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Mesozoic hybodont sharks from Asia and their relationships to the genus *Ptychodus*

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ABSTRACT:

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The affinities of the selachian genus *Ptychodus* is discussed and *Hemiptychodus* is here re-introduced as a subgenus characterized by unusual tooth ornamentation pattern. An overview of Asian hybodont genera showing tooth ornamentations pattern similar to that of *Ptychodus* is given. Lacking a triple-layered enameloid, *Ptychodus* may be a hybodont shark or a batoid, but both hypotheses are not without problems. Based only on dental characters, hybodont affinities for this genus are favoured here, although the evidence to do so is indeed weak.

Key words: Jurassic, Cretaceous, Hybodontiformes, Ptychodontidae, Asia.

INTRODUCTION

Ptychodus was a large selachian possessing a crushing dentition, showing a global distribution, and known from the Albian to the Campanian (CAPPETTA 1987). When erecting the genus, AGASSIZ (1839) considered *Ptychodus* to be closer to the hybodonts than to the batoids, but subsequent authors included this genus in the family Myliobatidae (WOODWARD 1889). Nowadays, the phylogenetic relationships of this genus are still poorly understood and it is variously included in the Hybodontiformes (CAPPETTA 1987, WELTON & FARISH 1993) or in the Neoselachii (MAISEY & *al.* 2004). The latter hypothesis is mostly supported by the association of calcified vertebral centra with teeth (EVERHART & CAGGIANO 2004), although WELTON & ZINSMEISTER (1980) noted that ‘articulated skeletons of *Ptychodus* are not known, and the finding of teeth and vertebrae in association should not be regarded as demonstrable proof that all are from the same genus’. Teeth of *Ptychodus* also possess a single-layered enameloid (Text-fig. 1A-B), a primitive character for elasmobranchs (GILLIS & DONOGHUE 2007) found in hybodonts and batoids. The presence of large holes in the enameloid (Text-fig. 1A) is however a feature that was not observed by the author in any of the hybodont or batoid teeth he has studied until now. Lacking a triple-layered enameloid, these teeth cannot belong to a galean or squalean shark (REES & CUNY 2007). Anyway, whether *Ptychodus* is considered a hybodont or a batoid, it is very difficult to identify another taxon sharing any of its dental characters, which in part explains the current uncertainty as to its phylogenetic affinities. This is why the discovery of Asian hybodont showing a tooth ornamentation pattern similar to that of *Ptychodus* is of interest.

