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THE CAUDAL SKELETON OF THE CRETACEOUS TELEOSTS
XIPHACTINUS, *ICHTHYODECTES*, AND *GILLICUS*, AND
ITS BEARING ON THEIR RELATIONSHIP WITH
CHIROCENTRUS

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VERY little is known concerning the tail-support structure of early teleosts, especially those from the Mesozoic. The discovery, in the University of Michigan Museum of Paleontology (UMMP), of a well-preserved caudal skeleton labeled "*Portheus molossus*" (UMMP 9358), from the Pierre Shale of Wyoming, has prompted me to investigate the caudal skeletons of the genera *Xiphactinus* (= *Portheus*), *Ichthyodectes*, and *Gillicus*.

These three genera form part of a closely interrelated group of Cretaceous marine fishes termed the "*Xiphactinus* Group" by Bardack (1965). In an extensive systematic study, Bardack attempted to demonstrate that phylogenetic connections exist between the *Xiphactinus* Group, certain Jurassic genera such as *Thrissops*, *Pachythrissops*, and *Mesoclupea*, and the Recent *Chirocentrus*. He has further chosen to treat these fishes as members of one family, the Chirocentridae. Bardack's discussion does not extend to a number of important structural details of the caudal skeletons (especially of *Xiphactinus* and *Chirocentrus*) which I take up in this paper.

In contrast to Bardack's phylogenetic conclusions, my findings strongly indicate that *Chirocentrus* has no close relationship with *Xiphactinus*, *Ichthyodectes*, and *Gillicus*, but belongs with the Clupeoidea, as most often held by systematists working with living fishes (Gosline, 1960; Whitehead, 1963; Greenwood *et al.*, 1966).

Recent clupeoids all possess a common type of caudal skeleton which is characterized by a number of distinct features as outlined below.

The progenitor of such a structural plan is as yet unknown among fossil teleosts. In an effort to throw some light on the subject I present brief accounts of the fossil clupeoid genera *Diplomystus* and *Knightia* from the Eocene, Green River formation of Wyoming. These forms, particularly *Diplomystus*, have a more "primitive" tail structure than the Recent clupeids and, when compared directly, raise the problem of structural levels of organization and genetic relationship in fishes.

MATERIALS AND METHODS

Nearly all of the available caudal material (some 21 specimens of *Ichthyodectes*, *Xiphactinus*, and *Gillicus* with tail skeletons in various states of preservation and preparation) in the University of Kansas Museum of Natural History (KU¹) has been examined for this study.

The Michigan specimen referred to above, UMMP 9358, is in one nicely articulated unit. It consists of nine caudal vertebrae, the caudal fin supports, and the proximal parts of the lower caudal fin rays. Both sides of the specimen have been prepared and the complete series of urodermal bones on the left side has been removed to expose the up-turned caudal centra. I believe that the taxonomic assignment of this specimen is incorrect and that it actually represents a species of *Ichthyodectes*. The neural and haemal spines appear to be more appressed through the caudal peduncle than they are in *Xiphactinus*; the lateral ridges and grooves of the vertebrae are closer to those found in *Ichthyodectes* and *Gillicus*; and the shape of the hypural I element resembles *Ichthyodectes* more than it does *Xiphactinus*. Except where the very large size can be used as a criterion to separate parts of the tail skeletons of *Xiphactinus*, the three genera, *Ichthyodectes*, *Xiphactinus*, and *Gillicus*, can be easily confused. I refer to all three as possessing in common an "*Ichthyodectes*-type" of caudal skeleton.

Other UMMP specimens examined, with measurements, in mm, of standard length, are: *Diplomystus* sp.: No. 52891, 84; 52899, 50; 52894, 66; 1108, 89; 52890, 62; 21425, 84; 52892, 81; 52895, 144; 52900, 122. *Diplomystus dentatus*: No. 15743, 355; 26314, 168; Middle Eocene, Green River formation, Wyoming. *Knightia eocaena*: No. 52903, 133; 52904, 105; 52889, 89; 52907, 116, Middle Eocene, Green River formation, Wyoming.

