HYBODONT SHARKS FROM THE MESOZOIC KHORAT GROUP OF THAILAND

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Abstract

Isolated teeth of seven hybodont genera, including *Hybodus, Acrodus, Thaiodus* and *Heteroptychodus,* are described from the freshwater Khorat Group of Thailand (Uppermost Jurassic – Aptian). These sharks show a wide range of diet and many of them were restricted to freshwater environment and thus endemic to the Khorat Plateau. The distribution of *Thaiodus* and *Heteroptychodus,* known in other Asian locations, may be explained by a mode of life similar to that of the modern sawfish *Pristis perotteti.*

Key words: chondrichthyes, hybodontiformes, Thailand, upper jurassic, lower cretaceous.

Introduction

The first hybodont sharks may have appeared as early as the Early Devonian (Mader, 1986) and they disappeared at the end of the Maastrichian (Cappetta *et al.,* 1993), but it is generally admitted that they showed a maximum diversity during the Triassic and that their numbers were greatly reduced by Cretaceous times (Thies & Reif, 1985; Carroll, 1988). Moreover, they appear to have mainly inhabited freshwater environments during the Cretaceous due to overwhelming competition from the neoselachian sharks in the marine realm (Rees, 1998). This would suggest that from the Jurassic onwards, the hybodont sharks were unable to compete with other sharks and by Cretaceous times, they were already some kind of living fossils taking refuge in fresh waters.

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However, new data from the Early Cretaceous of Thailand show that they were still very successful at that time. With at least 7 genera, they show a remarkable adaptation to freshwater environment. Moreover, this shark fauna shows affinities with those of Japan, Tibet, Kirghisia and Mongolia, but is unknown outside Asia, suggesting, they might have followed the Asiatic coast to spread into many freshwater ecosystems.

1. Material and method

The shark teeth described in the present work have been obtained by screen washing sediments using 0.5 and 1.7 mm mesh-sized sieves, and by surface collecting for the largest specimens. 1,200 kilograms of sediment have been processed from the Khok Pha Suam locality. The fossils will be housed at the Sahatsakhan Museum of Palaeontology (TF numbers) in Sahatsakhan, Kalasin Province, but some teeth also come from the Srisuk House Museum (Phetchaburi Province, SHM numbers).

2. Geological settings

The Khorat Group is a set of sandstones, clays and freshwater limestones deposited during the Mesozoic in Northeastern Thailand (and parts of adjacent Laos and Cambodia). It ranges in age from the Late Jurassic (Phu Kradung Formation) to the Cenomanian (Maha Sarakham Formation), and its total thickness is nearly 3200 m. These deposits occurred after the collision of the Shan-Tai (= Sibumasu) terrane with the Indochina block (Metcalfe, 1996; Charusiri *et al.*, 1997; Racey et al., 1997a). The Khorat Group has yielded a succession of nonmarine vertebrate assemblages (see Buffetaut & Suteethorn, 1998 for a recent review) but the stratigraphy and palaeoecology of its different formations is still poorly known (Racey *et al.,* 1994, 1996, 1997b; Metcalfe, 1998). Hybodont shark remains have been so far retrieved from the Phu Kradung Formation (Uppermost Jurassic), the Sao Khua Formation (Neocomian) and the Khok Kruat Formation (Aptian, Racey *et al.,* 1996).

3. Systematic description

Class: Chondrichthyes Huxley 1880

Subclass: Elasmobranchii Bonaparte 1838

Order: Hybodontiformes Maisey 1987

Family: Hybodontidae Owen 1846

Subfamily: Hybodontinae Maisey 1989

Genus: H*ybodus* Agassiz 1837

Hybodus sp. A

Material: 125 more or less complete teeth (including TF 7645), with only one being reasonably complete (TF 7644). One tooth (TF 7658) has been embedded in resin and cut for SEM study.

Occurences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

The complete tooth is also the largest, being 19.5 mm mesio-distally, 4 mm labio-lingually and 6 mm high at the level of the main cusp. All the teeth show a low main cusp flanked by up to two pairs of lateral cusplets (Fig. 1A-C). The first pair may be almost as high as the main cusp, while the second pair is half that height. One incomplete tooth (TF 7645) shows a minute accessory cusplet on the labial face of the main cusp, near the valley separating the main cusp from a lateral cusplet. As this was recorded in no other teeth, this is probably due to some anomaly in the development of this tooth. The crown is ornamented by a dense pattern of fine anastomosed ridges that cover the whole crown, except the lingual shoulder that is smooth. There is a moderately developed longitudinal crest that is interrupted at the tip of each cusp and cusplets although this may be the result of wear. There is no labial node at the base of the crown, but very rarely faint lingual nodes may be seen near the mesial or distal extremities of the crown. When preserved, the root is nearly as high as the crown and is not projected lingually. Its basal face is flat. The whole root is perforated by a multitude of foramina randomly distributed with the addition of a row of large foramina at the base of the root, crossing it labio-lingually.

