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## A TELEOST FROM THE LIVINGSTON FORMATION OF MONTANA

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### INTRODUCTION

The single specimen of a fossil fish described in this paper represents the first reasonably complete fossil vertebrate to be recorded from the so-called Livingston formation. It was found in 1947 by James A. Wilsey, a graduate student at Princeton University, in the Madison Range of southwestern Montana in fresh-water varved shales associated with basalts, volcanic agglomerates, and tuffs. Repeated attempts to obtain additional specimens have been unsuccessful, but the unique occurrence of this individual plus its curious assemblage of characters make it worthy of detailed consideration.

It was hoped that the fish would provide some clue regarding the age of the beds in which it was found. Although all indication of actual bone has disappeared, the remaining impression of the specimen is preserved in the finest detail, and it has been possible to prepare accurate and informative latex impressions. The question of taxonomic affinity, at first considered to be of no particular difficulty, became more and more involved as the observable characters were assembled and evaluated. It became obvious that the specimen cannot supply the desired data as to geologic age, even in a broad sense, and that its systematic position cannot be determined with absolute surety.

The higher categories of fishes are based, perhaps to a greater degree than equivalent categories in any other vertebrate group, on suites of characters that are not mutually exclusive. This implies that there are often many characters shared in common by categories of equal rank and that the characters themselves are

not so important taxonomically as the particular diagnostic combination in which they occur. This situation has led to extreme differences of opinion regarding the composition and relationships of many of the systematic units. It would appear that one of the greatest problems in teleost classification has been the difficulty of evaluating taxonomically a reasonably consistent series of morphological characters (including those that can be observed in fossils) that are of probable diagnostic value. Obviously, within the various ramifications of teleost phylogeny different morphological characters or character complexes will be of diagnostic significance at a given taxonomic level. The taxonomic evaluation will depend to a large degree on the tempo and mode of evolution observable in the various major and minor categories. Much has already been accomplished in this direction, but a new synthesis of taxonomic characters at familial and ordinal levels is badly needed. For this purpose new data, in addition to those present in the literature, are required.

The problem just discussed has been brought forcefully to mind in attempting to classify the form herein described. For example, the internal structure of the caudal fin and the form of the pelvic bones can be determined with considerable accuracy, as they can in most fossil teleosts that are fairly well preserved. The characteristics of these structures have been little used taxonomically, however, and the specimens are not at hand for extended comparisons, particularly among the living fishes.

As the observable diagnostic characters of the fish from the Livingston formation do not clearly place it in any known family of teleosts, the specimen was submitted to several ichthyologists for their consideration. All agree that it represents a real taxonomic puzzle, and at least one feels that it is a representative of a new family.

Wilsey was planning to prepare a synopsis of the pertinent stratigraphic evidence, but this was unfortunately not accomplished before his regrettable death from poliomyelitis on January 10, 1949. The writer is indebted to Dr. G. L. Jepsen for supplying such information as is now available. He is also obligated to Drs. C. M. Breder, Jr., G. A. Myers, E. M. Nelson, and L. P. Schultz for their opinions regarding the possible systematic position of the specimen.

TAXONOMY AND DESCRIPTION  
 ORDER ?ISOSPONDYLI  
 SUBORDER ?CLUPEOIDEA  
**OSTARIOSTOMIDAE, NEW FAMILY**

TYPE: *Ostariostoma*, new genus.

DISTRIBUTION: Known only from Livingston formation, Upper Cretaceous or Paleocene, North America.

DIAGNOSIS: Small, fusiform, isospondylous-like fish of doubtful ordinal and subordinal affinity. Gape small and nearly vertical, jaw articulation in front of orbit, upper jaw bordered by premaxillary and maxillary, teeth on premaxillary and dentary. Inter-muscular bones minute or possibly absent. Postcleithrum absent or completely covered by cleithrum. Last two vertebrae up-turned, ultimate forming elongated urostyle, hypurals moderately expanded and unfused. Dorsal and anal fins characin-like in form and arrangement.

