

THE FIRST MESOZOIC CARIBBEAN SHARK IS FROM THE TURONIAN OF CUBA: *PTYCHODUS CYCLODONTIS* SP. NOV. (?NEOSELACHII)

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Teeth of *Ptychodus* are known from the uppermost Lower Cretaceous and throughout the Upper Cretaceous (Albian to Maastrichtian), and have been reported from North and West Africa, Asia, Belgium, England, France, Germany, Italy, Arizona, Nebraska, and Texas (Cappetta, 1987; Williamson et al., 1991; Brito and Janvier, 2002). Brito and Janvier (2002) redescribe a museum find, a peculiar fragment of a ptychodontid dentition, which is of enigmatic origin, and they interpret it to be from the Upper Cretaceous of northern South America, from “Nouvelle-Grenade” (according to the specimen label; original description in Larrazet, 1886). The matrix surrounding the dentition fragment is apparently non-fossiliferous and of equivocal affinities, and the age of the specimen remains unsettled. We report here a second, remarkably similar specimen and museum find from “Constancia, Cuba.”

The systematic position of *Ptychodus* Agassiz, 1838, is problematic. Patterson (1966) included *Ptychodus*, *Hylaeobatis* Woodward, 1916, and *Heteroptychodus* Yabe and Obata, 1930, in Ptychodontidae Jaekel, 1898, and suggested that *Ptychodus* shares an ancestor with *Hylaeobatis*, which is no longer considered to be a “ptychodont” (see below; Herman, 1977; Stewart, 1980; Rees and Underwood, 2002). *Steinbachodus* Reif, 1980, is considered to be a close relative of *Ptychodus*. Recently reported, more complete remains also suggest a close relationship of *Heteroptychodus* and *Ptychodus* (Cuny et al., 2003). “Ptychodontid” teeth have been assigned to Hybodontiformes Maisey, 1987, on the basis of an anaulacorhizous root structure (Patterson, 1966; Cappetta, 1987; Brito and Janvier, 2002), but this feature is probably plesiomorphic (see Maisey [1982] for a review). *Ptychodus* has been interpreted to possess calcified vertebral centra (Stewart, 1980) and might therefore be neoselachian. However, all publications purportedly revealing “associated teeth and centra” of *Ptychodus* (most recently Everhart and Caggiano, 2004) fail to demonstrate unambiguous skeletal articulation. Furthermore, no synapomorphy has been defined for the family Ptychodontidae Jaekel, 1898, since the amended diagnosis by Patterson (1966:332–333), which leaves us to describe this new species of *Ptychodus* as a ?neoselachian incertae sedis.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Subcohort ?NEOSELACHII Compagno, 1977
Order incertae sedis
PTYCHODUS Agassiz, 1838
PTYCHODUS CYCLODONTIS sp. nov.

Holotype—AMNH 8031 (American Museum of Natural History, New York): 13 articulated teeth plus tooth fragments (Fig. 1).

Remarks—The specimen is labeled “?Colobodus, Jurassic, Constancia(?), Cuba, Acc. 260 from Dr. Carlos De la Torre”. The thin section plus matrix is stored under the catalogue number AMNH 8031-T1.

Microfossils were studied in polished thin section AMNH 8031-T1 under the light microscope and in freshly broken rock surfaces under the scanning electron microscope.

Type Locality and Age—Constancia (north central Cuba, Fig. 2); Carmita Formation; Cenomanian–Turonian (stratum unknown, but see discussion below).

Etymology—“cycl-” (Ancient Greek, Engl., meaning round) and “odont” (Ancient Greek, Engl., tooth) refer to the characteristic dome-shaped tooth crown.

Referred Specimen—MNHN 1898-3 (Muséum national d’histoire naturelle Paris, fragment of dentition), ambiguous provenance: probably ?La Luna Formation in Colombia (supposedly middle Cenomanian–Turonian; see Brito and Janvier [2002]).

Diagnosis—Dentition homodont; teeth high crowned; crown cone-shaped, pointed but blunt, with basal reticulate ornament and apically numerous radiating and ramifying ridges; reduced marginal area; root and basis of crown osteodont.

Description

Specimen AMNH 8031 (Fig. 1) consists of 13 complete or half-complete teeth, and about 10 tooth fragments in situ embedded in a small piece of limestone matrix containing various Late Cretaceous microfossils (see below). The teeth are homodont and the crowns show a pointed but blunt tip. The teeth measure up to 9 mm in height and up to 10 mm in width. The crown’s surface is weathered at the top and has been partly etched by acid preparation prior to discovery of the specimen.

