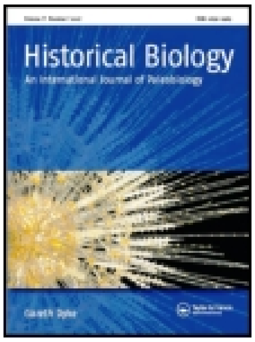

Historical Biology

Taylor & Francis
Taylor & Francis Group

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: http://www.tandfonline.com/loi/ghbi20

Early Middle Jurassic vertebrate microremains from the Three Gorges area, southern China

Qinghua Shang , Gilles Cuny & Lide Chen

Historical Biology
Vol. 20, No. 2, June 2008, 87–99

Taylor & Francis
Taylor & Francis Group

ARTICLES

Early Middle Jurassic vertebrate microremains from the Three Gorges area, southern China

Qinghua Shang[a]*, Gilles Cuny[b] and Lide Chen[c]

[a]*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, People's Republic of China;* [b]*Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark;* [c]*Yichang Institute of Geology and Mineral Resources, Yichang, People's Republic of China*

Vertebrate microremains were collected from the Middle Jurassic freshwater deposits of the Lower Member of the Xietan Formation in the Three Gorges area, Hubei Province, People's Republic of China. They include remains of hybodont sharks (*Hybodus* aff. "*H.*" *parvidens, Hybodus* sp., cf. *Parvodus* sp., *Polyacrodus* sp. and *Hubeiodus ziguiensis* gen. et sp. nov.), an actinopterygian fish, and a crocodyliform. The diversity of hybodont sharks in the Xietan Formation and the appearance of a peculiar pattern of tooth morphology in *Hubeiodus ziguiensis* suggest the adaptive radiation of these sharks in freshwater systems in China during the Middle Jurassic. This diversification led to the rich endemic hybodont faunas of the Lower Cretaceous in Asia.

Keywords: Actinopterygii; China; Crocodylomorpha; Elasmobranchii; Middle Jurassic; Three Gorges

Introduction

The Jurassic fossil record of sharks include neoselachians and hybodonts (Cappetta 1987). However, the Jurassic elasmobranch fossil record of China consists only of freshwater hybodonts and is completely devoid of neoselachians (Young 1941, 1942; Liu 1962; Wang 1977; Xue 1980; Lu et al. 2005). These hybodont faunas in China are represented only by isolated teeth and fin-spines and show low diversity and low abundance.

A new collecting effort was carried out in the Lower–Middle Jurassic beds from the Three Gorges area of southern China (Figure 1). It resulted in the discovery of many vertebrate microremains. The purpose of this paper is to describe these remains, which consist of hybodont, actinopterygian and crocodyliform teeth, and to discuss their biostratigraphic, palaeoecological, and palaeobiogeographic significance.

Geological setting

During the Early–Middle Jurassic, the vast Chinese hinterland was covered with regional-scale lakes and intramountainous basins where non-marine sediments were deposited (Chen 2003). The Three Gorges area is situated in western Hubei Province and comprises the northeastern margin of the ancient Chuan-Dian Lake. The Lower and Middle Jurassic strata in this region consist of the coal-bearing Xiangxi Formation (150–200 m), variegated mudstones and siltstones of the Xietan Formation (350 m) and red beds of the Chenjiawan (760 m) and Shaximiao (> 1000 m) Formations (Figure 2). These formations contain abundant fossil plants and bivalves and represent alternating sequences of fluvial and lacustrine deposits (Meng and Li 2004).

The vertebrate microremains described in this paper are all derived from the Xietan Formation. Well exposed outcrops of this formation, characteristic of a lacustrine system, mainly occur in the Zigui area of the eastern Three Gorges. According to Meng and Zhang (1987), two unnamed members can be distinguished within this formation corresponding to different depositional cycles. The Lower Member is about 150 m thick and further subdivided lithologically into two parts. The lower part is mainly composed of mudstone, siltstone and quartz sandstone, intercalated with thin coal seams and carbonaceous shale; whereas the upper part consists largely of calcareous siltstone and calcareous mudstone, intercalated with minor shelly limestone. The Upper Member is about 200 m thick and composed of mudstone, siltstone and fine-grained quartz sandstone, occasionally intercalated with shelly limestone. The Xietan Formation yielded a rich fauna of bivalves (Yu 1987), many palynomorphs (Chen and Zhang 2002), and some fossil plants (Meng 1987). This paper adds vertebrate microremains to this list.

*Corresponding author. Email: shangqinghua@ivpp.ac.cn

ISSN 0891-2963 print/ISSN 1029-2381 online

DOI: 10.1080/08912960701616935
http://www.informaworld.com

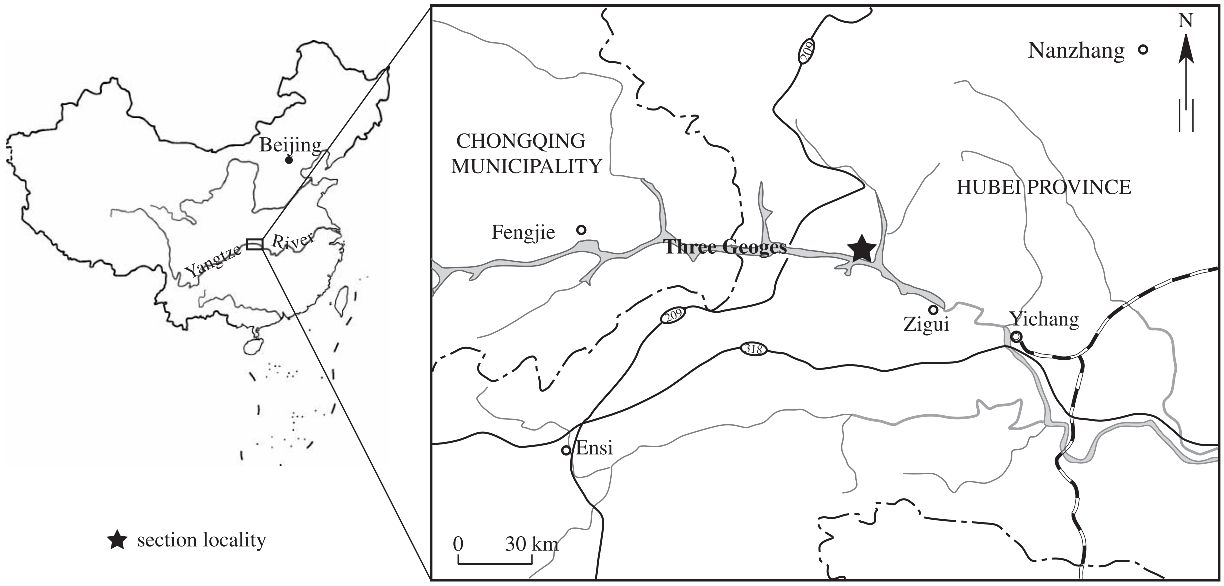

Figure 1. Regional map showing the locality where the section of the Xietan formation was investigated.

