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FOSSIL FISH STUDIES<sup>1</sup>

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## PART 1

## HELICOPRION (ELASMOBRANCHII, EDESTIDAE) FROM THE BONE SPRING FORMATION (LOWER PERMIAN) OF WEST TEXAS

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## ABSTRACT

The rare organ-genus, *Helicoprion*, is reported from the Guadalupe Mountains of west Texas, and its geographic distribution is reviewed. Although *Helicoprion* has been cited as an index fossil with a Uralian to Artinskian range, undisputed reports are restricted to the Early Permian.

## INTRODUCTION

Despite the wide geographic distribution of *Helicoprion*, this organ-genus is sufficiently rare and unusual to warrant the report of new occurrences. *Helicoprion* is known from a number of localities in North America and it has recently been reported from the Skinner Ranch Formation of Texas (Kelly & Zangerl, 1976). An additional specimen has been collected by F. R. West from the Guadalupe Mountains in west Texas. It was found *in situ* in the black limestone beds of the

Bone Spring Formation, 0.4 km east of Williams Ranch in Bone Canyon, Culberson County, Texas (University of Kansas Locality KU-TX-18). This specimen (KUVF 30606) is now in the collection of fossil vertebrates of the Museum of Natural History, University of Kansas. The Bone Spring Limestone is Early Permian (Leonardian) in age and represents a limy mud deposited in a deep stagnant basin (Harms, 1974).

## SYSTEMATIC DESCRIPTION

Family EDESTIDAE Jaekel, 1899

Genus HELICOPRION Karpinsky, 1899

HELICOPRION sp. indet.

Figure 1

Taxonomic assignment follows that of Kelly and Zangerl (1976) and terminology follows that used by Bendix-Almgreen (1966). Affinities of the genus are controversial, particularly as to placement within the Edestidae (see Moy-Thomas & Miles, 1971).

*Description.*—The specimen is a partial symphyseal tooth-spiral, which is broken apically and sagittally to reveal the interior of the tooth-crowns and compound root. Little detail is revealed, and the effect is that of an outline of the specimen. Parts of three volutions, composed of a total of 41

tooth-crowns are preserved: 8 on the first volution, 12 on the second, and 21 on the third. Part of the juvenile tooth arch may be present. Only tooth-crowns in the third (outermost) volution are sufficiently well preserved to permit accurate measurements. Of these tooth-crowns, that designated "A" (Fig. 1) has an apical angle of 45 degrees, a volution height of 92.1 mm, and a tooth blade width of 7.0 mm. The largest tooth-crown, "B" (Fig. 1), has a tooth blade width of 8.5 mm.

*Discussion.*—*Helicoprion* occurs widely and is presently known from Alberta, British Columbia, the Canadian Arctic, California, Nevada, Idaho (Nassichuk, 1971; Wheeler, 1939), Wyoming (Dunkle & Van Sickle, 1968), Texas (Kelly & Zangerl, 1976) and Mexico (Mullerried, 1945).

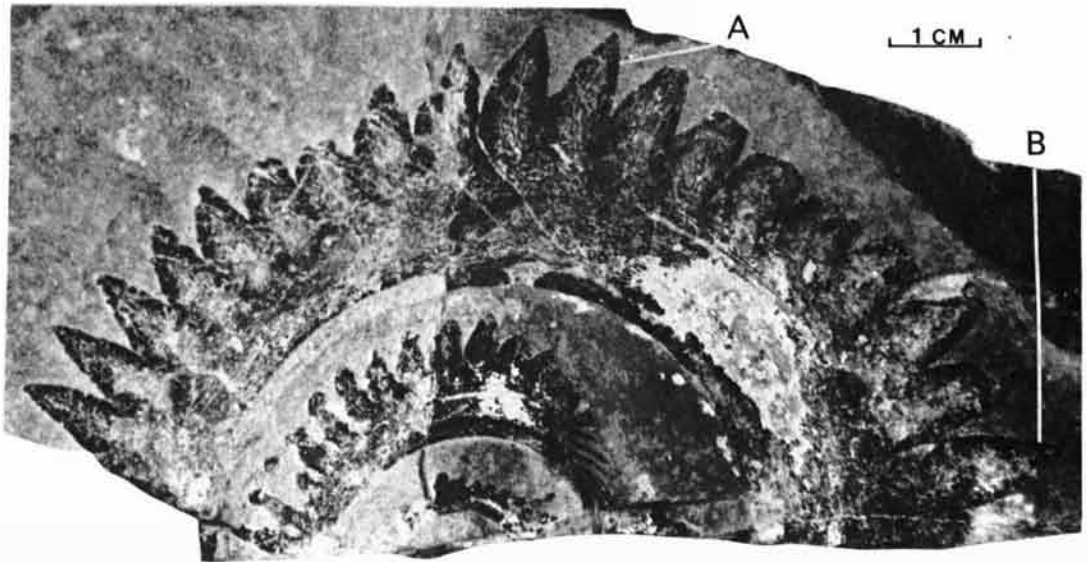


FIG. 1. *Helicoprion* sp., lateral view (KUVF 30606). Representative tooth-crowns designated A and B.

Outside North America it has been reported from the Soviet Union, Japan, Australia, Spitsbergen (for references, see Nassichuk, 1971), Laos (Wheeler, 1939), and possibly from Iran (Ob-ruchev, 1964). Mullerried (1945) has described *H. mexicanus* from the state of Coahuila, but subsequent reviewers have overlooked that report from Mexico. *Helicoprion* has also been reported from the Upper Productus Limestone in the Salt Range of India (now Pakistan) (Koken, 1901; Wheeler, 1939), but was assigned to another genus, *Helicampodus*, by Branson (1935; see also Teichert, 1940).

Virtually all well-known occurrences of *Helicoprion* are from the latter part of the Early Permian (Nassichuk, 1971). *Helicoprion* has been reported to have a Permo-Carboniferous distribution (e.g., Romer, 1966; Moy-Thomas & Miles, 1971) and has been used as an index indicating Late Pennsylvanian (Uralian) to Early Permian

(Artinskian) age (Kelly & Zangerl, 1976). Nevertheless, a review by Nassichuk (1971) failed to reveal any undisputed occurrence of *Helicoprion* in the Pennsylvanian, and the genus is presently known only from the Early Permian. Confusion as to the stratigraphic range of *Helicoprion* may have resulted from the description by Karpinsky (1922) of *Campyloprion ivanovi* from the Upper Carboniferous of the Soviet Union, which he incorrectly placed in *Helicoprion*. Licharev, in a personal communication to Wheeler (1939), mentioned an undescribed specimen, now lost, from the Uralian (Late Carboniferous) of the Donetsk basin, Soviet Union, but such a record is inadequate to demonstrate the presence of *Helicoprion* in the Late Carboniferous. The specimen described from the Wolfcampian of Texas (Kelly & Zangerl, 1976) is the earliest well-documented occurrence of this genus.