**OSTARIOSTOMA,<sup>1</sup> NEW GENUS**

GENOTYPE: *Ostariostoma wilseyi*, new species.

GENERIC DIAGNOSIS: A fish of possible isospondylous relationship, but differing from all known genera in this order by the following combination of characters: Body fusiform, elongate, skull contained in total body length about 5.5 times. Greatest depth about one-sixth of total length. Premaxillary and dentary with relatively large, conical, pointed teeth. Maxillary wide distally, entering jaw margin, edentulous. Supramaxillary bones not definitely indicated. Gular probably absent. Ossified inter-orbital septum absent. Preopercular L-shaped, opercular bone large and almost covering subopercular. Branchiostegals five. Vertebrae well ossified, 39-41, abdominal 19-21, caudal 20, including urostyle. Last vertebra modified into elongated urostyle. About nine unfused, expanded, delicate hypurals. Ribs long, delicate, reaching ventral border. Parapophyses reduced. Origin of pectoral fin low, with about eight rays. Pelvic fin origin abdominal, about halfway between origins of pectoral and anal, about seven rays. Single dorsal fin triangular with origin near middle of body, eight rays, longest about equal to skull length. Anal fin extended, 19 rays, origin posterior to that of

<sup>1</sup> ὀστάριον, small bone, and στόμα, mouth. The name is not meant to imply any demonstrated relationship to the Ostariophysi.

dorsal. Caudal fin moderately forked, epichordal and hypochordal lobes of about equal size.

***Ostariostoma wilseyi*, new species**

TYPE: Princeton University Geological Museum No. 14728. Only known specimen consists of a detailed impression of a complete fish.

HORIZON AND LOCALITY: Fresh-water varved shales of the Livingston formation, Upper Cretaceous or Paleocene. Wilsey's field notes indicate, with a fair degree of certainty, that the specimen was obtained at Raw Liver Creek (? trib. Indian Creek), Sec. 17, T. 8 S., R. 3 E., Madison County, Montana. During the summer of 1948, Wilsey discovered a rather prolific fossil leaf horizon in the same general area, which may permit a more accurate dating of this portion of the Livingston formation. The complexity of the geologic structure, however, made it impossible to determine the exact stratigraphic relationship between the plant-bearing beds and the fish horizon.

SPECIFIC DIAGNOSIS: Only known species of the genus.

MEASUREMENTS, IN MILLIMETERS

(Longitudinal measurements were taken from the tip of the premaxillary along the axis of the vertebral column)

Total length.....	49.0
Standard length (incl. urostyle).....	39.5
Skull length.....	8.3
Distance from snout to anterior border of:	
Dorsal fin.....	22.7
Pelvic fin.....	16.5
Anal fin.....	26.5
Body depth at origin of dorsal fin.....	7.0

DESCRIPTION: The skull roof is smooth and without indication of excavation in the otic region. The supraoccipital lacks a crest projecting above the general level of the roof. The superior border of the orbit is bounded by an elongate, splint-like element that is probably a supraorbital or prefrontal. It bears about the same relationship to the "lacrymal" as the similarly situated bone in many primitive clupeoids and some characins. The parietal, if correctly identified, extends as far medially as the probable median border of the frontal and presumably joined its fellow of the opposite side. The otic and occipital areas are obscure, and little can be determined regarding them. The parasphenoid runs obliquely

