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A LARGE PYCNODONT FROM THE NIOBRARA CHALK

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Among the fossils collected on the Yale Scientific Expedition of 1872 are fragments of the skull and dentition of a large pycnodont fish. These were found by O. C. Marsh in the Cretaceous chalk exposures along the Smoky Hill River in Kansas on November 6, 1872. They are of particular interest as an example of extreme reduction of the dentition in an aberrant member of this family of durophagous fishes, and also because of their unusually large size. The specimens confirm the distinctness of a genus described by Leidy from the Cretaceous of Mississippi. It is quite fitting that the species should be named for their discoverer.

CLASS PISCES (OSTEICHTHYES)

Order Pycnodontoidea

FAMILY PYCNODONTIDAE

Hadrodus marshi new species

Type: Premaxillary, left and part of right splenials, and fragments of skull roof of one individual, Y.P.M. Catalogue of Vertebrate Palentology, no. 1950.

Type locality: "South side Smoky Hill River, 2 miles east of North Fork." This places it in Logan Co., Kansas, about five miles west of Russell Springs.

Formation and age: Probably upper Niobrara Chalk, early Senonian.

Diagnosis: Two-thirds the size of *Hadrodus priscus* Leidy, premaxillaries shorter and much higher than in that species and not excavated anteriorly; anterior prehensile tooth smaller than posterior. Splenials with 4 rows of irregularly oval teeth, some of which bear apical cusps; teeth of the lateral row slightly larger than the others; 4 to 5 teeth in each row.

DESCRIPTION

Premaxillary: A left premaxillary lacking the dorsal extremity is tall and short, of fairly stout proportions, more similar to *Gyrodus* (Hennig, 1906, pl. X) than to such forms as *Proscinetes* [*Microdon*]. There is no trace of a horizontal process along the border of the mouth. It is about twice the size of that of the large specimen of *Gyrodus circularis* Agassiz figured by Hennig. The median surface is straight and bears throughout its length a suture for the opposite premaxillary; these bones must have been closely united throughout their length, in a normal fashion, not diverging as they have been restored in *Gyrodus* (Hennig, 1906, p. 148, pl. X). On its posterior margin is a large oval, vertically elongate depression, its upper end merging with the lateral surface of the bone. Two large, bicuspid, prehensile teeth are ankylosed to the oral margin. These differ from those of *H. priscus* figured by Leidy (1873, pl. 19, figs. 17-20) in somewhat greater disparity in size, and in the less distinct groove separating the cusps on the outer surface of the crown. They lack the posterior concavity characteristic of most pycnodont "incisors." The premaxillary bone itself differs markedly from Leidy's figure in its relatively greater height—which may be due to incompleteness of that specimen—and in the absence of an excavation in the anterior border. Leidy (1873, p. 294) interpreted the excavations above the roots of the teeth as spaces for developing replacement teeth. In the opinion of most students of the pycnodonts (cf. Woodward, 1895, p. 194) there was no tooth replacement. Neither the form of the cavity in the premaxillary of *Hadrodus* nor its remoteness from the dentigerous border suggests that it was an alveolus; however, Saint-Seine (1949, p. 121) has observed unworn replacement teeth in just this position in *Proscinetes* [*Microdon*] *sauvanausi* Thiollière. Hence Leidy's inference may be correct, although the mechanism of replacement and ankylosis of the teeth to the premaxillary remains an enigma. A more plausible interpretation is offered by Smith-Woodward (1895, p. 193) who suggests that the excavation lodged the nasal capsule.

Measurements of the Premaxillary

	mm.
Maximum length, anteroposterior	26.0
Height as preserved, including teeth	66.0
Length of first tooth	10.1
Width of first tooth	7.3
Length of second tooth	12.4
Width of second tooth	8.7

