REASSESSMENT OF THE AFFINITIES OF THE EXTINCT GENUS *CYLINDRACANTHUS* (OSTEICHTHYES)

David C. Parris and Barbara Smith Grandstaff
Bureau of Natural History
New Jersey State Museum
Trenton, NJ 08625-0530

Gorden L. Bell,Jr.
Guadalupe Mountains National Park
Salt Flat, TX 79847

ABSTRACT

The perplexing fossil genus *Cylindracanthus* has long been a taxonomic problem. Virtually a form genus of ribbed spine-like marine fish fossils (Cretaceous-Eocene), it has only recently been definitively shown to be rostral, based on bilateral symmetry and the presence of teeth. Best-known from circum-Atlantic sites, the first South Dakota specimen revealed the teeth for the first time and gave impetus for this review. Although the study is on-going, an emergent concept of relationships of the genus is now hypothesized, as well as potential biostratigraphic utility.

Traditionally *Cylindracanthus* was discussed in relation to the billfishes (marlins and swordfishes), particularly by those who considered the fossils to be rostral fragments. Aside from the anatomical considerations, such a relationship is awkward for biostratigraphic and evolutionary reasons. The extant billfish are highly derived Perciformes, an order that is virtually confined to the Cenozoic. *Cylindracanthus* and associated genera originated during the Cretaceous, which would place them among the earliest perciform genera, if correctly referred. In fact, they are in some respects even more derived than the living billfish, presumably with a skeleton entirely of cartilage except for the rostrum. (Extant billfish are bony, not cartilaginous.) It is thus unlikely that *Cylindracanthus* would have appeared so much earlier than supposedly related forms which are less derived.

Ancestral Acipenseriformes (sturgeons and related forms) appeared in the geologic record at about the same time in the Cretaceous as did *Cylindracanthus* , and a significant number of acipenseriforms survived the Cretaceous/Tertiary extinction event, as did *Cylindracanthus*. All of the living members of the order have tendencies toward projecting rostral development, and all are highly cartilaginous. As many taxonomic groups of fishes have produced experiments in bill-like projections of the rostrum, it is reasonable to speculate that *Cylindracanthus* was such an experiment among the acipenseriforms, with which all known features are consistent. Of known actinopterygians, only

Acipenseriformes have a projecting rostrum entirely anterior to the mouth, and this appears to have been the case in *Cylindracanthus* as well.

Among these features are the teeth, now known from the South Dakota specimen, which resemble those of juvenile *Polyodon* and of the various toothed species and growth stages of *Acipenser*. The same specimen exhibits insertion grooves with the bones posterior to the rostrum which resemble the insertion grooves in Acipenseriformes. The ventral rostral bones, cylindrical in Polyodontidae, are comparable to *Cylindracanthus*, particularly if homology to the vomer (generally a tooth-bearing element) is hypothesized. Microscopic structures and chemical analyses are thus far consistent with such a reference.

The teeth of *Cylindracanthus* were vestigial at the earliest known appearance of the genus, but became even more so during the course of evolution. This aspect may have some biostratigraphic value when more fully studied. Presumably *Cylindracanthus* became extinct when Eocene billed fishes of more modern aspect, such as *Blochius,* became too competitive for survival of similar, but archaic, forms.

Keywords

Fossil Fish, Acipenseriformes, Cretaceous, South Dakota

INTRODUCTION

Few fossil vertebrates have challenged understanding as much as has the fossil fish genus *Cylindracanthus* Agassiz. From the time it was first described (Agassiz, 1843) it was effectively a form taxon of cylindrical spines of Cretaceous through Eocene age. Easily recognized and fairly common in marine sediments from both sides of the Atlantic Ocean (Casier,1966; Lauginiger,1984; Robb,1989; Russell,1987), the specimens were nonetheless invariably incomplete and unassociated with any other skeletal material. Even the anatomical position of *Cylindracanthus* specimens remained unresolved. A possible relationship to the genus *Blochius* (of the Monte Bolca fauna of Italy) was advocated by Woodward (1917) and more or less accepted by many subsequent authorities (Fierstine, 1974). That hypothesis was the last major advance in knowledge; most subsequent publications have been notes of occurrence or discussions of form species and supposedly related form genera. Whether the genus was chondrichthyan or osteichthyan was still to some degree debatable.