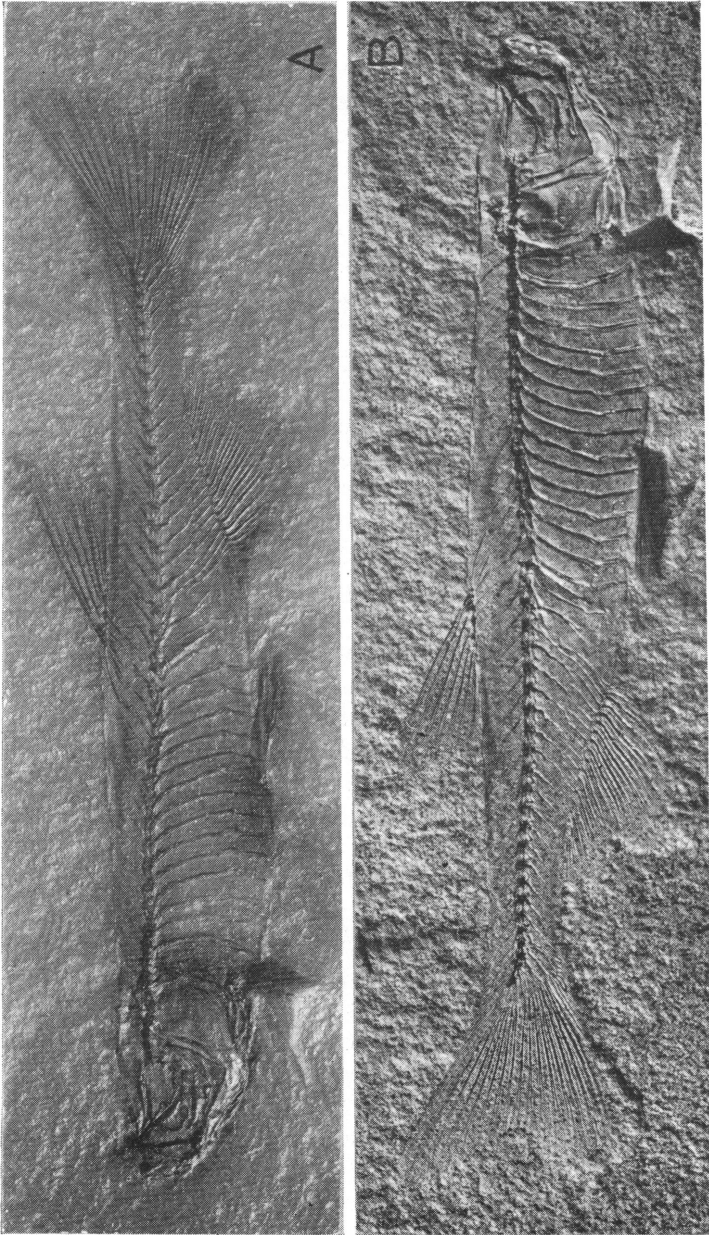


FIG. 1. *Ostariostoma wilseyi*. A. Latex cast of type,  $\times 3/1$ . B. Princeton Mus. No. 14728, type and only known specimen, preserved as a complete and detailed impression,  $\times 3/1$ .

downward and posteriorly in a manner suggestive of *Chatoëssus*. The braincase extends backward to about the middle of the dorsal surface of the opercular, a relationship commonly associated with forward jaw suspension.

The elements involved in the jaw suspension have undoubtedly been displaced forwardly and dorsally, resulting in an anterior and upward displacement of the upper and lower jaws. The dentigerous portion of the premaxillary is about half the length of the maxillary. It supports between 15 and 20 relatively long, pointed teeth of more or less equal size, closely spaced, and, as nearly as can be determined, in a single row. The posterior border of the premaxillary has a rather prominent rounded process that presumably fitted against the outer surface of the maxillary, indicating that the latter partially overlapped about the lower third of the premaxillary. The ascending process of the premaxillary appears to be very short, suggesting but a slight degree of protrusion, if any.

The maxillary is edentulous and widens rapidly ventrally. The presence of one or more supramaxillaries cannot be definitely demonstrated, although the marked distal expansion of the maxillary plus certain indications on the latex cast suggest that they may be present. The dentary has a rounded symphyseal region. Its dentigerous border rises rather rapidly to the coronoid region, resulting in a fairly deep mandible that is characteristic of many fishes with a forwardly directed suspensorium. The teeth, as in the premaxillary, are relatively long, pointed, single cusped, and circular in cross section. There are at least 10 teeth indicated in the specimen.

