

**Article VIII.—THE AFFINITIES OF THE FISH *LYCOPTERA*
*MIDDENDORFFI*¹**

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Plate III; Text Figure 1

Among the interesting fossils obtained by the Third Asiatic Expedition of The American Museum of Natural History in 1922 were numerous fishes from the Ondai Sair formation of Mongolia, ascribed to the Lower Cretaceous. These appear on examination to be old and young of a single species, *Lycoptera middendorffi*, described by Johannes Müller in 1848 from shales supposed to be of Jurassic age, occurring in the Transbaikal region of Siberia. The problem of stratigraphy and correlation has been discussed as fully as circumstances permit in another paper, and it remains only to give a fuller account of the fish remains, which are of quite unusual interest.

Lycoptera is referred by Doctor A. S. Woodward to the family Leptolepidæ, of which he writes:²

The Leptolepidæ differ from the two preceding families [Pholidophoridæ and Oligopleuridæ] in the absence of fulcra on the fins [whereby they agree with all living Isospondylous fishes], and are remarkable as being the earliest family in which intermuscular bones occur. These elements, forming so conspicuous a feature among modern fishes, appear to be arranged here only in a single series above the vertebral column in the abdominal region; though there may perhaps be traces of them sometimes also in the lower half of the caudal region. The vertebral centra of *Leptolepis* itself exhibit interesting gradations in the degree of development according to the geological age of the species, these centra never being more than delicate constricted rings or cylinders in the Upper Lias, and always strengthened by secondary peripheral calcifications in the Oxfordian [Middle Jurassic] and upwards. In *Thrissops*, which ranges as far at least as the Lower Cretaceous, the vertebral centra are still more robust. These fishes, it will be noticed, approach very closely the Clupeidæ, among which they are sometimes included; but they are distinguished by the meeting of the parietal bones in the median line, by the non-fusion of the hæmal spines at the base of the tail, and by the presence of a thin film of ganoiné on the scales. [Remarks in brackets are mine.]

Jordan and Branner³ say of the Leptolepidæ:

This family stands almost intermediate between the Ganoids and the Isospondyli. It has the general fin arrangement of the latter, but the scales are more or less diamond-shaped and ganoid on their exposed parts, and the last vertebrae are more or less turned upward, although the tail is usually or always forked. The orbital plates cover the cheek as in the Elopidae, but there is no gular plate, so far as known.

¹Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 39.

²1895, 'Catalogue of Fossil Fishes in the British Museum (Natural History),' III, p. xxi.

³1908, Smithsonian Miscellaneous Collections, LII, Part 1, p. 13.

However, a gular plate is clearly shown in Reis's figure of *Lycoptera middendorffi*.

Boulenger¹ separates the Leptolepidæ from other malacopterygian families only by the perforation of the vertebral centra, at least so far as his table shows. He recognizes that the coating of the scales with ganoin is not a family character.

We may readily gather from all this that the Leptolepidæ, beginning in the Upper Lias, represent the line of development which first points distinctly to the modern dominant isospondylous and related fishes. It is a group which therefore deserves minute analysis to determine what characters were evolving and in what manner. Gregory² has recently remarked: "The Jurassic Leptolepidæ are the earliest known true teleosts, with their cycloid scales, vertebral centra nearly complete, no fin fulcra, intermuscular bones present, and head and jaws remarkably like those of primitive Clupeidæ. The homocercal tail sometimes develops hypural bones of primitive teleost type." He here refers to Woodward's figure of tail of *Leptolepis dubius*.

An analysis of the above statements and of the known characters of the fishes serves only to bring out more clearly the relationship to existing families. The supposed family character of more or less ganoid scales breaks down entirely, as Gregory has indicated. As regards the vertebral centra, in some forms at least they appear to be well ossified, and *Lycoptera* during its lifetime goes through about the same stages described by Woodward as existing in successive species of *Leptolepis*. The distinct elevation of the end of the vertebral column corresponds to the condition found in the young of *Salmo* and other fishes.