It is somewhat unusual for a single specimen of a fossil taxon to clarify relationships after many years of confusion. This is particularly true when the specimen comes from a lithic unit which is notorious for poorly preserved fossils. It is thus with some bemusement that we describe a specimen of *Cylindracanthus* which is very helpful to interpretations of the genus, and effectively raises its status from form taxon to biologic taxon.

In the course of describing this specimen, we have assembled others of good quality and have re-examined the genus thoroughly. We began to question traditional assignments of *Cylindracanthus* (including those which we

had been formerly willing to accept), based on both stratigraphic and anatomical grounds. The new anatomical evidence suggests affinities to the Acipenseriformes, the sturgeon-like fishes, a hypothesis that we develop in detail herein.

AREA OF INVESTIGATION

Cylindracanthus has a wide distribution, but is particularly well known from circum-Atlantic sites of Cretaceous and Eocene age. Our comparative materials have been primarily from North America, both Cretaceous and Eocene sites. Of particular interest is the specimen from South Dakota, first publicly announced by Parris *et al.* (1996), which extended the range of the genus to the Western Interior. Other specimens included within this study are from the Atlantic and Gulf Coast states from New Jersey to Texas.

METHODS

Much of our investigation has consisted of examination of fossil specimens to determine the presence or absence of teeth and tooth bases or remnants. This generally included gross examination followed by binocular microscopy, recorded notes, sketches and in some cases, photographs. We have also attempted to determine whether the fossils consist of acellular (massive) bone, but have not yet prepared thin sections specifically for this purpose, only examining existing sections and broken ends of specimens. Examination of recent acipenseriform specimens included inspection of prepared complete skulls and skeletons and of liquid-preserved entire specimens, under binocular microscopy.

RESULTS

Systematic Paleontology

Genus *Cylindracanthus* Leidy 1856

Type Species: *Cylindracanthus rectus* Agassiz 1843

Amended Diagnosis: Osteichthyan fish known primarily from cylindrical rostrum, gradually tapering and possessing longitudinal ridges corresponding to wedge-shaped sector of the rostrum. Bilateral symmetry often reflected in median partition of a central cavity and in paired grooves which may bear teeth or tooth bases.

Type Species: *Cylindracanthus ornatus* Leidy 1856

Amended Diagnosis: Rostrum bearing 32 to 55 longitudinal ridges, some pairs uniting into single ones toward the narrow end. Teeth or tooth remnants, when present, spaced about 10 per centimeter of rostrum length.

Referred Specimen: SDSM 30638, a fragment of rostrum with teeth. Repository is Museum of Geology, South Dakota School of Mines and Technology (Fig. 1).

Provenience: Pierre Formation, Verendrye Member, from Locality V952 in Hyde County, South Dakota, with precise locality data on file at South Dakota School of Mines and Technology (SDSM). Precise stratum is two meters above the designated iron-stained layer, a marker bed in the lower Verendrye Member noted in the stratigraphy of Hanczaryk *et al.* (1996).

Age: Cretaceous, Campanian.

Description: Restored length of the specimen is 261 mm and its diameter varies from 7.8 mm to 12.9 mm. The number of longitudinal ridges varies from 21 to 44. In cross-section, the specimen exhibits vaguely the familiar double cavity described by Leidy (1856) and subsequently illustrated by various authors, including Fowler (1911) and Schultz (1987).