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## PART 2

# AFFINITIES OF THE CHONDRICHTHYAN ORGAN-GENERA LISTRACANTHUS AND PETRODUS

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### ABSTRACT

The name *Listracanthus* has been used for elements that occur in various chondrichthyans. *Petrodus*-type denticles are also widely distributed among fishes of this subclass. New material from the Fort Scott Limestone (Middle Pennsylvanian of Kansas) indicates that these spines and denticles were associated in the same animal, at least in Pennsylvanian black shales. *Edestus* dentitions may have been associated with these spines and denticles. *Listracanthus* spines are modified dermal denticles and occur closely spaced and in great numbers in the skin of a large chondrichthyan. Synonymy of all *Listracanthus* material with *Deltoptychius* is unwarranted. *Listracanthus* and *Petrodus* should be formally regarded as *nomina dubia* and retained to represent organ-genera only.

### INTRODUCTION

The organ-genus *Listracanthus* was established by Newberry and Worthen in 1870 on the basis of two spines. *Petrodus*, also an organ-genus, is known from denticles, first described by McCoy in

1848. Both genera are relatively common in Carboniferous black shales of Europe and North America.

Since the description of these forms little

progress has been made in establishing their zoological affinities. Moy-Thomas (1935) believed that *Petrodus* denticles found with a hyodont shark from the Pennsylvanian were derived from the shark, which he described under the name *Petrodus*. That association has been questioned by Zangerl and Richardson (1963). Based on the presence of *Listracanthus*-like spines on the type specimen of *Deltoptychius armigerus*, Patterson (1965) considered *Listracanthus* to be a synonym of *Deltoptychius* (Order Chimaerida, Sub-

order Menaspoidei). He also noted the presence of *Petrodus*-like denticles in the head and trunk region of the type specimen. Zidek (1973) has further discussed the affinities of *Petrodus*.

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#### LOCALITY

Recently new material of *Listracanthus* and *Petrodus* was collected by the junior author from a limestone quarry near Fort Scott, Kansas. The block containing the specimen had been removed as a result of commercial quarrying and it has not been determined which surface of the specimen was originally the upper one. Thickness and lithology, however, definitely indicate derivation from a black shale, approximately 15 cm above the top of the Summit Coal. This places the shale in

the Little Osage Shale Member of the Fort Scott Limestone, which is Middle Pennsylvania in age. The quarry (University of Kansas Locality KU-BOU-01), which is the type locality of the Fort Scott Limestone (Jewett, 1941), is located in the SE $\frac{1}{4}$  NE $\frac{1}{4}$  NW $\frac{1}{4}$  sec. 19, T. 25 S., R. 25 E., Bourbon County, Kansas, and is approximately 1.6 km north of the Fort Scott city limits and 0.8 km east of U.S. Highway 69. *Edestus* and *Cladodus* are also known from this locality.

#### DESCRIPTION

The specimen (KUPV 30604) consists of a mat of densely packed *Listracanthus* spines and *Petrodus* denticles preserved in a thin layer of black shale. Dimensions of the mat are approximately 62 cm in length, 41 cm in width, and between 6.5 to 7.0 mm in thickness. Spines appear on both surfaces. In some places *Listracanthus* spines are so closely packed that no matrix can be seen between them. For the most part they are randomly oriented, but in certain areas the spines are aligned in distinct rows (Fig. 2).

The spines conform in every way with the original description of *Listracanthus* and could probably be assigned to the common species, *L. hystrix*. Because most of the spines overlap each other, only a few are entirely visible. Eight of these were measured (from tip to corner of base on the concave side) and six are between 53 and 62 mm in length; the smallest spine is 36 mm and the largest is 76 mm in length. Toothlike projec-

tions are prominent along the concave side of each spine but are less conspicuous along the convex margin. From 8 to 11 ridges (carinae) are present near the base of each spine (Fig. 3,C).

*Petrodus* denticles or their impressions occur on one surface of the specimen. Almost all of the well-preserved denticles (27 of 31) are oriented with the base parallel to the shale surface and the crown pointing away at right angles. Individual *Petrodus* denticles are all much alike (Fig. 3,A), differing chiefly in size. Most are set on round bases but the crown and base of the largest observed denticle is elongated, measuring 3.5 by 2.1 mm at its base.

Also appearing on the same surface as the *Petrodus* denticles, and only in localized patches, are numerous small strongly arched denticles that have a truncated base (Fig. 3,B). One or more ridges are present on the sides of each of these denticles.



FIG. 2. Part of KUVF 30604 showing densely packed *Listracanthus* spines. Note the alignment of the bases, below left of center.

### DISCUSSION

Based on the material described above, and the work of Zangerl and Richardson (1963), we contend that *Listracanthus* spines and *Petrodus* denticles were present in the same chondrichthyan. The idea that these two elements were present on the same animal dates back to Bradley (1870), who noted that spines and denticles were commonly recovered from the same locality. Woodward (1903, p. 488) also suggested that denticles from the Lower Carboniferous of Russia, which he referred to as *Petrodus acutus*, were "essentially a squat *Listracanthus* with deepened lateral ridges and an exaggerated basal expansion."

*Listracanthus* spines and *Petrodus* denticles are two of the most common vertebrate fossils found in black shale where there seems to be a high correlation between the relative abundance of the

two genera. They often occur together as the only vertebrate remains at certain black-shale localities; however, both genera are known from localities where the other has not been reported, but this could result from sampling bias, hydraulic sorting, or differential preservation.

Plots of the horizontal distribution of *Petrodus* denticles and *Listracanthus* spines at Mecca Quarry in Indiana, are similar and were thought by Zangerl and Richardson (1963) to indicate that the decomposition and means of dispersal were similar in both forms. They also suggested that similar distribution patterns might indicate further similarities between the genera, that both possessed only a limited number of preservable elements, and that the size of the body might be similar for both animals.