The cone-shaped crowns are twice to three times taller than the roots and are ornamented by two main ridges running transverse and perpendicular to each other (Fig. 1A). These most prominent ridges radiate from the center and continue downwards from the apex of the crown. About halfway down and increasingly so farther down the crown, the ridges ramify and grade into a reticulate type of ornament. The reticulate ornament occurs just above the marginal area that separates the crown from the root. The marginal area shows projections and depressions that are variably well developed, and the roots form a tile-like arrangement in the dentition. The labial portion of the marginal area projects labiad and overlaps the marginal lingual area of the preceding tooth. Striae or minor ridges in the crown ornament originate from the dentitions’ inferred linguo-labial axis and from the axis perpendicular to it (Fig. 1A–C).

Tooth histology is largely osteodont (Fig. 1D–F): the roots and the basal portions of the crowns contain an extensive network of large cavities and trabecular dentine (sensu Cappetta, 1987), whereas the apical portions of the crowns consist of a less extensive system of vascular cavities but rather elongate canals (ca, stippled in Fig. 1E) with more numerous radiating dentinal tubules (dt, Fig. 1F). The latter type of tissue may be described as transitional: from osteodentine-orthodentine (os-o) to orthodentine (o), since the cavities grade into elongate canals towards the tooth surface. The fairly straight and long canals run vertically in the osteodentine-orthodentine and branch peripherally in the dense orthodentine, where canals run perpendicular to (and open into) the tooth’s surface (“tubular” and “pallial” dentine in Patterson, 1966). The enameloid layer is almost uniformly thin and covers the crown completely.

Provenance of the Holotype

The specimen label indicates provenance from “Constancia, Cuba,” which probably means a place near the village Constancia, located in