The remarkable aspect of SDSM 30638 is that it bears well-developed teeth, the first specimen known to us to retain them. The teeth are typically acrodont and appear to be composed of vitrodentine. Curved strongly at the bases, the teeth are oriented with a long axis at an acute angle with the long axis of the rostrum, pointing toward its larger diameter, the presumed basal or posterior end. The teeth do not rise significantly above the groove in which they are placed, thus they could scarcely serve as barb retainers in the generally ex-

Figure 1. *Cylindracanthus ornatus* Leidy. SDSM 30638, partial rostrum from the Verendrye Member, Pierre Formation, (Cretaceous,Campanian), Locality V952, Hyde County, SD.

pected manner. Indeed, the apex of each tooth overlaps the basal portion of the adjacent more posterior tooth. They are of regular size (approximately two mm long), and are spaced quite evenly at 10-11 per centimeter. They are translucent and appear to have internal open structure, but have closed pointed tips (so presumably did not serve as venom-conducting fangs). Some replacement teeth are visible, emerging beside the functional row, so it may be presumed that regular tooth replacement followed shedding or losses from the main row. There are six to fifteen ridges between the tooth rows.

One other conspicuous feature of SDSM 30638 is a sulcate groove on the surface which we interpret to be the dorsal side. The bilateral symmetry plane passes through it and the two tooth rows are paired closer to the other side. This sulcus, positioned at one end, appears to expand toward the base of the specimen and may represent the insertion of another pair of skeletal elements.

Another specimen with teeth preserved has been noted in the collections of the Alabama State Museum, catalogued as ASM-PV 994.2.111, and which has been loaned to us for inclusion in this study (Fig. 2). Also referable to the species *Cylindracanthus ornatus,* it is from the Bluffport Marl Member of the Demopolis Chalk in Marengo County, Alabama. (Precise locality information is known and catalogued.) It is quite similar to the South Dakota specimen in general form, with a number of loose teeth preserved in matrix within the ventral grooves. The teeth are no different from those in the South Dakota specimen.

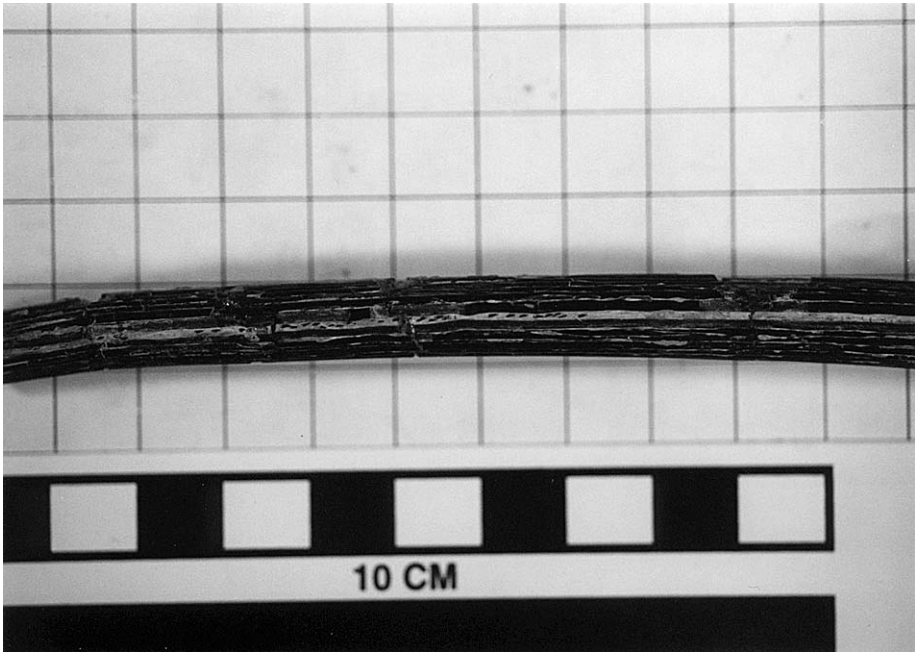

Figure 2. *Cylindracanthus ornatus* Leidy. ASM-PV 994.2.111, partial rostrum from the Bluffport Marl Member, Demopolis Chalk, (Cretaceous), Marengo County, AL. Precise locality information on file.