Histology

The studied tooth is osteodont (Fig. 2A) and the crown is covered with a rather thick (100 μ m) single-layered enameloid (Fig. 2B).

Discussion

The density of the ornamentation of these teeth is reminiscent to that of *Hybodus brevicostatus* from the Wealden of Britain (Patterson, 1966). However, the teeth from Thailand are easily distinguished from those of *H. brevicostatus* by the much better developed main cusp and lateral cusplets and the absence of lingual nodes at the base of the crown. These teeth also show an

ornamentation quite similar to those of *Hybodus* sp. described from the Upper Jurassic of Ethiopia (Goodwin *et al.,* 1999), but again are easily distinguished on the basis of the first pair of lateral cusplets almost as high as the main cusp and the absence of fine, short non-branching ridges on the cutting edge. The teeth from Thailand, with their first pair of lateral cusplets almost as high as the main cusp, appear to be fairly unique and probably belong to a new species.

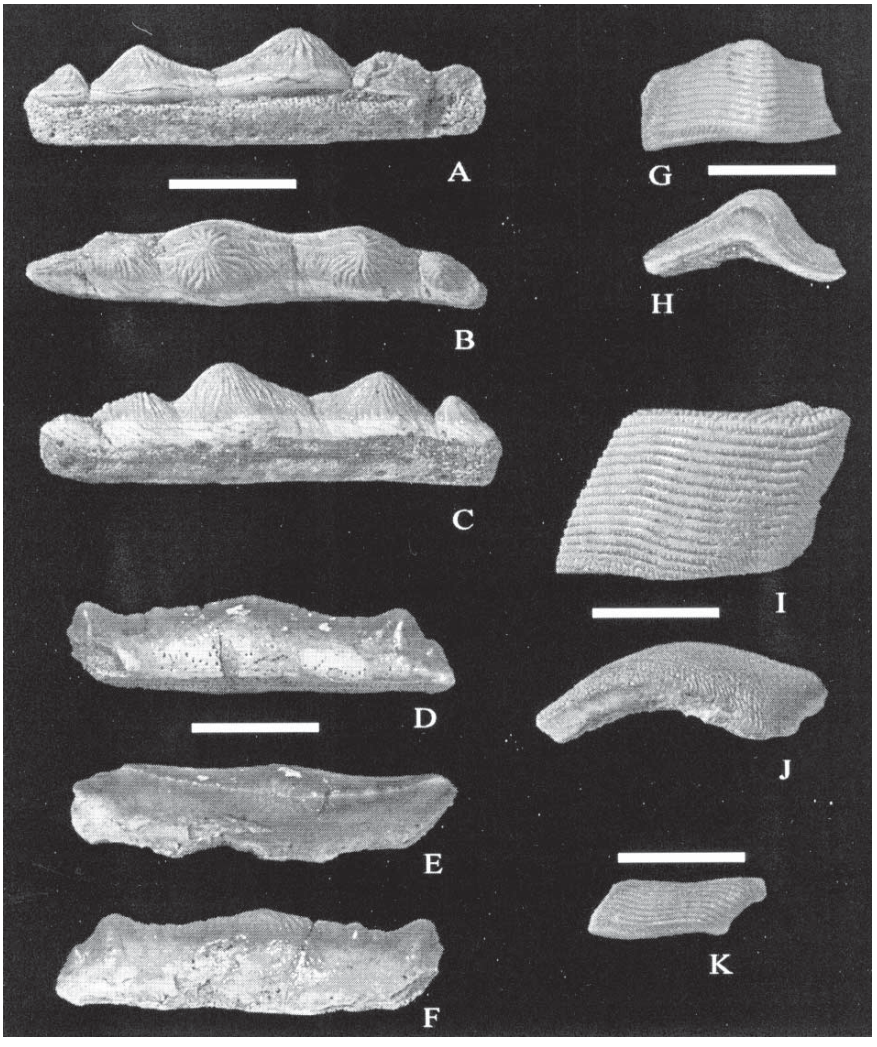

Fig. 1: A-C: Tooth (TF 7644) of *Hybodus* sp. A in A: labial, B: apical and C: lingual view. D-F: Tooth (TF 7646) of *Thaiodus ruchae* in D: labial, E: apical and F: lingual view. G-K: *Heteroptychodus steinmanni.* G-H: anterior tooth (TF 7647) in G: apical and H: labial view. I-J: lateral tooth (TF 7648) in I: apical and J: labial view. K: posterior tooth (TF 7649) in apical view. All scale bars: 5 mm. All the specimens come from Khok Pha Suam.

Hybodus sp. B

Material: 160 fragmentary crowns.

Occurences: Phu Phan Thong, Nong Bua Lamphu province, Sao Khua Formation.