Material and methods

The vertebrate material was extracted from two lenticular calcareous siltstone beds, here referred to as Beds 1 and 2, at the top of the Lower Member of the Xietan Formation (Figure 3). These strata are exposed along a road following the north side of the Yantze River. The vertebrate microremains were first found by one of us (L.C.) and then systematic collection and sampling were organised by Q.S. in the autumn of 2005. Samples of 50 kg were screen-washed from three calcareous

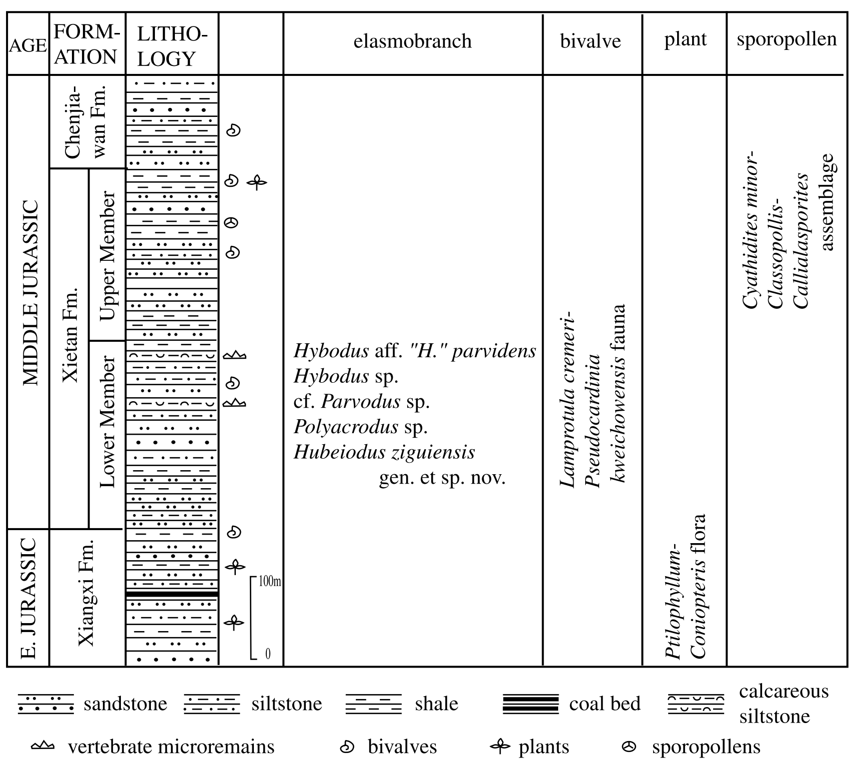

Figure 2. Stratigraphic column and palaeontological content of the early to middle Jurassic succession in the Zigui area in the Three Gorges.

Figure 3. Outcrops of the calcareous siltstone of Xietan formation (left: Bed 1, right: Bed 2). The arrows indicate the fossiliferous layers.

siltstone lenses, up to 20 cm thick, but only two yielded vertebrate microremains.

Quite diverse and abundant teeth have been obtained, but many are broken and lack their root. Breakage is likely to be the result of acid preparation and screen-washing of the sample. Apart from breakage, the teeth show no indication of abrasion, indicating a rather short transport before burial. All specimens described here are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China.

Systematic descriptions

Class: Chondrichthyes Huxley 1880
Subclass: Elasmobranchii Bonaparte, 1838
Order: Hybodontiformes Maisey, 1987
Family: Hybodontidae Owen, 1846
Subfamily: Hybodontinae Owen, 1846 *sensu* Maisey, 1989
Genus: *Hybodus* Agassiz, 1836
Hybodus aff. "*H.*" *parvidens* Woodward, 1916
(Plate 1 Figures 1–2)

Material

IVPP V15133, one tooth from Bed 2.

Description

The tooth is 1.9 mm long mesio-distally and 1.2 mm high. The main cusp is slightly bent distally and is flanked by three pairs of lateral cusplets. The distal set of lateral cusplets has been broken during micrographic mounting but has been kept separately. The lateral cusplets show a regular decrease of their height, each being half the height of the preceding pair. The third pair is very reduced and protrude from the mesial and distal extremities of the crown, giving them a hook-like shape. The longitudinal crest is well developed, without interruption between the cusps and cusplets. On the labial face, the main cusp is ornamented by four ridges, the two central reaching the apex of the cusp, whereas one bifurcates basally. The basal part of the main cusp is broken, but it is likely that there was a labial node (*sensu* Duffin 1993) there. The first and second lateral cusplets show a single ridge reaching the apex and bifurcating basally on the first cusplet. The ridge does not reach the base of the crown, leaving a smooth shoulder at its base. The lingual face shows two to three ridges on each cusp and cusplets, except the third one, which sometimes bifurcate basally. They do not reach the crown base.

The root is slightly projected lingually. The labial face is shallow, representing a fifth of the height of the main cusp, and shows a row of large, irregular foramina at its mid-height. The lingual face is less shallow than the labial face and shows two rows of large, irregular foramina.

Discussion

IVPP V15133 differs from all other *Hybodus* teeth described here in lacking a gap between the main cusp and the lateral cusplets. Xue (1980) erected the species *H. clavus* from the Yaojie Formation (Middle Jurassic) in Gansu Province. Teeth of this taxon show more developed ornamentation than IVPP V15133. However, the teeth described by Xue (1980) probably belong to two different species (see discussion below). Xue (1980) also mentioned the presence of *H. antingensis* in the Middle Jurassic Anding Formation in Shan'Xi Province. Xue's (1980, Figure 4) specimen possesses however a more robust main cusp than IVPP V15133. *H. antingensis* was first described by Liu (1962) from the same formation, but the tooth figured by Liu (1962, Figure 1) shows an ornamentation reaching the base of the crown, whereas this is not the case on the tooth figured by Xue (1980). One may therefore question whether these two teeth belong to the same species, and how *H. antingensis*