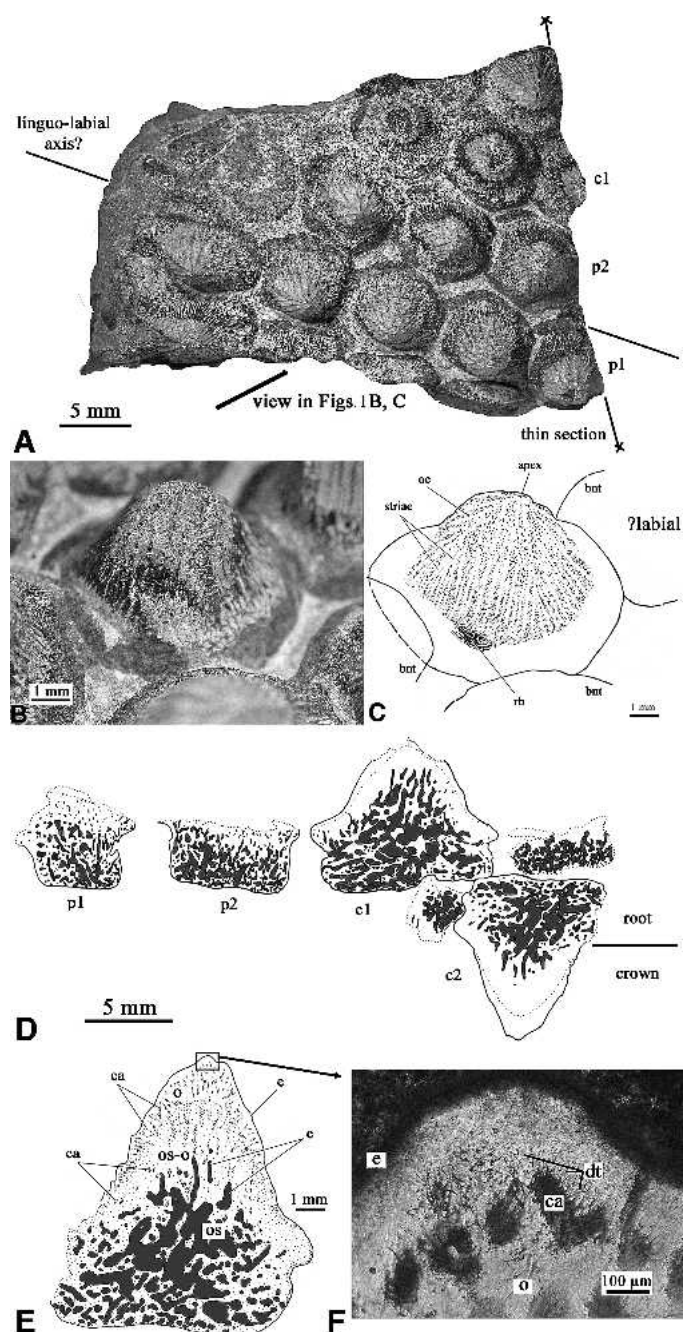


FIGURE 1. Tooth histology and morphology of *Ptychodus cyclodontis* sp. nov., specimen AMNH 8031; **A**, the dentition as preserved in occlusal view; **B**, a single tooth in oblique occlusal view, showing the pattern of striae in the crown and the partly preserved reticulate relief in the marginal area; **C**, sketch of single tooth in oblique-occlusal view; **D**, sketch of oblique thin section (holotype specimen AMNH 8031-T1, orientation shown in Fig. 1A) showing the histology of crown and root (teeth **p1** and **p2** are peripheral cuts and teeth **c1** and **c2** are central cuts); **E**, enlarged sketch of tooth **c2** showing extend of enameloid layer and dentine; **F**, close-up of apex, showing vascular canals in osteodentine, extensive dental tubules, and enameloid. **Abbreviations:** **bnt**, marginal area of neighboring tooth; **c**, cavities; **ca**, vascular canals; **dt**, dental tubules; **e**, enameloid layer; **o**, orthodentine; **os-o**, osteodentine-orthodentine; **oc**, canal opening (in surface); **os**, osteodentine; **rb**, reticulate ornament at crown/root junction (marginal area).

north central Cuba, along the outcrops of the so-called Placetas belt, where strongly deformed Jurassic and Cretaceous marine rocks are developed (Fig. 2).

The matrix where the fossil is preserved is a grey biomicritic limestone which contains microfossils of Late Cretaceous age, predominantly planktonic foraminifera (*Marginotruncana* aff. *sigali*, Heterohelicidae sp., and *Hedbergella* sp.; Fig. 3A–D), which suggest an early Turonian age. Taking into account this lithology and date, it can be postulated that the shark-bearing rock may be the late Cenomanian to early Turonian, 20 to 200 meters-thick Carmita Formation, composed of well-bedded limestones and radiolarian chert, with interbeds of marl and shale. This formation and equivalent facies are presently found in the Guaniguanico Terrane of western Cuba, and along the Placetas belt of northern Cuba, between Matanzas and Holguín (Pushcharovski et al., 1988; Pszczolkowski and Myczyński, 2004). These rocks were deposited in a bathyal zone between the aragonite compensation depth and the calcite compensation depth (Pszczolkowski and Myczyński, 2004), and represent continental rise and basinal deposits of the Proto-Caribbean sea (Iturralde-Vinent, 1998). Within the Carmita Formation are found distal turbiditic intercalations (calcirudites to calcarenites), but the specimen is embedded in biomicrite, suggesting that it may have reached the sea bottom by direct deposition without transportation. In this context, the fragmentary character of the teeth of *Ptychodus* suggest that the specimen suffered from complex taphonomic processes before fossilization. The fact that the specimen was acid prepared prior to its re-discovery does not allow further observations of matrix-teeth relationships.

DISCUSSION

Specimens AMNH 8031 and MNHN 1898-3 (Brito and Janvier, 2002) resemble each other closely in the presence of moderately coarse ridges radiating from the apex of the crown. The tooth crowns in MNHN 1898-3 are less acuminate and more voluminous than in AMNH 8031, and the whole “tooth battery” is more densely packed in the former specimen. The striae on the crowns are more densely spaced and the ornament in the marginal area is somewhat more reticulate in MNHN 1898-3. The matrix of the MNHN specimen was thin sectioned but appears to be free of microfossils (Brito and Janvier, 2002), and the age of that specimen thus remains unsettled.

However, MNHN 1898-3 may have had a similar “strato-paleogeographic” occurrence, because isolated teeth of *Ptychodus* are abundantly found in defined horizons of various localities in North America and Europe, taxa are restricted in stratigraphic distribution, and show little “provinciality” in their morphologic variation (Reinhart, 1951; Williamson et al., 1991; Welton and Farish, 1993). This phenomenon may be explained by the fact that late Cenomanian and early Turonian pan-tropical seas were generally well connected (Ricardi, 1991; Scotese, 2004).

In overall morphology, *Ptychodus cyclodontis* sp. nov. comes closest to *Ptychodus mortoni* Mantell, 1838, from the Austin group, Texas, occurring from Coniacian to Santonian. Jaekel (1894:137) had proposed to place this species in a separate new genus *Hemiptychodus*, but this suggestion was not generally accepted (Woodward, 1912; Patterson, 1966). *P. mortoni*, however, resembles *P. cyclodontis* sp. nov. more closely than any other species of *Ptychodus* currently known.