Description

The material is fragmentary, lacking either a complete crown, or a tooth with a root preserved. The maximum estimated height of these cusps is 6 mm. Two morphotypes can be recognized in the material at hand. The first one shows cusps that are slightly compressed labio-lingually with well-developed cutting edges. The labial side is ornamented by numerous, up to 15, short ridges, while the lingual side is ornamented by stronger, longer ridges, which are not anastomosed. Only one cusp has its apex preserved and the lingual ornamentation does not reach it. This cusp is sigmoid in mesial and distal view.

The second morphotype encompasses cusps with an almost circular cross-section at their base. Both the lingual and the labial sides are ornamented by strong ridges reaching the apex and anastomosing near the apex of the cusp. The cutting edges are less developed than in morphotype1.

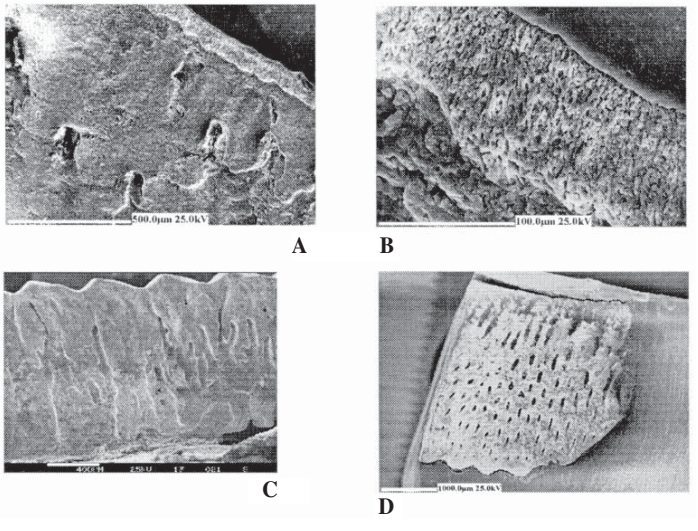

Fig. 2: A-B: Longitudinal section of a tooth (TF 7658) of *Hybodus* sp. A etched 30 sec in 10% HCl. A: Dentine and enameloid, B: detail of the single crystallite enameloid. C: Section of a tooth of *Heteroptychodus steinmanni* etched 95 sec in 10% HCl. The specimen has been destroyed for further study. D: Transverse section of a tooth (TF 7660) of genus #2 etched 6 min in 10% HCl. Please note that this section is upside down.

Discussion

With no complete teeth at hand, the assessment of a possible heterodonty is almost impossible, and it is very difficult to decide if the two morphotypes identified in the material belongs to one or two species. The sigmoid curvature of the only complete cusp belonging to morphotype 1 may also indicate that it belongs to *Egernotodus* rather than to *Hybodus* (Rees, 2002), but again we cannot reach a firm conclusion with such fragmentary teeth. This material is thus tentatively attributed to a single *Hybodus* species pending the discovery of more material.

Hybodus sp. C

Material: 11 fragmentary crowns.

Occurrences: Chong Chat, Nong Bua Lamphu Province, Phu Kradung Formation.

Description

The cusps are low, slightly compressed labio-lingually, and ornamented by 5-6 coarse ridges on the labial and lingual sides, which never anastomose. The ridges run from the base up to the apex of each cusp. There is no cutting-edge.

One fragmentary tooth shows three accessory, broken teeth, and part of the root is preserved. It is projected lingually, anaulacorhize with a row of enlarged foramina just under the crown/root junction on the labial side.

The highest isolated cusp is 2.5 mm high and 3 mm mesio-distally at its base. The fragment with three broken accessory cusps is 2 mm mesio-distally. A maximum width for these teeth could then be estimated to be in the range of 7-8 mm.

Discussion

Rather similar teeth attributed to *Hybodus* sp. have been described in the Phu Kradung Formation at the Wang Din So locality (Phitsanulok Province) by Srisuk (2002). However, the teeth from Wang Din So show ridges anastomosing near the base of the crown, and are thus quite easy to separate from those of Chong Chat. The poor preservation and the small number of teeth recovered so far prevent a determination at specific level for the time being.

Family: Acrodontinae Maisey 1989

Genus: *Acrodus* Agassiz 1837

Acrodus sp.

Material: One fragmentary crown from Chong Chat and one tooth from Wang Din So (SHM-WD 219).

Occurrences: Chong Chat, Nong Bua Lamphu Province, Phu Kradung Formation; Wang Din So, Phitsanulok Formation, Phu Kradung Formation.

Description

The fragmentary crown from Chong Chat measures 2 mm mesio-distally. The crown is ornamented with a well-developed double longitudinal crest, separated by a groove (Fig. 3E). The labial (?) one attain the mesial or distal extremity while the lingual (?) one stops well before. The crown is ornamented by irregular ridges originating from the base of the crown, sometimes attaining the longitudinal crests, sometimes not. Short ridges also originate from the crests.