Comparisons

The type material of *Cylindracanthus ornatus* (Fig. 3) was made available for comparison by the repository, the Academy of Natural Sciences of Philadelphia (ANSP). Leidy (1856) described the species from three fragments, ANSP 5186-5188. Additional description was contributed by Fowler (1911), whose notations on the number of ridges remain as part of the specific diagnosis. However, his description of the genus indicates absence of denticles, when in fact all three fragments show evidence of two rows of tiny teeth on the outer surface, separated by two to four ridges (Fig. 3). The grooves in which these tooth remnants are located are wider than the other grooves. The central lumen is divided into two sides, presumably left and right, and the two tooth remnant tracts seem to be associated in the same left and right portions, one tooth tract on each of the two sides.

It would appear that the type material of *Cylindracanthus ornatus* comes from a larger individual (or individuals) than does SDSM 30638. Because the range of variation in this taxon is uncertain and because SDSM 30638 seems to match ANSP 5186-5188 in all major features (Fowler's diagnosis notwithstanding) we refer SDSM 30638 to the species. It is probable that they differ substantially in age, however, SDSM 30638 being Campanian and ANSP 5186-5188 being almost certainly Maastrichtian. Although Fowler (1911) gave a range of potential formation proveniences for the type material, its preservation is highly indicative of the Navesink Formation.

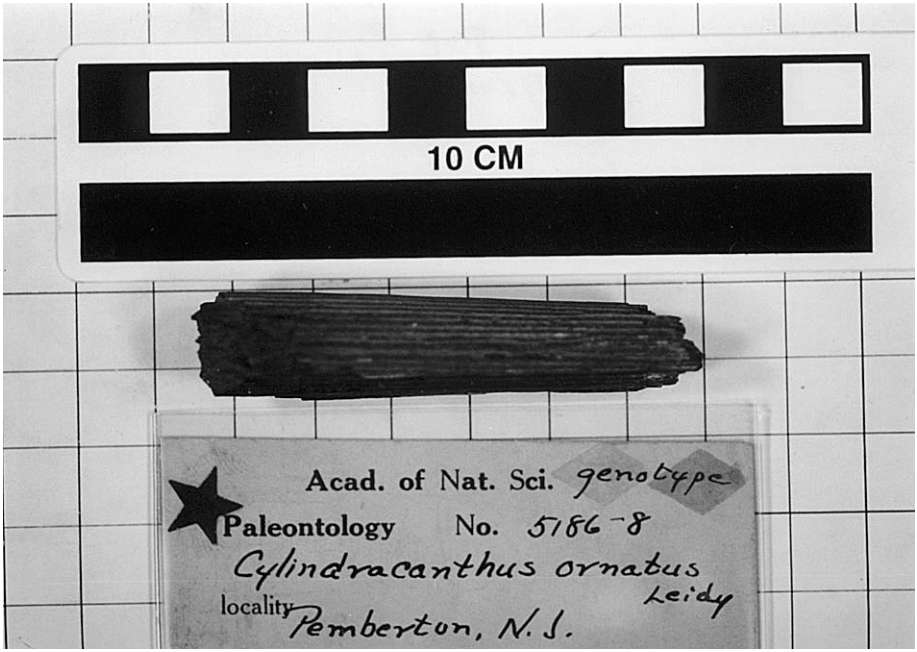

Figure 3. *Cylindracanthus ornatus* Leidy. ANSP 5186-5188, from Pemberton, Burlington County, NJ. TYPE. Believed to be from the Navesink Formation.

Specimens of Eocene age have also been referred to *Cylindracanthus ornatus* (and more often to the species *Cylindracanthus rectus* Agassiz, which was originally described as a species of *Coelorhynchus* and which is sometimes considered a senior synonym of *Cylindracanthus ornatus* Leidy). This is especially true of Gulf Coast area specimens (Woodward, 1891; Thurmond and Jones,1981).