The infraorbital series consists of four or five elements and has a marked ventral curvature which is probably real and not due to crushing. The preorbital is the largest of the series, and the posterior members show no evidence of expansion as in the chirocentrids, characins, and other groups of suggested affinity.

The nature of the hyopalatine complex cannot be observed. The quadrate is present below the second suborbital and is of the usual triangular shape. Its extreme forward position indicates a reduced pterygoid and palatine and probably much expanded entopterygoid and metapterygoid elements. The hyomandibular has a slight forward inclination or is nearly vertical. The symplectic is elongated, rod-like, and nearly horizontal.

The horizontal and vertical rami of the preopercular are of

equal length and meet at essentially a right angle. The horizontal ramus is about half the total skull length. The opercular is much larger than the subopercular and is very similar in shape to that of the cyprinids. The dorsal border of this bone is essentially horizontal, while the posterior and ventral borders form a continuous curve that meets the straight anterior border in a sharp point. The latex cast shows some indication of concentric growth lines on the opercular as well as a few radiating ridges near the posterior border. The subopercular is also of a form similar to that found in the cyprinids. The interopercular is elongated along with the horizontal arm of the preopercular. The hypobranchial skeleton is not exposed. Five rod-like branchiostegals extend from under the interopercular.

There are 39 to 41 vertebrae, including the urostyle, of which 19 to 21 are abdominal and 20 caudal. Repeated examination has failed to indicate any positive evidence of modification towards the Weberian condition in the first three abdominal vertebrae. Until this can be demonstrated on the basis of additional specimens, or until other exclusively ostariophysal characters are found, relationship with this group cannot be properly considered. The first two vertebrae seem to lack the slender neurapophyses characteristic of the more posterior vertebrae, and there is some indication of short, expanded, neural processes that may be fused. This is by no means certain, however. The ribs in this area are obscured by the shoulder girdle and opercular. The vertebral centra are well ossified, although crushing, particularly of the anterior abdominals, prevents detailed examination. They are hourglass shaped and appear to have a single lateral lamina. The length of an individual centrum is about a third greater than the diameter. The ribs articulate low on the centra without the intervention of well-defined parapophyses; they extend to the ventral border and remain almost of the same width throughout their length. The haemapophyses are slightly expanded proximally, tapering to a point distally. The neurapophyses are delicate throughout the length of the column and show little if any regional variation in length or diameter.

The apparent absence of intermuscular bones is difficult to understand if *Ostariostoma* is an isospondyl or, for that matter, a member of any derived order normally possessing them. A few very faint markings are indicated on the specimen, which suggest these elements were very delicate, to the extent of making practi-

cally no impression. The undisturbed condition of the entire skeletal impression seems to preclude any possibility of removal of the intermuscular bones by predators, current action, or other external agency.

The dermal shoulder girdle consists of the posttemporal, supra-cleithrum, and cleithrum. The posttemporal is a relatively large triangular element that has most certainly been displaced ventrally and somewhat caudally. It is most unusual in having but a single, much elongated process that may be the extension articulating with the pterotic. In all other teleosts examined the process reaching the epiotic or supraoccipital is usually much longer and more robust. In the case of *Ostariostoma*, the possible complete absence of an epiotic process as an ossified structure is striking. It may very well have existed as a ligamentous connection, a situation that is known to exist to varying degrees for the pterotic process. As preserved, the large posttemporal practically covers the splint-like supra-cleithrum, the latter being very suggestive of its shape in the cyprinids. The apparent absence of a postcleithrum in *Ostariostoma* must be regarded with caution as it may be covered entirely by the cleithrum. This element is present in all the families considered with the exception of the Dalliidae, and the possible exception of the Esocidae, where it is said to be absent (Chapman, 1934) or present as a single ray of bone (Starks, 1904). There is no indication of this bone in any of the prepared skeletons of *Esox* examined for this study. The presence or absence of the postcleithrum in *Paleoesox* (Voigt, 1939) cannot be determined, as the pertinent area is covered by the opercular.