In the University of Michigan Museum of Zoology (UMMZ) *Chirocentrus dorab*, No. 180095, Java, one cleared and stained specimen, 101; *Alosa pseudoharengus*, No. 183684, 65, Michigan, one cleared and stained specimen.

¹ Numbers under 10,000 are those originally assigned to the specimens.

The terminology used to describe the bony elements in the supporting structure of the tail is that of Nybelin (1963). Stated briefly, the ural centra are defined as those that follow the last caudal vertebra with a haemal arch enclosing the caudal artery, and the hypurals are the median ray-supporting elements associated with and positioned below and posterior to the urals. With respect to Gosline's (1960, 1961) terminology urals 1 and 2 replace his postterminals 1 and 2; hypural 1 is equal to his hypural 2. Gosline (1965: 191, footnote) has since followed Nybelin's revision except for the use of the term urodermal for uroneural. Nybelin (1963) presented fossil (but not embryologic) evidence supporting his view that the paired "uroneurals" are of dermal origin, and pointed out that Regan (1910a) was incorrect in postulating the derivation of the "uroneurals" from fused neural arches. I believe Nybelin is right in his interpretation.

RESULTS

Figure 1 (A and B) shows a reconstruction of the "*Ichthyodectes* type" of caudal skeleton with and without the urodermals in place. The reconstruction is based mainly on UMMP 9358.

In general aspect the most striking characteristic of this tail skeleton is its compact appearance formed by the strongly appressed neural and haemal spines that sweep sharply backward. Through the peduncle, these spines grip the centra firmly. In addition they are flattened dorsoventrally to give a markedly slender yet strong caudal peduncle and tail-support. The constriction of the caudal peduncle appears to be slightly more pronounced in *Gillicus* and *Ichthyodectes* than in *Xiphactinus*. *Chirocentrus* does not share this character. Approximately 5 neural spines and 6 haemal spines are involved in caudal-ray support. The last three or four centra of the vertebral column turn sharply upward. These are preural 1, ural 1, and ural 2. Each of these centra is tapered posteriorly and each appears to retain its individuality with completely dividing articular surfaces. Ural centra 1 and 2 are much reduced in size.

Behind the tapered posterior end of ural 2 is a long narrow space where four of the upper hypurals are seated. This space was probably occupied by cartilage (Hollister, 1936). Preural 1 seems to have a neural arch fused to it but I cannot find an attached spine. In the tail section perhaps all of the neural and haemal arches are fused to or firmly united with the centra. The last four haemal arches increase in size caudad. The final arch, which is attached to preural 1, is outstanding for its great development and lateral expansion. The sides