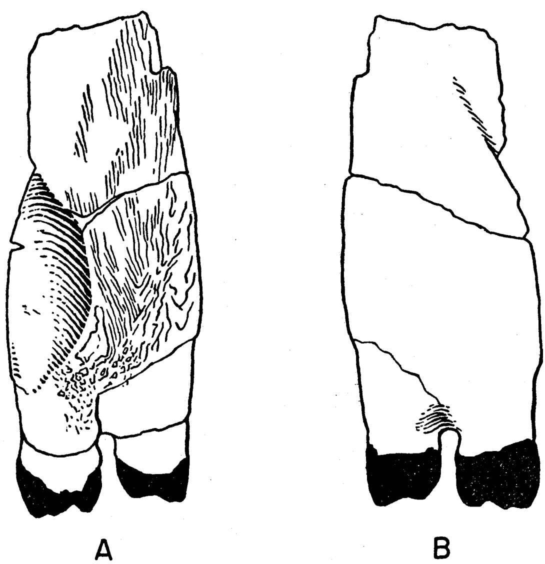

Figure 1. *Hadrodus marshi,* n. sp. Type specimen, Y.P.M. 1950. A. Medial view of premaxillary showing interpremaxillary suture and pocket for olfactory capsule in posterior border. B. Lateral aspect of premaxillary. x 1.

Splenials: A large left splenial with extremely deep anterior symphysis and only moderate coronoid process, and the posterior part of its left homologue show that the lower jaw of this genus differed in detail from other pycnodonts. It is only slightly longer than that of *G. circularis*, but much deeper, especially anterior to the front teeth where it reaches its maximum depth. The symphysial area is short, deep, with a straight posterior boundary. Its lower fourth forms a nearly round facet separate from the remainder of the denticulate suture. Possibly this small area met the opposite splenial, and the coarser suture was with the dentary. If so, the latter bone was further reduced than in *Mesturus* (Woodward, 1895, pl. 15; Saint-Seine, 1949, p. 107, fig. 38) or *Gyrodus* (Hennig, 1906, pl. X and Weitzel, 1930, p. 93), but perhaps no more than in *Proscinetes* [*Microdon*] (Saint-Seine, p. 112, fig. 41). There is no indication of contact with the dentary on the lateral surface of the splenial, except possibly at the extreme front. This is a characteristic pycnodont condition and supports the reference of *Hadrodus* to this Order in spite of considerable differences in dentition.

The large size of the upper prehensile teeth suggests that lower incisors should likewise have been prominent. It is possible that the dentary was larger than suggested above and the lower jaw as a whole about twice the size of that of *Gyrodus circularis*, with proportions similar to that species.

Four rows of irregularly oval teeth with one to three cusped crowns are present. Unlike other pycnodont genera, the lateral row contains the largest teeth; they are subequal in size, about 9 mm. in their long diameters, separated by spaces of about 1 mm. The most posterior bears three cusps in a straight line along its crown; the second from the front bears an obscure single, laterally placed cusp. In the second and third rows the teeth are slightly smaller and more variable in shape. A single large tooth with two apical cusps forms the fourth, innermost row. Variability in both number and shape of the teeth is indicated by the fragment of the right splenial in

