POLYPTERUS A PALAEONISCID?

By

EDWIN S. GOODRICH

(Oxford).

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Among the many brilliant contributions made to Palaeontology by Professor LOUIS DOLLO few have attracted more attention than his paper „*Sur la phylogénie des Dipneustes*" (1895). The conclusion he reached that *Dipterus*, with its thick scales, separate dorsal and anal fins, heterocercal tail, and more complete ossification is the most primitive known Dipnoan has been generally accepted. Indeed the evidence since brought to light about the structure of early *Dipnoi* is all in favour of DOLLO'S interpretation.

But, when discussing the phylogeny of the *Dipnoi*, DOLLO incidentally deals with the position of the „*Crossopterygii*", (including under that name both the ancient *Osteolepidae* and the modern *Polypterini*), his conclusions seem less well-founded. Much new evidence on the structure and affinities of these interesting fishes has been obtained since 1895, and although I have already elsewhere discussed the systematic position of *Polypterus* ('07, '09, '24), this would seem to be an appropriate occasion to review the whole question in the light of recent knowledge.

It was HUXLEY who first included *Polypterus* and *Osteolepis* in the one group *Crossopterygii* in his important paper on „The Systematic arrangement of the Fishes of the Devonian Epoch", 1861. Twenty years ago I ventured to maintain that HUXLEY was mistaken in thinking that *Polypterus* is closely allied to *Osteolepis*, and that most of the resemblances between these two fishes, in the scales, dermal cranial bones, paired gulars, lobate paired fins, on which he relied, are chiefly either primitive characters inherited from a remote common ancestor, or superficial likenesses due to convergence. In short I urged that *Polypterus* is much more nearly related to the *Actinopterygii (Chondrostei, Amioidei, Lepidosteoidei, Teleostei)* than to the *Osteolepidae* or *Dipnoi*.

Although this view was further developed later ('09) HUXLEY'S classi-

fication has become so firmly established that it still persists in most text-books and even in the works of specialists[1]). Let us now examine the evidence.

The Scales: — It is true that the scales of *Polypterus* and *Osteolepis* are superficially very alike, are shiny and rhomboid; but, whereas those of *Osteolepis* belong to the very distinct type known as ‚cosmoid', those of *Polypterus* are of the true ‚ganoid' type (GOODRICH '08). The former type is composed of a layer of typical cosmine of peculiar and elaborate structure on the exposed outer surface, fixed to an underlying plate of true bone. This plate is made up of an innermost layer of lamellated bone, and a layer with vascular spaces next to the cosmine. There is good reason to believe that the cosmine represents a mosaic of specialised denticles. It is a distinctive character of the cosmoid scale that it grows only by the addition of new cosmine at its edge and new bone on its inner surface. In the living fish the scales presumably lay immediately below the epidermis in continuity with the basement membrane. Such typical cosmoid scales are not found in any living fish, but are characteristic of the most primitive *Dipnoi (Dipterus)*, and *Osteolepidae*.

The scale of *Polypterus*, on the other hand, is of quite different structure, belongs to the ganoid type, lies buried in the dermis, and grows by the addition of concentric layers of bone on its inner and modified bone or ganoine on its exposed outer surface. Ganoid scales are characteristic of *Actinopterygii* and are of two kinds: the palaeoniscoid type and the lepidosteoid type (GOODRICH '08, '09). The latter (or some modification of it) is found in *Amioidei*, *Lepidosteoidei*, and *Teleostei;* the former is typically developed only in *Palaeoniscoidei* among extinct fishes, and in *Polypterini* among living fishes. This variety of the ganoid scale is characterised by the presence between the outer ganoine and inner bony layers of a middle layer with dentine and vascular spaces. Therefore in the structure of its scales and dermal bones it is not the Osteolepids but the Palaeoniscids that *Polypterus* resembles.

The dermal bones of the head: — The superficial dermal bones of the head (and pectoral girdle) in Osteolepids are of the cosmoid structure, and are so disposed as to form a fairly constant and characteristic pattern for the most part primitive, but also subject to minor specialisations (PANDER, TRAQUAIR, A. S. WOODWARD, WATSON & DAY, BRYANT, GOODRICH, STENSIÖ, and others). In the Palaeoniscids, where these bones are of course of the same histological structure as the scales, they likewise form a characteristic

[1]) To emphasize this conclusion in my book on „Cyclostomes and Fishes" ('09), *Polypterus* and *Calamoichthys* were placed in an Order *Polypterini,* and the *Osteolepidae* with the related families *Holoptychiidae, Glyptopomidae, Rhizodontidae, Onychodontidae,* and *Tarrasiidae* were included in a new Order *Osteolepidoti.* Huxley's name *Crossopterygii* has, however, been so universally adopted that it would probably have been wiser to retain it for this new Order of extinct fishes in a restricted sense.