The anterior and dorsal limbs of the cleithrum are about of equal length. The ventral surface of the anterior limb is not expanded, and the elongated ventral process of the coracoid appears to be exposed, extending anteriorly about as far as the cleithrum. A poorly preserved rugose mass above the origin of the pectoral fin may represent that portion of the scapula and adjoining coracoid articulating with the fin radials.

The pectoral fin is incomplete, and its ventrally directed position indicates that the median side is exposed. About six delicate rays can be counted, but there may have been more. The fin was long and narrow.

The pelvic bones are narrow, elongated triangles with no indication of anterior forking or of the presence of posterior processes.



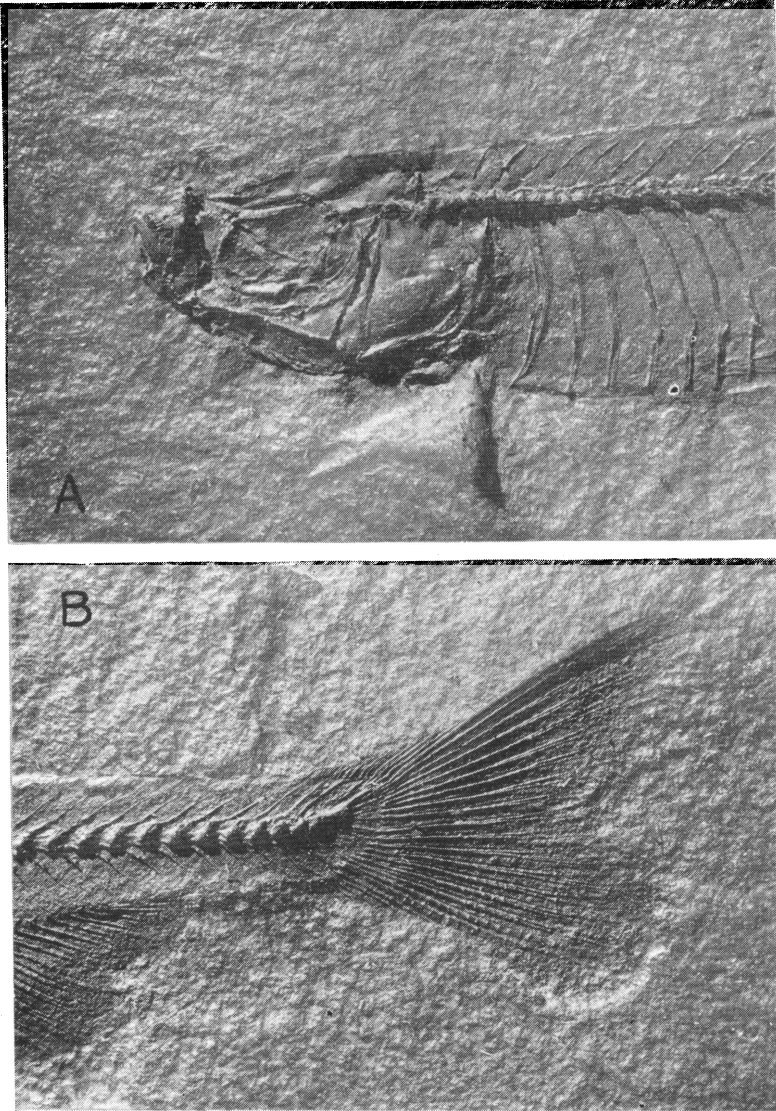


FIG. 2. *Ostariostoma wilseyi*. A. Latex cast of head region,  $\times 5/1$ . B. Latex cast of caudal fin,  $\times 5/1$ .

They are located between the fifth and ninth ribs, a position undoubtedly very close to the real one in spite of body compression. The shape and size of the pelvic fins cannot be accurately

determined. Remnants of six rays are indicated. The origin of this fin is about halfway between that of the pectoral and anal.

