SYSTEMATIC PALAEONTOLOGY OF THE FIRST CRETACEOUS FISH FAUNA FROM MALAYSIA

TENG YU HE

FACULTY OF SCIENCE
UNIVERSITY OF MALAYA
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2017

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TENG YU HE

DISSERTATION SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

GEOLOGY DEPARTMENT
FACULTY OF SCIENCE
UNIVERSITY OF MALAYA
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2017

ABSTRACT

The fluvial/lacustrine red-beds in Pahang, Peninsular Malaysia, produced a fossil fish assemblage that comprises mainly isolated teeth, bone fragments and fish scales. The red-beds are equivalent to part of the Tembeling Group of Jurassic-Cretaceous age, which is distributed along the eastern part of the Central Belt of Peninsular Malaysia. Specimens have been collected from the site and prepared using mechanical matrix removal method in the Palaeontological laboratory. A total of nine taxa have been identified from approximately 100 specimens collected from the site. They are six forms of sharks (two species of *Heteroptychodus*, and one of *Hybodus*, *Isanodus*, *Mukdahanodus* and *Isanodus*? sp.) and three forms of ray-finned fishes (*Lepidotes* sp., *Caturus* sp. and Semionotidae genus indet). A non-marine depositional environment is implied by the presence of *Heteroptychodus*, *Isanodus* and *Mukdahanodus* as they have previously been found only in brackish/freshwater sediments. *Heteroptychodus kokutensis*, *Isanodus*, *Mukdahanodus* and *Isanodus*? sp. are endemic to Thailand and Malaysia, while *Hybodus* and *Lepidotes* and *Caturus* are cosmopolitan. This Malaysian fish fauna is closely similar to that of the Sao Khua Formation of the Khorat Group in Thailand. The Malaysian fish fauna is interpreted to be coeval with the fish fauna of the Sao Khua Formation, therefore is dated at upper Barremian to lower Aptian age. Strong similarities between these two fish faunas also indicate a possible pathway for freshwater fauna interchange between Peninsular Malaysia and the Khorat Plateau during the late Early Cretaceous.

ABSTRAK

Fosil ikan berusia Kapur pertama di Semenanjung Malaysia telah ditemui di dalam batuan merah berusia Kapur Awal di Pahang. Fosil-fosil ini terdiri daripada serpihan tulang, gigi dan sisik ikan. Semua spesimen telah disediakan dengan menggunakan kaedah penyingkiran matriks secara mekanikal di dalam Makmal Paleontologi. Projek ini telah mengenalpasti sebanyak lapan taksa ikan daripada kira-kira 100 spesimen yang dikumpul dari kawasan ini. Mereka adalah enam bentuk jerung (dua species *Heteroptychodus*, *Hybodus*, *Isanodus*, *Mukdahanodus* dan *Isanodus*? sp.) dan tiga bentuk ikan bersirip kipas (*Lepidotes* sp., *Caturus* sp. dan Semionotidae genus indet). Kewujudan *Heteroptychodus*, *Isanodus* dan *Mukdahanodus* mengimplikasikan sekitaran pengendapan bukan marin, kerana mereka hanya dijumpai di dalam sedimen payau /air tawar sebelum ini. *Heteroptychodus kokutensis*, *Isanodus*, *Mukdahanodus* dan *Isanodus*? sp. dilaporkan hanya dari Thailand sebelum ini, manakala genera *Hybodus*, *Lepidotes* dan *Caturus* ialah ikan jenis kosmopolitan. Fauna ikan Malaysia ini menunjukkan persamaan dengan fauna ikan zaman Kapur Awal dari Kumpulan Khorat di Thailand, terumatanya dengan Formasi Sao Khua. Oleh demikian, kedua-dua fauna ikan tersebut dianggap wujud pada zaman yang lebih kurang same, iaitu atas Barremian – bawah Aptian. Selain itu, persamaaan yang ditunjukkan oleh fauna ikan Malaysia dengan fauna ikan Formasi Sao Khua juga implikasikan sambungan di antara Peninsula Malaysia dan Tanah Tinggi Khorat pada zaman Kapul Awal, membolehkan penghijrahan ikan air tawar.