pattern resembling in so far as it is primitive that of the Osteolepid, but diverging from it in certain ways (TRAQUAIR, '77; WATSON, '25). Without going into a detailed comparison of the bones in these two groups, it may be pointed out that a striking feature of the Palaeoniscid is the covering of the ‚cheek' by the extension forwards above the maxillary of the preopercular. *Polypterus* is distinguished by a similarly enlarged preopercular enclosing the hyomandibular lateral-line canal behind and extending forward over the lateral temporal region[1]). Another point of resemblance is the absence of a median element behind the parietals in the transverse series of bones which harbour the transverse occipital lateral-line canal. Considerable importance has been attached to the supposed presence in *Polypterus* of two large ventral gular plates similar to those found between the lateral gulars of Osteolepids. However, as already pointed out (GOODRICH, '07), the plates in *Polypterus* belong, not to the median intergular fold which is quite small, but to the paired lateral folds, and probably represent the two anterior lateral gulars which are already becoming much enlarged in many Palaeoniscids. The smaller and more posterior lateral gulars have been lost in Polypterini.

The skull: — Our knowledge of the structure of the skull in early fossil Teleostomes has recently been greatly increased by the researches of BRYANT ('19), WATSON ('26) and STENSIÖ ('22). It is now clear that the chondrocranium in Osteolepids was peculiar in that its ossifications are combined in two portions separated by an unossified tract: an orbito-ethmoidal region in front supported by the frontals above and the parasphenoid below, and an occipito-otic region behind under the parietals. Some motion seems to have been possible between these two regions. No such specialisation occurs in *Polypterini* and other *Actinopterygii*, the skull being of normal rigid structure, with a large parasphenoid extending far back under the otic and occipital regions (TRAQUAIR '71, BRIDGE '88, ALLIS '22).

Further, there is developed in *Polypterus* a median ventral aortic canal through the basioccipital, and along which the median dorsal aorta runs forwards to the paired parabasal canals between the parasphenoid and basis cranii (BRIDGE '88, ALLIS '22). Just such a median aortic canal has recently been described by WATSON ('25) in the basis cranii of Palaeoniscids. Although it is true that a similar, but probably not strictly homologous canal, exists in some Teleosts, its presence in two such primitive forms as *Palaeoniscus* and *Polypterus* may be taken as striking evidence of near relationship.

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[1]) Three bones, preopercular, squamosal and quadratojugal may often be distinguished covering this region in *Osteolepidoti;* but in *Osteolepis* itself (Goodrich '19, Watson, '26) the squamosal seems to have grown very large at the expense of the other two, which have nearly (preopercular) or quite disappeared (quadratojugal).

The nostrils: — It is a familiar fact that in *Dipnoi* both the external and the internal nostrils are situated on the ventral surface of the snout, and that the internal nostrils open into the buccal cavity. In the *Actinopterygii*, on the contrary, both sets of nostrils are brought up from their primitive ventral position on to the latero-dorsal surface well away from the mouth, and there is no communication with the buccal cavity. It has long been inferred from the shape of the roof of the snout that in *Osteolepis* the external nostrils could not have been on its dorsal surface[1]), and now we know from the observations of WATSON ('26) that the internal nostrils in these fishes were situated well within the margin oft the mouth in much the same position as in primitive *Stegocephalia*. The nostrils of *Polypterus* are typically Actinopterygian in structure and position, and this in spite of the fact that the ‚airbladder' opens ventrally and is somewhat lung-like in structure and function.

The median fins: — The phylogenetic history of the series of dorsal finlets of the *Polypterini* is still quite unknown, but it may well have arisen by the subdivision of a single elongated dorsal fin such as occurs in many Actinopterygians. The caudal fin likewise offers little definite evidence of special relationship to any other particular group. It clearly belongs to a modified heterocercal tail which has secondarily acquired a somewhat symmetrical outward shape; and its heterocercal nature is betrayed in the adult by the presence of ventral hypural bones and the upturning of the tip of the notochord. Moreover the relative shortening of the notochord and extension of the caudal fin far beyond it recalls similar modifications found only in the *Actinopterygii*.

The paired fins and girdles: — HUXLEY'S name *Crossopterygii* refers to the fringe of lepidotricha round the scale-covered lobe of the pectoral fin of *Polypterus* and *Osteolepis*. Nevertheless the pectoral fins in these two genera differ considerably in structure, and may indeed be considered as built on fundamentally different plans in so far as they have diverged from some common ancestral form, the exact structure of which is still a matter of conjecture. For whereas in *Osteolepidoti* the pectoral and even the pelvic fins possessed an ‚archipterygial' endoskeleton, with median jointed axis provided with preaxial and traces of postaxial radials (TRAQUAIR '74, A. S. WOODWARD '91, GOODRICH '01, '09), in *Polypterus* the pectoral fin has apparently a posterior axis bearing only preaxial radials, and the pelvic fin preserves only four preaxial radials. BUDGETT'S description of an early stage in the development of the pectoral fin-skeleton of *Polypterus*, shows that it may be interpreted as a modification of the uniserial type seen in all *Actinopterygii*,

[1]) In some Osteolepidoti the external nostril seems to have been more dorsally situated.

