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This volume is dedicated to Dr. Rainer Zangerl

### Paracanthopterygian and Acanthopterygian Fishes from the Upper Cretaceous of Kansas

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Numerous Cretaceous teleostean fishes belonging to paracanthopterygian and acanthopterygian groups are known from northern Europe and Tethyan deposits, such as those in England and Westphalia (Patterson, 1964), Lebanon (Patterson, 1967; Gaudant, 1969), Morocco (Arambourg, 1954), and Yugoslavia (Bardack and Radovčić, 1973). In contrast, only a single, intact Cretaceous fish of these groups, a holocentrid acanthopterygian, *Kansius* (Hussakof, 1929) has been described from North America. But because many of the teleostean families which have been described from the Upper Cretaceous of North America are found also in northern European and/or Tethyan localities, one should expect additional acanthomorph (Rosen, 1973) fishes in North America as existing collections are re-examined and/or new collections are made. Such expectations are fulfilled by discoveries in the Niobara Formation of Kansas and the Taylor Marl of Texas which include the first polymixiid from North America, additional specimens of *Kansius*, a different and probably new holocentrid, and a trachichthyid. The trachichthyid will be described in another paper. This report focuses on the new Kansas material.

The preservation of most of the Kansas specimens described here is unusual in that they are found on shells of the clam *Inoceramus*. This mode of preservation differs from that of the European and Tethyan fishes and, indeed, from that of most other Kansas chalk vertebrates and raises questions as to the manner of their accumulation after death.

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Abbreviations used in figures:

d2	.....	second uroneural
e 1-3	.....	epurals
h 1-6	.....	hypurals
hap	.....	hypurapophysis
npu2	.....	neural spine of second preural centrum
ph	.....	parhypural
pu 1 + u 1	.....	fused first preural and ural centra
pu 2, pu 3	.....	preural centra
St.	.....	stegural
u 2	.....	second ural centrum

## SYSTEMATICS

### Superorder Paracanthopterygii

Series Polymixiomorpha Rosen and Patterson, 1969

Order Polymixiiformes Rosen and Patterson, 1969

Family Polymixiidae Gill (1862)

Genus *Omosoma* Costa (1857, p. 106)

*Diagnosis and type species.* — See Patterson (1964).

*Omosoma garretti* new species. Figures 1-3.

*Diagnosis.* — *Omosoma* 4-7 cm. in standard length. Maximum depth of trunk two-fifths to one-half standard length and half again as deep as head length. Head  $2\frac{1}{2}$ - $2\frac{3}{4}$  in standard length. Vertebrae 27-28 with 17-18 caudal. Anal fin with 4 spines and about 23 soft rays. Dorsal fin with 4 spines and about 28 soft rays.

*Derivation of specific name.* — Named in honor of the Garret family, owners of the ranch on which FMNH PF 3040 was found.

*Holotype.* — FMNH PF 3040.

*Material examined and localities.* — FMNH PF 3040, Sec. 16, T. 11S, R. 24W, Trego Co., Kans.; KU 135, western Kans.; AMNH





FIG. 1. *Omosoma garretti* n. sp. on *Inoceramus platinus*, FMNH PF 3040, holotype. About  $\times \frac{1}{2}$

9837 A and B and AMNH 9838 A and B both from NE $\frac{1}{4}$ , Sec. 16, T. 13S, R. 26W, Gove Co., Kans.; AMNH 9840, one-half mile S. Castle Rock, Gove Co., Kans.

*Geological horizon.*—Upper Cretaceous (lower Senonian) Niobrara Formation, Smoky Hill Chalk member.

*Description.*—Specimens referred to various species of *Omosoma* are all small fishes and none are well preserved. The Kansas material is no exception even though there are more individual fish than from the European or Tethyan regions. Some specimens are preserved on the clam *Inoceramus platinus*, the parts of which total nearly 2,000 cm.<sup>2</sup> in surface area but the fish are concentrated on one piece about 600 cm.<sup>2</sup>. The new material is noteworthy because it represents the first Cretaceous record of this group in North America. Four groups of fishes from three localities are included in *O. garretti*. These are elongate, slightly ovate fishes whose standard length ranges from 4-7 cm. (figs. 1, 2). The body depth is between 2-3 cm. and, where measurable, this dimension is about half again as long as the head length. The heads are similar to those of *O. sahelal-mae* (Patterson, 1964) in so far as their fragmentary nature permits

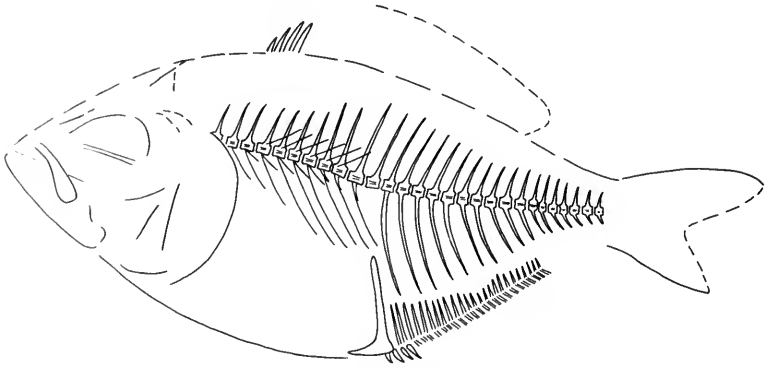


FIG. 2. *Omosoma garretti* n. sp. restoration based on AMNH 9837, 9838, and FMNH PF 3040. About  $\times 2$

examination. The supraoccipital crest is high, medially thickened and arises above the rear of the orbit. The suspensorium as in other polymixiids is inclined slightly forward. The mandible is long with a low coronoid area. The operculum is rounded posteriorly and its length is about one-half its height. There is no evidence that scales covered this bone but such scales could have been lost. Branchiostegals number at least 8.