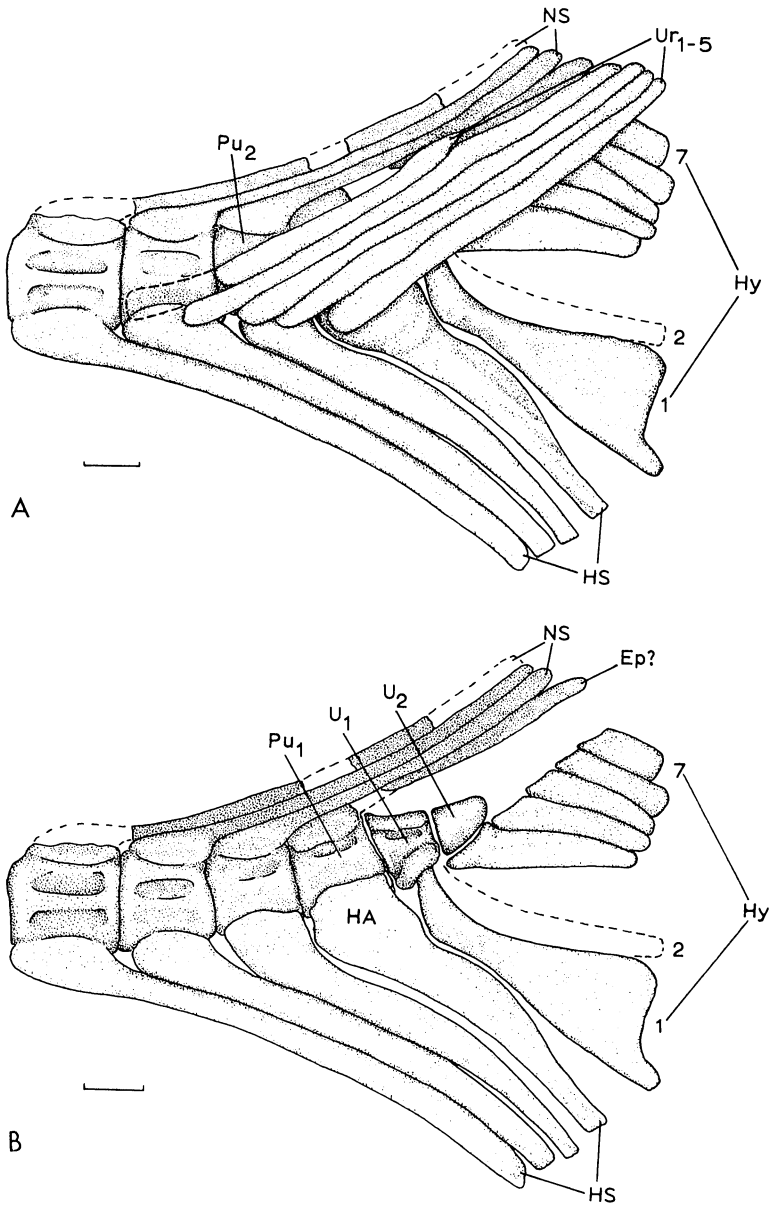


FIG. 1. "*Ichthyodectes* type" of caudal skeleton based on UMMP 9358, Pierre Shale, Wyoming. (A) urodermals in place; (B) urodermals removed. Abbreviations: Ep, epural; HA, haemal arch; HS, haemal spine; Hy, hypural; NS, neural spine; Pu, preural centrum; U, ural centrum; Ur, urodermal. Scale 1 cm.

of this arch extend upwards covering part of the centrum above. KU 168, consisting of a portion of the tail-supporting assembly of *Xiphactinus audax*, gives a good view of the last haemal arch (see Stewart, 1900: Plate XLVII-B, fig. 1).

The last three or four haemal spines are swollen in diameter as pointed out by Bardack (1965) and much less dorsoventrally compressed than those preceding. The spine belonging to preural 1 shows a slight lateral compression and is grooved where it articulates with the caudal rays. The other haemal spines that articulate with fin rays are laterally compressed at their distal ends.

There appear to be seven individual elements in the hypural series of the "*Ichthyodectes* type" of tail skeleton. Two hypurals belong to the lower caudal lobe and five to the upper. UMMP 9358 shows only one lower hypural. I believe the second hypural is missing in this specimen since such an element is seen resting along the dorsal border of hypural 1 in *Xiphactinus audax*—KU 103 (Pl. I).

Hypural 1 is by far the most interesting bone in the whole caudal complex. It is at once distinct from the other hypurals by its shape and by its manner of articulation with ural centrum 1. Figure 2 shows a separate hypural 1 of *Gillicus*. The anterior portion of this bone is rod-like with a condylar end. Posteriorly the bone is expanded into a spatulate plate. The lower part of the hypural is differentiated into a rod-like form that projects beyond the vertical posterior border of