CONCLUSIONS

Although the exact “strato-paleogeographic” provenance of both holotype specimen AMNH 8031 and specimen MNHN 1898-3, and the Late

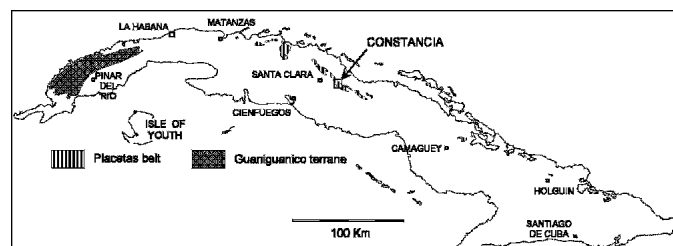


FIGURE 2. Location of the area where the specimen may have been collected, and distribution of the tectonostratigraphic units where the Carmita and equivalent formations occur.

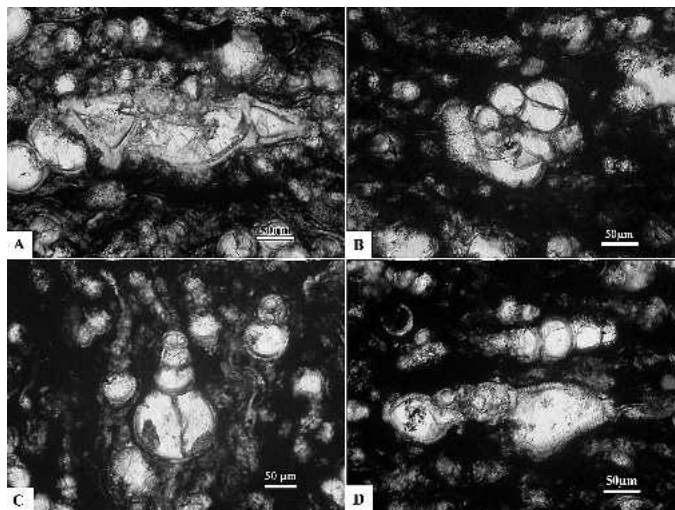


FIGURE 3. Planktonic foraminifera as preserved in specimen AMNH 8031; **A**, *Marginotruncana* aff. *sigali*; **B**, *Hedbergella* sp.; **C**, *Heterohellicidae* sp.; **D**, various planktonic foraminifera.

Cretaceous age of specimen MNHN 1898-3 are interpretive, the morphologic similarity showing a “cone-shaped triturating surface” (tooth-type 3 in Cappetta, 1987) strongly suggests inclusion of both specimens in the same species, *Ptychodus cyclodontis* sp. nov. Previous studies of Late Cretaceous *Ptychodus* confirm presence of little provinciality (i.e., Reinhart, 1951; Williamson et al., 1991) and corroborate the conspecific nature of both these museum finds despite the enigmatic provenance of MNHN 1898-3.

Quite in contrast to other species of *Ptychodus*, *P. cyclodontis* is remarkably homodont. However, the majority of species is known by isolated teeth only (Stewart, 1980; Maisey, 1982; Cappetta, 1987; Welton and Farish, 1993), in which the respective degree of heterodonty is almost impossible to assess.

Both *Ptychodus cyclodontis* sp. nov. and *Ptychodus mortoni* Agassiz, 1843, show a pattern of radial enameloid ridges and differ in this respect from all other known species of *Ptychodus*, in which the pattern in the enameloid relief is dominated by transverse ridges. Further research upon discovery of more complete dentitions of *P. mortoni* and *P. cyclodontis* will be necessary for assessment of the degree of homodonty in these two species and the validity of the genus *Hemiptychodus* Jaekel, 1894.