Zangerl and Richardson (1963) did not believe

that correlation between the vertical distribution of *Petrodus* denticles and *Listracanthus* spines at the Mecca Quarry was close enough to indicate a single animal. Measurements from Zangerl and Richardson (1963, fig. 32) yield a correlation of 0.75 (product-moment correlation coefficient) for these two forms. Correlation of this magnitude is not sufficient to demonstrate a strong relationship between *Listracanthus* and *Petrodus*; however, it does not preclude the possibility.

After considering the size, shape, and delicate structure of *Listracanthus* spines, Zangerl and Richardson (1963) tentatively suggested that they were borne by a chondrichthyan of fairly small size. *Petrodus* was believed to be a relatively large animal with individuals carrying a large number of denticles.

Concentrations of *Listracanthus* spines and *Petrodus* denticles are rare in the Indiana black shales, but they do occur in a few large gastric residues (regurgitated, partially digested stomach contents). From the West Montezuma locality, Zangerl and Richardson (1963, p. 196, 197) recorded what they interpreted to be the "ill-packed gastric residue from a predator of enormous size." That residue contained many *Petrodus* denticles

and numerous *Listracanthus* spines. Considering the apparent low predation rate (only three gastric residues contained *Listracanthus* spines in Mecca Quarry; none definitely contained *Petrodus* denticles), it is surprising that they should occur together in a gastric residue, unless, as we contend, they represent the same animal.

Specimen KUVF 30604 is interpreted as a piece of shagreen from an undetermined chondrichthyan. The orderly alignment of many *Listracanthus* spines and the uniform orientation of most of the *Petrodus* denticles rules out the possibility of mechanical concentration. Because no other remains are associated with this specimen, it probably represented only a small part of the fish's dermal covering. It follows that a large chondrichthyan is represented, and this is consistent with the fact that only large gastric residues contain concentrations of *Listracanthus* spines and *Petrodus* denticles in the Indiana black shales.

One difficulty in assigning *Petrodus* denticles to a particular chondrichthyan is that these denticles are probably not diagnostic even at the generic level. In actuality, similar denticles probably occur in various members of a family or higher taxon. It is not impossible that denticles

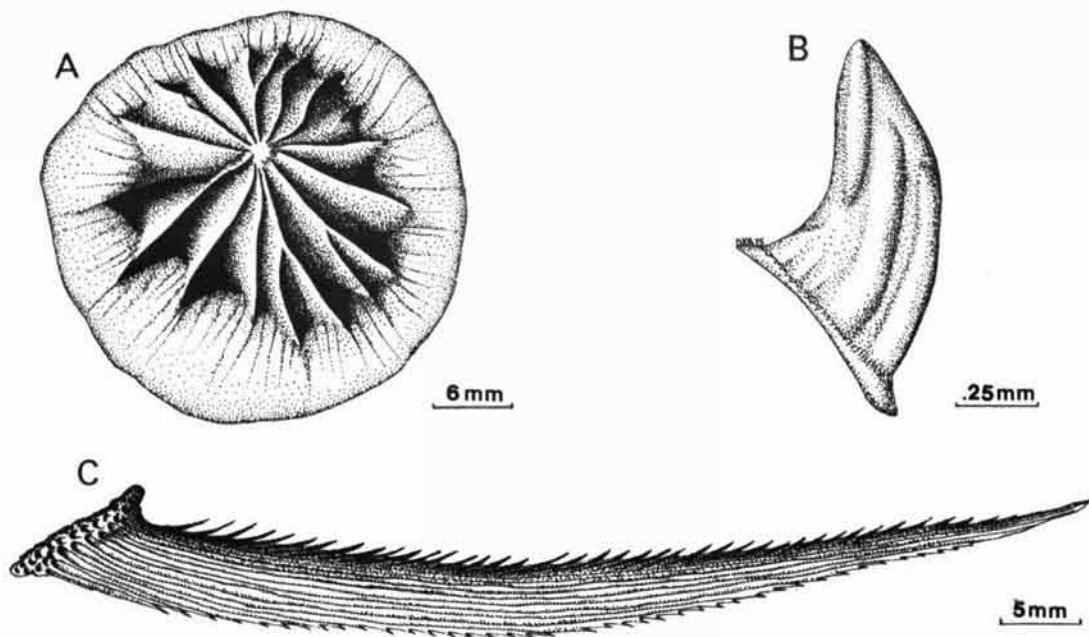


FIG. 3. *Petrodus* denticle in dorsal view (A), associated dermal denticle in lateral view (B), and *Listracanthus* spine in lateral view (C).

of this general morphotype occur in diverse groups as a result of independent origin and parallel evolution. Woodward (1903) noted the close similarity between *P. patelliformis* and *Hybodus* denticles, and he implied that *P. patelliformis* might represent a hybodont shark. Obruchev (1964) stated that such denticles probably appear on various coeliodonts and other bradyodonts. We have already noted the presence of *Petrodus*-like denticles on the head and trunk of *Deltotoptychius* (Patterson, 1965). In reference to specimens of *Petrodus patelliformis*, thought to be from the type locality of the genus, Ford (1964, p. 5) stated that they "appear to grade into the form described from Indiana as *Petrodus* sp. by Newberry (1873) and into a form from Illinois described by Newberry and Worthen (1866, p. 72 and Pl. IV, Fig. 17), as *P. acutus*."

Spines referred to *Listracanthus* may also represent more than one genus, although the complex nature of these spines seemingly does not support this view. Nevertheless, spines of this nature are known to occur in *Deltotoptychius* from the Mississippian, even though the crushing dentitions of this genus and other menaspoids are unknown from the Indiana black shales (M. E. Williams, 1975, pers. commun.) and possibly from black shales in general. Considering the great number of *Listracanthus* spines recovered by Zangerl and Richardson (1963), and the complete lack of menaspoids from these shales, we believe the synonymy of all *Listracanthus* with *Deltotoptychius* (see Patterson, 1965) is unwarranted.

Until Paleozoic sharks are better known, we recommend that *Listracanthus* and *Petrodus* be retained as terms that are useful as long as it is clearly understood that they are organ-genera only. Although these forms occur together in Pennsylvanian black shales, at the present time, they probably can not be satisfactorily distinguished from similar organs found in other chondrichthyans.