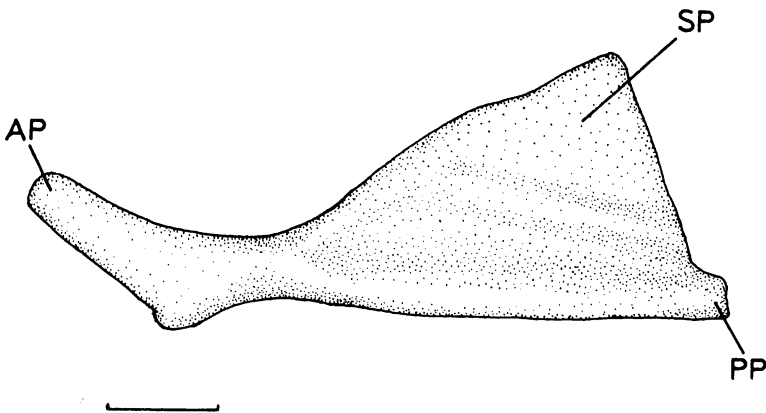


FIG. 2. Hypural 1 of "*Gillicus arcuatus*," KU 947. Abbreviations: AP, anterior condylar process; PP, posterior process; SP, expanded spatulate portion of hypural. Scale 1 cm.

the hypural. This lower part of hypural 1 resembles that of the haemal spine just below it.

The rounded articulating end of hypural 1 is received by ural centrum 1 which is equipped with a facet on its ventral surface. KU 1 and KU 10274 both show ural 1 in an exposed condition. The facet is circular, rather deep, and appears to be formed originally from a separate ossification that is possibly a modified haemal arch. In KU 10274 the hypural elements are out of proportion to the haemal spines (the latter being larger) indicating that parts of two individuals are present.

The distinct hypural 1 is a characteristic of the three genera examined: *Ichthyodectes*, *Xiphactinus*, and *Gillicus*. Specimens showing this hypural are: *Ichthyodectes*—KU 210, 112, 1, 11663 (determination tentative); *Xiphactinus*—KU 168, 103; and *Gillicus*—KU 13648, 250, 10274, 947.

Hypural 2, mentioned above, is a slender, laterally compressed bone situated directly above and in close juxtaposition with hypural 1. I was not able to ascertain whether hypural 2 articulates with a ural centrum or with the rod-like anterior end of hypural 1. The other five hypurals, as seen in UMMP 9358, are short and blade-like and each is slightly curved (dorsal border convex). They decrease in length in ascending order. Hypural 3 articulates with ural centrum 2, but the other four are above the last ossified centrum. The upper hypurals in *Gillicus* may be proportionately longer and more curved, as evidenced in KU 13648.

The paired urodermals are also of considerable interest since they are exceedingly well developed compared with those known in other teleosts. UMMP 9358 possesses five separate strap-shaped bones on the left side and four on the right side. These urodermal elements, lying along the upturned vertebral column, fit closely together to form remarkable supporting and strengthening units. In *Xiphactinus* (KU 103, Pl. I) the proximal ends of the urodermals are expanded. The most anterior element (urodermal 1) in this specimen extends forward to preural centrum 4.

Five pairs of urodermals may be the typical number in the "*Ichthyodectes* type" of caudal skeleton. KU 103 and National Museum of Canada 8151, *Xiphactinus*, each has 5 urodermals on the right side; KU 995 and KU 1011, *Ichthyodectes*, each has 5 on the right side; KU 13648, *Gillicus*, has 4 on the left side; and University of Nebraska State Museum 70026, *Gillicus*, has 5 urodermals on the right side.

In its general structural organization the "*Ichthyodectes* type" of caudal skeleton is similar to that of many of the most primitive known living and fossil teleosts. Characters such as the upturned vertebral column with two ural centra, the separate, unfused hypurals usually divided into two lower and four or five upper elements, and the well-developed urodermal bones (usually in a series) are shared by such teleost genera as *Hiodon*, *Esox*, *Salmo*, *Elops*, *Pterothrissus*, *Alepocephalus* (Gosline, 1960, 1961), *Denticeps* (Greenwood, personal communication), and *Allothrissops* (Nybelin, 1963). As interpreted through the recent classification of Greenwood *et al.* (1966), these genera represent all of the major divisional lines of teleostean evolution. As far as the tail skeleton is concerned the assumed phyletic lines probably possessed, in their early stages, the same basic plan of organization which can be traced to the pholidophoroid level if *Leptolepis* is considered as such. Gosline (1965) has already remarked on this. One primitive teleost that does not fit the picture is the Eocene osteoglossid *Phareodus*, which does not possess the strap-shaped urodermals (Cavender, 1966).