Specimens show 27-28 centra of which at least 10 are abdominal. Seventeen to 18 caudal vertebrae include the fused preural 1 and ural 1. Ribs are sessile on anterior abdominal vertebrae and on the last three or four abdominal centra ribs are attached to transverse processes. The ribs on these processes arise more distal to the centrum in an antero-posterior direction. Abdominal vertebrae bear very thin epineurals and epipleurals. Whether the latter also are present on anterior caudal centra as in *O. sahelalmae* is uncertain.

The caudal skeleton (fig. 3) is sufficiently preserved to permit description of its basic form. Patterson (1968) was unable to illustrate the caudal skeleton of his *Omosoma* specimens but he noted strong similarities between them and *Berycopsis*. The North American material strongly supports this suggestion. Preural 1 and ural 1 (pu 1, u 1) are fused and bear the parhypural (ph), a distally expanded hypural 1 (h1), and a slender hypural 2 (h2) which is missing the distal end in the one specimen on which this structure can be examined. Ural 2 (u2) is short with a dorso-posteriorly extended process. Hypurals 3 and 4 (h3, h4) are closely set and fit under this process. Hypurals 5 and 6 (h5, h6) are short. The stegural (St) is not greatly expanded over preural 1 and ural 1. Distally, the stegural overlaps a long second uroneural (d2). Three short epurals (ep 1-3)

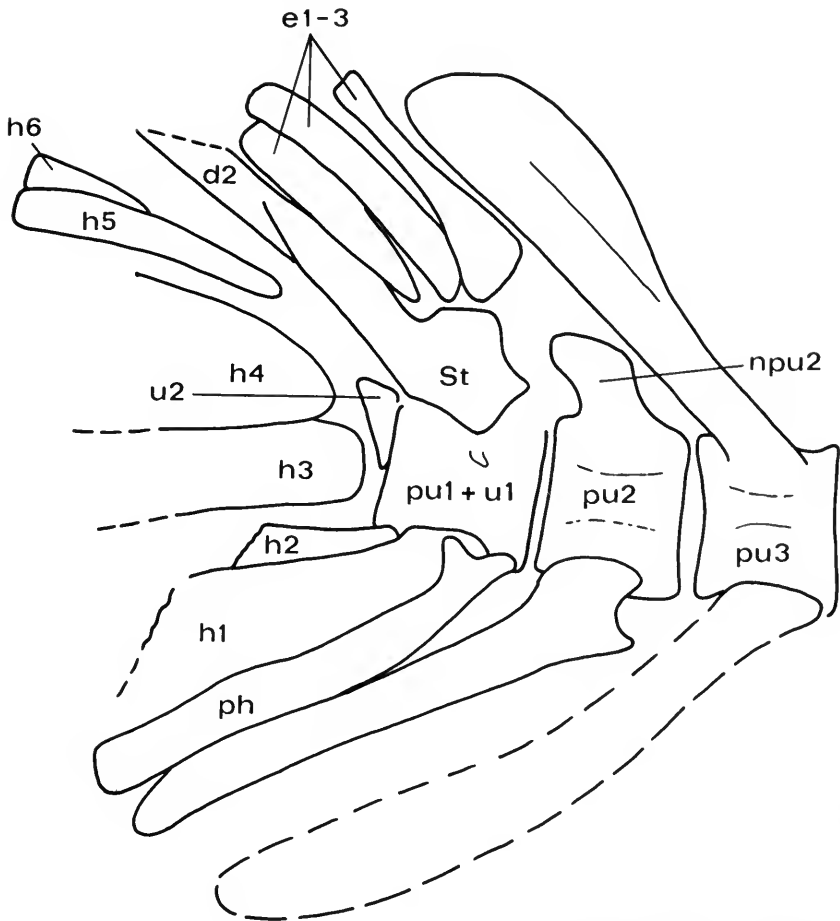


FIG. 3. *Omosoma garretti* n. sp. caudal skeleton of FMNH PF 3040, standard length 4.5 cm. For abbreviations see p. 356.

fit into the area above the stegural and uroneural 2. Preural centrum 2 (pu2) has an elongate spine (npu2) which is fused to the centrum as are more anterior neural spines. The hemal arch on preural centrum 2 is not fused to the centrum while that on preural 3 is fused. The first lower principal caudal fin ray is attached to the parhypural.

No paired fins are preserved. Of unpaired fins, the caudal includes 18 principal rays. The principal ray of the lower lobe of the caudal fin is preceded by 2 segmented and 4-5 unsegmented rays. The antermost of these rays extends forward to the hemal spine of the

third preural centrum. An elongate dorsal fin covers most of the back and includes about 4 spines and 28-30 soft rays. The first spine is supported by a stout radial which bears an anteriorly directed hook. Predorsal radials cannot be identified with certainty. The anal fin has 4 spines. The first two are short, about 1 mm. in length. There are 23 soft rays. The first anal radial is characteristically hooked but less expanded centrally than in *O. sahelalmae*.

The cleithrum is a stout, elongate, expanded "C." Elongate post-cleithra are preserved but other features of the girdle are inadequately preserved for description.

Scales show fine circuli. It cannot be determined whether ctenii were present.