ACKNOWLEDGEMENTS

I would first like to thank my thesis advisor Associate Professor Dr. Masatoshi Sone of the Geology Department at the University of Malaya. Dr. Masatoshi has provided guidance and help that steered me in the right direction whenever I needed it.

I would also like to thank the experts who have given me suggestion and guidance for this research project: Prof. Gilles Cuny, Prof. Hirayama Ren, Dr. Toshi Komatsu, Dr. Komsorn Lauprasert, Dr. Ng Tham Fatt, Mr. Masataka Yoshida and Ms. Suchada Khamha. Also, thanks to Dr. Suravech Suteethorn and staff from the Paleontological Research Center (PRC) of the Mahasarakham University, for providing me access to the fossil specimens in the PRC. Without their kind help and input, the study could not have been successfully conducted.

Finally, I must express my very profound gratitude to my parents and to my husband for providing me with unfailing support and continuous encouragement throughout my years of study and through the process of researching and writing this thesis. This accomplishment would not have been possible without them. Thank you.

Table of Contents

Figures

Tables

List of Appendix

CHAPTER 1 INTRODUCTION

The Mesozoic Era, also known as the "Age of Reptiles", is a period of diversification of all land-based life. Especially during the Jurassic–Cretaceous periods ca. 200–66 million years ago (J–K hereafter), land was dominated by both large and small dinosaurs, turtles, and crocodiles, while the marine environment was occupied by giant marine reptiles, such as plesiosaurs and mosasaurs. It was also during the Cretaceous that the first flowering plants occurred on Earth. Previous studies also found petrified coniferous forest in northern China, offering an insight into the rich floral diversification during the Early Cretaceous.

In 2012, a team of palaeontologists from the University of Malaya discovered fossil beds containing the first vertebrate fossil remains of Early Cretaceous age in Pahang, Peninsular Malaysia. Two types of dinosaur were identified among these fossil remains, providing evidence of a terrestrial/freshwater ecosystem in this part of the world during the Cretaceous. The dinosaurs, are identified as a spinosaurid and an ornithischian dinosaurs, reported in the media in February 2014 and November 2014. Beside the dinosaur remains, the fossils unearthed also include isolated fish teeth, scales, turtle shells and crocodile teeth, offering an insight into the palaeoenvironment of the Cretaceous world in Southeast Asia. This study deals with the first Cretaceous fish fauna from Malaysia.

The rock formation where this fossil deposit was found is equivalent to part of the Tembeling Group. The Tembeling Group was interpreted by the previous workers as fluvial/lacustrine deposits (see Chapter 2. Literature Review). The strata form a hilly topography along the eastern side of the central belt of Peninsular Malaysia. Palynology was in general the main tool used to date the sediments of the Tembeling Group by previous workers, but the age range of each formation within the group is not well-established. The Tembeling Group is in need of more fossil evidence for having better biostratigraphical controls. The newly discovered fossilised fish teeth provide new information on this matter.

Objectives

The main objectives of this study are

1. To carry out taxonomic identification of the fish fauna found in the central part of Pahang.
2. To carry out age dating through correlation with fish faunas previously reported from other countries.

Fossil preservation and fossil locality

The fish fossils were deposited in clastic sandstone and mudstone strata. Some fossils are severely abraded, indicating the possibility that they were transported through the fluvial system from their original habitat(s) prior to deposition.

As per agreement with the Pahang State Government, the information about the fossil locality has to be kept confidential. It will not be revealed anywhere, including in this report, until proper protection measures are in place. Information about the fossil locality should be referred to the state government or Geology Department, University of Malaya (Dr. Masatoshi Sone).