Observations on caudal organization at a more specific plane show that the "*Ichthyodectes* type" of caudal skeleton can be distinguished from that of most other teleosts by these features: (1) the distinctive shape of hypural 1, with its rounded anterior process and spine-like posterior projection; (2) ural centrum 1 possesses on its ventral surface a deep facet for receiving the condylar process of hypural 1; (3) the long, well-developed urodermals are arranged in parallel and form a compact structural unit; and (4) the massive haemal arch on preural 1.

I believe that this type of caudal skeleton is not only primitive but also sufficiently distinctive to set the genera that possess it apart into a closely interrelated group. It characterizes *Ichthyodectes*, *Xiphactinus*, and *Gillicus*, but may also be found in other members of Bardack's (1965) "*Xiphactinus* Group." Elsewhere within Bardack's "*Chirocentridae*" the caudal skeleton of the Upper Jurassic "*Thrissops*" *salmoneus* (= *Allothrissops salmoneus*, Nybelin, 1964) has been described by Nybelin (1963: fig. 11). It is not surprising to find that there is a close agreement between this genus and *Ichthyodectes* in the development of the urodermals. *Allothrissops* has five long, strap-shaped urodermals in a fairly compact series. Judging from Nybelin's illustrations, the hypural arrangement in *Allothrissops* resembles that of *Leptolepis* (Nybelin, 1963).

The caudal skeleton of *Chirocentrus* has been described by Gosline

(1960). He has shown that it differs only in minor details from that found in the Recent Clupeidae. Figure 3 (A and B) gives a direct comparison between the caudal skeletons of *Chirocentrus dorab* and *Alosa pseudoharengus*. Of considerable interest is the uniformity of occurrence of this particular type of tail structure throughout the Recent Clupeidae as defined by Whitehead (1963). Specifically, caudal skeletons of the following genera have been investigated: *Jenkinsia*, *Anchoviella*, *Harengula*, *Opisthonema*, *Sardinella* (Hollister, 1936), *Dussumieria*, *Nematalosa* (Gosline, 1960), *Clupea* (Ramanujam, 1929, and Regan, 1910b), *Chatoessus* (Regan, 1910b), *Alosa*, *Brevoortia*, *Dorosoma*, and *Anchoa* (personal observation). The specialized characters that identify the clupeid-*Chirocentrus* caudal skeleton are as follows: (1) In the adult, hypural 1 is completely separated from ural centrum 1, having no basal articulation; (2) hypural 2 is fused with all or part of ural centrum 1, the latter being reduced to a small prominence at the base of the hypural (see Gosline, 1960: 336); (3) there are usually three pairs of urodermals of which the largest and most anterior pair is normally fused to preural centrum 1; and (4) preural 1 is sharply tapered at its posterior end, the ural centra following it are greatly reduced and, along with the first two pairs of urodermals, are directed abruptly upwards. It is worth noting that hypural 1 often possesses an anterior (basal) projection directed toward ural centrum 1. Hollister (1936: text fig. 48) has figured such a projection in a 22-mm *Harengula*. Hollister found that in a few young specimens of *Jenkinsia*, hypural 1 (equal to Hollister's hypural 2) is attached to ural centrum 1 as in *Elops*, *Megalops*, and *Albula*. This arrangement she considers to be the primitive condition.

The suggestion made by Bardack (1965) that the caudal skeletons of *Xiphactinus* and Recent *Chirocentrus* are similar is not convincing. The similarity extends only to the abrupt upward orientation of the ural centra and urodermals from the horizontal vertebral axis, the sharp tapered appearance of preural centrum 1, and the reduced ural centra (the latter are reduced to a greater degree in *Chirocentrus*). The differences are much more pronounced. Where *Chirocentrus* has three pairs of urodermals, the first two of which are long, *Xiphactinus* has five pairs, all long and all extending to the level of preural 1 as in *Allothrissops*. Where *Chirocentrus* possesses a hypural 1 element free from ural centrum 1, *Xiphactinus* has a hypural 1 with a strong basal articulation. Where *Xiphactinus* has five upper hypurals, *Chirocentrus* has four; and, finally, in *Chirocentrus* the appressed nature of the neural and haemal spines is absent.