The tooth from Wang Din So is 8 mm mesio-distally, 2 mm labio-lingually and 3 mm high. The crown shows a low main cusp and a moderately developed longitudinal crest (Fig. 3A-D). It is ornamented by irregular, anastomosing ridges. Because of wear, it cannot be determined with any certainty whether or not they attain the base of the crown, although this is likely. The root is approximately a third of the height of the crown, quadrangular in outline with a flat basal side, and slightly projected lingually. A well-developed furrow separates the crown from the root on the lingual side, but it is less developed on the lingual side. The vascularization is anaulacorhize, and the root shows no enlarged foramina.

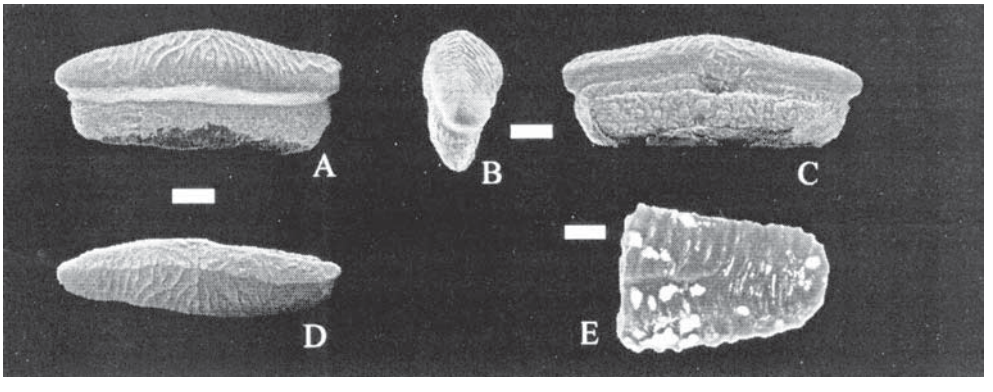

Fig. 3: A-D: Tooth of *Acrodus* sp. (SHM-WD 219) in A: labial, B: mesial or distal, C: lingual, and D: apical view. E: Crown of *Acrodus* sp. from Chong Chat in apical view. Scale bars: A-D: 1 mm, E: 200 μm.

Discussion

This is the first unquestionable mention of the genus *Acrodus* in Thailand, for its earlier mention in the Khok Kruat Formation (Pitakpaivan *et al.,* 1969) corresponds in fact to *Thaiodus* (Cappetta *et al.,* 1990). The presence of a double longitudinal crest in the crown fragment of Phu Phan Thong is reminiscent of *Acrodus spitzbergensis* from the Lower Triassic of Sptizbergen and the Middle Triassic of Nevada (Stensiö, 1921; Rieppel *et al.,* 1996; Cuny *et al.,* 2001). In *A. spitzbergensis,* the double longitudinal crest is present in lateral teeth, but not in anterior ones (Stensiö, 1921; Rieppel *et al.,* 1996; Cuny *et al.,* 2001). It is thus not impossible that the tooth from Phu Phan Thong and the one from Wang Din So belong indeed to the same species, although the stratigraphic gap makes it unlikely that the uppermost Jurassic Thai teeth belong to the Triassic *A. spitzbergensis.* The lack of a sufficient number of teeth prevents the erection of a new species for the time being.

Family: Steinbachodontidae? Reif 1980

Genus: *Thaiodus* Cappetta, Buffetaut & Suteethorn 1990

Thaiodus ruchae Cappetta, Buffetaut & Suteethorn 1990

Material: 192 more or less fragmentary teeth plus one large complete crown (TF 7646).

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation; Ban Khok Kruat, Nakhon Ratchasima Province, Khok Kruat Formation.

Description

The complete crown is 16.5 mm mesio-distally, 5 mm labio-lingually and shows a maximum height of 4.5 mm. It is elongated mesio-distally with a low central cusp flanked by a pair of lateral cusplets (Fig. 1D, F). The labial face is gently convex while the lingual one is slightly concave and flared basally. The main cusp is ornamented by short, but well developed, radiating ridges that are longer on the lingual face than on the labial one. The lateral cusplets, more compressed labio-lingually than the main cusp, are well separated from the latter. Between the main cusp and each of the lateral cusplets, there are 7 to 9 denticles of irregular size. Each of these denticles is serrated, although most of the serration has been worn away. The lateral cusplets, which are also serrated, are almost as high as the main cusp. Mesially and distally from the lateral cusplets, there is another serrated denticle. In apical view, the longitudinal crest is concave labially (Fig. 1E). The smaller teeth do not show ridges ornamenting the main cusp, and lateral cusplets are lacking. Only denticles can be seen mesially and distally from the main cusp. There is no tooth with the root preserved.