CHAPTER 2 LITERATURE REVIEW

The generally accepted model for Southeast Asia is that the Sibumasu (=Shan-Thai) Block and the mainland Indochina Block collided during the Late Triassic, when the Paleo-Tethys Ocean was closed and formed the landmass of the Sundaland (e.g. Hutchison, 2007; Sone & Metcalfe, 2008). Being part of the Sundaland, the Western Belt of Peninsular Malaysia belongs to the Sibumasu (=Shan-Thai) Block, whereas the Central and Eastern belts were interpreted as the southern extension of the Sukhotai island-arc terrane (Mitchell, 1977; Sone & Metcalfe, 2010).

No post-Triassic marine deposition has been known within Peninsular Malaysia. The palaeoenvironment has changed from shallow marine during the Permian–Triassic, to a terrestrial environment during the Jurassic–Cretaceous. This is supported by an Indosinian unconformity that is marked between the Middle–Upper Triassic marine strata and the overlying J–K redbeds in the Jengka Pass road-cut (Ichikawa et al., 1966) and elsewhere in Peninsular Malaysia. Most J–K rocks in Peninsular Malaysia are distributed to the east of the Bentong-Raub Suture and are found along the eastern margin of the Central belt (Figure 2.1). Three main areas where the J–K rock formations were mapped are: 1). The Gagau Group and the Koh Formation in the northern part; 2) The Tembeling Group and the Bertangga Sandstone in the central part; 3) Patches of unconnected J–K rock bodies, which are the Paloh Formation, the Ulu Endau Beds, the Panti Sandstone and the Ma' Okil Formation in the southern part (Hutchison & Tan, 2009; Tjia, 1996).

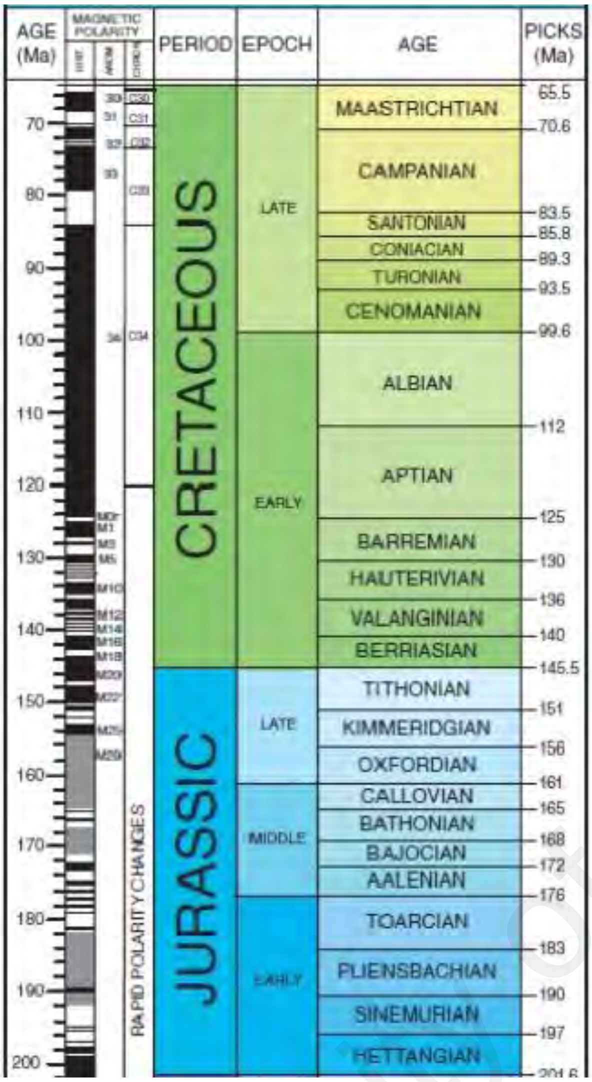


Figure 2.1 Geological time scale modified after the International Chronostratigraphic Chart (Cohen et al., 2013).