I am particularly fortunate in being able to present some enlarged figures of the scales of *Leptolepis* and *Thrissops*, photographed by Mr. Herring under the direction of Doctor A. S. Woodward at the British Museum. The type of *Leptolepis* is *L. coryphænoides* (Bronn)³ from the Upper Lias. It may be that *L. dubius* (Blainville) from the Lithographic Stone of Bavaria is not strictly congeneric, in which case *Ascalabos* Munster may be available in a subgeneric sense. A photograph of the scales of *L. dubius* (which may possibly differ somewhat from those of the type of the genus and family) shows the following characters: scales cycloid, broader than long, apex very broadly rounded, base truncate, laterobasal angles obtuse; nucleus central; circuli fine and distinct,

¹1904, 'Cambridge Natural History,' VII, p. 544.

²1923, Bull. Amer. Mus. Nat. Hist., XLVIII, p. 241.

³*Cyprinus coryphænoides* Bronn, 1830; *Leptolepis bronnii* Agassiz, 1832.

concentric; no radii. The laterobasal circuli cut the more central ones somewhat as indicated in Geinitz's figure of *Kymatolepis*, but about half-way between nucleus and margin. A distinct ridge on each side passes from the region of the nucleus to the laterobasal corner.

Now it is singular that the features of this scale, even to the interference of the circuli laterally and the indication of ridges from the nucleus to the laterobasal corners, are very nearly those of the living *Caranx hippos* (Linnaeus), or *Carangus hippos* as Jordan has it. The ridges, however, are just as well seen in certain salmonoid scales, such as *Leucichthys nigripinnis* (Gill). The fish *Leptolepis dubius* is of course quite distinct from the Salmonidæ, and still more so from the Carangidæ, but I believe that the scale-structure may be regarded as prophetic. That is to say, the scale type of the modern fishes was acquired earlier than many of the other structures, and hence when found in a fossil may be used to indicate the line of development initiated by the latter. If this generalization is valid, it affords us a very important clue to the evolution of fishes. In the case of *Thrissops*, I am fortunate in having a photograph of the scales of the type species, *T. formosus* Agassiz, from the Lithographic Stone of Bavaria. The scales are extremely broad and very different from those of *Leptolepis*. They may be described as follows: scales transverse, very much broader than long; apical margin simple, broadly rounded or slightly angular; some distance below the margin, but well above the nucleus, is usually a more or less irregular or wavy band, interpreted as an annulus; occasional feeble rudiments of apical radii, but distinct basal radii of the type seen in *Ichthyodectes*; circuli extremely fine, concentric.

These scales much resemble those of the Cretaceous *Hypsodon*, lacking, however, the prominent tuberculation of the apical area. There is a superficial, but probably not significant, resemblance to the scales of the modern Hemirhamphidæ and Exocetidæ.

Coming now to *Lycoptera middendorffi*, we find still another quite diverse type of scale (Fig. 1). The scales are minute, about 1.2 mm. across, cycloid, transversely broad oval, without corners; nucleus central; circuli fine and concentric; apical and basal radii, the basal (about 14) extending up the sides nearly to meet the apical; apical radii about 13 but weaker and shorter, irregular. In some scales the radii are less developed or evanescent.

This scale is practically identical with that of the European minnow, *Phoxinus phoxinus*. I am unable to point out any difference which could be called generic. *Lycoptera* has so much the aspect of a

cyprinid that Egerton long ago proposed to place it in the cyprinid genus *Aspius*. It is a freshwater fish, and in it I think we must see the ancestor of the Cyprinidæ and their allies.

That it is not a cyprinid is shown by the following characters.

1.—Teeth are present on the premaxilla, maxilla, and dentary, though extremely small. I could not demonstrate these teeth in my material and for a time believed them absent, but in one specimen I was able to see small sockets, and a specimen from the original (Siberian) lot in the British Museum clearly shows the teeth. Through the kindness of Doctor A. S. Woodward, I am able to present an enlarged figure of this specimen.