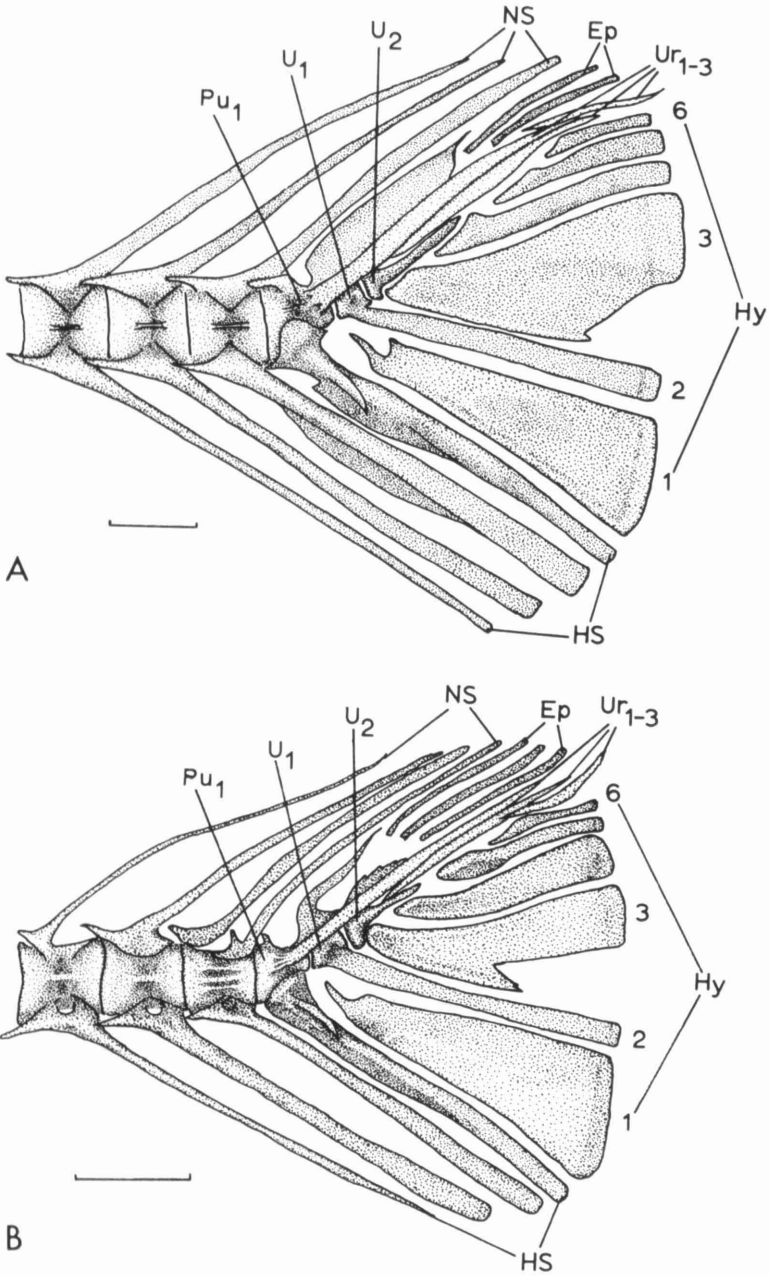


FIG. 3. Caudal skeletons of *Chirocentrus dorab* (A), UMMZ 180095, standard length, 101 mm., and *Alosa pseudoharengus* (B), UMMZ 183684, standard length, 65 mm. Abbreviations as in Fig. 1. Scale 1 mm.