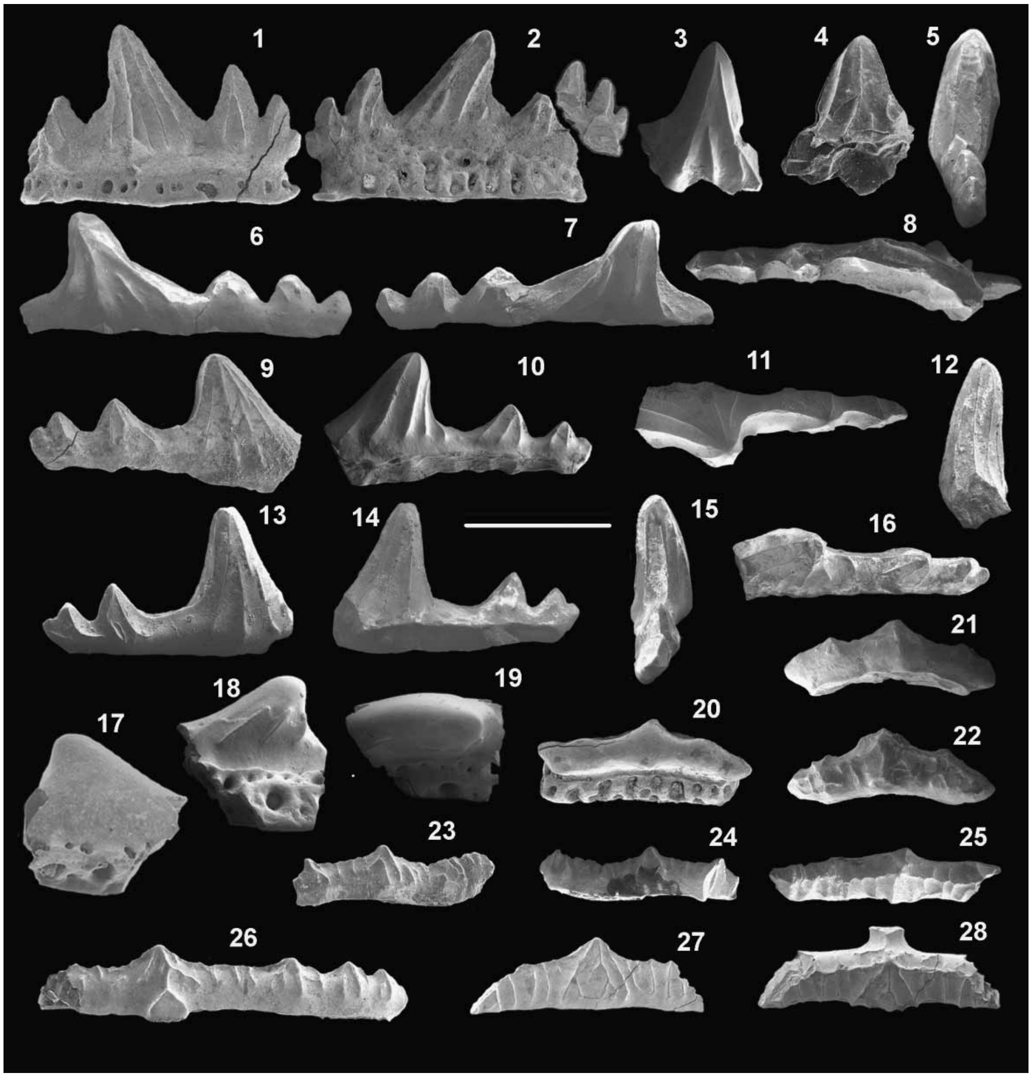

Plate 1. Figures 1–2 *Hybodus* aff. *H. parvidens* IVPP V15133: 1-labial view, 2-lingual view; Figures 3–19 *Hybodus* sp. 3–4 IVPP V15134.1: 3-labial view, 4-lingual view; 5–8 IVPPV15135: 5-distal view, 6-labial view, 7-lingual-apical view, 8-apical view; 9–11 IVPP V15136: 9-labial view, 10-lingual view, 11-apical view; 12–16 IVPP V15137: 12-distal view, 13-labial view, 14-lingual view, 15-mesial view, 16-apical view; 17–19 IVPP V15134: 17-labial view, 18-lingual view, 19-apical view; Figures 20–22 cf. *Parvodus* sp. 20 IVPP V15139 – lingual view, 21–22 IVPP V15138: 21-labial view, 22-apical view; Figures 23–28 *Polyacrodus* sp. 23–25 IVPP V15141: 23-labial view, 24 lingual view, 25-apical view; 26–28 IVPP V15140, X22 (part was broken between picture 27 and 28 during SEM preparation): 26-labial view, 27 lingual view, 28-apical view; scale bar = 1 mm.

is related to *H. clavus*. It should also be noted that the tooth described by Wang (1977) as *H. huangnidanensis* is nearly identical to the holotype of *H. antingensis.* However, the tooth described by Wang (1977) measures 10 mm mesiodistally, although one set of lateral cusplet is lacking, while the tooth described by Liu (1962) is only 7 mm mesiodistally. The former also possess a higher main cusp than the latter (pers. obs.). It is thus quite probable that the tooth described by Wang (1977) is an anterior tooth belonging to a rather large individual, whereas the tooth described by Liu (1962) is a more posterior tooth belonging to a smaller individual. We therefore propose *H. huangnidanensis* as a junior synonym of *H. antingensis*, and note that IVPP V15133 can be assigned to neither *H. clavus* nor *H. antingensis.*

Hybodus songaensis from the Late Jurassic–Early Cretaceous of Congo possesses a labial ornamentation that is less developed than on IVPP V15133 (Saint-Seine and Casier 1962). *Hybodus delabechei, H. reticulatus, H.* ?*cloacinus* and *H. hauffianus* from the Lower Jurassic of Europe possess on the contrary a much denser ornamentation than IVPP V15133 (Casier 1959; Maisey 1987; Duffin 1993, 1997; Rees 1998). Teeth of *H. medius* possess a more robust main cusp than IVPP V15133 (Woodward 1889; Duffin 1993), whereas teeth of *H. raricostatus* are more elongated mesiodistally than

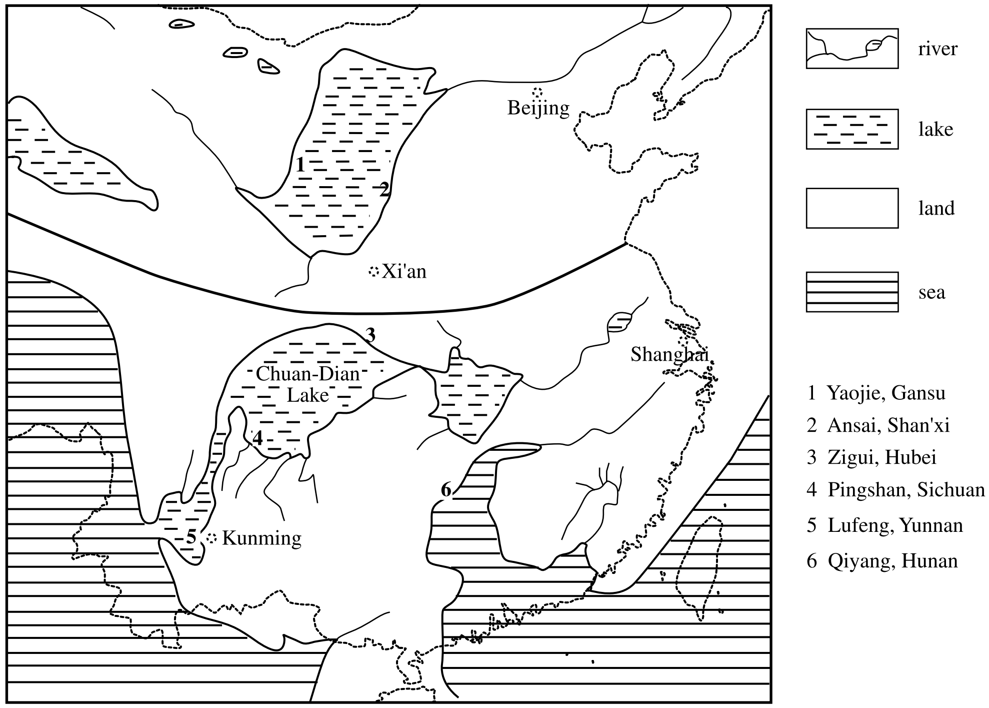

Figure 4. Map showing the palaeogeography (modified after Chen, 2003) and the *Hybodont* shark localities of middle Jurassic in Southern and Central China. The dotted line oulines the recent geography of southern and central China.

IVPP V15133, possessing four to eight pairs of lateral cusplets (Duffin 1993).

Contrary to what can be seen on IVPP V15133, the ornamentation of the teeth of *H. grossiconus* and *H. obtusus* from the Middle–Upper Jurassic of Europe and of those of *Egertonodus basanus* from the Lower Cretaceous of Europe and Morocco does not reach the apex of the main cusp (Agassiz 1836; Woodward 1889; Maisey 1983; Duffin and Sigogneau-Russell 1993). IVPP V15133 seems more similar to those of *"Hybodus" parvidens*, sharing its sparse and branching ornamentation (Patterson 1966; Rees 2002; Underwood and Rees 2002). However, as the basal part of the main cusp is broken, it is difficult to say if IVPP V15133 possesses a keel like the tooth of *"H." parvidens*. The lateral cusplets are also unusually large for *"H." parvidens* (Patterson 1966; Rees 2002; Underwood and Rees 2002). This species has been variously attributed to the genus *Hybodus* (Patterson 1966; Rees 2002) or *Polyacrodus* (Underwood and Rees 2002), highlighting the need for a revision of these two genera. Because of its high-crowned teeth and the lack of a pyramidal main cusp, we consider this species phylogenetically closer to *Hybodus* than to *Polyacrodus*, although it could as well belong to a different, new taxon. Nevertheless, IVPP V15133 is more similar to *"H." parvidens* than to any other Jurassic hybodont species. However, its small size may indicate that it comes from a juvenile, making comparisons even more difficult. More material is needed in order to decipher its exact relationships.

Hybodus sp.
(Plate 1 Figures 3–19)

Material

74 incomplete teeth from Bed 1, including IVPP V15136, V15137, and V15137.1-V15137.72; 92 incomplete teeth from Bed 2, including IVPP V15134, IVPP V15134.1, V15135 and V15135.1-V15135.89.