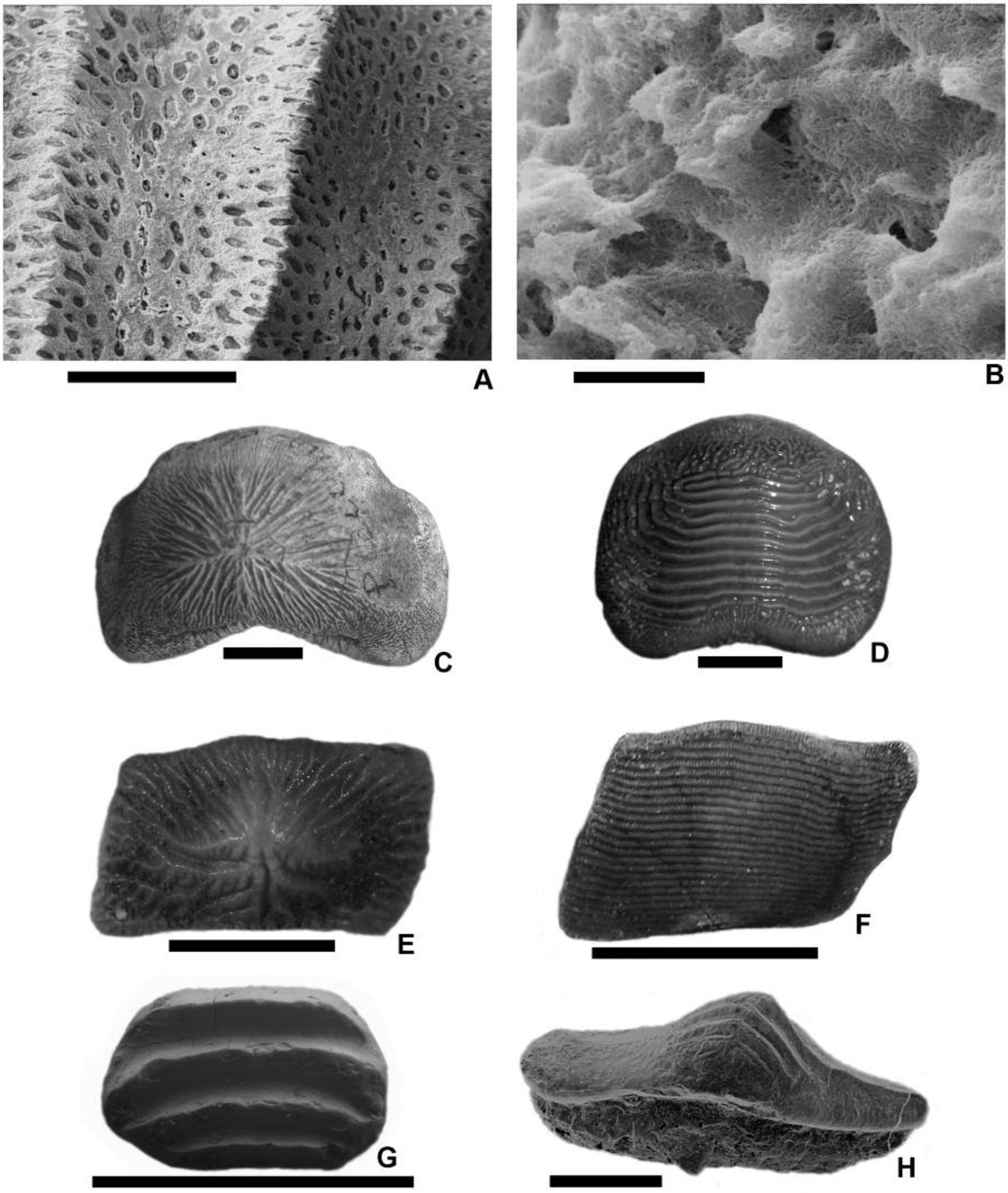

Fig. 1. A-B – *Ptychodus* sp. from Craie du Blanc-Nez (Cenomanian-Turonian, Boulonnais, Northern France). Tooth etched 34 min. in 10% HCl, A – Surface of the crown, B – Details of the single crystallite enameloid, C – Tooth of *Ptychodus (Hemiptychodus) mortoni* in apical view; specimen from the collection of the Museum of Comparative Zoology, Harvard University, MCZ 13202, Cretaceous of Alabama, D – Tooth of *Ptychodus decurrens* in apical view; MCZ 5730, Lower Chalk, Holborough, Kent, England, E – TF 7651 (Sirindhorn Museum, Department of mineral resources, Sahatsakhan, Kalasin Province, Thailand) from Khok Pha Suam (Ubon Ratchathani Province, Thailand, Khok Kruat Formation, Aptian-Albian) in apical view, F – Tooth of *Heteroptychodus steinmanni* from Phu Wat (Nong Bua Lamphu Province, Thailand, Sao Khua Formation, Lower Cretaceous) in apical view; specimen from the collection of the Srisuk's House Museum (Khao Yoi, Phetchaburi Province, Thailand), unnumbered, G – Tooth of a new hybodont from Guizhou (Zigui County, Hubei Province, China, Xietan Formation, Middle Jurassic) in apical view; specimen from the collection of the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China, IVPP V15148, H – Posterior tooth of *Isanodus paladeji* from Phu Phan Thong (Nong Bua Lamphu Province, Thailand, Sao Khua Formation, Lower Cretaceous) in linguo-apical view; specimen from the Sirindhorn Museum, Thailand, unnumbered. Scale bars: A, E, G, H – 1 mm; B – 10 μm; C, D, F – 10 mm