It remains to discuss the obvious similarity between the caudal skeletons of *Chirocentrus* and the Clupeoidea. If Bardack is correct in the phylogenetic interpretation of his "Chirocentridae," then the chirocentrids are only indirectly allied to the clupeoids through the common ancestral pholidophoroid stock. The clupeoids, he states, originated from the pholidophoroids by way of the leptolepids, and the chirocentrids evolved directly from the pholidophorids with *Allothrissops* as the stem chirocentrid genus. The possession of the same type of caudal skeleton in Recent *Chirocentrus* and Recent clupeoids, then, cannot be explained through a close genetic relationship but rather as a result of independent attainment of the same structural plan. Such parallelism in locomotor and feeding mechanisms in fishes has recently been discussed by Schaeffer (1965). With *Chirocentrus*, however, the problem of structural similarity to the clupeoid fishes is not just limited to the tail but occurs in a number of other parts of the animal as well. Whitehead (1963) has listed some of the important Recent clupeoid characters, all of which are shared by *Chirocentrus*. Bardack (1965) in his discussion of the "Origins and Relationships of Early Clupeiformes" has listed nine cranial characters common to both *Chirocentrus* and clupeids. When postcranial features are considered the list can be easily expanded to over twenty similar structures that have, at one time or another, been taken by fish taxonomists to indicate relationship. The evidence weighs heavily in favor of regarding *Chirocentrus* as a clupeoid with strong affinities to the Clupeidae.

A brief look at some fossil clupeoids may give a better understanding of how the clupeoid tail skeleton evolved. Two fossil genera of the Clupeidae are available—*Knightia* and *Diplomystus* from the Eocene Green River formation, Wyoming.

Knightia eocaena has heavy scales that obscure the detailed internal structure. Its tail skeleton appears to agree closely with that of living clupeids. The only significant difference that I find is in the hypural 1 element which seems to possess a weak basal articulation with ural centrum 1. *Diplomystus* (Fig. 4) on the other hand exhibits a number of distinctive features. First, there are three well-defined upturned centra. Ural centrum 1 is not greatly reduced. The vertebral axis bends gradually toward the upper caudal lobe and not abruptly as in some clupeids. Hypural 1 articulates with ural centrum 1 by means of a tapered anterior projection. Hypural 2 is firmly attached to the posteroventral part of ural centrum 1. Hypural 3 is a greatly expanded, tri-

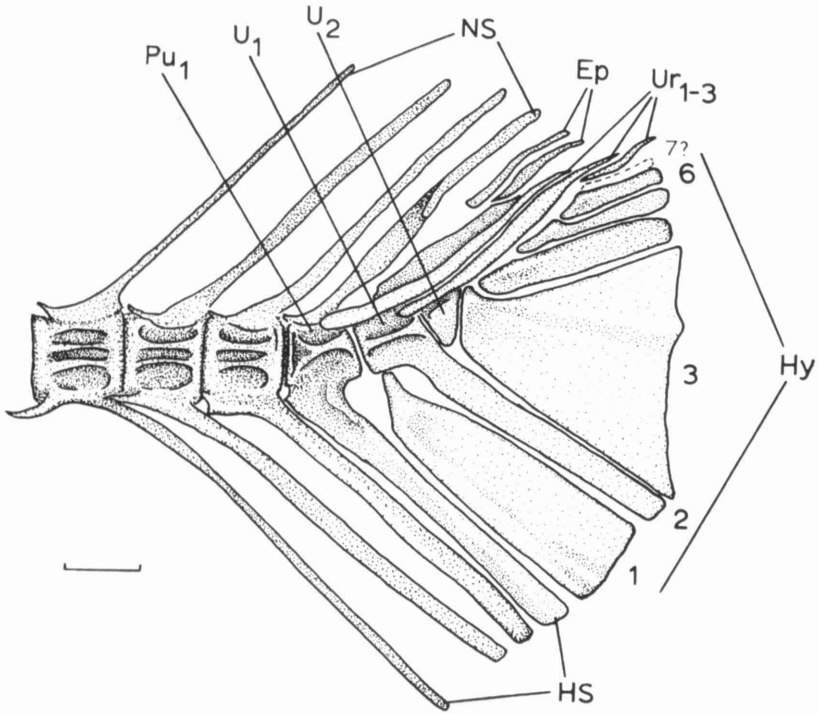


FIG. 4. Caudal skeleton of *Diplomystus* sp., UMMP 52891, standard length, 84 mm., Green River formation, Wyoming. Abbreviations as in Fig. 1. Scale 1 mm.