Other chondrichthyan remains from Pennsylvanian black shales are of uncertain affinities and may also occur with *Listracanthus* and *Petrodus*. The organ-genus *Edestus* may be the dentition of such an animal, but this can not yet be demon-

strated. *Edestus* is known chiefly from isolated teeth and symphyseal dentitions and is commonly found in, but not restricted to, black shale. Size and morphology of *Edestus* teeth indicate a large chondrichthyan, at or near the top of the trophic pyramid (see Eaton, 1962, for conflicting view). Animals occupying this position in a food chain are, as a rule, seldom preyed upon, long lived, and not abundant relative to the organisms upon which they prey. This is consistent with the fact that the symphyseal dentitions of *Edestus*, which must represent the death of the animal, are rare elements in those faunas in which the genus occurs.

The study by Zangerl and Richardson (1963) and the present paper indicate that two attributes (infrequently preyed upon, large body size) were probably also shared by the chondrichthyan bearing *Listracanthus* spines and *Petrodus* denticles. Thus, it is possible that these teeth, spines and denticles all derive from the same animal. The great abundance of *Petrodus* denticles and *Listracanthus* spines in the Indiana black shales is consistent with the above if many of these elements are considered to have been shed from a living animal (see Zangerl & Richardson, 1963, for discussion of shedding of *Petrodus* denticles). As early as 1946, Olson implied that these three forms may not be generically distinct. Moreover, the skeleton of the chondrichthyan that bore these spines and denticles was probably histologically unsuited for fossilization in the black-shale depositional environment (i.e., it was probably not composed of the same type of calcified cartilage as were other chondrichthyans in the environment). Skull material from two species of edestids has been recovered from Logan Quarry, Indiana (Zangerl, 1973), and is also poorly calcified and consequently poorly preserved (R. Zangerl, 1976, pers. commun.). Contrary to this hypothesized relationship, we note that *Listracanthus*-like spines have recently been reported from the Lower Triassic of Wapiti Lake, British Columbia (Schaeffer & Mangus, 1976), whereas *Edestus* is unknown from rocks later than Permian in age.

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## PART 3

# ENTEROSPIRAE (FOSSIL INTESTINES) FROM THE UPPER CRETACEOUS NIOBRARA FORMATION OF WESTERN KANSAS

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### ABSTRACT

Gross morphology and microscopic study of ground sections reveal that heteropolar spiral "coprolites" from the Upper Cretaceous Niobrara Formation of western Kansas are of the same nature as those described as enterospirae (fossilized intestines) of xenacanth sharks by Williams (1972). These are the first recognized enterospirae in Mesozoic deposits. Analysis of faunal assemblages indicates that the Niobrara enterospirae are not attributable to any known selachians or other vertebrates of the fauna, and supports a hypothesis of the presence of diminutive and heretofore undetected selachians in the Niobrara fauna.

## INTRODUCTION

Williams (1972) studied a collection of heteropolar coprolites from the Lower Permian of Kansas and compared them to the spiral valves of modern sharks. He concluded that: 1) the structures described as mucosal folds confirmed the suggestion of Fritsch (1895) that they are fossilized intestines; 2) judging from their contents and the associated fauna, they are from xenacanth sharks; and 3) amphipolar forms are coprolites in the strict sense. Williams used Fritsch's term "enterospirae" to designate such fossil intestines of a coiled nature.

Vertebrate coprolites were first reported from North America by Dekay (1830) in a letter to Buckland, which was published along with Buckland's reply in the *Philosophical Magazine*. Dekay's specimens came from the Cretaceous of New Jersey. Case (1967) has illustrated coprolites from the Navesink Formation of New Jersey; Waldman (1970) analyzed the contents of a coprolite from the Oldman Formation of Alberta; Waldman and Hopkins (1970) utilized Upper Cretaceous coprolites for their floral content; and Stokes and Balsley (1973) mentioned "gastric concretions," possibly coprolitic, from the Ferron Sandstone of Utah and the Fox Hills Formation of South Dakota. To my knowledge, this is the extent of the study of North American Upper Cretaceous macrocoprolites, although several authors have studied microscopic fecal material from these deposits.

Mantell (1822) studied coprolites from the Mesozoic of England and suggested an animal

origin for them. Buckland (1829) recognized the fecal nature of these spiral forms and later (1841) referred them to ichthyosaurs, although most authors have disputed this assignment. In reference to these English specimens, Williams (1972) stated that they are almost certainly not from pleuracanth and that they might or might not prove to represent enterospirae. He further concluded that thin-section studies and analyses of the related faunal assemblages would be necessary to determine whether or not specimens from any localities and geologic horizons other than those of his study were actually enterospirae and to what taxonomic groups they should be assigned.

In recent years I have collected heteropolar spiral coprolites from the Niobrara Formation of the Kansas Upper Cretaceous. In accordance with Williams' suggestions, I undertook a study of ground sections and an analysis of the fauna. All specimens used in this study are deposited in the University of Kansas Vertebrate Paleontology collections, and are numbered with the prefix KUVP.

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## DISCUSSION

Examples of enterospirae from the Niobrara Formation are shown in Figure 4. None of the specimens collected from the Niobrara Formation are complete. Some have lost ends due to weathering, and outer whorls have spalled off from others. Many show collapse, although others are nearly round in cross section. They range in length from 28 to 48 mm and from 9 to 18 mm in maximum width. The general appearance is of a wide ribbon coiled around itself in cone-shaped whorls, the whorls pointing anteriorly. The anterior end is composed of the last whorls and is more acutely pointed than the posterior end,

which shows the coiled nature of the structure (Fig. 4,4). Each whorl is oriented nearly perpendicular to the long axis of the structure.