The dorsal fin is triangular, with the rays progressively decreasing in size anteroposteriorly. There are eight rays, clearly subdivided and jointed for about half their length. The longest ray is equal in length to the distance from the tip of the premaxillary to the posterior border of the opercular. The anterior radials show a moderate expansion, and probably all the radials were widened to some degree.

The elongated anal fin consists of 19 rays. The first two rays are relatively short and are supported by a single radial. The remainder, although not completely preserved, undoubtedly progressively decreased in size anteroposteriorly. The base length of the anal fin is about equal to the depth of the skull at the anterior border of the opercular, or about one-seventh of the total body length. The origin of this fin is well behind the middle of the body and the base of the dorsal fin.

The caudal fin, which is externally homocercal and moderately forked, is internally heterocercal (stegurous). The last vertebra is modified into an elongated, rod-like urostyle, resembling that found in certain of the more generalized isospondyls. There are probably three short epural elements dorsal to the urostyle, the last one being closely applied to the urostyle. About nine expanded, unfused hypurals are indicated. Two vertebrae appear to be involved in the upturned caudal end of the column. Expanded hypurals are present on the last three and possibly the last four vertebrae. The arrangement of the lepidotrichia of the caudal fin permits a natural division into epaxial and hypaxial lobes. This division is also suggested in the external symmetry of the tail and bears no direct relationship to the column, as indicated by Hollister (1936). The dorsal lobe has 19 to 20 raylets plus rays, and the ventral lobe about 17. The rays increase in diameter dorsally and ventrally and are segmented in both lobes.

Scale impressions are absent, suggesting that the skin was naked or, more reasonably, that the scales had either completely disintegrated or were too delicate to leave an impression.

#### DISCUSSION

Several characters that are of diagnostic value cannot be observed in the specimen of *Ostariostoma*. These include the presence or absence of the mesocoracoid arch, the detailed nature of

the parietal-supraoccipital relationship, the ethmoid area, and the vomer. Others, such as the exact form of the upper jaw and the anterior abdominal vertebrae, cannot be determined with the desired clarity. The number of features that are thus available for ready comparison with the available diagnoses of recognized families and higher categories is seriously reduced.

*Ostariostoma* has been compared with a number of families in the Isospondyli, Ostariophysii, Iniomi, Haplomi, and Microcyprini. Other orders (or suborders) below the acanthopterygian level have been eliminated from consideration, as no possible affinity appears to be involved. Probably the most important available clue indicative of the evolutionary level represented by *Ostariostoma* is to be found in the internal structure of the caudal fin. Unfortunately this is one of the character complexes that has not been examined thoroughly from a systematic point of view, although there are a number of papers on caudal fin structure.

The skull pattern of *Ostariostoma* shows no definite relationship with that of any family considered. The relatively large premaxillary, strong teeth, forward jaw suspension, and the lack of a suborbital and gular are characters eliminating it from the Leptolepidae. Although the lycopterid skull has not been adequately described, the jaw structure alone in this group bears no resemblance to *O. wilseyi*. This is also true of the elopids with their wide, almost horizontal gape, and in addition the Elopidae have expanded circumorbitals, a relatively small premaxillary (a retained heritage character), a gular plate, and about five times as many branchiostegals.

Both the albulids and the chanids have a forwardly directed suspensorium which was already specialized in its present form in the earliest known Cretaceous members of both families, *Hajulia* and *Prochanos*, respectively. In both, the premaxillary excludes the maxillary from the functional gape which is essentially the case in *Ostariostoma*. The maxillary is relatively smaller than in *Ostariostoma*, and while all known chanids are edentulous, the albulids may have only minute teeth on the jaws. The completely ossified interorbital septum in the Albulidae is at variance with *O. wilseyi*, although it is absent in the chanids. There are also obvious differences in the shape and proportions of the cheek elements between these families and the form from the Livingston formation.