We have had the opportunity to make detailed comparisons with three specimens described by Fallow (1964) through the courtesy of the University of North Carolina (UNC), and another which was loaned from the personal collection of Donald Clements of North Carolina. These specimens were not referred to any described species, but seem to be typical of Eocene specimens generally, except for those historically referred to the species *Cylindracanthus acus* Cope. Our comparisons, given as follows, offer some basis for distinction from Cretaceous specimens. Fallow's specimens are from the Castle Hayne Formation of North Carolina and the Santee Formation of South Carolina UNC 3595, 3596, 3597). Details of the ossification are more observable in these specimens, at least in binocular magnification, than in the Cretaceous specimens seen by us (Fig.4).

Grooves in these specimens seem to represent areas which are intensely vascularized and/or innervated relative to the ridges. Small pores are visible on the surfaces at the bottoms of the grooves. Where breaks have occurred, usually along the grooves (which apparently are weak positions), a network of fine interior grooves may be seen, suggestive of a capillary bed. Calcified tis-

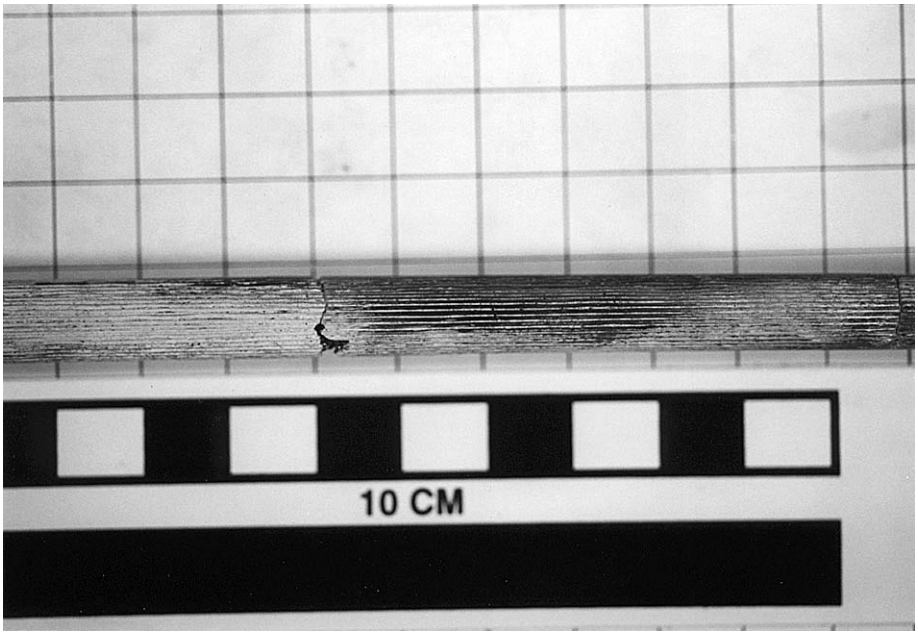

Figure 4. *Cylindracanthus rectus* Agassiz. ASM-PV 989.4.200, from the White Hills Locality, Lisbon Formation(Late Eocene) near Melvin, Choctaw County, AL.

sue of the ridges, when broken, generally appears granular, unlaminated, and in no way trabecular in contrast to the broken grooves.

The inner wall of the lumen of the specimens shows pores on the surface, appearing like vascular foraminae, which presumably are vessel passages to the central tissue mass. In some of the specimens the lumen is partially occluded by mounds of what appear to be secondary calcified tissue, developed inside the radially structured bone of the major portion of the specimen. Although lacking the radial structure, this secondary calcified tissue (which may be dentine or calcified cartilage) does have some vascular channels which run parallel to the long axis.

One specimen (UNC 3597) shows evidence on a broken end surface of organized calcification of the ridges. In each ridge there are patterns of organization of calcified tissue radiating outward (on a curving diagonal) from the center line of the ridge toward the outer surface of the cylinder and the outer surface of the ridge, presenting a feather-like pattern in end view. The vascular traces in the specimen are not absolutely straight, and it appears that there may be secondary osteons in the area of the internal midline ridge. The feather-like pattern suggests a pattern of calcification perhaps similar to teeth. The bone lining the lumen has a longitudinal (almost fibrous) structure.