*Remarks.* — Four genera of polymixiids occur in the Upper Cretaceous, *Berycopsis*, *Omosoma*, *Pycnosterinx*, and *Homonotichthys*. Characteristics of each are given by Patterson (1964, 1968). The new North American fishes differ from three of the four genera and most closely resemble *Omosoma* in the following features. For example, *Homonotichthys* has 9-11 dorsal fin spines and 8 pelvic fin rays compared to 4 and 7 respectively in *Omosoma*. *Pycnosterinx* has a vertical suspensorium, rather than one inclined slightly forward as in *Omosoma*, and fewer soft rays in the dorsal and anal fins. *Berycopsis* is a larger fish with more dorsal fin spines (6-8 *vs.* 3-4) than in *Omosoma*.

The usual incomplete preservation of *Omosoma* material makes it difficult to present an extensive characterization of the new American species. Indeed, the four previously described Old World species are not well differentiated. *Omosoma sahelalmae* and *O. pulchellum* from the Santonian of Lebanon are quite similar, differing only in body proportions and numbers of fin rays in the unpaired fins. *Omosoma garretti* differs from *O. sahelalmae* in having fewer soft rays (28-30 *vs.* 35) in the dorsal fin and regularly 4 spines in the anal fin *vs.* 3-4 in *O. sahelalmae* and *O. pulchellum*. *Omosoma monasteri* from the Upper Senonian of Westphalia and *O. simum* from the Lower Cenomanian of Morocco may belong to a different genus (Patterson, 1964). Both have about 20-22 anal soft rays thus resembling *O. garretti* but each has 3 anal fin spines. Both the Old World species and *O. garretti* agree in having 10 abdominal centra but the former differ in having only 15-16 caudal centra compared to 17-18 in the North American species. The new North American fishes surely pertain to *Omosoma* as defined by Patterson, but if better material should become available, re-examination may demonstrate

that several distinctly different fishes compose the cluster of species referred to *Omosoma*.

The four genera of Cretaceous polymixiids occur at one or more localities in the northern European or Tethyan realm. *Homonotichthys* and *Berycopsis* are restricted to northern European deposits including the Upper Cenomanian and Turonian of England (*Homonotichthys* and *Berycopsis*) and the Upper Senonian of Westphalia (*Berycopsis*). While *Pycnosterinx* is confined to the Upper Santonian of Lebanon (Ejel and Dubertret, 1966), *Omosoma* has the broadest geologic and geographic range of the polymixiids being found in the Lower Cenomanian of Morocco, Upper Santonian of Lebanon, and the Upper Senonian of Westphalia. The North American record thus represents a major expansion in geographic distribution of the genus and its occurrence in the Lower Senonian (probably Coniacian)—an extension of its geologic range. More interestingly, it suggests another link in the emerging pattern of similar fish groups in Tethyan and mid-North American biogeographic realms in the Upper Cretaceous.

#### Superorder Acanthopterygii

##### Order Beryciformes

##### Family Holocentridae Richardson (1846)

##### Genus *Kansius* Hussakof, 1929

*Diagnosis.*—Holocentrid fishes attaining 100 mm. or more in standard length. Skull roof and opercular bones with pebbly texture and small mucus cavities. Supraoccipital crest stout. Suspensorium inclined slightly forward. Vertebrae 25-26 with 12 abdominal. Dorsal fin X + 11-12, anal IV - V + 8-10; third spinous ray may be enlarged.

*Type species.*—*Kansius sternbergi*, Hussakof, 1929

*Kansius sternbergi* Hussakof, 1929. Figures 4-6.

*Diagnosis.*—See genus, only species.

*Holotype.*—SMM 25.

*Material examined.*—SMM 25, one-half mile SW of Castle Rock, Gove Co., Kans.; SMM 8123, 12 miles S. Quinter, Gove Co., Kans.; ?KU 345, 6 miles W. of Castle Rock, Gove Co., Kans.

*Geological horizon.*—Upper Cretaceous, Niobrara Formation, Smoky Hill Chalk member.

*Kansius* was described by Hussakof (1929) from two incomplete specimens, each in large part represented by impressions on a block



FIG. 4. *Kansius sternbergi* on *Inoceramus platinus*, SMM 8123. About  $\times \frac{1}{2}$ .

of chalk. A third fish on this block is too incomplete for study. The few subsequently discovered small, spiny-rayed fishes from the Niobrara Formation were curatorially assigned to this genus, but some of these clearly represent different kinds of fishes which are, in this paper, assigned to the Polymixiidae. In addition to the type, two other specimens remain for consideration. One is KU 345, consisting of a piece of the shell of the clam, *Inoceramus platinus*, (about 30 by 45 cm.) which contains slight impressions and a few largely fragmentary bones of two fishes, the largest of which is perhaps 15 cm. in length. These impressions indicate a spiny-rayed fish with jaw fragments suggesting a holocentrid. This specimen represents the largest of the Niobrara spiny-rayed fishes, but the material is too poorly preserved for description. Its assignment to *Kansius* is most uncertain.

