygium,' and the question is, Has this been formed by the shortening up and degeneration of an originally elongated and biserial one, or on the other hand, do we find here a condition in which the stage last referred to has not yet been attained? This question is inseparable from the next, whether the Rhizodonts or the Holoptychians form the most advanced type.

The Holoptychiidæ resemble the Rhizodontidæ extremely closely in their external head-bones, in their rounded, deeply imbricating scales, and in the form and arrangement of their median fins. But the teeth show a more complex and specialized structure than those of the Rhizodontidæ; the simple vertical vascular tubes formed by the repeated folding of the dentine in that family being connected by lateral branches around which the dentine tubules are grouped in such a way as to give rise in transverse sections to a radiating arborescent appearance; hence the term 'dendrodont.' In this respect, then, the Holoptychiidæ show an advance on the Rhizodontidæ—what then of the paired fins? While the ventral remains subacutely lobate, as in the previous family, the pectoral has now assumed an elongated *acutely lobate* shape, with the fin-rays arranged along the two sides of a central scaly axis exactly as in the Dipnoi; and though the internal skeleton has not yet been seen, yet, judging by analogy, we cannot escape the belief that it was in the form of a complete biserial 'archipterygium.'

What, then, is the condition of affairs in the oldest known Dipnoan?

The oldest member of this group with whose configuration we are acquainted is *Dipterus*, which likewise appears in the middle of the Devonian period simultaneously with the Osteolepidæ, Rhizodontidæ, and Holoptychiidæ. In external form it closely resembles a Holoptychian, having a heterocercal caudal fin, two similarly placed dorsals, one anal, and circular imbricating scales, which, however, have the exposed part covered with smooth ganoine. But now we have the ventrals as well as the pectorals acutely lobate in shape, and presumably archipterygial in structure; the top of the head is covered with many small plates, there is no longer

a dentigerous maxilla, the skull is autostylic, and the palatopterygoids and the mandibular splenial are like those of *Ceratodus* and bear each a tooth-plate with radiating ridges.

Now, comparing *Dipterus* with the recent *Ceratodus* and *Protopterus*, the first conclusion we are likely to draw is, that the older Dipnoan is a very specialized form, that its heterocercal tail and separate dorsals and anal are due to specialization from the continuous diphycercal dorso-ano-caudal arrangement in the recent forms, that the Holoptychiidæ were developed from it by shortening up of the ventral archipterygium, as well as by the changes in cranial structure, and that the Rhizodontidæ and Osteolepidæ are a still more specialized series in which the pectoral archipterygium has also shared the fate of the ventral in becoming shortened up and uniserial.

Five years ago, however, M. Dollo proposed a new view to the effect that the process of evolution had gone exactly in the opposite direction;[1] and after long consideration of the subject I find it difficult to escape from the conclusion that this view is more in accordance with the facts of the case, though, as we shall see, it also has its own difficulties.

I have already indicated above that we are, on account of the more specialized structure of the teeth, justified in considering the Holoptychians, with their acutely lobate pectorals, a newer type than the Rhizodonts, even though they did not survive so long in geological time. What, then, of the question of autostyly?

We do not know the suspensorium of *Holoptychius*, but that of the Rhizodontidæ was certainly hyostylic, as in the recent *Polypterus*. Now, as there can be no doubt that the autostylic condition of skull is a specialization on the hyostylic form, as seen also in the Chimæroids and in the Amphibia, to suppose that the hyostylic Crossopterygii were evolved from the autostylic Dipnoi is, to say the least, highly improbable; in my own opinion, as well as in that of M. Dollo, it will not stand. And if we assume a genetic connection between the two groups it is in accordance with all analogy to look on the Dipnoi as the children and not as the parents of the Crossopterygii.

M. Dollo adopts the opinion of Messrs. Balfour and Parker that the apparently primitive diphycercal form of tail of the recent Dipnoi is secondary, and caused by the abortion of the termination of the vertebral axis as in various 'Teleostei,' so that no argument can be based on the supposition that it represents the original 'protocercal' or preheterocercal stage. Very likely that is so, but it is not of so much importance for the present inquiry, as both in the Osteolepidæ and Rhizodontidæ we find among otherwise closely allied genera some which are heterocercal, others more or less diphycercal. *Diplopterus*, for example, differs from *Thursius* only by its diphycercal tail, and in like manner among the Rhizodontidæ *Tristichopterus* is heterocercal, *Eusthenopteron* is nearly diphycercal, and

[1] "Sur la Phylogénie des Dipneustes": Bull. Soc. belge géol. paléont. hydr.,' vol. ix (1895).

there can be no doubt that in spite of this their caudal fins are perfectly homologous structures.