PTYCHODUS TOOTH ORNAMENTATION PATTERN

Ptychodus teeth are easily identifiable based on their large size, up to more than 50 mm labio-lingually, and their crown divided in two distinct areas. In most species, the central area is more or less elevated and ornamented by a set of longitudinal crests oriented mesio-distally, while the marginal area is ornamented with small tubercles and fine enameloid wrinkles (Text-fig. 1D). Three species however differ from this pattern: *Ptychodus mortoni* AGASSIZ, 1839 (Turonian-Santonian, North America, Europe and Africa), *P. cyclodontis* MUTTER & *al.*, 2005 (Cenomanian-Turonian, Cuba) and *Ptychodus* sp. (BRITO & JANVIER 2002, Upper Cretaceous, South America) whose teeth possess radiating ridges instead of longitudinal crests in the central area (Text-fig. 1C). JAEKEL (1894, p. 137) had proposed to place the species *P. mortoni* in a separate genus, *Hemiptychodus,* but this suggestion was generally not accepted (PATTERSON 1966, CAPPETTA 1987). This name accounts however nicely for the existence of two very different tooth ornamentation patterns among these sharks, and I propose to reintroduce *Hemiptychodus* as a subgenus, in which we can include the three species mentioned above. This definition of two subgenera in *Ptychodus* is only based on the ornamentation pattern, and for the time being high crowned species which retain an ornamentation made of a set of parallel longitudinal crests, like for example *Ptychodus whipplei,* are retained in *Ptychodus sensu stricto.*

ASIAN HYBODONTIFORMES

Heteroptychodus was first described as a Myliobatidae by YABE & OBATA (1930) before being considered as a junior synonym of *Ptychodus* by CAPPETTA (1987). The ornamentation pattern of *Heteroptychodus* clearly indicates that it is a valid genus, and its root structure confirms its hybodont status (CUNY & *al.* 2003, 2006, CAPPETTA & *al.* 2006). This genus encompasses two known species: *H. steinmanni* from the Early Cretaceous of Japan and Thailand (YABE & OBATA 1930, CUNY & *al.* 2006, 2008) and *H. chuvalovi* from the Aptian-Albian of Mongolia (CUNY & *al.* 2008), which was first described as *Asiadontus chuvalovi* (see NESSOV 1997). The teeth of *Heteroptychodus* show a pattern of ornamentation quite similar to those of *Ptychodus,* differing mainly by a reduced marginal area, a denser pattern of parallel longitudinal crests, and the presence of small ridges perpendicular to the longitudinal crests (Text-fig. 1F), although several teeth from Thailand attributed to juveniles show a reduced number of crests lacking short perpendicular ridges (CUNY & *al.* 2003, 2006). *Heteroptychodus* has therefore been attributed to the family Ptychodontidae (PATTERSON 1966, CUNY & *al.* 2003, 2006, CAPPETTA & *al.* 2006). The oldest record of *Heteroptychodus* is so far from the Phu Kradung Formation (latest Jurassic-earliest Cretaceous) in Thailand.

Isanodus paladeji was described from the lower part of the Sao Khua Formation (Berriasian-Barremian) in Thailand (CUNY & *al.* 2006). The presence of a labial peg, low cusp and low root indicates that the teeth of *Isanodus* belong to the family Lonchidiidae. In addition, they share a similar ornamentation pattern with the teeth of *Heteroptychodus*, with parallel mesio-distal crests (Text-fig. 1H) from which originate short, non-branching secondary ridges only in lateral teeth (CUNY & *al.* 2006).

One tooth (TF 7651) from the Aptian/Albian Khok Kruat Formation in Thailand (CUNY & *al.* 2003, 2008) is also of interest to this discussion. It has a rectangular outline in apical view, being mesio-distally longer than labio-lingually wide. The crown is ornamented with a dense pattern of radiating, often anastomosing ridges, but on the lingual side of the cusp, two pairs of ridges become parallel to the longitudinal crest (Text-fig. 1E). The longitudinal crest and some main ridges show short, non branching ridges perpendicular to them, a pattern similar to that seen in *Heteroptychodus* and *Isanodus* (CUNY & *al.* 2003, 2006), but its general pattern of ornamentation is also similar to that in *Hemiptychodus,* although its crown is not as high as in the latter subgenus. TF 7651 probably represents a new taxon, but a single tooth does not suffice to erect a new genus and species, and it was therefore left in open nomenclature.

A fourth taxon of interest to this discussion has recently been found in the early Middle Jurassic Xietan Formation (Hubei province, southern China), which is currently under study, and will be described in details elsewhere (SHANG, CUNY & CHEN, submitted). The Chinese teeth show two to four parallel longitudinal crests, without small perpendicular ridges, and are devoid of a marginal area (Text-fig. 1G). The posterior teeth show a labial protuberance. The insertion area of the root is elliptical or triangular, like in the Lonchidiidae, while it is quadrilateral in *Heteroptychodus* and *Ptychodus.*

IS *PTYCHODUS* CLOSELY RELATED TO THE ASIAN HYBODONTS?