Another specimen, SMM 8123 (fig. 4), also on a block of *Inoceramus platinus* measuring about 20 by 40 cm., shows about 50 fish superimposed, helter-skelter across the block. Only one individual is more or less intact from head to base of tail. None shows the unpaired fins in their entirety. SMM 8123 appears to be referable to *Kansius sternbergi* because both specimens share the forward inclination of the suspensorium, a similar pebbly texture of the skull roof bones and up to 5 anal fin spines with the third enlarged. The intact individual is about 50 per cent longer than the type of *Kansius sternbergi* and differs somewhat in body proportions. The

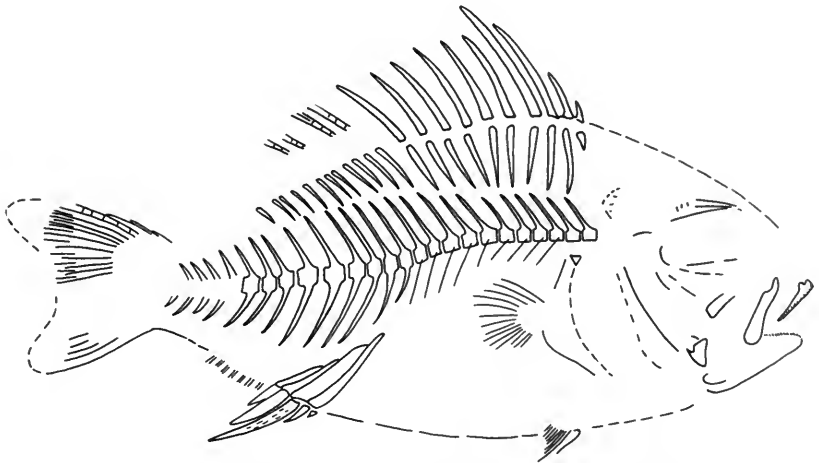


FIG. 5. *Kansius sternbergi* restoration based on SMM 25. About  $\times 2$ .

type of *Kansius sternbergi* measures approximately 60 mm. in standard length and about 25 mm. in maximum depth at the insertion of the paired fins. The depth is contained thus about  $2\frac{2}{5}$  times in the length. The intact specimen of SMM 8123 measures about 90 mm. in standard length and 30-35 mm. in depth for a ratio of  $2\frac{1}{2}$ -3. Although only two specimens may be compared, these differences do not seem significant considering that similar proportional ranges are indicated for single species of holocentrids (Woods and Sonoda, 1973).

Both specimens will be described separately so that individual features of each as they are preserved may be cited.

Few features of the head skeleton are preserved on SMM 25 (fig. 5). Impressions of the frontals suggest a knobby surface, as in *Caproberyx* (Patterson, 1964). The supraorbital crest is short and thickened anteriorly. The ascending process of the premaxillary is short, about one-quarter the length of the toothed ramus and slightly longer than the articular process. The fine band of dentition on the premaxillary appears to extend along most of the length of this bone. The edentulous maxillary is long and not apparently expanded significantly behind the premaxillary as in *Stichocentrus*, *Alloberyx*, or *Caproberyx*. The mandible, about 1 cm. in length, reaches approximately 6 mm. in height via a rapidly rising dental border. This is a sharper rise than in *Caproberyx* or *Stichocentrus*. Short, acute teeth are present.

Of the operculars, only fragments are preserved. A single, short, broad opercular spine appears below the level of the vertebral col-

umn. The preoperculum has a stout, central vertical ridge but its distal border is not preserved.

The vertebral column has 25 centra, 11 abdominal, and 14 caudal. No intermuscular bones are present. The last two to three abdominal ribs appear to be attached to transverse processes. The caudal skeleton is not preserved.

The dorsal fin comprises 10 spines plus 11-12 soft rays. This fin arises at the back of the head and extends to about the fifth from last caudal centrum. The fourth spine is the longest and the stoutest. Spines are more slender than in *Caproberyx* or *Stichocentrus* and are not alternately inclined. Dorsal fin radials are longer than the neural spines and more or less alternate with these spines. The height of the soft portion of the dorsal fin is uncertain despite Husakof's statement that it was lower than the spinous portion because distal ends of this part of the fin are not preserved. The anal fin arises below the soft dorsal fin and comprises five spines and eight soft rays. Both individuals of SMM 25 show five spines based upon counts of impressions and preserved elements. The first two spines are short, less than 2 mm. and 3 mm. in length, respectively. The third spine nearly 12 mm. long, thick and characterized by anastomosing lines and pits is followed by a nearly as long fourth and a fifth spine. The presence of two spines beyond the enlarged third is unique among holocentrids, leading Patterson (1967) to question whether there actually are five anal fins spines in *Kansius*. Although the fifth skeletal element of the anal fin is incomplete, its basal thickness and absence of segmentation along its preserved length of nearly 5 mm. suggest that it is a spine and not a soft ray. There are eight soft rays. The first two anal radials are broad and basally expanded. The caudal fin shows the usual 19 principal rays of holocentrids.

Paired fins include a pectoral of 13 rays originating half way between the vertebral column and the ventral margin of the body. The pelvic fins arise below the pectorals and include a spine and at least six rays but the specimen is poorly preserved in this area.

SMM 8123 is assigned to *Kansius* for reasons stated above. The head shows an anteriorly thickened supraoccipital crest. The fragmentary skull roof bones have a rippled, knobby surface. A deep fossa is developed in the sphenotic, parietal, and epiotic, as in *Caproberyx*. Intact jaws are not preserved. The hyomandibular is small in proportion to the head, about as long as the supraoccipital crest. Below the opercular process, the hyomandibular angles forward unlike that of *Caproberyx* or *Stichocentrus*, but similarly to that of