The South Carolina specimen (UNC 3595) has the tip preserved and has a large foramen opening by the tip (possibly a sensory nerve passage) and the tip also appears worn rather evenly all around. The specimen loaned by Mr. Clements is from the Castle Hayne Formation at the Lanier Pit, Maple Hill, Pender County, North Carolina. It has a large groove, an indentation of the entire structure, possibly homologous to the grooves which bear dentition or dentition remnants, but it is sufficiently worn to have obliterated any actual remnants. A Cretaceous specimen loaned by Eugene Hartstein of Delaware came from the Mt.Laurel Formation spoil piles of the Chesapeake and Delaware Canal in New Castle County, Delaware. It has relatively large tooth bases, measuring approximately 1.58 millimeter diameter, with spacing at 28 per centimeter. There are four ridges between the tooth rows and a total of twenty in the entire circumference, none of them anastomosed within the short length of the specimen as preserved (less than 2 centimeters). The specimen is of particular interest in that the central lumen is not of normal orientation, but instead has an axis oblique to the tooth rows, despite the overall persistence of bilateral symmetry.

No teeth were mentioned by Fallow (1964) in his specimens, but in fact they are present as tiny remnants, readily seen if magnification is sufficient. Two rows of tooth bases are observable in UNC 3595 and a few remnants are visible in UNC 3596. Grooves are narrower on the Eocene specimens, and the tooth remnants consequently are much smaller than in the Cretaceous specimens.

Less detailed comparisons to other specimens, none of them published, confirmed the general observations listed above. We have examined approximately 200 such specimens of the genus ranging in age from Cretaceous to Eocene, and geographically from New Jersey to Texas. In addition to those institutions previously listed, we have viewed and borrowed specimens from

Louisiana State University (LSU) and the Mississippi Museum of Natural Science (MMNS). (There are reportedly some specimens from younger horizons, but we have not reviewed the validity of such records.) With regard to the species *Cylindracanthus ornatus,* there seems to be consistency in the lesser development of tooth base remnants in the younger horizons. While various authorities have placed *Cylindracanthus ornatus* Leidy and *Cylindracanthus acus* (Cope) in synonomy with *Cylindracanthus rectus* Agassiz, it seems clear to us that the latter species is perceived as having virtually no bilateral symmetry nor tooth base development, and is characteristically found in strata of Eocene age, as was the Agassiz type material (Arambourg,1952;Thurmond and Jones,1981; Weems,1999). *Cylindracanthus ornatus,* which exhibits tooth development, is Cretaceous through Eocene, but with diminished tooth development in specimens from younger strata. Because a rigorous taxonomic revision would require examination of the type material of Agassiz, we provisionally suggest that the three species should be retained as distinct, and restrict our primary comments on the teeth to the species *Cylindracanthus ornatus* Leidy.

DISCUSSION

Cylindracanthus has a lengthy history of recorded specimens and discussion of its affinities (Fierstine, 1974,1990; Schultz, 1987). We concede that only better specimens will ever reveal a definite taxonomic position for the genus. We at least have a better specimen than any found previously, and thus have some basis to form our own hypothesis. A complete historical review of the supposed relationships of the genus is beyond the scope of this present work, but it will suffice to note that many authorities have proposed that *Cylindracanthus* is related to the extant billfishes (Schultz, 1987). While we ourselves have discussed the genus as a possible xiphioid relative, the biostratigraphic record shows this to be a very awkward arrangement.

The extant xiphioids are very derived members of the order Perciformes, an order that is virtually confined to the Cenozoic. As some authors have noted (Weems, 1999), to place the genus *Cylindracanthus* in that group would make it one of the earliest taxa of the order, because of its appearance in the Cretaceous. However, it would appear that *Cylindracanthus*, if considered to be a perciform, is even more derived than the extant xiphioids, because in all probability the skeleton was cartilaginous except for the acellular bones of the bill. Extant xiphioids are bony, not cartilaginous, and it is highly unlikely that *Cylindracanthus* would have appeared so much earlier than other, supposedly related forms, which are less derived.