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LITERATURE CITED

- Agassiz, L. 1833–44. *Recherches sur les Poissons fossiles*. 5 vols. Petit-Pierre, Neuchâtel et Soleure, 1420 pp.
- Bonaparte, C. L. 1838. *Selachorum tabula analytica*. *Nuovi Annali Scienze naturali* (Bologna) 1(2):195–214.
- Brito, P. M., and P. Janvier. 2002. A ptychodontid (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of South America. *Geodiversitas* 24(4):785–790.
- Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii; in H.-P. Schultze (ed.), *Handbook of Paleichthyology*. Vol. 3B, Gustav Fischer, Stuttgart, New York.
- Compagno, L. J. V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17:303–322.
- Cuny, G., V. Suteethorn, E. Buffetaut, and M. Philippe. 2003. Hybodont

- sharks from the Mesozoic Khorat Group of Thailand. *Maharakham University Journal* 22(special issue):49–68.
- Everhart, M.J., and Caggiano, T. 2004. An associated dentition and calcified vertebral centra of the Late Cretaceous elasmobranch, *Ptychodus anonymus* Williston 1900. *Paludicola* 4(4):125–136.
- Hay, O. P. 1902. *Bibliography and catalogue of the fossil vertebrata of North America*. *Bulletin of the United States Geological Survey* 179:1–868.
- Herman, J. 1977. Les sélaciens des terrains néocrétacés & paléocènes de Belgique & des contrées limitrophes. *Eléments d'une biostratigraphie intercontinentale*. *Mémoires pour servir à l'explication de Cartes Géologiques et Minières de la Belgique*. *Sérvise Géologique de Belgique* 15:1–401.
- Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880: 649–662.
- Iturralde-Vinent, M. 1998. Synopsis of the Geological Constitution of Cuba. *Acta Geologica Hispanica* (IGCP 433) 33(1–4):9–56.
- Jaekel, O. 1894. *Die eocänen Selachier vom Monte Bolca*. Berlin, 176 pp.
- Jaekel, O. 1898. Über *Hybodus* Ag. *Sitzungsbericht der Gesellschaft naturforschender Freunde Berlin* 1898:135–146.
- Larrazet, M. 1886. Des pièces de la peau de quelques Sélaciens fossiles. *Bulletin de la Société géologique de France* séries 3, 14(16):255–277.
- Maisey, J. G. 1982. The anatomy and interrelationships of Mesozoic hybodont sharks. *American Museum Novitates* 2724:1–48.
- Maisey, J. G. 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. *American Museum Novitates* 2878:1–39.
- Mantell, G. 1838. *The Wonders of Geology*. 2 vols. Relfe and Fletcher, London, 821 pp.
- Patterson, C. 1966. British Wealden sharks. *Bulletin of the British Museum (Natural History) Geology* 11:283–350.
- Pszczolkowski, A., and R. Myczyński. 2004. Stratigraphic constraints on Late Jurassic–Cretaceous paleotectonic interpretations of the Place-tas belt in Cuba; pp. 545–581 in C. Bartolini, R. T. Buffler, and J. Blickwede (eds.), *The Circum-Gulf of Mexico and the Caribbean: Hydrocarbon Habitats, Basin Formation, and Plate Tectonics*, American Association of Petroleum Geologists, Memoir 79.
- Pushcharovski, Yu. M. (ed.). 1988. *Mapa geológico de la República de Cuba escala 1:250,000*. Academia de Ciencias de Cuba y Academia de Ciencias de la URSS, 42 sheets.
- Rees, J., and C. J. Underwood. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontidae (Selachii). *Journal of Vertebrate Paleontology* 22:471–479.
- Reif, W.-E. 1980. Tooth enameloid as a taxonomic criterion: 3. A new primitive shark family from the lower Keuper. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 160:61–72.
- Reinhart, R. H. 1951. A new shark of the family Ptychodontidae from South America. *University of California Publications—Bulletin of the Department of Geological Sciences* 28(8):195–202.
- Ricardi, A. C. 1991. Jurassic and Cretaceous marine connections between the Southeast Pacific and Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* 87(1–4):155–189.
- Scotese, Ch. R. 2004. PALEOMAP project site. <http://www.scotese.com/>
- Stewart, J. D. 1980. Reevaluation of the phylogenetic position of the Ptychodontidae. *Transactions of the Kansas Academy of Sciences* 83(3):154.
- Welton, B. J., and R. F. Farish. 1993. *The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas*. Before Time, Lewisville, 204 pp.
- Williamson, T. E., S. G. Lucas, and J. I. Kirkland. 1991. The Cretaceous elasmobranch *Ptychodus decurrens* Agassiz from North America. *Geobios* 24(5):595–599.
- Woodward, A. S. 1912. The fossil fishes of the English Chalk. Part VII. *Palaeontographical Society (London) Monographs* 56(57):225–264.
- Woodward, A. S. 1916. The fossil fishes of the English Wealden and Purbeck formations. *Palaeontographical Society of London (Monograph)* 1:1–48.
- Yabe, H., and T. Obata. 1930. On some fossil fishes from the Cretaceous of Japan. *Japanese Journal of Geology and Geography* 8:1–8.

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