These observations are in accord with Williams' (1972) description of Permian enterospirae. He also observed a series of subparallel folds inclined at an angle of about 60 degrees to the long axis on many specimens, and stated that these folds have usually been interpreted to result from passage of fecal material over mucosal folds of the outer sheath of the intestine. Similar folds are present in Niobrara enterospirae (Fig. 4,2,3). They generally have an angle of inclination to

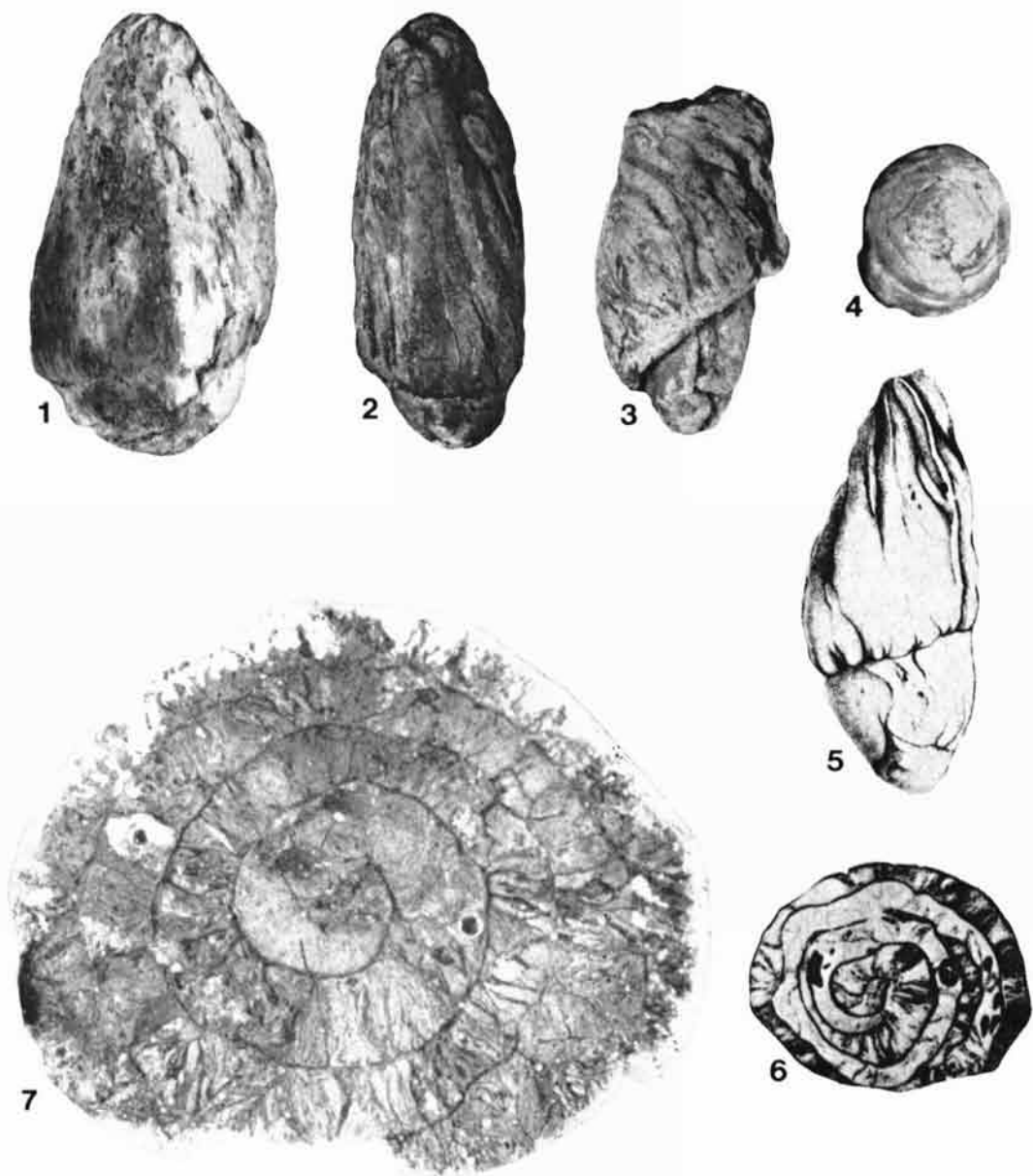
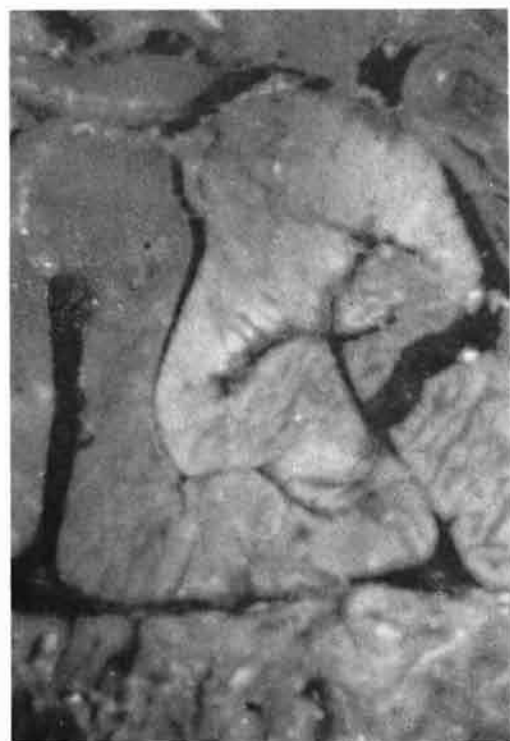


FIG. 4. Enterospirae from the Niobrara Formation in Kansas (1-4,7) and from the Lias of England (5,6).—1. Specimen from the Niobrara showing general morphology (KUVV 43074),  $\times 2$ .—2,3. Niobrara enterospira showing external mucosal folds (KUVV 43073, KUVV 43071), both  $\times 2$ .—4. Posterior end of Niobrara enterospira showing coiling (KUVV 43072),  $\times 2$ .—5. Specimen from the Lias of Lyme Regis, England (size not given, mod. from Buckland, 1841, pl. 15, fig. 14).—6. Cross section of enterospira from the Lias of Lyme Regis, England (size not given, mod. from Buckland, 1829, pl. 28, fig. 12).—7. Cross section of Niobrara enterospira (KUVV 43068, sec. 2),  $\times 17.7$ .

the long axis of between 20 to 30 degrees. Williams (1972, pl. 1, fig. 1-7) showed that these folds in Permian enterospirae frequently have an

angle of inclination that is considerably less than 60 degrees. There is no possibility that these are marks resulting from the passage of fecal material