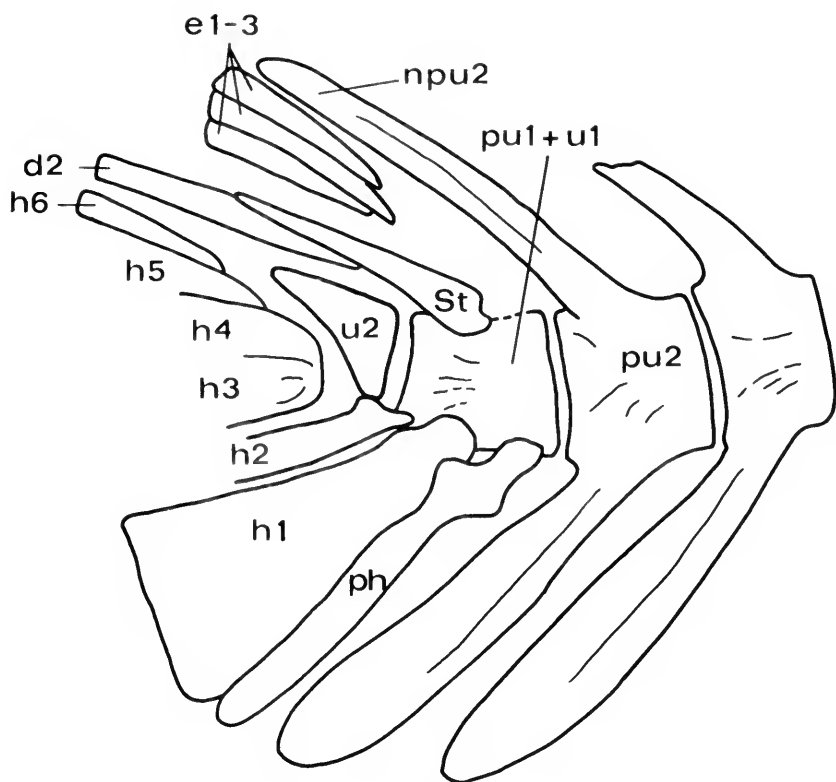


FIG. 6. *Kansius sternbergi* caudal skeleton of SMM 8123. For abbreviations see p. 356.

*Kansius* as suggested by the position of the quadrate in the holotype. Opercular fragments lack margins so that the nature of spinous development is uncertain. The lateral surfaces of the operculars show a linear, pebbly texture.

There are about 26 centra with 14-15 caudal. The centra are slightly constricted with a longitudinal, midlateral ridge. Pleural ribs are stout but their mode of origin from the centra, especially posterior abdominal centra, is unclear. A relatively well-preserved caudal skeleton (fig. 6) shows a large fused preural 1 and ural 1 and a short, free ural 2, as in *Caproberyx* and *Stichocentrus*. The parhypural is a long, slender bone attached to the fused preural 1 and ural 1 and it sends a slender hypurapophysis (hap) over hypural 1 as in the living holocentrid *Myripristis* (Patterson, 1968). Hypural 1 has a broad base and expands posteriorly, while hypural 2 has a slender base.

Hypurals 3 and 4 are broad based, closely appressed, but apparently not fused with each other. Hypural 5 is an elongate slender bone, while hypural 6 is short. The broad stegural is not fused with the underlying centrum as in *Stichocentrus*. A short second uroneural is attached to a posterior extension of the stegural. Three epurals lie above the stegural. The neural spine of preural centrum 2 is short, while the neural spine of the third preural centrum is elongate and distally broadened. Hemal spines of preural centra 2 and 3 are elongate and not expanded distally. The relationship of the foremost caudal fin rays to the caudal skeleton is indeterminable. The caudal skeleton of *Kansius* is most like that of *Caproberyx*.

Of paired fins, the pelvics bear a spine and seven soft rays while the pectorals include 13 rays. Of the unpaired fins, the number of spiny rays in the dorsal is probably 10; soft rays cannot be counted. There are at least two predorsal radials preceding this fin and lying above centra one and two. The number of anal fin spines varies. At least one individual shows the five spines typical of *Kansius* with the third spine thickened but, unlike *Kansius*, shorter than the fourth spine. However, another individual appears to have but four spines. In the former specimen the first two spines are small as in the holotype. Where four spines are preserved, the first may have been lost or perhaps not developed for there remain two spines beyond the thickest spine, as in the holotype. There are 10 soft rays as indicated by a count of basal radials.

*Remarks.*—*Kansius* was recognized as a holocentrid by Hussakof (1929) and this assignment is supported by later workers (Conrad, 1941); Patterson, 1964), as well as by this first re-examination of the type specimen. Thus *Kansius* is a holocentrid and not a trachichthyid based on the more than eight spinous rays in the dorsal fin, the seven soft rays in the pelvic fin, the enlarged third anal fin spine, and the small cranial mucus cavities.

Eight genera of holocentrids have been described from the Upper Cretaceous. These are: *Caproberyx* from the Turonian of England and Bohemia, the lower Cenomanian of Morocco and the middle Cenomanian of Lebanon; *Trachichthyoides* from the Cenomanian of England, *Stichocentrus* from the Cenomanian of Lebanon and *Alloberyx*, *Serratocentrus*, *Ctenocephalichthys*, and *Holocentropsis* from the Santonian of Lebanon (Patterson, 1964; Gaudant, 1969). *Kansius* is thus the only intact North American Upper Cretaceous representative of this group (although some scales have been referred to this family, see David, 1946).