2.—As shown by Reis, there is a gular plate resembling that of *Amia*.

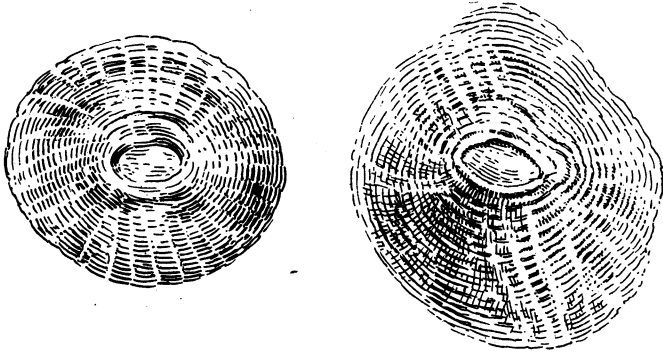


Fig. 1. Two scales of *Lycoptera* from the Ondai Sair shales, showing their general character.

3.—The end of the vertebral column turns upward, though the caudal fin is bifurcated and entirely like that of a cyprinid in appearance.

4.—The anterior vertebræ are not modified.

Characters 2 and 3 suggest a certain affinity with *Amia*, but the scales are wholly different. The dorsal fin is far posterior, about opposite the anal, as in the cyprinid genus *Engraulicypris*. In the adult the vertebral centra are solid, yet apparently always with a central canal for the notochord.

Doctor A. S. Woodward has described a second *Lycoptera*, *L. sinensis*, from the Lower Jurassic (?) of the Province of Shantung, China. Our specimens are, however, referable to *L. middendorffi*.

I think it is now evident that the Leptolepidæ of authors must be subdivided, at least to the following extent.

1.—Leptolepidæ. Marine (or sometimes brackish water ?) fishes, definable as indicated above,

a.—Leptolepinæ, new subfamily. Type *Leptolepis*, with scales as described above. (For other characters of these genera see Woodward.)

b.—Thrissopsinæ, new subfamily. Type *Thrissops*, with broad scales as described above. From the position of the dorsal fin opposite the anal, we might infer affinity with *Lycoptera*, but the scales are entirely different; so also the *Coryphæna*-like caudal fin.

2.—Lycopteridæ. Freshwater fishes, with scales resembling those of *Phoxinus*. *Lycoptera*, two species, or three if we include *Prolebias davidi* of Sauvage, 1880, from the supposed Tertiary of northern China.

Other genera referred to Leptolepidæ will have to be left in a rather uncertain position until their scales can be critically examined, but there is no indication that any one of them belongs to Lycopteridæ. In the Kimmeridge shale at Ringstead, Dorset, England, I collected circular or subcircular scales, 3 to 4 mm. diameter, with concentric circuli, strong annuli, and no radii. Doctor A. S. Woodward believes they must belong to Leptolepidæ, but they seem to represent a genus distinct from *Leptolepis dubius*.

PLATE III

Fig. 1. Enlarged figure of head of *Lycoptera middendorffi*. British Museum, P. 1841.

Fig. 2. Median dorsal scales of *Thrissops formosus*. Lithographic Stone, Solnhofen, Bavaria. British Museum, P. 913a.

Fig. 3. Anterior dorsal scales of *Leptolepis dubius*. Lithographic Stone, Solnhofen, Bavaria. British Museum, P. 924.

Figs. 4-8. *Lycoptera middendorffi*, from Ondai Sair.

Fig. 4. General view of a small specimen.

Fig. 5. A larger specimen that preserves the head and pelvic fins fairly well.

Fig. 6. A large fish, in which the pectoral pelvic and anal fins are well preserved. The scales, shown in text figure 1, are drawn from the specimen.

Fig. 7. Well-preserved anal and part of a dorsal fin.

Fig. 8. A good caudal fin.