The general form of the skull of *Ostariostoma* bears some resemblance to that of the chirocentrids, particularly in the orientation of the jaws and the relative size of the teeth. This family, however, has a toothed maxillary and a relatively smaller premaxillary (with the exception of *Chirocentrus*). The suspensorium is forwardly directed to only a slight degree in spite of the obliquity of the jaws, and the preopercular is gently curved rather than L-shaped. The Cretaceous representatives have considerably expanded suborbitals, again lacking in *Ostariostoma*.

Relationship of the *Ostariostoma* skull with that of the Clupeidae appears to be ruled out on the basis of tooth development, the teeth of the clupeids being either absent or feeble. Other observable skull characters might fit into this family, although the forward jaw suspension is more extreme and the gape differently oriented than in such types as *Pseudoberyx* and *Chatoessus*, and there is no indication of temporal fenestration. Furthermore, the clupeid opercular has a dorsal extension above the hyoman-dibular articulation that is lacking in *O. wilseyi*.

The jaw structure and cheek area of the salmonids and osteoglossids with a toothed maxillary and expanded circumorbitals eliminate these families. The extensive mesethmoid (dermethmoid) exposure of the salmonids is likewise apparently missing, and the nasals are relatively smaller than in the osteoglossids, although their exact form or size cannot be determined. The wide, horizontal gape of the Inioini and related structure of the cheek region go back essentially unmodified to the late Cretaceous along with the complete exclusion of the maxillary from the jaw and exclude any relationship with *Ostariostoma*.

Two families in the Haplomi, the Umbridae and the Dalliidae, have a number of skull characters in common with *O. wilseyi*. These are for the most part related to the similarly displaced suspensorium. There are differences, however, in the shape and relative size of the premaxillary and maxillary and in the opercular elements, as well as in the absence of the infraorbitals in these families.

Resemblance between the skull of *Ostariostoma* and that of most of the cyprinodonts is even more striking, particularly in the form and arrangement of the opercular elements. This is apparently again a case of convergence due to the forward jaw suspension, for the Cyprinodontidae differ in having the maxillary excluded from the jaw margin. Unfortunately virtually none

of the skull characters mentioned by Myers (1931) as diagnostic of this family can be observed.

Within the limits of the Characinidae and the Cyprinidae, most of the observable features of the skull of *Ostariostoma* can be found, including an almost exact duplication of the cheek pattern, the forward jaw suspension, similar premaxillary-maxillary relationship, and relatively robust pointed teeth. There are also other characters in the post-cranial skeleton mentioned below that suggest additional similarity to the more generalized Ostario-physi.

The vertebral column, excluding the last few vertebrae, offers little of diagnostic value. The parapophyses extend laterally very slightly, and it is not possible to determine whether or not they are coalesced with the centra. The rib heads are expanded in a manner suggestive of the characins and cyprinids. The presence or absence of a notochordal canal cannot be observed.

All the families of isospondyls examined (Leptolepidae, Lycoperidae, Elopidae, Albulidae, Chirocentridae, Chanidae, Clupeidae, Salmonidae, and Osteoglossidae) show at least some degree of heterocercy in the adult condition. In *Leptolepis*, Arambourg and Schneegans (1935) have pointed out an interesting transition in the structural series ranging from the early Jurassic *L. coryphaenoides* to the basal Upper Cretaceous *L. congolensis*. This series demonstrates a gradual reduction in the number of vertebrae involved in the upturned axis and in providing attachment for expanded hypural elements. In *L. coryphaenoides* about six vertebrae are involved, while in *congolensis* no more than two. In *Lycoptera middendorffi* (Berg, 1940) and *Lycoptera fragilis* three to four vertebrae enter the upturned axis. The Elopidae have retained the more primitive condition with four vertebrae upturned.