The incomplete cranial remains of the North American material preclude extensive comparisons between *Kansius* and Old World genera. Except for *Stichocentrus* and *Caproberyx*, the other Lebanese genera have received only preliminary descriptions. *Alloberyx* apparently has a more deeply expanded posteroventral end of the maxillary than in *Kansius* and only eight spinous rays in the dorsal fin, but it does show five spinous rays in the anal fin as in *Kansius*. However, Gaudant has only tentatively assigned *Alloberyx* to the holocentrids. *Serratocentrus* is primarily distinguished by characteristics of the operculars and infraorbitals which are not well preserved in *Kansius*. In *Ctenocephalichthys*, likewise, cranial features are critical, but this genus appears to have fewer dorsal and anal fin spines and possibly a few more centra than *Kansius*. *Holocentropsis* has fewer dorsal (at least four) and anal (three) fin spines and soft rays than *Kansius*. *Trachichthyoides* is known only by the head. More meaningful comparisons can be made with *Stichocentrus* and *Caproberyx*. *Kansius* differs from the latter in having more (10 vs. 7) dorsal-fin spines and an enlarged third anal-fin spine. The caudal skeletons of both, as shown above, are quite similar. Differences between *Stichocentrus* and *Kansius* in number of dorsal fin spines and their length pointed out by Patterson (1967) are supported by this study. However, with regard to the number of anal fin spines, it appears that *Kansius* does have five. Despite earlier doubts (Conrad, 1941; Patterson, 1967), Hussakof's interpretation is correct and we now know of several other Cretaceous holocentrids which have five anal spines. In *Stichocentrus*, the five spines increase in length from front to rear, unlike *Kansius* in which the third or fourth is the longest. *Kansius* is also unique among holocentrids in the pattern of rugose, anastomosing lines and pits which appear on the third and to a lesser extent on the fourth anal fin spines. *Caproberyx superbus* (Patterson, 1967) occasionally has five spines and if SMM 8123 is properly assigned, *Kansius* may occasionally have four. If *Alloberyx* is a holocentrid, it too has five spines and Gaudant (1969) also indicates that *Serratocentrus* may have four-five spines.

Until the cranial skeleton is better known, subfamily assignment of *Kansius* remains uncertain. It does differ from the Caproberycinae (Patterson, 1967) at least in having the third rather than the penultimate spine enlarged.

#### Holocentridae

**Genus and species incertae sedis. Figures 7-9.**

An additional specimen (fig. 7) of a beryciform fish from the Kansas chalk is SMM 11543 found 7-8 miles NE of Ellis, Ellis Co., Kans.

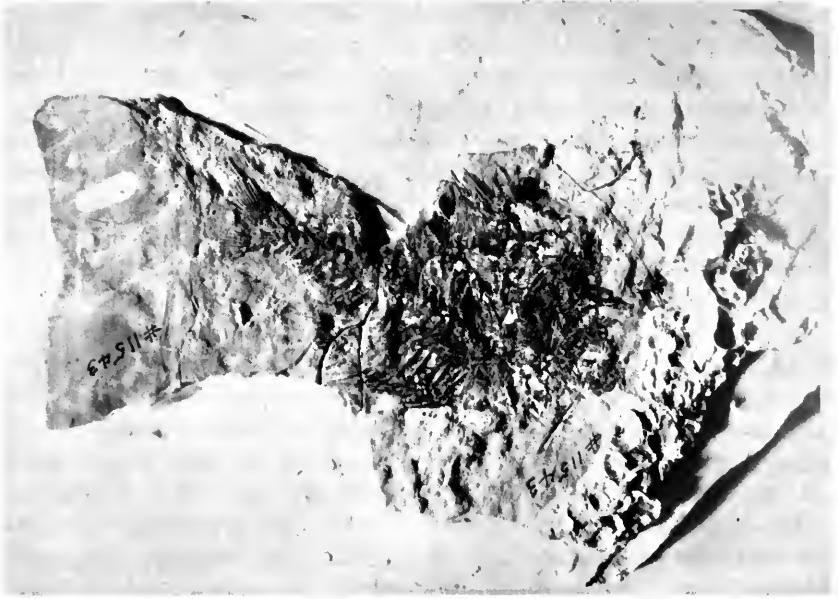


FIG. 7. Holocentrid gen. and sp. incertae sedis. SMM 11543. About  $\times 1$ .

(specifically "2 mi. N, 2 mi. E, and 4 mi. N. of the rendering plant"). This single specimen, preserved on a fragment of *Inoceramus platinus*, is from the Niobrara Formation, Smoky Hill Chalk member. The specimen (fig. 8) lacks the upper half and anterior end of the head and parts of the mid body including the anal fin. The fish was probably 90 mm. in standard length and had a maximum depth of 45 mm.

The posterior supramaxillary is similar to that of *Caproberyx* or *Stichocentrus*. The lacrymal (fig. 8) is most characteristic, resembling that of *Caproberyx* (Patterson, 1964) rather than *Stichocentrus*. It is about 12 mm. long and shows an elongate posterior process below which 4-5 large spines point posteroventrally. Several more smaller spines are directed ventrally from the ventral margin of this bone. These spines are more developed than in *Caproberyx* or *Stichocentrus*, but similar to those of *Ctenocephalichthys*. A ridge running the length of the medial surface of this bone must be the facet for articulation with the lateral ethmoid. A 1.7 cm. long parasphenoid and T-shaped vomer are present. It is uncertain whether teeth are present on the vomer. The ventral margin of the preoperculum is serrated as in holocentrids and the posterior border of the operculum shows a few short spines.

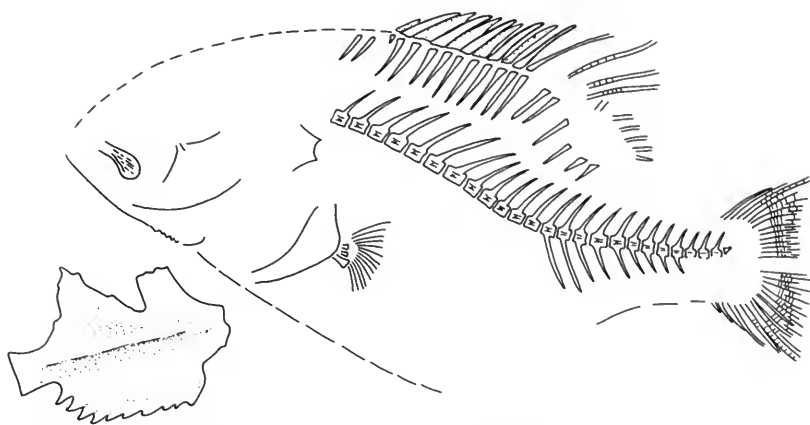


FIG. 8. Holocentrid gen. and sp. incertae sedis. SMM 11543. About  $\times 1$ . Lower left inset: medial view of lacrymal. About  $\times 4$ .