Description

All specimens of this taxon in our sample are incomplete. The largest tooth (IVPP V15135) does not exceed 2.5 mm mesiodistally and 1 mm in height. The largest isolated cusp (IVPP V15137.1) reaches 2 mm in height. All teeth show numerous well-developed ridges. In labial view, each cusp has between one and eight ridges, whereas there are two to seven ridges on the lingual face. These ridges reach the apex of the cusp where a basal protuberance may be present on the labial median ridge. Branching of the ridges is observed only in the lower half of the cusp, but does not occur in every tooth. The cutting edge is moderately developed and reaches the base of each cusp. The cusps are slightly compressed labio-lingually, with a labial face more convex than the lingual face (the smaller the cusp, the less compressed they are). No more than three pairs of lateral cusplets are present in our samples. The first pair of lateral cusplets is widely separated from the main cusp, but the cutting edge shows no interruption in between. The first pair of cusplets is up to two third the height of the main cusp. The second and third pairs of cusplets are set closely to the first pair, their height decreasing regularly.

IVPP V15134.1, which preserves a main cusp and a lateral cusp widely separated from each other, shows an ornamentation pattern different from the teeth described above (note: the lateral cusplet was not photographed, because they are broken and lost during preparation). In lingual and labial views, both the main cusp and the lateral cusplet show a single ridge reaching the apex of the cusp. In addition, there are four short ridges on the basal part of the labial face, and one on the lingual face. Such short basal ridges were not observed in any of the remaining 73 teeth from Bed 1.

Two isolated cusps (IVPP V15134, IVPP V15137.2) preserve part of their root. It is projected lingually almost perpendicular to the axis of the crown. The labial face shows a row of small foramina, and the lingual face a row of large foramina. In IVPP V15134, there is a row of small foramina on top of the basal row of large ones. In basal view, there is a wide labial groove with numerous large foramina.

Discussion

As only one tooth out of 165 displays a different pattern of ornamentation, whereas showing the same general morphology, it is rather unlikely it represents a separate species. It more probably is an abnormal tooth, which perhaps has experienced growth problem after the shark was injured.

The most striking feature of all these incomplete teeth is the main cusp widely separated from the first pair of lateral cusplets. One of the *Hybodus clavus* teeth illustrated by Xue (1980, Figure 1d) displays a first pair of cusplets widely separated from the main cusp like in our sample. To the best of our knowledge, no other *Hybodus* species displays such a gap between the main cusp and the rest of the lateral cusplets. Xue's (1980) specimen is approximately 9 mm mesio-distally, whereas our specimens do not apparently exceed 5 mm mesio-distally possibly representing juvenile teeth. On the other hand, the other teeth illustrated by Xue (1980, Figures 1a–c, e–g) as belonging to *H. clavus* show a first pair of lateral cusplets close to the main cusp. It is therefore very probable that the material referred to as *H. clavus* by Xue (1980) encompasses at least two different species.

Because of the lack of complete teeth in our sample and the need for a comprehensive taxonomic review of Jurassic *Hybodus* species from China, we consider premature to assign our material to a specific species.

Family: Lonchidiidae Herman, 1977
Genus: *Parvodus* Rees & Underwood, 2002
cf. *Parvodus* sp.
(Plate 1 Figures 20–22)

Material

IVPP V15138, crown of posterior tooth from Bed 2; IVPP V15139, one nearly complete posterior tooth from Bed 2.

Description

IVPP V15138 measures 1.5 mm mesio-distally, 0.5 mm labio-lingually, and is 0.5 mm high. It is arched lingually in apical view, and shows a low, blunt main cusp flanked by a pair of lateral cusplets. The main cusp shows a well-developed labial peg as well as a smaller lingual one. The longitudinal crest is well developed. The crown is ornamented by sparse, irregular and branching ridges, but the ornamentation is denser on the labial face than on the lingual one. The ornamentation originates from the longitudinal crest, but does not reach the base of the crown, which is smooth. There is a strong constriction at the base of the crown at its mesial and distal extremity.

IVPP V15139 preserves a root with a crown that is similar to IVPP V15138: low, blunt main cusp flanked by a pair of lateral cusplets, with a well-developed labial peg and a smaller lingual one, and there is a strong constriction at the mesial and distal ends of the crown. However, the crown is smooth, without ornamentation. The root is projected lingually and shows large, irregular foramina.

Discussion

The presence of a well-developed labial peg and the pattern of ornamentation of the isolated crown is reminiscent of *Parvodus pattersoni* (Bathonian of Great-Britain, Duffin 1985; Rees and Underwood 2002) and *"Lissodus" multicuspidatus* (Kimmeridgian of Germany, Duffin and Thies 1997; Rees and Underwood 2002). The teeth of *"L." multicuspidatus* however show lateral cusplets with more pronounced labial nodes than in IVPP V15138. They also show lingual nodes, lacking on IVPP V15138. The latter appears more similar to the lateral tooth of *P. pattersoni* figured by Duffin (1985, Plates 7, Figure 1i–k), although the cusp and cusplets are lower and the labial peg less developed. The cusp and cusplets are however well demarcated, a character diagnostic of the genus *Parvodus* (Rees and Underwood 2002). The complete tooth is unusual for *Parvodus* in possessing a smooth crown, but as the crown pattern is very similar to that of the isolated crown, we tentatively assign them to the same genus. Two teeth are not sufficient to ascertain identification at a generic level. More material is needed to confirm the presence of *Parvodus* in the Xietan Formation, but it should be noted that the genus *Parvodus* has already been recorded in Asia in the Lower Cretaceous of Thailand (Cuny et al. 2006).

Family: Polyacrodontidae Gluckman, 1964
Genus: *Polyacrodus* Jaekel, 1889
Polyacrodus sp.
(Plate 1 Figures 23–28)

Material

Four teeth from Bed 1, including IVPP V15140, IVPP V15140.1-V15140.3; eight teeth from Bed 2, including IVPP V15141, IVPP V15141.1-IVPP V15141.7.

Description

Teeth of this taxon is characterised by their mesio-distally elongated shape and low cusp. The main cusp displays a labial peg at its base, and it is flanked by up to three pairs of lateral cusplets. The longitudinal crest of the crown is moderately developed, and densely branching ridges ornament the crown. The ridges originate from the longitudinal crest, giving to the latter a somewhat zigzag shape, but do not reach the base of the crown. On both the lingual and labial faces, the lower third of the crown is smooth.

Whereas the root is missing in all teeth due to damage, only one crown was complete, belonging to a posterior tooth (IVPP V15140). It showed a very low cusp displaced distally with a reduced labial peg. This crown measured 2.4 mm mesio-distally and 0.3 mm labio-lingually, but was damaged during SEM preparation.

Discussion

A labial peg is a feature that can be found in teeth of Lonchidiidae, *Polyacrodus* and *Hybodus* (Rees & Underwood, 2002). The mesio-distal elongation of the crown in our sample is not found among lonchidiid taxa and the cusp and cusplets are unusually low for a *Hybodus* tooth (Rees and Underwood 2002). In contrast, low cusps and mesiodistally elongated crown is found in *Polyacrodus,* such as *P. claveringensis* from the Lower Triassic of Greenland (Stensiö 1932). However, the rather poor quality of our sample does not allow meaningful comparisons to be made at species level.

Family *incertae sedis*
Genus: *Hubeiodus* nov. gen.

Derivation of name

From Hubei Province, where the specimens were found, and *odous*, tooth in Greek. Gender: masculine.

Type species

Hubeiodus ziguiensis nov. sp.

Diagnosis

Low crowned, flat teeth without cusp, showing at least two sharp mesio-distal crests. In addition of the main mesio-distal crests, crowns can also show a lingual and/or a labial row of tubercles, which can give an additional labial and/or lingual crest. The outline of the teeth in apical view is elliptical to quadrangular, with posterior teeth showing a labial protuberance. The root is quadrangular, which is as high as the crown, and is slightly projected lingually with a recess at mid-height on the labial side. Foramina are distributed randomly on the root surface but those in the lower part are larger than the upper part.