Discussion

The teeth of *Thaiodus ruchae,* currently known only from Thailand and Tibet (Cappetta *et al.,* 1990) show a unique morphology characterized mainly by the presence of irregular, obtuse, serrated denticles and a highly asymmetric crown, the lingual face being concave and flared basally while the labial face is gently convex. These characters clearly separate these teeth from those of any Hybodontidae, even if one accepts the broad definition of this family by Maisey (1989), which includes the genera *Palaeobates, Asteracanthus, Bdellodus, Acrodus, Egertonodus* and *Hybodus,* plus *Tribodus* (Brito & Ferreira, 1989; Maisey & de Carvalho, 1997) and *Priohybodus* (Duffin, 2001b). The inclusion of *Thaiodus ruchae* into the Hybodontidae by Cappetta *et al.* (1990), not justified by the possession of shared derived characters, seems therefore unlikely. On the other hand, the teeth of *Thaiodus ruchae* share a number of characters with those of *Steinbachodus*: raised cutting edge deflected to the labial edge of the crown, poorly defined cusps, labial face of the crown gently convex without a well-developed labial protuberance, lingual face concave and flared basally (Reif, 1980; Duffin, 2001a; Rees & Underwood, 2002) and the Steinbachodontidae are known up to the Cenomanian in Egypt (Duffin, 2001a; Rees & Underwood, 2002). *Thaiodus* would thus appear closer to the Steinbachodontidae than to the Hybodontidae, and is therefore cautiously attributed to this family in the present work.

New genus and species #1

Material: 87 fragmentary teeth, including TF 7656 and TF 7659.

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation

Description

The teeth of this genus are very elongated, rod shaped. Their labio-lingual width is generally around 1 mm although one tooth shows a width of 2.5 mm. The maximum mesio-distal length is unknown as no complete teeth have been found yet but it is at least six times the width in TF 7656. These teeth show a low coronal profile with a well-developed, zigzag-shaped longitudinal crest (Fig. 4B). Ridges originate from the longitudinal crest, often branching, but they do not attain the base of the crown (Fig. 4A, C). The crown is asymmetric with a short and convex labial face while the lingual face is flared basally although remaining slightly convex (Fig. 4D). As a result the longitudinal crest is displaced labially. There is a faint basal groove on the lingual face. At the mesial and distal ends of the teeth, there is a short basal bulge on the labial face. No tooth shows a completely preserved root.

Discussion

The low crown profile and elongated shape of these crowns suggest that they formed crushing batteries, as in *Asteracanthus* (Rieppel, 1981) or *Acrodus* (Mutter, 1998). But unlike these two Hybodontidae, they share with the teeth of *Thaiodus ruchae* an asymmetric crown with a convex labial face and a basally flared lingual face. Moreover, both kinds of teeth share a mesio-distally elongated crown. This strongly suggests that these two genera are closely related and we therefore consider genus #1 as a possible Steinbachodontidae, although the lingual face of the crown is not concave but slightly convex. However, this is to be considered tentative in the absence of a preserved root in both genera, which prevents detailed comparison with the Steinbachodontidae.