The relationships between the Chinese hybodont, TF 7651, *Isanodus, Heteroptychodus* and *Ptychodus* remain difficult to assess in the present state of our knowledge. A common pattern of ornamentation based on the multiplication of longitudinal crests and the fact that the Chinese hybodont, *Isanodus* and *Heteroptychodus* are restricted to Asia would certainly suggest that these sharks are somewhat related to each other. Moreover, the presence of a labial protuberance on posterior teeth is another shared character between the Chinese hybodont and *Isanodus*. CUNY & *al.* (2006, 2008) have proposed that Ptychodontidae, first represented by *Heteroptychodus,* originated from Asian freshwater Lonchidiidae that became increasingly adapted to durophagy. In this case, TF 7651 could be intermediate between *Isanodus* and *Heteroptychodus*. This hypothesis would also explain the similarities between the teeth of *Hylaeobatis,* another Lonchidiidae, and those of *Ptychodus* (PATTERSON 1966), although adaptation to durophagy probably appeared independently in these two lineages. This hypothesis means however that the family Lonchidiidae is paraphyletic.

The transition between *Heteroptychodus* and *Ptychodus* involves the development of marginal area on the crown of the teeth, the reduction in number of parallel crests and the loss of their perpendicular ridges. The presence of numerous longitudinal crests and reduced marginal area are considered primitive characters among *Ptychodus* (HERMAN 1977), which supports the idea of an evolutionary continuum between *Heteroptychodus* and *Ptychodus,* all the more since the oldest *Ptychodus* species, *P. decurrens,* known from the Albian, presents a reduced marginal area and up to 16 longitudinal crests (SIVERSON 1999). The loss of the small perpendicular ridges in *Ptychodus* could be the result of neotenic evolution as these ridges are not present in juvenile *Heteroptychodus* (CUNY & *al.* 2003, 2006). *Heteroptychodus-Ptychodus* relationship would also be suggested by the shape of posterior teeth of *Ptychodus rugosus,* which are elongated mesio-distally with an irregular outline in apical view (CASIER 1953), a pattern quite similar to what has been described in *Heteroptychodus steinmanni* (CUNY & *al.* 2003), although in the latter the reduction in size of these teeth is more important than in *P. rugosus.* Finally, the stratigraphic range of these two genera (Berriasian – Albian for *Heteroptychodus* and Albian – Campanian for *Ptychodus*) fits well with a close relationship between them.

The new Chinese hybodont could be basal to a *Isanodus* + *Heteroptychodus* + *Ptychodus* clade, which would fit nicely with its known stratigraphic distribution, but it could also be closer to *Ptychodus* than to *Isanodus* and *Heteroptychodus,* the latter sharing the presence of short perpendicular ridges between the longitudinal crests. The loss of labial protuberance in *Ptychodus* and *Heteroptychodus* would thus be the result of a convergence as it is present in both *Isanodus* and the Chinese hybodont, and the presence of small perpendicular ridges would be a synapomorphy of *Isanodus,* TF 7651 and *Heteroptychodus*.

It is also possible that the appearance of several parallel longitudinal crests in so many different genera is just the result of convergence, indicating that this character might not be so significant from a phylogenetic point of view. A similar ornamentation can indeed be observed in some batoids, like *Rhina* and *Ptychotrygon* (CAPPETTA 1987, LAST & STEVENS 1994), although it should be noted it is never associated with a tooth enlargement similar to that is observed in *Ptychodus* and the Asian hybodonts. Other characters that would oppose to a close relationship between *Heteroptychodus* and *Ptychodus* include the heterodonty pattern of these sharks, as the largest teeth in *Ptychodus* are in the symphyseal files on the lower jaws and in the parasymphyseal files on the upper jaws (LERICHE 1902), while they are in lateral positions in *Heteroptychodus* (CUNY & *al.* 2003). In addition, in *Ptychodus* the root is reduced and firmly attached to the crown, and the teeth from a same row show a labial peg and lingual socket interlocking system, although it should be noted that such a system could easily be derived from the lonchiidid labial peg. Other negative evidences that would oppose *Ptychodus* from being a hybodont include the fact that no dorsal or cephalic spines have ever been found in association with *Ptychodus* teeth, although a secondary loss of these structures among hybodonts is not impossible, the same way as many neoselachian lineages have lost dorsal spines. If indeed *Ptychodus* is not a hybodont shark, then it could be a batoid, a stem-neoselachian, or the sister-group of Galea + Squalea, as the loss of the triple-layered enameloid has never been documented among non-batoid neoselachian sharks (Text-fig. 2), even in durophagous form like *Heterodontus* (REIF 1973). The two latter hypotheses would suggest that the *Ptychodus* lineage appeared at least at the beginning of the Permian, when the first Synechodontiformes appeared in the fossil record (IVANOV 2005). However, such an ancient origin for this lineage has never been documented.