But of special interest is the question of the primitive or non-primitive nature of the continuity of the median fins in the recent Dipnoi. Like others I was inclined to believe it primitive, and that the broken-up condition of these fins in *Dipterus* was a subsequent specialization, and in fact gave the series *Phaneropleuron, Scaumenacia, Dipterus macropterus,* and *D. Valenciennesii* as illustrating this process of differentiation. This view, of course, draws on the imperfection of the geological record in assuming the existence of ancient pre-Dipterian Dipnoi with continuous median fins, which have never yet been discovered. But Dollo, using the very same series of forms, showed good reason for reading it in exactly the opposite direction.

The series is as follows :—

1. *Dipterus Valenciennesii,* Sedgw. & Murch., from the Orcadian Old Red, and the oldest Dipnoan with whose shape we are acquainted, has two dorsal fins with *short* bases, a heterocercal caudal, and one short-based anal.

2. *Dipterus macropterus,* Traq., from a somewhat higher horizon in the Orcadian series, has the base of the second dorsal much *extended,* the other fins remaining as before.

3. In *Scaumenacia curta* (Whiteaves), from the Upper Devonian of Canada, the first dorsal has advanced considerably towards the head, and its base has now become elongated, while the second has become still larger and more extended, though still distinct from the caudal posteriorly.

4. In *Phaneropleuron Andersoni,* Huxley, from the Upper Old Red of Fifeshire, the two dorsal fins are now fused with each other and with the caudal, forming a long continuous fin along the dorsal margin, while the tail has become nearly diphycercal, with elongation of the base of the lower division of the fin. But the anal still remains separate, narrow, and short-based.

5. In the Carboniferous *Uronemus lobatus,* Ag., the anal is now also absorbed in the lower division of the caudal, forming likewise on the hæmal aspect a continuous median fin behind the ventrals. There is also a last and feeble remnant of a tendency to an upward direction of the extremity of the vertebral axis.

6. In the recent *Ceratodus Forsteri,* Krefft, the tail is diphycercal (secondary diphycercy), the median fins are continuous, the pectorals and ventrals retain the biserial archipterygium, but the cranial roof-bones have become few.

7. In *Protopterus annectens,* Owen, the body is more eel-like, and the paired fins have lost the lanceolate leaf-like appearance which they show in *Ceratodus* and the older Dipnoi. They are like slender filaments in shape, with a fringe on one side of minute dermal rays; internally they retain the central jointed axis of the 'archipterygium,' but according to Wiedersheim the radials are gone, except it may be one pair at the very base of the filament.

8. Finally, in *Lepidosiren paradoxa,* Fitz., the paired fins are still

more reduced, having become very small and short, with only the axis remaining.

From this point of view, then, *Dipterus*, instead of being the most specialized Dipnoan, is the most archæic, and the modern *Ceratodus*, *Protopterus*, and *Lepidosiren* are degenerate forms; and instead of the Crossopterygii being the offspring of *Dipterus*-like forms, it is exactly the other way, the Dipnoi owing their origin to Holoptychiidæ, which again are a specialization on the Rhizodontidæ, though they did not survive so long as these in geological time. Consequently the *Ceratodus* limb, with its long median segmented axis and biserial arrangement of radials, is not an archipterygium in the literal sense of the word, but a derivative form traceable to the short uniserial type in the Rhizodonts. But from what form of fin *that* was derived is a question to which palæontology gives us no answer, for the progenitors of the Crossopterygii are as yet unknown to us.

Plausible and attractive as this theory undoubtedly is, and though it relieves the palæontologist from many difficulties which force themselves upon his mind if he tries to abide by the belief that the Dipnoan form of limb had a selachian origin, and was in turn handed on by them to the Crossopterygii, yet it is not without its own stumbling-blocks.

First as to the dentition, on which, however, M. Dollo does not seem to put much stress, it is impossible to derive *Dipterus directly* from the Holoptychiidæ, unless it suddenly acquired, as so many of us have to do as we grow older, a new set of teeth. The dendrodont dentition of *Holoptychius* could not in any way be transformed into the ctenodont or ceratodont one of *Dipterus*: both are highly specialized conditions, but in different directions. Semon has recently shown that the tooth-plates of the recent *Ceratodus* arise from the concrescence of numerous small simple conical teeth, at first separate from each other.[1] Now this stage in the embryo of the recent form represents to some extent the condition in the Uronemidæ of the Carboniferous and Lower Permian, which stand quite in the middle of Dollo's series.