The adult albulids (*Albula*) have a urostyle composed of two centra (Hollister, 1936) which support hypural elements, although as many as four distinct centra (urostyle segments) are involved in the larva of *Albula vulpes*. Instead of the more or less gradual upturning of the posterior end of the column that characterizes the preceding families (*Leptolepis congolensis* representing a known exception), there is a rather abrupt angle in *Albula* between the axis of the column and that of the urostyle elongation, usually about 40 degrees. The Chanidae, including the basal Upper Cretaceous *Parachanos*, the Chirocentridae, and Osteoglossidae,

show a similar condition. The Salmonidae have retained the gradual upturning, evident in *Salmo*, but even more extreme in the Eocene *Thaumaturus* (Voigt, 1934).

Among the Haplomi, the Eocene *Paleoesox* (Voigt, 1934) has three vertebrae involved in the upturned caudal axis. The hypurals are symmetrically arranged, however, on either side of the main vertebral axis. The Esocidae (Berg infers a close relationship of *Paleoesox* with the Umbridae), Dalliidae, and Umbridae have an elongated urostyle but also the symmetrical arrangements of the hypurals.

The reduction of the urostyle to a mere nubbin and the more or less symmetrical expansion of the hypurals on either side of the vertebral axis are characteristic of the Microcyprini, fossil and recent.

The Ostariophysi, while retaining a urostyle, approach a symmetrical arrangement of the hypurals. The haemopophysis of the last vertebra is robust, so that the urostyle and haemopophysis form a sort of symmetrical fork quite unlike the condition in *Ostariostoma*.

This brief survey of caudal fin structure suggests that the situation in *Ostariostoma* is about at the albulid-clupeid level of differentiation. It is clearly more advanced than that found in most leptolepids (with the exception of *L. congolensis*), the lycoperids, or the elopids. Among the chanids, it lacks the symmetry found in *Chanos* in the hypurals but does resemble more closely the condition in *Parachanos* (which Berg believes may be a leptolepid). There is no close resemblance in caudal fin structure to any of the other families considered.<sup>1</sup>

The shoulder girdle offers little more than has already been commented upon in regard to taxonomic characters. The exposure of the coracoid below the cleithrum occurs in varying degrees among the isospondyls as does the narrow supracleithrum. The posttemporal will require additional specimens for its proper interpretation. The elongated triangular form of the pelvic girdle does not resemble closely that of the leptolepids or lycoperids but is similar to the type occurring in the albulids, clupeids, salmonids, and even the cyprinids, except for the absence of a posterior process.

<sup>1</sup> Although the extent and nature of variation in caudal fin structure are unknown, the specimens examined indicate that certain basic patterns are constant for families and possibly lower taxonomic levels.

Dr. Myers (personal communication) has pointed out the remarkable similarity of the dorsal and anal fins to those structures in the characins and cyprinids. This resemblance includes the form of the fin margins, the relative length of the rays, the relative number of rays, as well as the positions of these fins. Fin form, as he states, is a character requiring experience for its proper evaluation, but is nevertheless of value. A survey of dorsal and anal fin form in the Isospondyli, Haplomi, Iniomi, and Microcyprini indicates no close duplication of the combination of characters presented by these fins in *Ostariostoma*.

In regard to the taxonomic position of *Ostariostoma*, the weight of available evidence would appear to indicate the following:

1. *Ostariostoma* cannot be assigned to any known family on the basis of the observed characters. It is therefore placed in a new family, the Ostariostomidae.

2. The family Ostariostomidae is tentatively assigned to the Order Isospondyli, Suborder Clupeoidea. This has been done in spite of the missing or poorly indicated intermuscular bones, the meaning of which is not evident, and because the general level of organization indicates this allocation at the present time rather than any other.

3. As the above description indicates, *Ostariostoma* exhibits many characters shared by the Ostariophysi, particularly the characins. The possibility exists, therefore, that this form is either representative of the ancestral ostariophysial stock, before any extended modification of the anterior vertebrae, or else that it represents a parallel modification in that direction. *Ostariostoma* certainly fills such a role in a more convincing manner than *Lycop-tera* which has been considered by some as a possible ancestor of the Ostariophysi (Cockerell, 1925; Hussakof, 1932).

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