Based on our new anatomical evidence from the teeth and posterior insertions of the rostrum, we suggest another possible relationship which seems consistent with all available evidence. The Acipenseriformes, sturgeons and related forms, have a substantial fossil record in the Cretaceous, appearing at about the same time as *Cylindracanthus*. As noted in the monographic reviews of Grande and Bemis, 1991,1996), the acipenseriforms have tendencies toward cartilaginous skeletons and substantial rostral development. Of known

actinopterygians, they are the only group known to have a projecting rostrum entirely anterior to the mouth, which was probably the case in *Cylindracanthus* as well, there being no evidence of an occlusion to a lower jaw on even the best of specimens. The acipenseriforms fared well during the Cretaceous, and also survived the Cretaceous/Tertiary extinction event (as did *Cylindracanthus*). They are extant in relatively small numbers and diversity, being somewhat at a competitive disadvantage with more derived forms (such as the Perciformes).

As many taxonomic groups of fishes have produced forms with bill-like projections of the rostrum, it is reasonable to speculate that *Cylindracanthus* was such a form among the Acipenseriformes, with which all known anatomical features are consistent. Among these features we can now cite the teeth, which greatly resemble those of juvenile paddlefish (*Polyodon*) and those of toothed species and growth stages of sturgeons *(Acipenser).* The South Dakota specimen also exhibits insertion grooves which resemble those on the rostrum of *Acipenser*. Furthermore, the ventral rostral bones,cylindrical in Polyodontidae (Grande and Bemis,1991) may be homologous to the vomer (Jollie,1980), commonly a tooth-bearing element in fishes.

Weems (1999) suggested that *Cylindracanthus* could be related to the Dercetidae. While based on the definite resemblance of the rostrum to that of *Rhynchodercetis* (Chalifa, 1989), the fully ossified skeleton, modest size, and fully functional dentition of dercetids lend little support for such a relationship. Furthermore, the resemblance of *Rhynchodercetis* is to *Cylindracanthus rectus* rather than to the Cretaceous specimens of *Cylindracanthus*, while *Rhynchodercetis* is early Cenomanian, considerably older than any taxa discussed here.

The trend in the dentition of *Cylindracanthus* is toward tooth reduction. The teeth were vestigial in the oldest specimens (Cretaceous) and became even more so, as noted within the species *Cylindracanthus ornatus.* This aspect may have biostratigraphic value when more fully studied. Presumably *Cylindracanthus* declined toward extinction when Eocene billed fishes of more modern aspect became too competitive for the survival of similar, but archaic forms. As a relatively common and widespread marine fossil that spans the Cretaceous/Tertiary boundary, the potential value of *Cylindracanthus* in biostratigraphy commands special interest, and it is to be hoped that yet more discoveries of better specimens will continue to improve our knowledge of it.

ACKNOWLEDGEMENTS

We are especially grateful to Dr. H. Fierstine for his advice and encouragement and his helpful comments. Drs. J.Carter (UNC), E.Daly (MMNS), E. Daeschler (ANSP), E. Hooks (ASM), J. Sankey (LSU), J. Schiebout (LSU), and E. Hartstein provided loans of specimens in their care. M.Turner, M.Sabaj, and R. Purdy assisted us with visits at their respective institutions. Dr. W. Gallagher, Dr. J.Martin, E. Manning, and P. Hanczaryk provided useful discussions. D.Clements and P. Mintz donated specimens for the sake of this investigation.

William N. Parris, a student at the Princeton Child Development Institute, assisted with the collecting of SDSM 30638. In grateful appreciation to this respected institute for autism research, the site is now designated as the PCDI Site.

REFERENCES CITED

Agassiz, L. 1843. Recherches sur les poissons fossiles, Tome V, 160 pages.

Arambourg, C.1952. Les vertebres fossils des gisements de phosphates (Maroc-Algerie-Tunisie). Notes et Memoires de la Service Geologique Maroc 92. 372 pages.