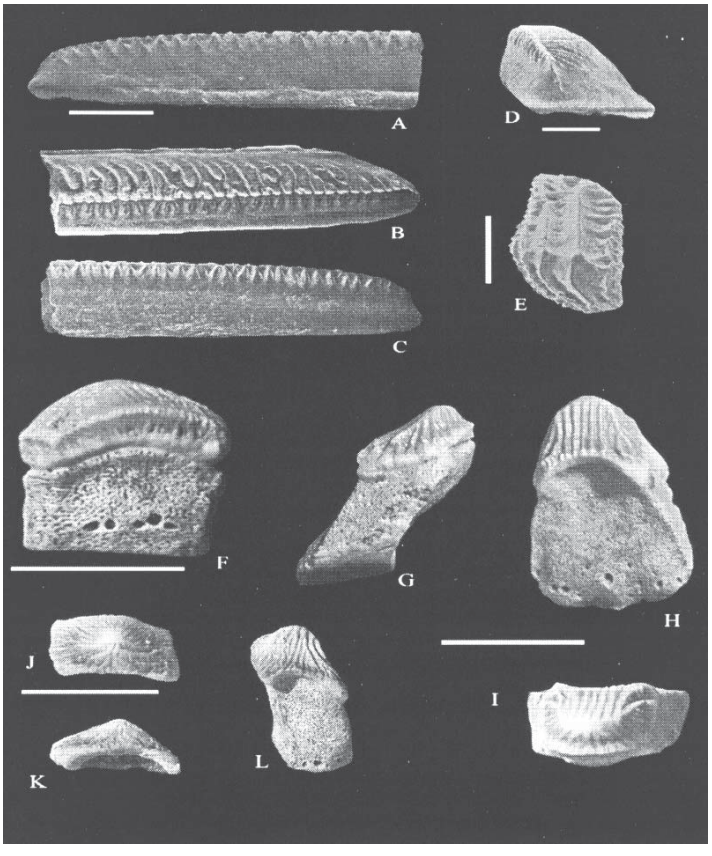

Fig. 4: A-D: Tooth (TF 7659) of genus #1 in A: lingual, B: apical, C: labial and D: mesial or distal view. E: tooth (TF 7655) of a juvenile *Heteroptychodus steinmanni* in apical view. F: Lateral tooth (TF 7650) of *Heteroptychodus steinmanni* in labial view. G-I: Tooth (TF 7657) of genus #2 in G: mesial or distal, H: lingual and I: apical view. J-L: Teeth of genus #3. J-K: TF 7651 in J: apical and K: lingual view. L: TF 7653 in lingual view. Scale bars: A-C, E: 1 mm, D: 0.5 mm, F-L: 5mm. All the specimens come from Khok Pha Suam.

Family: Ptychodontidae Jaekel 1898

Genus: *Heteroptychodus* Yabe & Obata 1930

Heteroptychodus steinmanni Yabe & Obata 1930

Material: 221 more or less complete teeth, including TF 7647-50, plus four teeth probably belonging to juveniles (including TF 7655). Two teeth have been embedded in resin and cut for SEM study.

Occurrences: Phu Phan Thong, Nong Bua Lamphu Province, Sao Khua Formation (103 teeth); Phu Wiang 1A, Khon Kaen Province, Sao Khua Formation (4 teeth); Phu Kum Khao, Kalasin Province, Sao Khua Formation (about 10 teeth); Phu Phok, Sakon Nakhon Province, Sao Khua Formation (2 teeth); Non Liam, Chaiya Phum Province, Sao Khua Formation (about 10 teeth); Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation (118 teeth).

Description

These teeth are parallelogram-shaped in outline. The largest crown, which is incomplete, is 15 mm mesio-distally and 11 mm labio-lingually. It comes from Khok Pha Suam. The ornamentation consists of up to 15 tightly packed parallel ridges running mesio-distally (Fig. 1G, I, K). From each of these main ridges originate short, non-branching secondary ridges. They are better developed on the lingual side of each of the main ridges. Labial ridges are seen only on the largest teeth. The marginal area of the crown is ornamented with fine, branching ridges. In many teeth, in labial or lingual view, the crown is arched, forming a bulge (Fig. 1H). These teeth are asymmetric, the bulge never being in a central position. It appears to be well developed on some teeth while others are completely flat, without any bulge. The flatter teeth are the smallest ones (Fig. 1K). The largest teeth show only a moderately developed bulge. It is therefore tempting to reconstruct the dentition of *Heteroptychodus* as follows: Anterior teeth (TF 7647, fig. 1G, H) with a well developed bulge not in the centre of the crown, large crushing lateral teeth (TF 7648, fig. 1I, J)) with a moderately developed bulge, and small, flattened posterior teeth (TF 7649, fig. 1K). Unfortunately, many teeth are fragmentary and it is not always possible to recognize to which category they belong. It is therefore difficult to assess the relative proportion of each kind, which makes any attempt to reconstruct the whole dentition highly hypothetical at best.

The crown-root junction is incised, and the crown overhangs the root labially. In some teeth, the crown covers the upper part of the root mesially and distally. One tooth (TF 7650, fig. 4F) shows a well-preserved root that is twice the height of the crown. Its basal face is flat, parallelogram-shaped with a surface smaller than that of the crown. The root does not protrude lingually beyond the crown. The whole root is perforated by a multitude of randomly distributed

foramina. On the labial face, there are five enlarged foramina in the lower third of the root, forming an irregular row.

Four parallelogram-shaped isolated crowns may belong to a juvenile *Heteroptychodus steinmanni.* In the best-preserved one (TF 7655, fig. 4E), measuring 1.8 mm mesio-distally and 0.8 mm labio-lingually, the crown is ornamented with three longitudinal ridges of decreasing length. On the mesial(?) part of the crown, each of the ridges shows a low cusp, decreasing in height from one ridge to another. Mesially(?), after the cusp, each ridge curves lingually(?). The marginal area of the crown is ornamented with radiating, branching ridges. The only difference between TF 7655 and the other three teeth is that the former appears flatter than the latter three, which are arched in lingual and labial view.

Histology

The teeth are osteodont, the vascular canals of the dentine being parallel to each other and arranged vertically (Fig. 2C). This type of dentine is often called 'tubular dentine' (Smith & Sansom, 2001). The crown is covered with a thin single-layered enameloid. *Ptychodus* also possesses osteodont teeth (Cappetta, 1987).