The dorsal fin includes 10 spines and probably 11-12 soft rays. The spines are thick, alternate left and right as in living holocentrids, and unlike those of *Kansius*. The soft rays appear distinctly longer than the spiny rays, unlike *Stichocentrus* in which they are about equal in length. There are at least two predorsal radials. The caudal fin appears to have 19 principal rays. The pectoral fin shows 13 rays and the pelvic has seven soft rays and an indication of the base of a spine.

Twenty-five centra comprise the vertebral column with 12 abdominal centra. These centra show a longitudinal lateral ridge which is subdivided by thinner longitudinal struts and grooves.

The caudal skeleton (fig. 9) is basically similar to that of *Kansius*. It includes a typically holocentrid fused preural 1 and ural 1. Ural 2 is separate, as in *Caproberyx*, but with a more elongate posterior process. The neural spine on the second preural centrum is short. There are three epurals. The stegural is fragmentary and its relationship to the second uroneural is uncertain. However, the stegural is not fused to underlying centra. The slender parhypural bears a hypurapophysis. Hypurals 1 and 2 are broadly expanded posteriorly while hypurals 3 and 4 are fused and greatly expanded posteriorly, as in *Caproberyx* and unlike *Kansius*. Hypurals 5 and 6 are narrow, elongate bones. The first principal ray of the caudal fin attaches to the parhypural. This ray is preceded by two short segmented rays and three unsegmented ones.

Whereas intact scales are not preserved on the other Kansas fishes described here, this specimen shows one abdominal scale

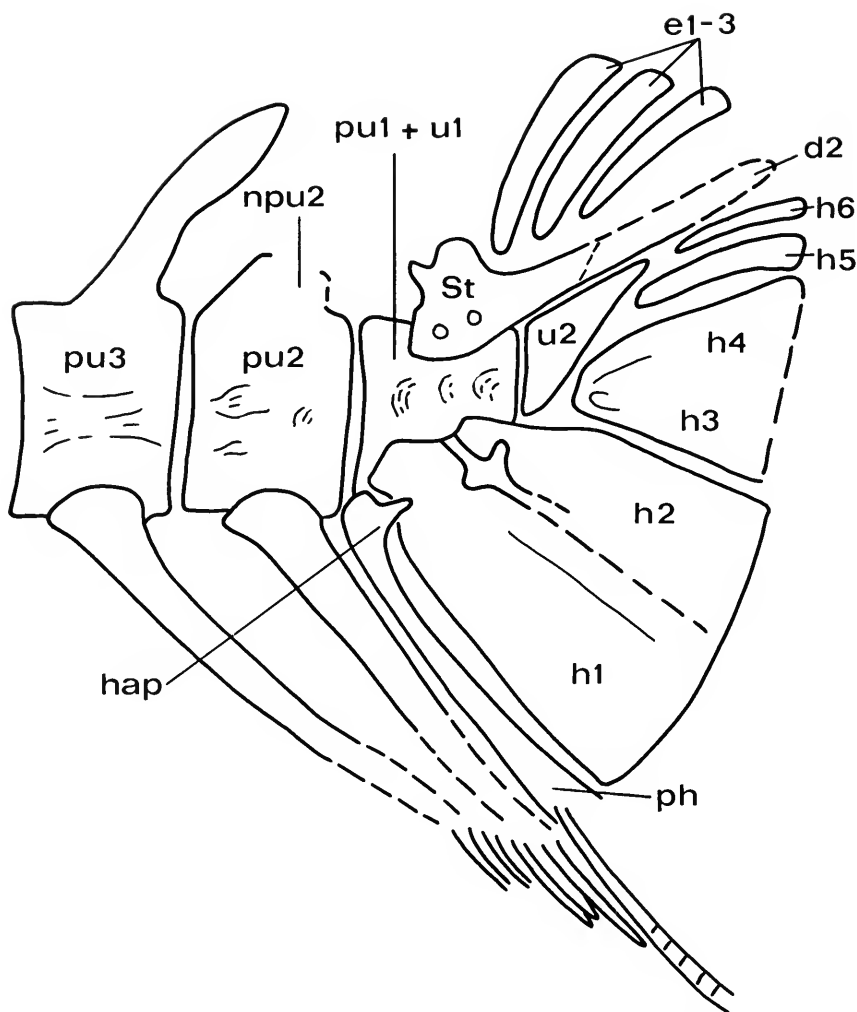


FIG. 9. Holocentrid gen. and sp. incertae sedis. SMM 11543. Caudal skeleton. For abbreviations see p. 356.

about 9 mm. high and 5+ mm. long. The focus is located toward the rear, about midway along the scale height. Many circuli characterize the scale which is approximately rectangular in outline and similar to that of living holocentrids (Woods and Sonoda, 1973). It is not possible to determine whether ctenii are present.