Casier, E.1966. Faune ichthyologique du London Clay. British Museum of Natural History. 2 volumes. 496 pages.

Chalifa,Y. 1989.Two new species of longirostrine fishes from the Early Cenomanian of Ein-Yabrud, Israel, with comments on the phylogeny of the Dercetidae. Journal of Vertebrate Paleontology 9, pages 314-328.

Fallow, W. 1964. *Cylindracanthus* from the Eocene of the Carolinas. Journal of Paleontology 38(1), pages128-129.

Fierstine, H.L. 1974. The paleontology of billfish — the state of the art. *in* Shomura, R.S. and Williams, F.,eds. Proceedings of the International Billfish Symposium. Kailua-Kona, Hawaii. Part 2. Review and Contributed Papers. NOAA Technical Report NMFS SSRF-675, pages 34-44.

Fierstine, H.L. 1990. A paleontological review of three billfish families (Istiophoridae, Xiphiidae, and Xiphiorhynchidae). *in* Stroud, R.H.,ed.. Planning the future of billfishes Part 2. Contributed Papers. Proceedings of the Second International Billfish Symposium. National Council for Marine Conservation, Inc. Savannah, Georgia, pages 11-19.

Fowler, H.W. 1911. A description of the fossil fish remains of the Cretaceous, Eocene, and Miocene formations of New Jersey. Geological Survey of New Jersey. Bulletin 4.185 pages.

Grande, L. and W.E. Bemis. 1991. Osteology and phylogenetic relationships of fossil and Recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. Journal of Vertebrate Paleontology 11, Memoir I, 121 pages.

Grande, L. and W.E.Bemis. 1996. Interrelationships of Acipenseriformes, with comments on "Chondrostei". *in* Stiassny, M.L., L.R. Parenti, and G.D.Johnson; Interrelationships of Fishes. Academic Press, pages85-115.

Hanczaryk, P.A.; K.G. Miller; W.B. Gallagher; M.D. Feigenson; and M.C. Van Fossen; 1996 Stratigraphy of the Campanian-Maestrichtian Pierre Shale of Central South Dakota: Geological Society of America; Rocky Mountain Section, Annual Meeting (Abstract).

Jollie, M. 1980.Development of head and pectoral skeleton and scales in *Acipenser*. Copeia 1 1980 (2), pages 226-249.

Lauginiger, E.M. 1984. An Upper Campanian vertebrate fauna from the Chesapeake and Delaware Canal, Delaware. The Mosasaur II, pages 141-149.

Leidy, J. 1856. Description of two ichthyodurulites. Proceedings of the Academy of Natural Sciences of Philadelphia 8. page 12.

Parris, D.C.; B.S.Grandstaff, and G.L.Bell. 1996. *Cylindracanthus* in the Cretaceous of South Dakota. Geological Society of America; Rocky Mountain Section, Annual Meeting (Abstract).

Schultz, O. 1987. Taxonomische Neugruppierung der Uberfamilie Xiphoidea (Pisces, Osteichthyes). Annalen des Naturhistorischen Museums in Wien 89, pages 95-202.

Robb, A. 1989. The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen County, North Carolina. The Mosasaur IV. pages 75-92.

Russell, D.A. 1988. A checklist of North American marine Cretaceous vertebrates including freshwater fishes. Occasional Papers of the Tyrrell Museum of Paleontology 4: 58 pages.

Thurmond, J.T. and D.E. Jones. 1981. Fossil Vertebrates of Alabama, University of Alabama Press, pages 106-107.

Weems, R. 1999. Actinopterygian fishes from the Fisher/Sullivan Site: Virginia Division of Mineral Resources Publication 152, pages 53-61.

Woodward, A.S. 1891. Catalogue of the fossil fishes in the British Museum. Part II. pages 120-122.

Woodward, A.S. 1917. Exhibition of specimen of *Coelorhynchus* from Nigeria, Proceedings of the Geological Society 62: part I, page xxvii.