Among all the J–K formations described and mapped by previous workers, the Tembeling Group has the most extensive area with most detailed information. It was first proposed by Koopmans (1968) as the Tembeling Formation. The type section is located along the Tekai River in the north of the Pahang district. The extent of the formation was traced further south towards Maran area, further east towards Bukit Berkelah, and further west towards Gunung Tungku and Jerantut.

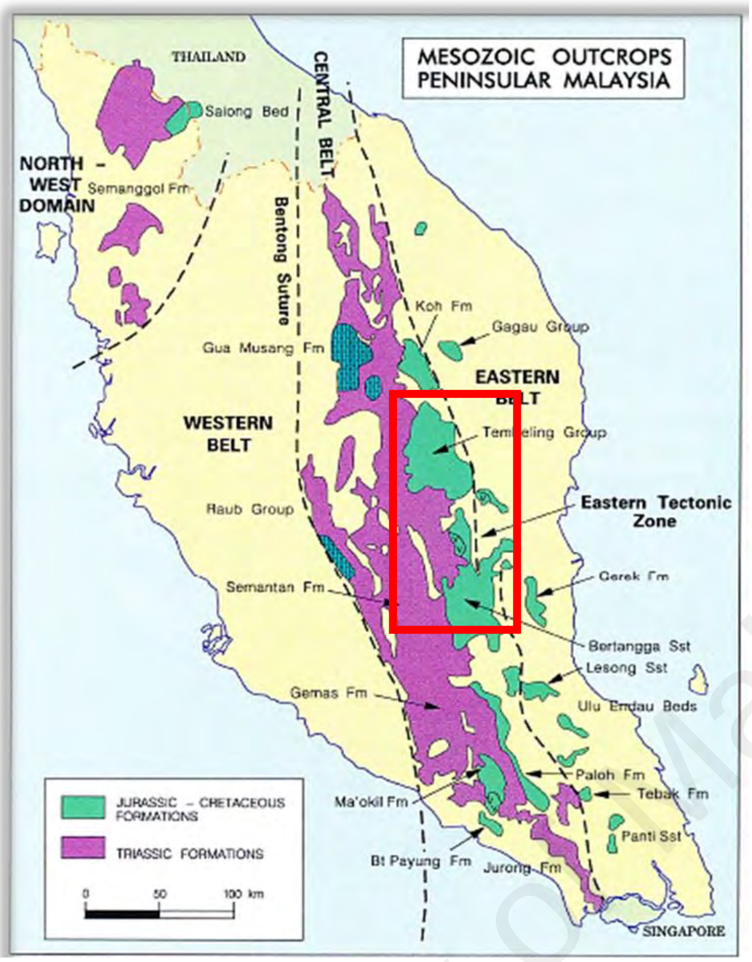


Figure 2.2 Simplified geological map of Peninsular Malaysia showing Jurassic – Cretaceous formations in green and Triassic formations in purple (modified after Tjia, 1996 in Hutchison & Tan, 2009). Red box: fossil locality. Note: Information about the fossil locality is kept confidential according to an agreement with the Pahang State Government.

Koopmans (1968) considered a layer of conglomerate mapped in Tanjung Murau, namely, the Murau Conglomerate, as the possible basal unit for the Tembeling Formation. This decision was merely based on lithological similarity where the Murau Conglomerate was said to share the same reddish polymict character with the basal conglomerate found in the type section of the Tembeling Formation. Later, the Tembeling Formation was upgraded to the Tembeling Group by Khoo (1977) who defined four formations within the group. They are the Kerum Formation, the Lanis Conglomerate, the Mangking Sandstone, and the Termus Shale upwards in ascending order. The Murau Conglomerate was since being removed from the Tembeling Group. Lithological descriptions of each formation are summarised in Table 2.1.