Hubeiodus ziguiensis gen. et sp. nov.
(Plates 2 Figures 1–4, 6–22, 26–27, 28–29)

Derivation of name

From Zigui, the locality where the specimens were found.

Holotype

IVPP V15142, a nearly complete anterolateral? tooth from Bed 2 (Plates 2 Figures 1–4).

Paratypes

IVPP V15143, V15146 – V15147 tooth crowns from Bed 1; IVPP V15144 – V 15145, V15148 tooth crowns from Bed 2.

Other material

21 teeth from Bed 1 (IVPP V15147.1-IVPP V15147.21); 10 teeth from Bed 2 (IVPP V15148.1-IVPP V15148.10).

Type locality

Approximately 1 km east of the town of Guizhou, Zigui County, Hubei Province, China.

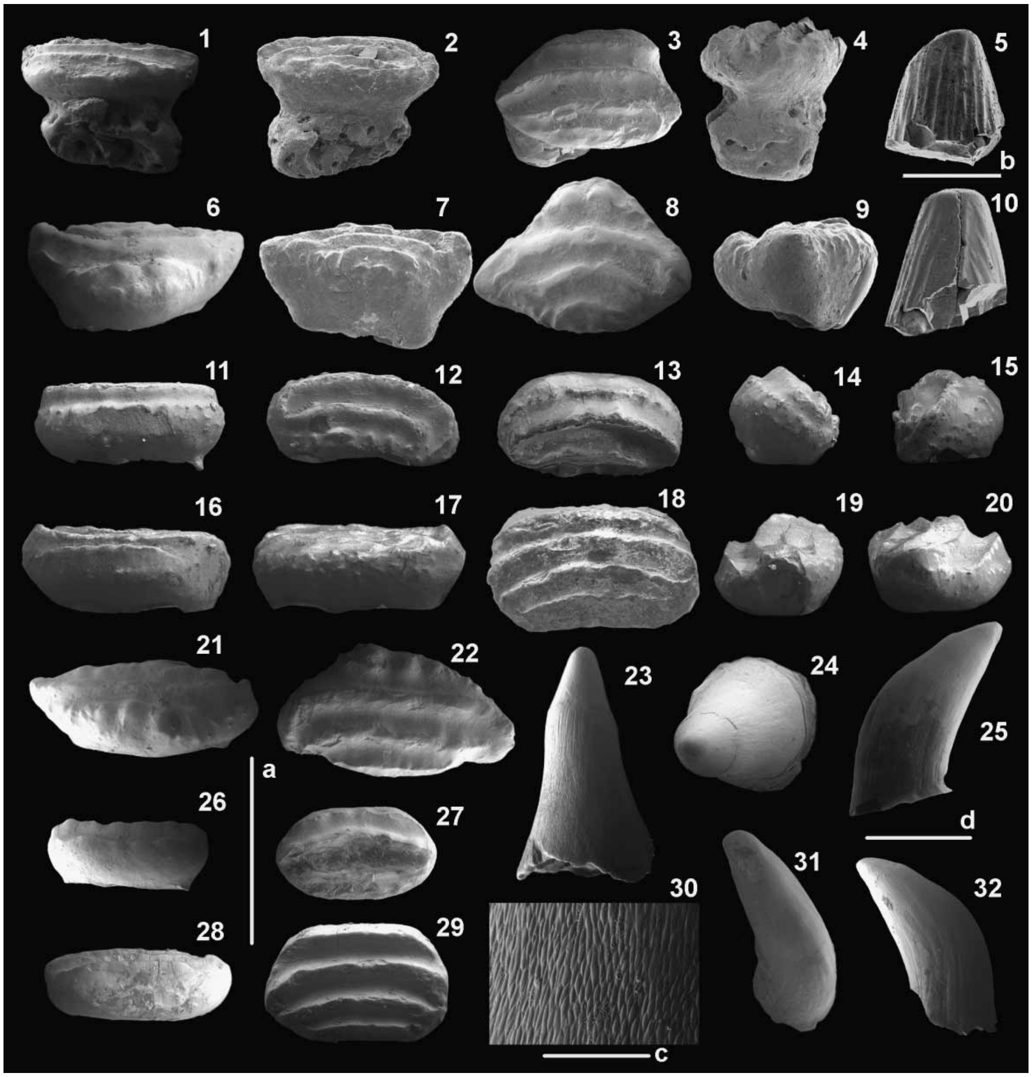

Plate 2. Figures 1–4, 6–22, 26–27, 28–29 *Hubeiodus ziguiensis* gen. et sp. nov. 1–4 IVPP V15142 (holotype): 1-labial view, 2-lingual view, 3-apical view, 4-lateral view; 6–9 IVPP V15143 (paratype): 6-labial view, 7-lingual view, 8-apical view, 9-lateral view; 11–15 IVPP V15144 (paratype): 11-labial view, 12-lingual view, 13-apical view, 14-lateral view (mesial?), 15-lateral view (distal?); 16–20 IVPP V15145 (paratype): 16-labial view, 17-lingual view, 18-apical view, 19-lateral view (mesial?), 20-lateral view (distal?); 21–22 IVPP V15146 (paratype): 21-labial view, 22-apical view; 26–27 IVPP V15147 (paratype): 26-labial view, 27-apical view; 28–29 IVPP V15148 (paratype): 28-labial view, 29-apical view; Scale bar a = 1 mm. Figures 5, 10 Indeterminate tooth of Crocodyliformes IVPP V15150: 5-lateral view, 10-antero-posterior view, scale bar b = 1 mm. Figures 23–24, 30 indeterminate tooth of actinopterygian IVPP V15149: 23-lateral view, 24-apical view, scale bar a = 1 mm; 30-enlarged surface ornamentation of the lower part of this specimen, scale bar c = 100 um. Figures 25, 31–32 Indeterminate tooth of actinopterygian in lateral views IVPP V15149.1, scale bar d = 1 mm.

Type stratum

Top of the Lower Member of the Xietan Formation, Middle Jurassic.

Diagnosis

Same as for genus.

Description

This taxon is characterised by their flat crown, absence of cusp, and the presence of two to four mesio-distal sharp crests. The largest tooth measures 2 mm mesio-distally and 1 mm labio-lingually. In apical view, teeth with two crests display an elliptical outline (e.g., IVPP V15144; Plate 2, Figure 13), whereas teeth with four crests display a quadrangular outline (e.g., IVPP V15148; Plate 2, Figure 29), but posterior teeth add a well-developed labial protuberance (Plate 2, Figures 6, 8). The pattern of ornamentation is rather variable. Some teeth show only two parallel, strong, sharp crests, which sometimes appear roughly serrated (Plate 2, Figures 11–15). Other teeth add a labial row of tubercles to these two main crests, and then a lingual row of tubercles, which gives an additional labial crest, and then an additional lingual crest. These labial and lingual crests are always shorter mesio-distally than the two main crests. When present, the labial crest develops on the labial protuberance (Plate 2, Figure 8). The largest tooth of the sample (IVPP V15146; Plate 2, Figures 21, 22) shows three crests and a lingual row of tubercles, whereas the holotype, which measures 1 mm mesio-distally and 0.7 mm labio-lingually, shows four crests. On anterior teeth (e.g., IVPP V15147; Plate 2, Figure 27), these crests appear roughly parallel to each other and to the mesiodistal axis of the crown, although the main crests are sometimes arched lingually at their mesial and distal extremities. On more posterior teeth, the crests can be more irregular in shape (e.g., IVPP V15144; Plate 2, Figure 12), almost zigzag shaped, or they can be arched lingually (e.g., IVPP V15143; Plate 2, Figure 8). The labial and lingual faces of the crown are ornamented by short vertical ridges and/or granulae (small, irregular elevations of the enameloid: Rees and Underwood 2002).