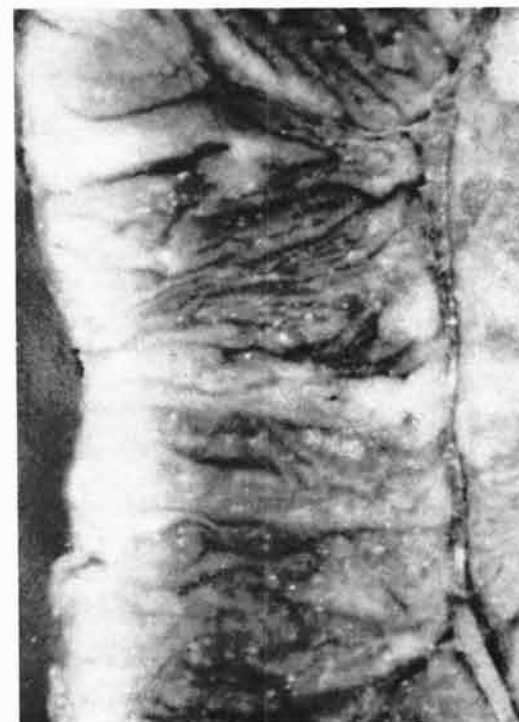
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FIG. 5. (See facing page.)

over the mucosal folds of a spiral valve, because that would produce marks parallel to the direction of coiling and approximately perpendicular to the folds in question. Furthermore, these are undoubtedly casts of the mucosal folds because tangential sections indicate that they are internally continuous with the mucosal folds. None of the posterior ends of these enterospirae have a matrix-filled cavity as do those described by Williams, and the spiral is always completed to the center (cf. Williams, 1972, pl. 1, fig. 8).

Ground sections show that, whereas the whorls are somewhat thinner and more numerous than those of Williams' embryonic *Squalus acanthias*, they are not as numerous as those of Permian enterospirae from Texas and Kansas. The concentric pattern of the whorls continues to the center in some specimens (Fig. 4,7) or is replaced by loose irregular foldings in others (Fig. 5,1,2). The folds are nearly identical to those of xenacanth enterospirae. They commonly bifurcate and are much higher, thinner, and more elaborate and irregular than those of *Squalus acanthias*. Those of the outer whorls are better defined and more regular than those of the central whorls. The mucosal folds are rarely linear interfingerings (Fig. 6,1), and are more often dendritic (Fig. 6,2-4). These folds are double layered and continuous from fold to fold as are those of xenacanth enterospirae. The position of the submucosa is occupied by either a void or by calcite infillings (Fig. 5,3,4). The best hypothesis to explain these complex structures is that they are actually fossilized intestinal contents.

Inclusions of bone are not apparent in the sections, but oblong to spherical calcite infillings are seen between some mucosal folds. These never transgress the boundaries of the intestinal wall and may represent voids left by rotted organic material or by digestive gases trapped within the apatite paste. Calcite-filled cracks intersect the intestinal wall in some instances, and are of diagenetic origin.

As has been shown, the Niobrara specimens resemble Williams' (1972) enterospirae in nearly every detail, and should be considered to be enterospirae. No other enterospirae have been previ-

ously recognized as such from the Mesozoic, but illustrations of spiral coprolites from the Lias of England, which were studied by Buckland (1829, 1841), indicate from cross section and gross morphology that they, too, are enterospirae (Fig. 4,5,6).

One enterospira, KUVV 25868, was collected from the Smoky Hill Chalk in the NE $\frac{1}{4}$  sec. 12, T. 8 S., R. 22 W., Graham County, Kansas (KU Locality KU-GRA-11). Associated fauna includes the invertebrates *Pycnodonte congesta*, *Volviceramus grandis*, and *Tusoteuthis longa*. Associated vertebrates include *Ptychodus mortoni*, *Squalicorax falcatus*, *Cretolamna appendiculata*, *Cimolichthys nepaholica*, *Enchodus gladiolus*, *Stratodus apicalis*, *Xiphactinus audax*, Toxochelyidae, Mosasauridae, *Ichthyornis victor*, and *Ichthyornis* cf. *I. tener*. The absence of *Inoceramus platinus* and the presence of *Volviceramus grandis* indicate that the fauna is of late Coniacian age.

A second locality that has produced enterospirae is in the E $\frac{1}{2}$  sec. 27, T. 14 S., R. 26 W., Gove County, Kansas (KU Locality KU-GOV-05). This locality, like the preceding one, is in what could be called a coprolitic zone. These zones of abundant coprolites are also associated with an abundance of other vertebrate fossils. The zones are probably local and of little stratigraphic significance. It appears that not all coprolitic zones produce enterospirae; however, more than 30 enterospirae are among the coprolitic material collected at this locality. The associated fauna includes the invertebrates *Pycnodonte congesta*, *Volviceramus grandis*, *Inoceramus platinus*, *Durania maxima*, *Tusoteuthis longa*, and *Texasites* sp. (*Spinptychus sternbergi*). Vertebrates include *Squalicorax falcatus*, *Cretolamna appendiculata*, *Cretoxyrhina mantelli*, *Protosphyraena* sp., *Xiphactinus audax*, Ichthyodectidae (*Gillicus* or *Ichthyodectes*), *Apsopelix anglicus*, *Pachyrhizodus* sp., Plethodidae, *Cimolichthys nepaholica*, *Enchodus dirus*, *Enchodus petrosus*, *Toxochelys latiremis*, *Chelosphargis advena*, Mosasauridae, and *Pteranodon* sp. This fauna is also of late Coniacian age. Although *Spinptychus* has been considered to be indicative of Santonian age (Kennedy & Klingler, 1972), the presence of *Volvice-*

FIG. 5. Enterospirae from the Niobrara Formation. All figures approximately  $\times 45$ .—1,2. Irregular folding in the center of KUVV 43070, sec. 1.—3,4. Outer whorl of KUVV 43068, sec. 3, showing loss of submucosa and subsequent calcite infilling (along the right border).

*ramus grandis* and *Squalicorax falcatus* indicates that it ranges into the late Coniacian as well.