angular element. It has a broad articulation with the sharply tapered ural centrum 2. There are four or five upper hypurals (five occur in UMMP nos. 26314, 15743, 52892) versus four upper hypurals in *Knightia* and other clupeids. The urodermals are well-developed, separate elements. Two on each side are long and strap-shaped. The third and most posterior urodermal is a short, slight bone lying alongside the distal end of urodermal 2. The most anterior urodermal (urodermal 1) is not fused to preural centrum 1 as in the Recent Clupeidae and *Chirocentrus*.

Thus, in *Diplomystus* we find a caudal skeleton approaching the type that is widespread among the lower teleosts (e.g., *Elops*, *Hiodon*). Actually it is somewhat intermediate in structure between the "primitive type" and that of the Recent clupeids. It lends good evidence to support the idea that the modern clupeid caudal skeleton must have

evolved from a "lower" structural level of organization present, for example, in the Leptolepidae at least as far back as the Lower Jurassic (Nybelin, 1963). *Diplomystus* and *Knightia* are members of the double-armored herring group; the former is one of the oldest known clupeid genera. Schaeffer (1947) has constructed a tentative phylogeny of the double-armored herrings that shows two principal phyletic lines. One incorporates *Diplomystus*, with species ranging from Upper Cretaceous to Miocene, and the other contains the Eocene *Knightia*, which probably gave rise to the Recent double-armored herrings such as *Hyperlophus*. It would be worthwhile to trace changes in the caudal skeletons in species of both lines. From the evidence shown here it appears that by Eocene times the *Knightia* line represented by *K. eocaena* had progressed further in the structural organization of its tail than had *Diplomystus* (specifically *Diplomystus dentatus*). This assumes that the two genera possessed the same type of caudal skeleton at their origin. A common ancestry was proposed by Schaeffer.

As the evolution of "higher levels of organization" in fishes becomes better understood it is tempting to rely on parallelism to explain the origin of similar structures where fossil lineages are missing. Some genera mentioned in this paper, such as *Mesoclupea*, are too incompletely known to make a firm taxonomic assignment possible. Although Bardack allied *Mesoclupea* with the chirocentrids, Yakovlev (1966) has recently placed the genus with the Lycoperidae.

Among the Chirocentridae and Clupeidae the origin of such structures as their particular type of swimbladder-ear connection and the recessus lateralis of the cephalic lateral-line system remain unsolved. As yet the fossil "chirocentrids" have not yielded the answers. The cephalic sensory structures have been emphasized in the latest classification of Recent bony fishes (Greenwood *et al.*, 1966). Here the Clupeomorpha, as part of a major teleost division, are defined by three principal characters: the tail skeleton, the swimbladder-ear connection, and the recessus lateralis. It is implied within their proposed phylogeny that the Clupeomorpha have had an independent history since their origin from the pholidophoroids and that the defining characters probably were present in the group from Mesozoic times. The evidence presented here concerning the *Diplomystus* caudal skeleton does not entirely agree with this conclusion. On the other hand the "type" of caudal skeleton as exhibited by the Jurassic *Clupavus* shows that certain higher levels of caudal organization within the teleost group were attained early in its evolutionary history. It is my opinion that

investigation into the osteology of fossil and Recent teleost fishes has not yet been carried out with the thoroughness needed to yield the information necessary for constructing phyletic lines.

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PLATE I

Photograph of the tail of *Xiphactinus audax*, KU 103, Niobrara formation, Kansas, showing five urodermals on the right side. About 1/2 natural size.



PLATE I