In basal view, the root insertion area of anterior teeth is elliptical in outline. In posterior teeth, the root insertion area is triangular, following the appearance of a labial protuberance on the crown. Two teeth from Bed 2, including the holotype and IVPP V15148.1 have their root preserved. The holotype shows a crown with a rectangular outline in apical view and four crests fully developed (Plate 2, Figures 1–4), whereas the other tooth has a damaged crown showing two serrated crests and a labial row of tubercles. The root is as high as the crown, slightly projected lingually, and shows a recess at mid-height in labial view. In labial or lingual view, the root has a quadrangular outline. The vascularisation system is made of large foramina in the basal part of the root, and smaller ones in the upper part, which are otherwise randomly distributed.

Discussion

The presence of a row of tubercles in labial and lingual positions and the serrated aspect of the crest when unworn strongly suggest that the formation of the crests is the result of the accretion of rows of tubercles. Our samples show teeth showing the following sequence: 1) teeth with only two crest, 2) teeth with two crests plus a row of labial tubercles, 3) teeth with two crests with a row of labial and lingual tubercles, 4) teeth with three crests and a row of lingual tubercles, and 5) teeth with four crests. It seems thus that the teeth add the labial row of tubercles or crest before the formation of the lingual one. Teeth with rows of tubercles might thus belong to younger specimens than teeth possessing four fully formed crests, although there is no significant size differences between the different kind of teeth. This could therefore also be related to monognathic or dignathic heterodonty as the largest tooth in our sample has three crests and a row of lingual tubercles, whereas the smaller holotype possess four crests. Another possibility would be that the presence of row of tubercles rather than crests is related to a sexual dimorphism. It is also possible that both ontogeny, heterodonty, and sexual dimoprhism play a role in the rather important variability observed among our sample, but the number of teeth available is not sufficient to actually test this kind of hypothesis.

The presence of more than two parallel longitudinal crests was hitherto quite rare in hybodont shark teeth. The condition is recorded so far in only three genera: *Ptychodus, Heteroptychodus*, and *Isanodus*, which the latter two are restricted to Asia. *Hubeiodus* shows heterodonty much different from that of *Isanodus,* and show a different ornamentation pattern (Cuny et al. 2006). *Hubeiodus* is also different from *Heteroptychodus* because its teeth lack a marginal area on the apical face of the crown, lack the numerous small ridges perpendicular to the main crests, and have an elliptical or triangular insertion area for the root, whereas it is quadrilateral in *Heteroptychodus*. Shape of the root insertion area and the lack of a marginal area on the crown allow also to easily differentiating *Hubeiodus* teeth from those of *Ptychodus* (Cuny et al. in press). Moreover, there is no indication that the crests are the result of the accretion of tubercles in any of the three aforementioned genera. The erection of a new genus is thus justified.

The assessment of the relationships among *Hubeiodus, Isanodus, Heteroptychodus*, and *Ptychodus* are difficult. The presence on their teeth of more than two parallel longitudinal crests and the fact that *Hubeiodus*, *Isanodus*, and *Heteroptychodus* are restricted to Asia suggest their close affinity. Moreover, the presence of a labial protuberance on posterior teeth is another shared characteristic between *Hubeiodus* and *Isanodus*. Cuny et al. (in press) proposed that *Isanodus, Heteroptychodus*, and *Ptychodus* are closely related to each other. *Hubeiodus* could thus be sister to the clade uniting these three genera, which would correspond well with their known stratigraphic distribution, *Hubeiodus* being restricted to the Middle Jurassic while *Heteroptychodus* and *Isanodus* do not appear before the latest Jurassic, and *Ptychodus* not before the Albian. It is also possible that *Hubeiodus* is sister to *Ptychodus* and that *Isanodus* is sister to *Heteroptychodus*, if the presence of a peculiar ornamentation pattern made of numerous small ridges perpendicular to the longitudinal crests is used to unite the latter two genera. If so, the loss of a labial protuberance in *Ptychodus* and *Heteroptychodus* would represent the result of a convergence because it is present in both *Isanodus* and *Hubeiodus*. However, such phylogenetic hypotheses are difficult to test based only on isolated teeth.

Class: Osteichthyes Huxley, 1880
Subclass: Actinopterygii Klein, 1885
Actinopterygii indet.
(Plate 2 Figures 23–25, 30–32)

Material

34 teeth from Bed 1, including IVPP V15149, IVPP V15149.2-IVPP V15149.33; 19 teeth from Bed 2, including IVPP V15149.1, IVPP V15149.34-IVPP V15149.52

Description

Teeth of this taxon are conical and exhibit a smooth acrodine cap representing up to 25% of the total crown height. Maximum height of these teeth does not exceed 2.5 mm. Most of them are upright, but the largest one from Bed 2 is bent distally like a hook (Plate 2, Figures 25, 31–32). The ganoine can be smooth or finely ornamented by irregular ridges (Plate 2, Figure 30).

Discussion

The tooth morphology of this taxon is simple, and the ornamentation pattern of the ganoine is widely distributed amongst the teeth of piscivorous palaeonisciforms and halecomorphs (Delsate et al. 2002). Thus, their exact taxonomic identification cannot be ascertained.

Class: Sauropsida Goodrich, 1916
Subclass: Diapsida Osborn, 1903
Infraclass: Archosauromorpha Huene, 1946
Subdivision: Crurotarsi Sereno & Arcucci, 1990
Superorder: Crocodylomorpha emend. Walker, 1968
Order: Crocodyliformes Hay, 1930
Crocodyliformes indet.
(Plate 2 Figures 5, 10)

Material

IVPP V15150, one fragmentary tooth from Bed 2.

Description

The specimen represents the apical part of a crown, which is conical, 1.2 mm in height, and 1 mm in preserved basal diameter It possesses moderately developed carinae, and the enameloid surface exhibits vertical ridges, more densely arranged on the labial side than on the lingual side.

Discussion

The specimen is too fragmentary that its taxonomic identity beyond Crocodyliformes cannot be ascertained.

Discussion

Biostratigraphy

The Xietan Formation, which yielded the vertebrate microremains described here, is dated as early Middle Jurassic based on bivalves, ostracods, palynomorphs, and a few plant fossils (Meng and Zhang 1987). The underlying Xiangxi Formation is a coal-bearing sequence, which can be widely correlated with other similar beds in southern China (Chen 2003). It yields a rich assemblage of plants, bivalves, and palynomorphs, all of which consistently suggest an Early Jurassic age. Chen and Zhang (2002) studied the palynomorphs from the Upper Member of the Xietan Formation and demonstrated its mid-Jurassic age based on the correlation with Middle Jurassic palynomorph assemblages from Great-Britain (Couper 1958). Based on the lithostratigraphy and distribution of fossil assemblages Meng and Li (2004) correlated the Lower-Middle Jurassic strata in the Three George region within the Chuan-Dian basin (Figure 4) and suggested that the Lower Member of the Xietan Formation is late Early Jurassic in age. However, revising the invertebrate fossils found in the type section, the senior author (Q.S.) found that the bivalves from the Lower Member of the Xietan Formation are very similar to those from the Upper Member. They include the non-marine genera *Pseudocardinia* and *Unio* and belong to the *Lamprotula* (*Eolamprotula*) *cremeri* – *Pseudocardinia kweichowensis* assemblage, which was widely distributed in the Middle Jurassic non-marine deposits of China (Gu 1982). Only a few fossil plants have been found from the Lower Member of the Xietan Formation, which include *Otozamites bengalensis*, *Ptilophyllum contiguum*, *Baiera furcata*, and *Sphenobaiera huangi*. These are common taxa in the Middle Jurassic of China (Meng and Zhang 1987).