Articulated vertebrate remains are quite common at these localities, as in most of the Smoky Hill Member. cursory examination reveals three taxonomic groups in common to these faunas: selachians, reptiles, and teleosts. Teleosts and reptiles are not known to have spiral valves. It is generally accepted that all chondrichthyans and all non-teleostean osteichthyans possess some type of spiral valve, but those of the Neopterygii appear to be rather rudimentary. The only non-teleostean osteichthyans known from the Niobrara Formation are one specimen of *Lepisosteus* sp. (Wiley & Stewart, in press), three specimens of pycnodonts (the holotype of *Hadrodus marshi* [Gregory, 1950] and the holotype of *Micropycnodon kansasensis* [Hibbard & Graffham, 1941], and a second specimen of *M. kansasensis* [Dunkle & Hibbard, 1946]), and four specimens referred to the Amioidea (Dunkle, 1969; Bardack, 1976). All these are neopterygians and presumably would not have had spiral valves as complex as those represented by the enterospirae. Furthermore, these are unknown from the two localities in question and, therefore, it is unlikely that the enterospirae would be from any of these.

At present, *Cretolamna appendiculata* and *Squalicorax falcatus* are the only selachian taxa known from both localities. It is probable, however, that extensive collecting will show these localities to also have *Ptychodus mortoni*, *Cretoxyrhina mantelli*, and *Scapanorhynchus raphiodon* in common.

Of the selachians in the Niobrara Formation, *Cretoxyrhina mantelli* is the largest. One complete skeleton (KUPV 43092) is approximately 5.5 m in length, and its trunk centra are 75 to 80 mm in diameter. *Squalicorax falcatus* is a rather small lamniform by comparison. The only reasonably complete representative of this species in the University of Kansas collection is that of a juvenile (KUPV 34916) with centra of the trunk region 21 to 25 mm in diameter. Some of the enterospirae described by Williams (1972) are much larger than those described herein, and could well have been from xenacanth. The diam-

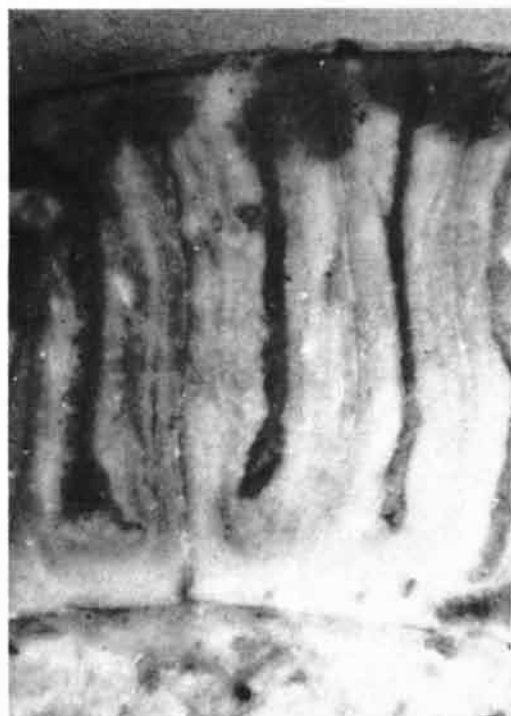
eter of the spiral valve in the extant shark *Squalus acanthias* is from four to five times the diameter of the centra in the trunk region (Gans & Parsons, 1964). By extrapolation, sharks having spiral valves the size of the Niobrara enterospirae would have centra from 2 to 3 mm in diameter. No selachians of this size, either juvenile or adult, are known from the Niobrara Formation.

From another perspective, only 16 teeth of *Squalicorax falcatus*, 11 of *Cretoxyrhina mantelli*, and 2 of *Cretolamna appendiculata* were found at the exposures that produced the 30 Niobrara enterospirae. With well over 200 teeth in the mouth at one time and those being gradually shed, theoretically, few individuals would be necessary to produce the observed quantity of teeth. Conversely, if an enterospira is correctly interpreted as a mortality, then at least 30 sharks were necessary to produce this concentration. Not only are the teeth known from this locality entirely insufficient to numerically account for the enterospirae, but they are all from sharks that were too large to possess such small spiral valves. A curious parallel is found in the Kansas Permian. Although Williams (1972) assigned his enterospirae to xenacanth, many more enterospirae were recovered than xenacanth teeth. If differential preservation is called upon to explain this phenomenon, it would be an anomalous situation indeed if coprolitic material were preserved, but not teeth.

The answer may well be that the teeth were too small to be detected by visual searching. Bulk acidizing of rock samples has produced extensive selachian microfaunas elsewhere in the North American Upper Cretaceous (Cappetta, 1973; Meyer, 1974), and might do the same in this instance. The most probable explanation of the Niobrara enterospirae is that they are from a very small selachian not previously detected in the Niobrara Formation. Further systematic collecting and study of coprolites and diminutive selachians from these and other localities should confirm or disprove this tentative explanation.

Only one enterospira, KUPV 43075, from the Gove County locality, produced identifiable vertebrate remains. It contained a tooth of *Enchodus* sp. Niobrara coprolites (*sensu stricto*) fall

FIG. 6. Enterospirae from the Niobrara Formation. All figures approximately  $\times 45$ .—1. Linear interfingering mucosal folds of the outer whorl of KUPV 43069, sec. 2.—2-4. Complete dendritic mucosal folds (KUPV 43070, sec. 1).



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FIG. 6. (See facing page.)

into five categories: 1) heteropolar with little internal structure preserved; 2) coprolites with convolutions similar to the external mucosal folds described above, but with no internal structure; 3) large oblong specimens loosely coiled around the narrow axis; 4) large oblong specimens coiled around the long axis; and 5) oblong specimens of all sizes, having no external or internal structure. Coprolites of category 1 often contain bone inclusions. They show some indication of a spiral structure and may actually represent spiral valves that decayed before the internal apatite paste had sufficiently consolidated to retain the structure of the mucosal folds. Those of category 3 rarely have in-

clusions. Those of category 5 frequently contain bones of teleosts. Remains of *Enchodus gladiolus*, *Stratodus apicalis*, and a small plethodid have been identified in this category. At present, none of these types can be definitely matched to any of the known members of the Niobrara fauna.

In summary, heteropolar spiral coprolites from the Niobrara Formation, herein described, are identified as enterospirae on the basis of gross and microscopic internal morphology. They are compared to the xenacanth enterospirae described by Williams (1972) and are tentatively assigned to small selachians previously undetected in the formation.

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## PART 4

BELONOSTOMUS SP. (TELEOSTEI, ASPIDORHYNCHIDAE)  
FROM THE UPPER CRETACEOUS TOMBIGBEE SAND  
OF ALABAMA

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## ABSTRACT

A small presymphyseal bone of the teleost *Belonostomus* is described from the Tombigbee Sand Member of the Eutaw Formation (Cretaceous, Campanian) in Alabama. This is the first report of an aspidorhynchid fish in the eastern Gulf Coastal Plain.