Discussion

This genus and species was hitherto known only from a handful of teeth found in the Lower Cretaceous of Japan (Yabe & Obata, 1930; Tanimoto & Tanaka, 1998). However, hybodont teeth attributed to the genus *Asiadontus* were reported from the Aptian-Albian of Kirghisia and Mongolia (Nessov, 1997). The ornementation of these teeth is very similar to that of *Heteroptychodus* and it is likely that that the two genera are synonyms. *Heteroptychodus* was thus present all around the Asian continent.

There are no significant differences between the teeth from the Sao Khua Formation and those from the Khok Kruat Formation. The largest teeth come from the Khok Kruat Formation, but on average the size difference is not significant, and there is no reason to think that we are dealing with two different species. *H. steinmanni* appears thus to have a rather large stratigraphic distribution.

The teeth of *Heteroptychodus* differ from those of *Ptychodus* by a reduced marginal area and a denser pattern of parallel longitudinal ridges ornamenting the crown. The teeth with a well-developed bulge recall what is seen in *Ptychodus whipplei* (Williamson *et al.,* 1993) or *P. rugosus* (Cappetta, 1987). The massive root, narrower than the crown, is also similar to that of *Ptychodus.* We therefore include *Heteroptychodus* in the family Ptychodontidae, which thus comprises two

genera: *Heteroptychodus* and *Ptychodus,* as *Hylaeobatis* is now considered better included in the family Lonchidiidae (Batchelor & Ward, 1990; Rees & Underwood, 2002).

The teeth of the juveniles are more reminiscent of the ornamentation pattern of *Ptychodus* showing well-separated longitudinal ridges devoid of secondary ridges although the marginal area is still very reduced. The main difference however is the presence of one cusp on each of the ridges. However, if we compare with modern sharks possessing a grinding dentition, Reif (1976) has documented that the juveniles of the modern *Heterodontus* show a dentition that is not as grinding as that of the adult. It is therefore reasonable to think that this may have also been true of some Mesozoic hybodonts, although similar cusps, to the best of the knowledge of the authors, have never been reported in the genus *Ptychodus.* The presence of secondary ridges in *Heteroptychodus* appears to be size-related as labial ones are present only in the largest teeth. Their absence on juvenile teeth is therefore not surprising. The attribution of TF 7655 and similar teeth to a juvenile *Heteroptychodus,* which must be considered tentative, relies therefore on the hypothesis that their diet was different from that of the adults, and the fact that the ornamentation is made of parallel longitudinal ridges with a reduced marginal area.

Family: *incertae sedis*

New genus and species #2

Material: 18 teeth including TF 7657. One tooth (TF 7660) has been embedded in resin and cut for SEM study.

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

In apical view, the crown is broadly rectangular with a slightly convex labial outline and a slightly concave lingual one. In TF 7657, the best-preserved tooth, the crown is 5 mm mesio-distally and 4 mm labio-lingually. The largest complete crown is 9 mm mesio-distally and 5 mm labio-lingually. There is a blunt cusp on the labial side that is almost as wide as the crown (Fig. 4G, I). The crown is ornamented with a dense pattern of primary anastomosed ridges originating from the longitudinal crest. These primary ridges attain the base of the crown. On large unworn teeth, there are short secondary ridges originating from both sides of the primary ridges on most of their length. In mesial or distal view, the labial face is slightly convex while the lingual face is strongly concave and flared basally.

The root is preserved in two teeth, including TF 7657, and is one and a half to two times the height of the crown. It is perforated by a multitude of randomly distributed foramina. As in *Hybodus* sp. A, *Heteroptychodus steinmanni* and genus #3, there is a rather irregular basal row of enlarged foramina, the central one always being the largest (Fig. 4H). The basal face is rectangular in shape and flat. The root is oriented lingually, with a convex labial face and a concave lingual face. The crown slightly overhangs the root lingually.

Histology

The microstructure is very similar to that of *Heteroptychodus steinmanni*, showing osteodont teeth, with 'tubular' dentine, covered by a thin single-layered enameloid (Fig. 2D).

Discussion

These teeth share with *Thaiodus ruchae* and genus #1 a convex labial face and a concave, basally flared lingual face, a character that would again suggest they belong to the family Steinbachodontidae. They are easily distinguished from the two previous taxa by a strong ornamentation and teeth that are moderately elongated mesio-distally. When compared with the Steinbachodontidae however, genus #2 shows some important differences in the root morphology, which is well developed, contrary to that of Steinbachodontidae, and shows a basal row of enlarged foramina, absent in Steinbachodontidae. According to the small number of teeth available and their rather poor preservation, the heterodonty of this species cannot be assessed. Therefore, the phylogenetic relationships of genus #2 are rather difficult to ascertain, and we prefer to leave this genus in open nomenclature for the time being.

New genus and species #3

Material: 10 teeth, including TF 7651-54.