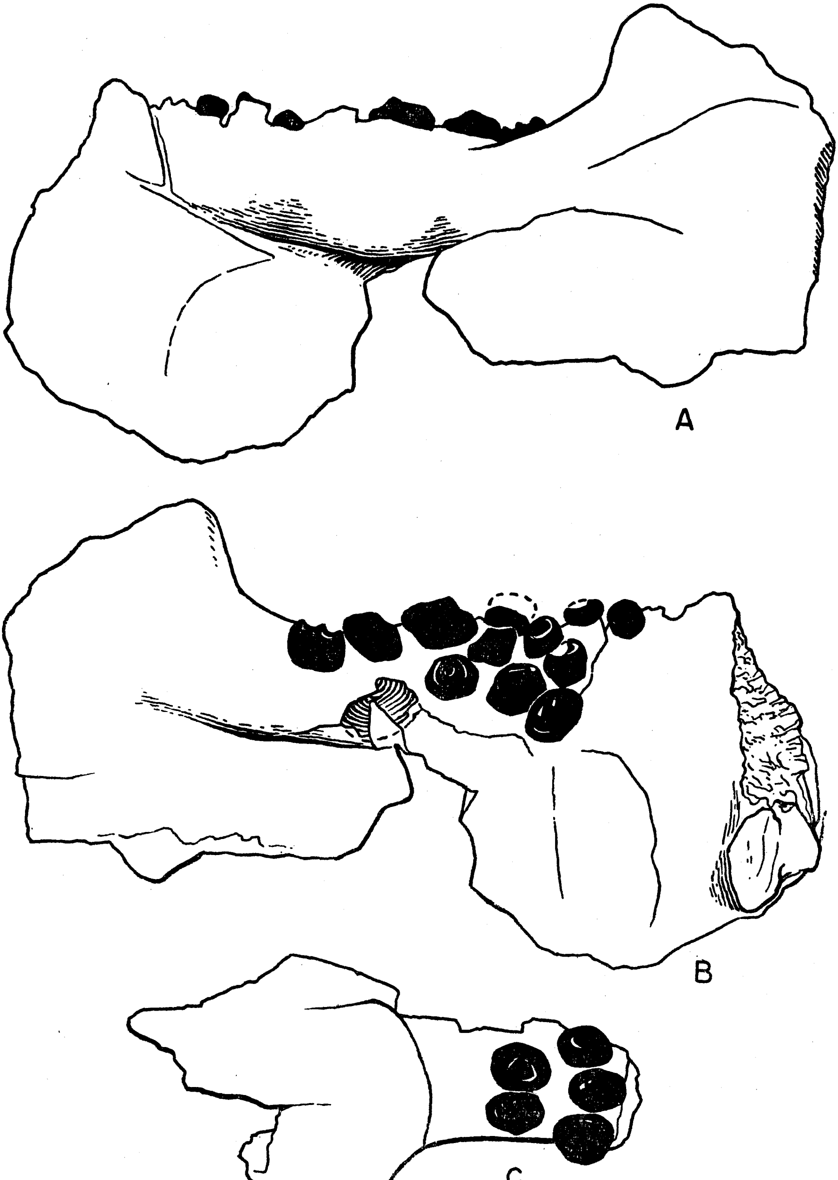

Figure 2. *Hadrodus marshi,* n. sp. Type specimen, Y.P.M. 1950. A. Left splenial, lateral aspect. B. Left splenial, medial aspect. C. Right splenial, dorsomedial aspect. x 1.

which the posterior tooth of the lateral row, as displayed on the left side, is absent, and the teeth of the second row are nearly as large as those of the lateral row.

The crowns of the teeth are smooth except for the papilla-like tubercles at the apex. In this they differ markedly from *Gyrodus* and are more similar to *Gyronchus* [*Mesodon*] or *Proscinetes* [*Microdon*]. There is no trace of the tendency toward transverse broadening of the teeth seen in *Coelodus* or *Anomoeodus*. Similar papillae are present on the crowns of tritoral teeth of *Acrotemnus faba* Agassiz. That species, however, differs from *Hadrodus* in the much greater transverse width of its tritoral teeth, in the presence of a marked transverse ridge along their crowns, and in having a group of papillae adjacent to but not upon this ridge line. In *Hadrodus* the papillae are upon the ridge, if any is present, and tend to be oriented anteroposteriorly if more than one papilla occurs.

Measurements of the Splenials

	mm.
Anteroposterior length (reconstructed from both)	120
Depth in front of crushing teeth	48
Anteroposterior length dental battery	47

Roofing bones: Several fragments of thick skull bone ornamented by closely but irregularly spaced, rounded tubercles are present. Most probably they are portions of opercular bones, although insufficient borders remain to determine their exact position. None shows traces of canals of the lateral line system. Some fragments show a lower radiating type of sculpture near the thin margins such as Hennig (1906, p. 161) describes on the preoperculum of *G. circularis*. The thick tuberculated layer of ganoine above extremely cancellous bone is characteristic of pycnodonts; *Hadrodus* shows coarse tuberculation commensurate with its large size. Such strong sculpture is found in *Gyrodus* and in *Gyronchus* [*Mesodon*] *hoeferi*, the earliest appearing pycnodont; other members of the family are said by Hennig (*Ibid.*, p. 179) to have considerably weaker tuberculation.

DISCUSSION

Dr. David H. Dunkle has called my attention to the resemblance of this specimen to certain semionotids. Bifid prehensile teeth are characteristic of *Dapedium*, whereas the incisors of pycnodonts have single crowns, concave internally. *Dapedium* also has crushing palatal teeth. However the shape of the premaxillary of *Hadrodus* differs greatly from that of *Dapedium* in its great vertical and short horizontal extent, and also in the absence of surface ornamentation. Conceivably the premaxillary of *Hadrodus* could be derived from that of the early Jurassic *Dapedium* by shortening and dorsal extension, but as *Dapedium* had already attained a deep body and relatively high, short skull without vertical elongation of the premaxilla, it seems unlikely that such a change would have occurred. Aside from the form of the incisors, there is no reason to postulate this relationship.