## INTRODUCTION

Aspidorhynchid fishes are known from Jurassic and Cretaceous deposits virtually worldwide. As presently defined the family contains only two genera—*Aspidorhynchus* and *Belonostomus*. In North America, *Belonostomus* has previously been described from the Lower Cretaceous of Mexico (Felix, 1891) and from several Upper Cretaceous localities: The Oldman and St. Mary River formations of Alberta (Lambe, 1902; Langston, 1975), the Judith River Formation of Montana, the Lance Formation of Wyoming (Estes, 1964), and the Austin Chalk of Texas (Bardack, 1968).

*Belonostomus* is here reported from the Tombigbee Sand Member of the Eutaw Formation in Alabama, which is Campanian in age, and approximately the same age as part of the Austin Chalk (Fig. 7). The member is predominantly composed of glauconitic cross-bedded marine sand. Bulk screening of the deposit in Alabama has produced a microvertebrate assemblage including a presymphyseal bone referable to *Belonostomus* sp. The specimen, deposited in the Kansas University Museum of Natural History, (KUVP 36120) was recovered from the Tombigbee Member in Mont-

gomery County, Alabama (sec. 22, T. 16 N., R. 17 E.) approximately 6 m (20 ft) below its contact with the Mooreville Formation of the Selma Group. This is the first report of an aspidorhynchid from the eastern Gulf Coastal Plain.

The vertebrate fauna of the Eutaw Formation is poorly known. A plesiosaur has been described by Shannon (1974), a hadrosaurian dinosaur by Kaye and Russell (1973), and selachians by Meyer (1974). Tuomey (1850), Stephenson (1926), and Stephenson and Monroe (1940) noted the occurrence of the shell-crushing shark *Ptychodus mortoni* in the Tombigbee Member. The *Belonostomus* specimen was found associated with a rich selachian assemblage including *Hybodus*, *Cretolamna*, *Ptychotrygon*, *Cretoxyrhina*, *Scapanorhynchus*, *Odontaspis*, and *Squalicorax*.

## ACKNOWLEDGMENTS

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## SYSTEMATIC DESCRIPTION

Subdivision TELEOSTEI Müller, 1846  
Family ASPIDORHYNCHIDAE Woodward,  
1896

The placement of the Aspidorhynchidae within the Teleostei differs from Bardack (1968) and most other authors, but follows the assignment of

Patterson (1973) and Patterson and Rosen (1977).

Genus *BELONOSTOMUS* Agassiz, 1833  
*BELONOSTOMUS* sp.

Figure 8

*Description.*—Only part of a presymphseal bone was recovered. It is hollow and tapered, measuring 8 mm in length and 1.0 mm in maximum width. The sides are ridged and covered with a shiny ganoine layer. In cross section the element is oval and truncated dorsally by a median groove that originally bore 17 small, regularly spaced, dome-shaped teeth. The preserved teeth are hollow and translucent, measuring 0.23 to 1.37

mm in diameter at the base. Tooth caps, presumably of "vitrodentine," are not preserved. On ridges on either side of the median tooth row were approximately 25 lateral teeth, measuring up to 0.15 mm in diameter.

*Discussion.*—The Alabama specimen differs from those of the Austin Chalk described by Bardack (1968), from *Belonostomus longirostris* of the Western Interior of the United States (Estes, 1964), and from *B. cinctus* of the English Chalk (Woodward, 1908) by having the median presymphseal teeth closely spaced, short, and mammiform instead of widely spaced, high, and conical. Bases of the median teeth are neither buttressed as in the Texas specimens nor fluted as in *B. longiro-*

UPPER CRETACEOUS STAGES/SUBSTAGES	ALABAMA	TEXAS	REDBIRD, WYOMING	JUDITH RIVER
MAESTRICHTIAN	PRAIRIE BLUFF FORMATION	KEMP CLAY	* LANCE FORMATION	HELL CREEK FORMATION
			FOX HILLS SANDSTONE	FOX HILLS SS.
CAMPANIAN	RIPLEY FORMATION	CORSICANNA MARL	UPPER UNNAMED SHALE MEMBER	BEAR PAW SHALE
		NACATOC SAND	KARA BENTONIC MBR.	
		NEYLANDVILLE MARL	LOWER UNNAMED MEMBER	* JUDITH RIVER FORMATION
		TAYLOR GROUP	RED BIRD SILTY MEMBER	PARKMAN SANDSTONE
LOWER	MOOREVILLE FORMATION	* AUSTIN GROUP	MITTEN BLACK SHALE MEMBER	EAGLE SANDSTONE
	TOMBIGBEE SAND MEMBER*		SHARON SPRINGS MEMBER	
	EUTAW FORMATION		GAMMON FERRUGINOUS MEMBER	TELEGRAPH CREEK FORMATION
SANTONIAN			NIOBARRA FORMATION	COLORADO SHALE

FIG. 7. Generalized correlation of Upper Cretaceous strata of the Gulf Coast and Western Interior of the United States. Horizons from which aspidorhynchid fishes have been recovered are indicated by a star (mod. from Owens and others, 1970 and Gill & Cobban, 1973).

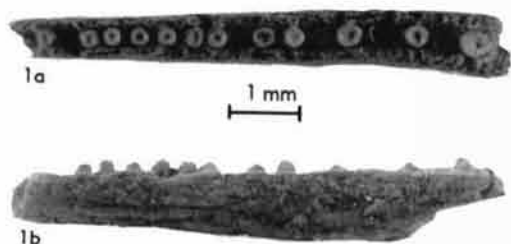


FIG. 8. *Belonostomus* sp. (KUVV 36120).—1a. Dorsal view of presymphyseal bone.—1b. Lateral view of same. Anterior is to the left.

*stris* and *B. cinctus*. The presymphyseals differ in cross section and external ornament; the Alabama and Wyoming fishes have oval cross sections with ganoine on the flanks, whereas those from the Austin Chalk have triangular cross sections and lack ganoine. Although these differences may indicate an undescribed species of *Belonostomus* from the Tombigbee Sand, the small size of the presymphyseal bone suggests a juvenile individual. Lacking more complete material, the specimen can be identified only to genus.

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