*Remarks.*—This single specimen is referable to the Berycoidei based upon its caudal fin with 19 principal rays, caudal fin skeleton

with a free second uroneural, and absence of epineurals. Within the suborder, the new fish must be referred to the holocentrids due to the number of spinous rays in the dorsal fin, their alternating right and left pattern and the number of soft rays in the pelvic fin. Due to the incompleteness of the specimen it is better not to establish a new genus and species. It differs from its contemporary, *Kansius* in some details of the caudal skeleton, the thickness of the dorsal fin spines, and their left, right alternation. Also, the few head bones preserved, particularly the lacrymal, suggest a more rugose surface sculpture than in the *Kansius* material. Clearly, more than one type of berycoid fish is to be found in Kansas.

### MODE OF PRESERVATION

The Niobrara Formation and specifically the Smoky Hill Chalk has yielded over the last century a vast number of different kinds of fishes, reptiles, and birds. These fossils are preserved directly in rock in contrast to the mode of preservation of the majority of fishes described in this paper. Of the eight cataloged specimens, with a total of nearly 100 individuals, five occur adhering to inner surfaces of the clam *Inoceramus platinus*. Two of the others (AMNH 9837, 9838) were found directly upon the large ichthyodectid fish, *Xiphactinus audax* (SMM 5026), while the third (SMM 25) lies on a particularly dense block of chalk. In addition to these acanthomorphs, at least four other specimens of fishes from the Smoky Hill Chalk are preserved on clam shells. These include the amioid, *Paraliodesmus* (Dunkle, 1969) on *I. platinus*, a different, undescribed amioid (SMM 11324) on *Volviceramus grandis* (a bowl-shaped rather than thin, flat inoceramid), and two fragments (KU 24201, 24202) with fossil amioid remains similar to SMM 11324 on *I. sp.* These fossils represent the only occurrences of amioids in the Niobrara Formation. In addition, one other genus, a nominal enchodontid, *Leptacodon* (represented by two individuals, KU 35, the holotype, and FMNH PF 3040 both of which occur on blocks with specimens of *Omosoma*) is known only from such shells.

Clearly, despite years of collecting in the chalk, few clam shells bearing fishes have been found. Because fossil collectors working in the chalk have concentrated their attentions on larger vertebrates, it is possible that smaller fishes similar to those on shells but preserved directly in rock have been bypassed. However, the occurrence of many small skeletons of *Enchodus*, apselicids, and probable albulids among described and undescribed chalk fossils suggests that this is not the sole factor. The growing number of a few

types of fishes found solely on clam shells suggests that particular conditions are required for their preservation and this accounts for their rarity.

Precise stratigraphic positions are known for few of the chalk vertebrates. However, the occurrence of such fossils from eastern to western ends of exposures of the chalk in Kansas indicates that many of the larger vertebrates may not be stratigraphically limited in their distribution in the chalk. The fish described here appear to be more limited in occurrence. In recent years Kauffman (1967) has developed a picture of the biostratigraphy of the chalk defining particular assemblages of macroinvertebrates and associated lithological sequences. Two of these macroinvertebrate assemblages, designated Y and Z, include the species of clam shells which contain fossil fishes.

Assemblage Y features very large, flat, thin-shelled inoceramids, especially *I. platinus* encrusted with *Pycnodonte*, reflecting an environment of soft carbonate substrates to which these broad (to 1 m. or more in diameter), thin shells were adapted for lying prone on the surface. According to Kauffman, this assemblage is characteristic of moderately deep, quite outer shelf waters possibly 300-500 ft. in depth. Assemblage Z is characterized by bowl-shaped inoceramids and particularly in the Smoky Hill Chalk by *Volvicerasmus grandis*. Kauffman suggests (most speculatively) that this assemblage represents outer shelf limes and muds less than 100 ft. in depth but below "effective wave base."

All fossils cited in this paper come from Assemblage Y except SMM 11324 which is from Assemblage Z. These are the first chalk vertebrates to be tied to a specific macroinvertebrate assemblage.

In life, these large shells lay on soft substrates and the upper valves became encrusted with the small clam *Pycnodonte*. Upon death, the shells sprung open and either by this means or with the aid of water currents the upper valves were laid on the sea bottom, lateral surface down. As the fish are almost exclusively on the epizoan free inner surface of the upper (right) valve, it would appear that they accumulated on the clams at this time. One might also expect fish to be preserved on the lower valves, but the shells with fish all show moderate to dense epizoan encrustations on the external surface, rather than bare shell which would be expected if fish were preserved on the lower (left) valve. In one case (FMNH PF 3040), a few fragments of *Omosoma* are preserved on the outer shell surface indicating that some fish may have been deposited while the clams were alive. However, most such individuals would have been



bacterially decomposed or mechanically disrupted before fossilization. The hard surface of the shells relative to the slurry lime of the bottom appears to have provided the suitable environment for intact preservation of these small vertebrates and may be an important factor accounting for their rarity as fossils. Those few specimens not on shells (AMNH 9837, 9838, and SMM 25) were deposited either on a large, firm-bodied fish or in denser chalk. Unfortunately, we do not know the specific macroinvertebrate assemblage in which these specimens were deposited.

Polymixiids and holocentrids today are mostly shallow water fish (Woods and Sonoda, 1973), but some occur along the shelf to depths of 60 or more fathoms. Presumably, these small fishes, characteristically schooling types, were swept together by current action in a short period of time in order to yield the large numbers of individuals on a single shell. There is no indication that the current was strong enough to orient the individual fish. Rather they face all directions and in the case of SMM 8123 lie two or three deep. Furthermore, the fact that the fish are relatively intact suggests that they were buried rapidly. Otherwise, due to bacterial action in these warm seas, they might have floated and been deposited as disarticulated fragments.

It is impossible to examine a large area at one level in order to determine the extent of deposition of fish on shells at one time, but other inoceramid shells within several yards of FMNH PF 3040 showed no indication of fish specimens.

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