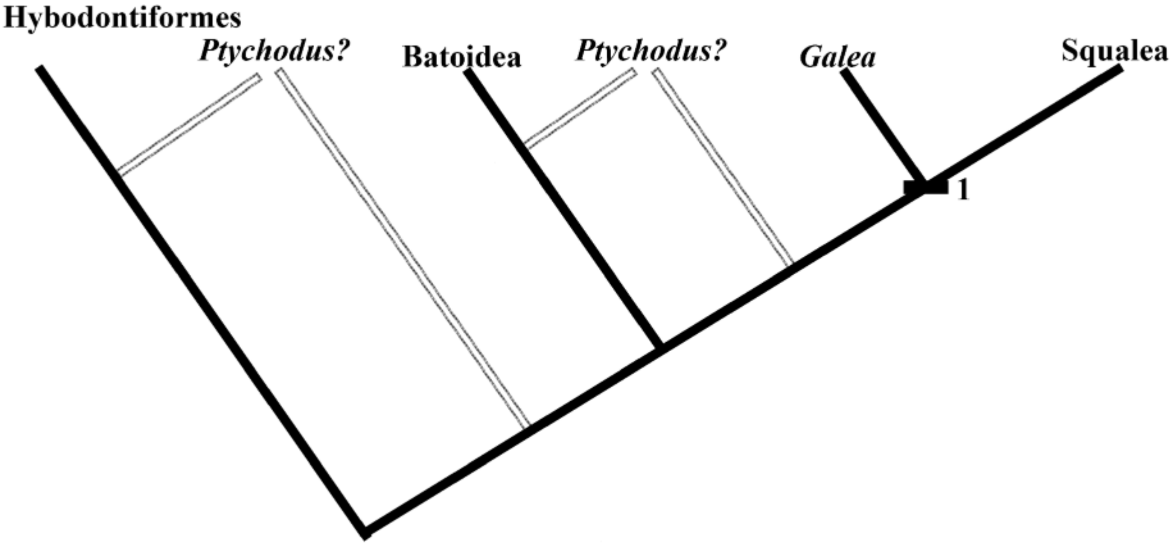

Fig. 2. Diagram indicating different possible phylogenetic relationships for the genus *Ptychodus.* 1 indicates the acquisition of a triple-layered enameloid among elasmobranchs

If *Ptychodus* is a batoid, there will be no contradiction with its appearance in the Albian, but this hypothesis is not without problems. As early as 1953, CASIER noted that the vascularization system observed in the teeth of *Ptychodus* is unlike that of any batoid, but would be closer to the hybodont type. The elongation of the jaws observed in *Ptychodus* (WOODWARD 1904) is also unknown among batoid, probably as a result of their euhyostylic jaw suspension. In addition, no synarcual has ever been found in association with *Ptychodus* teeth.

To consider *Ptychodus* as a hybodont is not without difficulties, but at the present stage of our knowledge, it might be the hypothesis that fits available data the best, mostly because it offers a reasonable explanation for the appearance of their most unusual dental ornamentation pattern among Asian forms within an acceptable stratigraphic frame. However, only the discovery of a *Ptychodus* skeleton in connection will definitively settle this discussion. The recent report of a partial skeleton from *Ptychodus anonymus* from the Late Cretaceous of Nebraska by SHIMADA & *al.* (2007) could indeed indicate that we are getting closer to an answer.

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