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

Seven teeth (including TF 7651 and TF 7652) have a rectangular outline in apical view, being mesio-distally longer than labio-lingually wide, while three are parallelogram-shaped (including TF 7653 and TF 7654) with a tendency to be wider than long. All teeth possess a single blunt, low cusp. The largest crown (TF 7652) is 6 mm mesio-distally and 4 mm labio-lingually, and shows a heavily worn central cusp with an almost circular cross-section. All crowns are ornamented with a dense pattern of radiating, often anastomosing ridges. The ridges all originate from the

longitudinal crest and attain the base of the crown. The longitudinal crest is not very well developed. On the lingual side of the cusp, in some teeth, as in TF 7651, one or two pairs of ridges become parallel to the longitudinal crest (Fig. 4J). In labial and lingual view, the base of the crown is arched (Fig. 4K).

The roots of two teeth (TF 7653 and TF 7654) have been preserved, although only one is complete. The basal face of the complete root (TF 7653) is flat and rectangular, wider than long, while the crown is parallelogram-shaped. The surface of the basal face of the root is smaller than that of the crown. The root is twice as high as the crown and is perforated by a multitude of foramina on all faces, as in *Hybodus* sp. A, *Heteroptychodus steinmanni* and genus #2. There is a basal row of four enlarged foramina crossing the root labio-lingually (Fig. 4L).

Discussion

With only ten teeth at hand and no precise idea about the heterodonty pattern, the affinities of this new genus are rather difficult to decipher. Several characteristics recall the teeth of *Heteroptychodus:* the parallelogram to rectangular shape of the crown with a very high root showing a row of basal enlarged foramina, the basal surface of the root smaller than that of the crown, the presence of some ridges parallel to the longitudinal crest, and a crown which is arched in lingual and labial view. However, the small number of teeth currently available makes the hypothesis of a relationship with *Heteroptychodus* difficult to ascertain. On the other hand, similarities in root morphology (Compare fig. 4H and L) may indicate that genus #2 and #3 are closer to each other than to *Heteroptychodus.* Pending the discovery of more material, we therefore prefer to leave this genus in open nomenclature.

4. Discussion and conclusion

The Khorat plateau has yielded a rich hybodont shark fauna, although it was deposited in a nonmarine environment. The diversity seems to increase from the uppermost Jurassic Phu Kradung Formation to the Aptian Khok Kruat Formation, although it should be mentionned that two new taxa of Lonchidiidae, not yet described, have been found in the Sao Khua Formation. One belongs to the genus *Lonchidion,* while the other one seems to represent a new genus. For the time being, we have thus 2 taxa in the Phu Kradung Formation, 4 in the Sao Khua Formation, and 6 in the Khok Kruat Formation.

The Thai hybodonts display a wide range of possible diets according to their dentition. *Hybodus* spp. and genus #2 were probably opportunistic feeders while the grinding dentition of *Acrodus, Heteroptychodus,* genus #1, and genus #3 indicate more durophagous sharks. Finally, the

cutting dentition of *Thaiodus* suggests a diet mainly consisting of large, soft-bodied preys. These sharks thus represented an important and diverse component of the freshwater ecosystems of the Khorat Plateau.

Genera #1, #2, and #3 are so far endemic to the Khorat Plateau and likely to have been infeoded to freshwaters, hence their endemism. *Hybodus* and *Acrodus* possess a worldwide distribution, but the exact affinities of the Thai material appear unclear due to a lack of material, except for *Hybodus* sp. A, which clearly belong to a new species that appears again to be endemic to the Khorat Plateau. *Thaiodus* on the other hand is known both from the Khorat Plateau and Tibet, where it has been found in a deltaic environment (Cappetta *et al.,* 1990). This shark was therefore able to tolerate some changes in salinity. Finally, *Heteroptychodus* has the largest distribution, having been recorded in Thailand, Japan, Kirghisia, and Mongolia (Yabe & Obata, 1930; Nessov, 1997; Tanimoto & Tanaka, 1998). The palaeobiogeographic distribution of the two latter taxa is difficult to explain if we consider these sharks as strictly confined to freshwaters. However, Maisey (1989) suggested that many hybodont genera (*Hamiltonichthys, Hybodus, Lissodus)* were in fact euryhaline. Such a mode of life would explain the distribution of *Heteroptychodus* and *Thaiodus* around the Asian continent, as it would explain how these hybodonts were able to follow the coastline to invade several freshwater systems. A similar strategy is seen today among the sawfish *Pristis perotteti*, which has colonized several lakes along the Atlantic coast of Central and South America (Thorson, 1982). Following a similar pattern, the spreading of *Thaiodus* and *Heteroptychodus-Asiadontus* would have been favoured by the Late Aptian sea transgression (Averianov & Skutschas, 2000). However, as these sharks are unknown outside Asia, they were probably unable to face open water.

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