Among the new discovered vertebrate microremains, *Hybodus* is well distributed worldwide from the Triassic up to the Cretaceous (Cappetta 1987). In the Jurassic of China, isolated teeth of Middle Jurassic *Hybodus* are known in northern China, such as from the Anding Formation in Shan'xi Province (Liu 1962) and Yaojie Formation in Gansu Province (Xue 1980), and in southern China, such as from the Tangjiawu Formation in Hunan Province (Wang 1977) and Laoluocun Formation in Yunnan Province (Lu et al. 2005). This genus is also known from the Early Triassic Luolou Formation in Guangxi Province in southern China (Wang et al. 2001) and Late Triassic Yanchang Formation in Shan'xi

Province in northern China (Liu 1962). Our specimens are similar to a *Hybodus* specimen found in the Middle Jurassic Yaojie Formation in Gansu (Xue 1980, Plate 1, 1d) by possessing lateral cusplets separated by a gap from the main cusp. *"Hybodus" parvidens* is only known from the Late Jurassic – Early Cretaceous interval in Europe (Rees 2002), which might suggest a younger age for our assemblage, but the tooth identified as *Hybodus* aff. *"H." parvidens* here (Plate 1, Figures 1–2) shows marked differences from typical European *"H." parvidens* teeth (see above), so its stratigraphic value is somewhat limited.

The taxon referred to cf. *Parvodus* here (Plate 1, Figures 18–20) is new to the fossil record of China. This genus is known with certainty from the Bathonian to the Valanginian, mainly in Europe, although it might have appeared as early as the Sinemurian (Rees and Underwood 2002). In addition a single ?*Parvodus* tooth was also found in the Yang Liu Jing Formation (Anisian, Guizhou Province, southern China) (Chen et al. in press).

Other taxa described here (*Hubeiodus ziguiensis, Polyacrodus* sp., Actinopterygii indet. and Crocodyliformes indet.) as well as other undescribed material (e.g., various shark dermal denticles) offer no useful stratigraphic information. Therefore, only the specimens of *Hybodus* sp. appear to confirm a Middle Jurassic age for the Lower Member of the Xietan Formation by correlation with the Yaojie Formation in Shan'xi Province.

Palaeoecology and palaeobiogeography

Meng and Zhang (1987) suggested that the depositional environment of the Xietan Formation was fluvial on the bivalves and plants. The occurrence of small freshwater hybodont teeth does not contradict this interpretation, (Cuny et al. in press). However, marine incursions were common during the Jurassic in the ancient Chuan-Dian Lake area in the Sichuang and Yunnan Provinces, and palaeogeographical reconstructions (Figure 4) show that this lake was connected with the Tethys ocean during the Early and Middle Jurassic. The sharks were therefore possibly euryhaline and anadromous.

In Sichuan Province, Middle Jurassic beds containing fish teeth and scales, which were deposited along the southern margin of the ancient Chuan-Dian Lake, have been recorded from the Shaximiao Formation but not yet studied in detail (BGMR-SP 1997). Middle Jurassic hybodonts also occur in the Laoluocun Formation in Lufeng and Kunming of Yunnan Province, which were situated in the southwest mouth area of the ancient Chuan-Dian Lake (Lu et al. 2005). Adding our new discovery to these shark faunas indicates the adaptive radiation of hybodont sharks in the Middle Jurassic freshwater system in southern China. The occurrence of *Hubeiodus ziguiensis* is consistent with this interpretation because of its unusual tooth pattern, which became widespread during the Lower Cretaceous in Asia as marked by the appearance of *Heteroptychodus* and *Isanodus* (Cuny et al. in press). The connection of the Chuan-Dian Lake with the Tethys also agrees with this interpretation that these sharks spread all around Asia following the coast-line (Cuny et al. 2006). It seems therefore that euryhaline hybodonts invaded many freshwater systems during the Jurassic and Cretaceous of Asia. They then underwent adaptive radiation leading to specialised durophagous sharks such as *Hubeiodus*, *Isanodus*, *Khoratodus*, and *Heteroptychodus*, but also unusual predators with cutting dentition such as *Thaiodus* from the Lower Cretaceous of Thai and Tibet (Cappetta et al. 1990). *Hubeiodus, Isanodus*, and *Heteroptychodus* are likely to share a common ancestry among lonchidiid sharks (Cuny et al. 2006). However, their exact phylogenetic relationships remain unknown, and we anticipate that more discoveries of fossil hybodont sharks on the Asian continent may shed some lights on their interrelationship.

Conclusions

The new hybodont shark fauna, containing *Hybodus* aff. "*H*." *parvidens*, *Hybodus* sp., cf. *Parvodus* sp., *Polyacrodus* sp. and a new taxon, *Hubeiodus ziguiensis*, does not contradict a deposition of this formation under freshwater conditions. Teeth similar to those of *Hybodus* sp. have so far only been found in the Middle Jurassic Yaojie Formation in Shan'xi Province, and none of the other hybodonts recovered from the Lower Member of the Xietan Formation contradicts a Middle Jurassic age for the latter Member. Along with the shark faunas described from the Lower Cretaceous of Thailand, Japan, Mongolia, and Khirghisia (Yabe and Obata 1930; Nessov 1997; Tanimoto and Tanaka 1998; Cappetta et al. 2006; Cuny et al. in press), this new fauna confirms a major adaptive radiation of freshwater hybodonts in Asia.

Acknowledgements

This study was financially supported by State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No. 063105) and by the Major Basic Research Projects (2006CB806400) of MOST (The Ministry of Science and Technology) of China. GC's work in China was made possible by a research grant from the Carlsberg Foundation. We also thank Jan Rees (University of Karlstad) for helpful discussions on some of the specimens described in this article. We are sincere thank to K. Shimada (DePaul University) for reviewing this manuscript, making helpful suggestions and clear-cut modifications.

References

Agassiz L. 1836. Recherches sur les poissons fossiles. In: Tome 3 contenant l'histoire de l'ordre des placoides. Neufchâtel (QU): Imprimerie de Petitpierre. 390 p.

Bonaparte CLJL. 1838. Selachorum tabula analytica. Nuovi Annali della Scienze. Naturali Bologna. 2(1):195–214.

Bureau of Geology and Mineral Resources of Sichuan Province (BGMR-SP). 1997. Stratigraphy (lithostratic) of Sichuan Province. Wuhan (China): China University of Geosciences Press. 417 p.

Cappetta H. 1987. Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii. In: Schultze H-P, editor. Handbook of paleoichthyology. Stuttgart (Germany): Gustav Fischer Verlag. 193 p.

Cappetta H, Buffetaut E, Cuny G, Suteethorn V. 2006. A new elasmobranch assemblage from the lower Cretaceous of Thailand. Palaeontology. 49(3):547–555.

Cappetta H, Buffetaut E, Suteethorn V. 1990. A new hybodont from the lower Cretaceous of Thailand. Neues Jahrb für Geol Paläontol Monatsh. 11:659–666.

Casier E. 1959. Contributions à l'étude des poissons fossiles de la Belgique – XII. Sélaciens et Holocéphales sinémuriens de la province de Luxembourg. Bull de l'Inst R des Sci Nat de Belg. 35:1–27.

Chen PJ. 2003. Jurassic biostratigraphy of China. In: Zhang WT, Chen PJ, Palmer AR, editors. Biostratigraphy of China. Beijing (China): Science Press. p. 423–464.

Chen L, Cuny G, Wang X. In press. The chondrichthyan fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China). Hist Biol. 19(4):291–300.

Chen HM, Zhang ZL. 2002. Sporopollen assemblage of the Middle Jurassic Xietan formation in the Zigui basin, Hubei. Acta Microplalaeontol Sin. 19(3):301–308 (Chinese with English abstract).

Couper RA. 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. Palaeontographica B. 103(4–6):75–179.