The form of the splenial teeth, particularly the development of one or a few papillae on the crown, is not unlike that of some species of *Lepidotes* such as *L. mantelli* Agassiz. Wide and irregular spacing of the splenial teeth, and lack of differentiation of these teeth into rows of small and large tritors are most unlike normal pycnodonts and far more like *Lepidotes*. Also, the deep anterior portion of the splenial is suggestive of that genus. No trace of tooth succession can be found, however, and the shape of the premaxillary bone is very unlike *Lepidotes* in which there is a well-developed alveolar ramus along the oral margin and a slender ascending process arising from the anterior end (Saint-Seine, 1949, p. 138, fig. 161, p. 140). Nor is there any trace of a separate coronoid bone such as occurs in the semionotids. The splenial alone forms the major portion of the lower jaw and its coronoid process, as in other pycnodonts. Thus the resemblances lack detail indicative of relationship and may reasonably be ascribed to convergence.

Only one other species of pycnodont is known from the Niobrara formation, *Micropycnodon kansensis* (Hibbard and Graffham). This is a small fish, scarcely one-third the size of *Hadrodus marshi,* which may readily be distinguished by its more typically pycnodontid splenial dentition, with two rows of small teeth lateral and one row internal to the principal row of enlarged crushing teeth. *Coelodus streckeri* Hibbard from the underlying Carlisle shale of Kansas is also of Turonian age. Pycnodonts are more numerous in the lower Cretaceous of the Gulf of Mexico embayment, several genera having been reported (Williston, 1900, Gidley, 1913).

The type locality and horizon of *Hadrodus priscus* Leidy are uncertain; Columbus, Mississippi, is on the Eutaw formation but only a short distance from the base of the Selma Chalk. The horizon may well be equivalent to the Niobrara and close to that of *H. marshi.* Whether the characters here used to seperate these species are valid remains to be determined by future discoveries of more complete material from these and other localities. Differences in the form of the premaxillary seem sufficient for specific distinction of the two forms.

Although it is difficult to estimate the size of the fish from such fragments as are available, especially when the proportions of the genus are not accurately known, it seems worthwhile to point out that *Hadrodus* may well have been the largest of the pycnodonts. If its proportions were similar to those of *Gyrodus circularis,* it may have exceeded a meter in length. The premaxillary is twice the size of that of a large specimen of *G. circularis* described by Hennig, and the splenial exceeds those of that species by 30 to 50 per cent.

Hadrodus shows the most reduced and specialized dentition thus far known among the pycnodonts. Reduction in number of teeth, increase in size of the external row and corresponding decrease in importance of the next to innermost row of the splenial teeth, and development of a diastema between teeth of the dentary and splenial are all divergent from the general trend of pycnodont evolution, and separate *Hadrodus* sharply from all other described genera. Closest resemblances, in dentition, appear to be with *Gyronchus* [*Mesodon*] and certain species of *Proscinetes* [*Microdon*], in which the crushing teeth are irregular in size and distribution. It is interesting to note that the dental evolution of the pycnodont line leading from *Gyronchus* to *Hadrodus* parallels that of the placodont reptiles from *Paraplacodus* through *Placodus* and *Cyamodus* to *Henodus* (von Huene, 1936).

Four main types of dentition have evolved among the pycnodonts. *Eomesodon*, the earliest form, and *Gyronchus* [*Mesodon*] have smooth crowned crushing teeth arranged in irregular rows and uneven in size. In *Mesturus* and *Proscinetes* [*Microdon*] the teeth attain regular arrangement in longitudinal rows; their crowns are smooth or with apical pits. This type of dentition persists into the Eocene *Pycnodus*. *Gyrodus* has similar rows of teeth, but the crowns are ornamented with concentric rings of mamillary papillae. *Coelodus* shows divergence in the transverse broadening of the enlarged teeth, beginnings of which may be observed in some species of *Proscinetes*. *Anomoeodus* may represent a further development of this line, with degeneration of the lateral rows of teeth. Finally, *Hadrodus* has greatly reduced the number of teeth and shifted emphasis from internal to external rows. It will be most interesting to discover the vomerine dentition which accompanied this modification.

ACKNOWLEDGMENTS

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