Again, the idea of the origin of the Dipnoi from the Crossopterygii in the manner sketched above cuts off every thought of a genetic connection between the biserial archipterygium in them and in the Pleuracanthidæ, so that we should have to believe that this very peculiar type of limb arose independently in the Selachii as a parallel development. It may be asked, Why not? We may feel perfectly assured that the autostylic condition of the skull in the Holocephali arose independently of that in the Dipnoi, as did likewise a certain amount of resemblance in their dentition. But those who from embryological grounds oppose any notion of the origin of the Dipnoi from 'Ganoids' might here say, if they chose, If so, why should not also the same form of limb have been independently evolved in Crossopterygii?

Accordingly, while philosophic palæontology is much indebted to M. Dollo for his brilliant essay, and though we must agree with him

[1] "Die Zahnentwickelung des *Ceratodus Forsteri*"; Jena, 1899

in many things, such as that the Crossopterygii were not derived *from* the Dipnoi, and that the modern representatives of the latter group are degenerate forms, yet as to the *immediate* ancestry of the Dipnoi themselves, and the diphyletic origin of the so-called archipterygium, we had best for the present keep an open mind.

In his "Catalogue of the Fossil Fishes" in the British Museum (vol. ii, 1891) Dr. Smith Woodward, following the suggestion of Newberry in 1875, classified the Coccosteans or 'Arthrodira' as an extremely specialized group of Dipnoi. At first I was much taken with that idea, but after looking more closely into the subject I began to doubt it extremely. My own opinion at present is that the Coccosteans are Teleostomi belonging to the next order, Actinopterygii; but Professor Bashford Dean, of New York, will not have them to be even 'fishes,' but places them in a distinct class of 'Arthrognatha,' which he places next to the Ostracophori (=Ostracodermi), even hinting at a possible union with them, whereby the old 'Placodermata' of McCoy would be restored. It will, therefore, be better to leave them out of consideration for the present, pending a thorough re-examination of their structure and affinities.

We come then to the great order of Actinopterygii, to which a large number of the fishes of later Palæozoic age belong, as well as the great mass of those of Mesozoic, Tertiary, and modern times. Of these we first take into consideration the oldest sub-order, namely, the Acipenseroidei or Sturgeon tribe, in which the dermal rays of the median fins are more numerous than their supporting ossicles, while the tail is, in most, completely heterocercal. The oldest family of Acipenseroids with which we are acquainted is that of the Palæoniscidæ, which, in addition to well-developed cranial and facial bones, has the body normally covered with rhombic ganoid scales furnished with peg-and-socket articulations. It endures up to the Purbeck division of the Jurassic formation, and in the Carboniferous *Cryphiolepis*, the Lower Permian *Trissolepis*, and the Jurassic *Coccolepis* we find the same degeneration of the rhombic scales into those of a circular form and imbricating arrangement, which we find repeated in other groups of 'Ganoids.'

In these Palæozoic times we notice also a side branch of the Palæoniscidæ, constituting the family Platysomidæ, in which, while the median fins acquire elongated bases, the body becomes shortened up and deep in contour. A most interesting series of forms can be set up, beginning with *Eurynotus*, which, though it has the platysomid head contour and a long-based dorsal, has only a slight deepening of the body, and still retains the palæoniscid squamation and a short-based anal fin. In *Mesolepis*, which resembles *Eurynotus* in shape, being only slightly deeper, we have now the characteristic platysomid squamation, and the base of the anal fin is considerably elongated. *Platysomus* has a still more elongated anal fin, and the body is rhombic; while in *Cheirodus* the body is still deeper in contour, with peculiar dorsal and ventral peaks, long fringing dorsal and anal fins, while the ventrals seem to have disappeared altogether. Here also, as in the allied genus *Cheirodopsis*, the separate cylindro-

conical teeth characteristic of the family are, on the palatal and splenial bones, replaced by dental plates, reminding us of those of the Dipnoi. Certainly the Platysomidæ seem to me to form a morphological series telling as strongly in favour of Descent as any other in the domain of palæontology.[1]

If we now return to the Palæoniscidæ we find that they dwindled away in numbers in the Jurassic rocks, and finally became extinct at the close of that epoch. But already in the Lias (leaving the Triassic Catopteridæ out of consideration for the present) we find that they have sent off another offshoot sufficiently distinct to be reckoned as a new and separate family, namely, the Chondrosteidæ, in which the path of degeneration, in all but the matter of size, seems to have been entered on.

In the genus *Chondrosteus*, though the palæoniscid type is clearly traceable in the cranial structure, there is marked degeneration as regards the amount of ossification, and though the suspensorium is still obliquely directed backward the toothless jaws are comparatively short, and the mouth seems now to have become tucked in under the snout as in the recent sturgeon. Then the scales have entirely disappeared from the skin except on the upper lobe of the heterocercal caudal fin, where they are still found arranged exactly as in the Palæoniscidæ.