Cuny G, Suteethorn V, Kamha S, Buffetaut E. In press. Hybodont sharks from the lower Cretaceous Khok Kraut formation of Thailand and hybodont diversity during the early Cretaceous. In: Cavin L, Longbottom A, Richter M, editors. Fishes and the break-up of Pangea. London (UK): Geological Society Special Publication.

Cuny G, Suteethorn V, Kamha S, Buffetaut E, Philippe M. 2006. A new hybodont shark assemblage from the lower Cretaceous of Thailand. Hist Biol. 18(1):21–31.

Delsate D, Duffin CJ, Weis R. 2002. A new microvertebrate fauna from the Middle Hettangian (early Jurassic) of Fontenoille (Province of Luxembourg, South Belgium). Memoirs Geol Surv Belgium. 48:1–84.

Duffin CJ. 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935). Palaeontographica, A. 188:105–152.

Duffin CJ. 1993. Teeth of *Hybodus* (Selachii) from the early Jurassic of Lyme Regis, Dorset (southern England): preliminary notes. Belgain Geol Surv, Professional Paper. 264:45–52.

Duffin CJ. 1997. The dentition of *Hybodus hauffianus* Fraas, 1895 (Toarcian, early Jurassic). Stuttg Beiträge zur Naturkunde Ser B (Geol und Paläontol). 256:1–22.

Duffin CJ, Sigogneau-Russell D. 1993. Fossil shark teeth from the early Cretaceous of Anoual, Morocco. Belgian Geol Surv, Professional Paper. 264:175–190.

Duffin CJ, Thies D. 1997. Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. Geol et Palaeontol. 31: 235–256.

Gluckman LS. 1964. Class Chondrichthyes, subclass Elasmobranchii. In: Obruchev DV, editor. Fundamentals of Paleontology. Acad. Nauk SSSR. 11:196–237 (In Russian).

Goodrich ES. 1916. On the classification of the Reptilia. Proc R Soc Lond B. 89:261–276.

Gu ZW. 1982. Distribution and development of nonmarine Mesozoic bivalves and formations in China. Sci Sin Ser B. 25(4):438–452.

Hay OP. 1930. Second bibliography and catalogue of the Fossil Vertebrata of North America, Vol. 2. Carnegie Institution of Washington, Washington D.C. 390(2):1–1074

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 des Cartes géologiques et minières de la Belg. 15(1975):1–450.

Huene F von. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. Biol Zentralbl. 65:268–275.

Huxley TH. 1880. 1. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proc Zool Soc. 1880:649–662.

Jaekel O. 1889. Die Selachier aus dem oberen Muschelkalk Lothringens. Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen. 3(4):274–332.

Klein EF. 1885. Beiträge zur Bildung des Schädels den Knochenfische, 2. Jahreshefte Vereins Vaterlandischer Naturkunde Würtenberg. 42:205–300.

Liu XT. 1962. Two new *Hybodus* from north Shensi, China. Vertebr PalaAsiatica. 6(2):150–156 (in Chinese with English summary).

Lu LW, Jin YG, Fang XS. 2005. A revision of Middle Jurassic *Hybodus houtienensis* Young (Chondrichthyes: Hybodontidae) from Yunnan. Geol Bull China. 24(2):145–148 (in Chinese with English summary).

Maisey JG. 1983. Cranial anatomy of *Hybodus basanus* Egerton from the lower Cretaceous of England. Am Museum Novitates. 2758:1–64.

Maisey JG. 1987. Cranial anatomy of the lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. Am Museum Novitates. 2878:1–93.

Maisey JG. 1989. *Hamiltonichthys mapesi*, g. and sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. Am Museum Novitates. 2931:1–42.

Meng FS. 1987. Fossil plants. In: Zhang ZL, Meng FS, editors. Biostratigraphy in the Eastern Yangtze Gorges (4), the Triassic – Jurassic fascicle. Beijing (China): Geological Publishing House. p. 239–257 (in Chinese).

Meng FS, Li XB. 2004. Correlation of the Early-Middle Jurassic strata in the Three Gorges area and discussion of sedimentary environments. Geol Min Res South China. 3:56–66 (Chinese with English abstract).

Meng FS, Zhang ZL. 1987. The Jurassic series. In: Zheng ZL, Meng FS, editors. Biostratigraphy in the Eastern Yangtze Gorges (4), the Triassic – Jurassic fascicle. Beijing (China): Geological Publishing House. p. 91–148 (in Chinese with English summary).

Nessov LA. 1997. Cretaceous Nonmarine vertebrates of Northern Eurasia. Saint Petersburg (Russia): Institute of Earth Crust, University of Saint Petersburg Press. 218 p.

Osborn HF. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Memoirs Am Museum Nat Hist. 1:449–507.

Owen R. 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. London (UK): Longman, Brown, Green, and Longmans. 308 p.

Patterson C. 1966. British Wealden sharks. Bull Br Museum (Nat Hist), Geol. 11(7):281–350.

Rees J. 1998. Early Jurassic selachians from the Hasle formation on Bornholm, Denmark. Acta Palaeontol Polonica. 43:439–452.

Rees J. 2002. Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden. Trans R Soc Edinb: Earth Sci. 93:59–71.

Rees J, Underwood CJ. 2002. The status of the shark genus *Lissodus* Brough 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (selachii). J Vertebr Paleontol. 22(3):471–479.

Saint-Seine P, Casier E. 1962. Poissons fossiles des couches de Stanleyville (Congo). Deuxième partie, La faune marine des calcaires de Songa. Musée royal de l'Afrique Centrale – Tervuren. Annales, Série in 8 – Sciences géologiques. 44:1–51.

Sereno PC, Arcucci AB. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. Neues Jahrb für Geol Paläontol Abhandlungen. 180:21–52.

Stensiö E. 1932. Triassic fishes from East Greenland collected by the Danish expeditions in 1929–1931. Meddelelser om Grønland. 83:1–305.

Tanimoto M, Tanaka S. 1998. *Heteroptychodus* sp. (Chondrichthyes) from the Lower Cretaceous Matsuo Group of Arashima, Toba city, Mie Prefecture, Southwest Japan. Chigakukenkyu. 47(1):37–40.

Underwood CJ, Rees J. 2002. Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England. Special Papers. Paaleontol. 68:83–101.

Walker AD. 1968. *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodiles. Geol Mag. 105:1–14.

Wang NZ. 1977. The Jurassic fish fossils from Liling – Hengyong region of Hunan and its biostratigraphical significance. Vertebr PalAsiatica. 15(4):233–243 (in Chinese).

Wang NZ, Yang SR, Jin F, Wang W. 2001. Early Triassic Hybodontoidea from Tiandong of Guangxi, China. Vertebr PalAsiatica. 39(4):237–250 (in Chinese with English summary).

Woodward AS. 1889. Catalogue of the fossil fishes in the British Museum (Natural History). Part 1: Catalogue of the fossil fishes in the British Museum (Natural History). Vol. 1. London (UK): British Museum (Natural History) Press. 474 p.

Woodward AS. 1916. The fossil fishes of the English Wealden and Purbeck formations part I. Monogr Palaeontographical Soc. 69:1–48.

Xue XX. 1980. New materials of Hybodontidae in Gansu and Shaanxi. Vertebr PalAsiatica. 18(1):9–15 (in Chinese with English summary).

Yabe H, Obata T. 1930. On some fossil fishes from the Cretaceous of Japan. Jpn J Geol Geogr. 8:1–8.

Young CC. 1941. On two new fossil fishes from southwestern China. Bull Geol Soc China. 21(1):91–96.

Young CC. 1942. Fossil Vertebrates form Kuangyuan, N. Szechuan, China. Bull Geol Soc China. 22(3–4):293–309.

Yu JS. 1987. Jurassic Bivalves. In: Zhang ZL, Meng FS, editors. Biostratigraphy in the Eastern Yangtze Gorges (4), the Triassic – Jurassic fascicle. Beijing (China): Geological Publishing House. p. 172–189 (in Chinese).