possibly specialised and enlarged to help in progression and supporting the body ('02). The reduced endoskeleton of the pectoral girdle of *Polypterus* conforms to the Actinopterygian plan. The pelvic fin-skeleton of *Polypterus* clearly resembles that of an advanced Actinopterygian; and the two pelvic bones (often, but I believe erroneously, called *basipterygia* ['01]) are remarkably like those of *Amia* and *Lepidosteus.*

Other points of resemblance between *Polypterus* and *Actinopterygii* may be briefly mentioned: — In the auditory labyrinth occurs a large solid otolith. The gut is provided with pyloric caeca. The urinogenital organs are built on the same plan, and show some of the same specialisations. The oviduct with its open funnel at the outer side of the ovary resembles that of *Acipenser, Amia,* and certain *Salmonidae;* lying close to the genital ridge it develops from the dorsal region of the coelom into which at first open the peritoneal funnels of the mesonephros (BUDGETT, '02). The oviducts of *Acipenser* and of *Lepidosteus* develop in the same way. The anus and urinogenital apertures open separately owing to the disappearance of the cloaca.

But it is perhaps in its brain that *Polypterus* shows most clearly its Actinopterygian affinities. There is the same absence of differentiation in the fore-brain with its membranous roof, and the hind-brain already shows that great development of the cerebellum as a thickened infolding projecting forwards below the roof of the mid-brain which gives rise to the valvula so characteristic of the *Actinopterygii* (KERR, '07).

Although the list of significant points of resemblance is probably by no means exhausted in the foregoing pages, yet it is amply sufficient to justify the inclusion of the *Polypterini* in that division of the *Teleostomi* known as the *Actinopterygii.* But while it seems certain that *Polypterus* belongs to the *Actinopterygii* its exact position within that group is still undetermined. With the *Teleostei* it obviously has no special affinities, nor can it be closely related to the *Holostei (Amioidei* and *Lepidosteoidei)* since it has neither in its bony endo-skeleton nor in its dermal bones and scales that peculiar ‚lepidosteoid' histological structure which occurs in the Holostean (GOODRICH, '13). On the other hand, there are several features of significance in which it resembles the *Palaeoniscoidei* in particular, and it may be expected that more will be discovered when the structure of these fishes becomes better known. It is on this account that I ventured to suggest ('24) that the *Polypterini* are the survivors of this large and varied group hitherto supposed to be extinct.

Department of Zoology and Comparative Anatomy, Oxford
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List of references.

Allis, E. P 1922. „The Cranial anatomy of *Polypterus.*" J. of Anat v. 56.
Bridge, T. W., 1888. „Some points in the cranial anatomy of *Polypterus.*" Proc. Phil. Soc. Birmingham, v. 6.
Bryant, W. L., 1919. „On the structure of *Eusthenopteron.*" Bull. Buffalo Soc. Nat. Sci. v. 13.
Budgett, J. S., 1902. „On the structure of the larval *Polypterus.*" Tr. Zool. Soc. London, v. 16.
Dollo, L., 1895. „Sur la phylogénie des *Dipneustes.*" Bull. Soc. Belg. Geol. v. 9.
Goodrich, E. S., 1901. „On the pelvic girdle and fin of *Eusthenopteron.*" Quart Journ. Univ. Soc. v. 45.
— 1907. „On the systematic position of *Polypterus.*" Rep. Brit. Assoc. 1907.
— 1908. „On the scales of Fish" Proc. Zool. Soc. London, 1908.
— 1909. „Cyclostomes and Fishes" Treatise on Zoology, part 9.
— 1913. „On the structure of bone in Fishes." Proc. Zool. Soc. London, 1913.
— 1919. „Restorations of the head of *Osteolepis.*" Jour. Linn. Soc. v. 34.
— 1924. „The origin of Land Vertebrates." „Nature" v. 114.
Huxley, T. H. 1861. „The systematic arrangement of the Fishes of the Devonian Epoch". Mem. Geol. Survey.
Kerr, J. G. 1907. „The development of *Polypterus.*" Budgett Memorial Volume.
Stensiö, E. A. 1921. „Triassic Fishes from Spitzbergen", Vienna.
— 1922. „Notes on certain Crossopterygians" Proc. Zool. Soc. London, 1922.
Traquair, R. H., 1871. „On the cranial osteology of *Polypterus.*" J. Anat. and Physiol. v. 5.
— 1874. „On the structure of *Tristichopterus alatus.*" Tr. Roy. Soc. Edinb. v. 27.
— 1877. *„Palaeoniscidae."* Monogr. Palaeontogr. Soc.
Watson, D. M. S., 1925. „The structure of certain Palaeoniscis". Proc. Zool. Soc. London, 1925.
— 1926. „The evolution and origin of the *Amphibia.*". Phil. Trans. Roy. Soc. London, B. v. 214.
Woodward, A. S., 1891. „Catalogue of the Fossil Fishes in the Brit. Museum", London, v. 2.