Chondrosteus in fact conducts us to the recent Acipenseroids—the Polyodontidæ (Paddle-fishes) and Acipenseridæ (Sturgeons). So the sturgeons and paddle-fishes of the present day would seem to be the degenerate, though bulky, descendants of the once extensively developed group of Palæoniscidæ, even as the modern Dipnoi are degenerated from those of Palæozoic times.

In the Upper Permian occurs the genus *Acentrophorus*, whose fellowship with *Semionotus*, *Lepidotus*, and all the rest of the series of Mesozoic semi-heterocercal 'Ganoids' is at once obvious. If we look at the configuration of a typical Jurassic member of this series, such as *Lepidotus* or *Eugnathus*, we shall at once see that we are a stage nearer the modern osseous fish. Though the scales are bony, rhombic, and ganoid, we are struck by the 'Teleostean'-like aspect of the external bones and plates of the head, the rays of the dorsal and anal fins are fewer and correspond in their number to that of the internal supports or 'interspinous' bones, while in the caudal we see the semi-heterocercal or abbreviate-heterocercal condition.

Then, if we refer to the tail of *Lepidosteus* itself, we shall observe how few are its rays and how evident it is that we have here to do only with the lower lobe of the original palæoniscoid caudal fin. For a convincing corroboration of this we have only to look at the tail of the embryo *Lepidosteus* as described and figured by Professor A. Agassiz to see that it in reality passed through an Acipenseroid stage, and the last we see of the upper lobe of this tail is in the form of a filament which projects from the top of the original lower lobe and then disappears.

[1] R. H. Traquair, "Structure and Affinities of the Platysomidæ": Trans. Roy. Soc. Edin., vol. xxix (1879), pp. 343–391.

Again, in these Lepidosteid forms we have a repetition of the same tendency for the thick rhombic, peg-and-socket articulating scales to become rounded and imbricating, as we saw in the Crossopterygii and again in the Palæoniscidæ. To such an extent does this go that in the recent *Amia*, whose skeletal structure so clearly shows it to belong to this group, the rounded scales are so thin and flexible that after it was removed from the Clupeoid family, or Herrings, and placed among the 'Ganoids," it was considered to be the type of a distinct sub-order of 'Amioidei.'

As the Acipenseroids dwindled away after the close of the great Palæozoic era, and are now scantily represented only by the degenerate paddle-fishes and sturgeons, so the Lepidosteid series, flourishing greatly in the Trias and Jura, in their turn declined in the Cretaceous, and in the Tertiary period became about as much a thing of the past as they are now, the North American *Lepidosteus* and *Amia*, of which remains of extinct species have also been found in Eocene and Miocene rocks, only remaining. These two genera, can, however, hardly be called 'degenerate.'

But that the fishes which succeeded the Lepidosteids in populating the seas and rivers of the globe were evolved from them there can be no reasonable doubt, while it is equally clear that they branched off at an early period, as already in the Trias we find the first representatives of the order of Isospondyli, which contains our familiar Herrings, Salmonids, Elopids, Scopelids, etc. For Dr. Smith Woodward has not only definitely placed the Jurassic Leptolepidæ and Oligopleuridæ in the Isospondyli, but also the Pholidophoridæ, which appear in the Trias and extend to the Purbeck. And it is of special interest that in the Pholidophori the scales are still brilliantly ganoid, and mostly retain the peg-and-socket articulation, while in the allied Leptolepidæ, although they have become thin and circular, a layer of ganoine mostly remains.

With the Isospondyli we now get fairly among the bony fishes of modern type—Teleostei as we used to call them—to which other sub-orders are added in Cretaceous and Tertiary times, and which in the present day have assumed an overwhelming numerical preponderance over all other fishes. The prevalent form of scale among these is thin, rounded, deeply imbricating, and with the posterior margin either plain (cycloid) or serrated (ctenoid). But that these 'cycloid' and 'ctenoid' scales are modifications from the rhombic osseous 'ganoid' type we cannot doubt after what we have seen. It is indeed strange that the same tendency to the change of rhombic into circular overlapping scales should have occurred independently in more than one group.

Incompletely as I have treated the subject, it cannot but be acknowledged that the palæontology of fishes is not less emphatic in the support of Descent than that of any other division of the animal kingdom. The modern type of bony fish, though not so 'high' in many anatomical points as that of the Selachii, Crossopterygii, Dipnoi, Acipenseroidei, and Lepidosteoidei of the Palæozoic and Mesozoic eras, is more specialized in the direction of the fish proper.