Table 2.1 Lithology descriptions of the Tembeling Group (Khoo, 1977)

Thickness	Age	Formation	Lithology
+1500 m	U. Jurassic – L. Cretaceous	Termus Shale	Reddish/puplish-red ferruginous Argillaceous rocks Interbedded with minor amount of reddish and non-ferruginous lithic sandstone and some quartzose sandstone
~ 2200 m		Mangking Formation	Greyish to Whitish Quartzose sandstone interbeded with grey to brown argillaceous rocks and some ferruginous reddish argillaceous rocks. Sandstone slightly conglomeratic with pebbles and granules mostly of quartz.
~ 900 m	?	Lanis Conglomerate	Interbedded reddish/purplish red pebble to granule lithic conglomerate, lithic sandstone and some reddish ferruginous siltstone mudstone and shale. Volcanic class abundant.
Actual thickness not known	?	Kerum Formation	Interbedded tuff/lava, tuffaceous sediments, lithic sandstone and reddish ferruginous argillaceous rocks. Some quartzose sandstone.

On the other hand, Harbury et al. (1990) suggested to exclude the Kerum Formation from the Tembeling Group due to the presence of tuffaceous volcaniclastics that recall the Kaling and Semantan formations of Triassic age. However, this suggestion was disagreed upon by Tjia (1996) in that the Kerum Formation comprises conglomeratic sandstone and purplish red mudrocks that are similar to those seen in the Lanis Conglomerate, the Mangking Formation, and the Temus Shale. Moreover, its thick to massive bedding structure do not resemble deep-water turbiditic stratification which is typical to a sequence of the Semantan Formation.

Palaeoenvironment of the Tembeling Group

In terms of palaeoenvironment, Koopmans (1968) suggested that the sediments of the Tembeling Group were deposited in a fluvial-deltaic-lacustrine environment. Evidence given consists of several points:

1. The occurrence of plant fossils and palynomorphs from the Tekai River outcrops (Mangking Sandstone); The occurrence of freshwater bivalves at Jengka Pass outcrop on top of the unconformity.
2. Lithology succession and sedimentary features, such as imbricate structure of pebbles in the Mangking Sandstone, suggesting a unidirectional fluvial current deposition.
3. The occurrence of coal shales and carbonaceous material indicating swampy depositional environment.
4. The occurrence of redbeds which indicates iron oxidation in a warm continental condition.

The earlier interpretation on the depositional environment of the Tembeling Group is based on minimal sedimentological analysis. Instead, Khoo (1977) suggested a continental aqueous environment based on the occurrence of non-marine bivalves at the base of the Termus Shale, together with the plant fossils *Gleochenoides gagauensis*, freshwater gastropods, and palynomorphs in the Mangking Sandstone. Harbury et al. (1990) suggested an alluvial system instead of fluvial-lacustrine-deltaic system based on the observable unidirectional palaeocurrent directions, which points towards the south-east in the sandstone and conglomeratic units. Later, a more detailed sedimentological study was carried out on the Mangking Formation exposed along the Tembeling River (Ainul et al., 2005), and its lithological and sedimentary characters suggested that the depositional environment was a meandering river system. Another J–K outcrop was recorded along the Karak Highway and the strata were also being interpreted as a meandering fluvial deposit based on detailed sedimentological study (Madon et al., 2010). Overall, depositional environment of the Mangking Sandstone is likely to be a fluvial setting, and the Temus Shale is likely to have been deposited in a low energy floodplain setting (Ahmad Jantan et al., 1991).

Palaeoclimate in Peninsular Malaysia during Early Cretaceous was interpreted to be sunny, warm, dry with seasons of draught (Smiley, 1970). This was based on plant fossil records, such as the presence of the family Gleichenianceae, the genera *Cyras* and *Ferenlopsis* from the Maran sandstone beds. Shamsudin Jirin & Morley (1994) concluded a semi-arid climate during the Early Cretaceous, based on the occurrence of the palynomorphs *Classopollis*, *Exesipollenites*, *Ephedripites*, and *pteridophytes* in the Temus Shale.

A correlation among the Tembeling Group, the Gagau Group, the Koh Formation, the Bertangga Sandstone, the Ulu Endau Formation, and the Panti Sandstone was attempted based on plant and palynolomorph fossils from the sandstone and mudstone units of these formations (Khoo, 1983). Unfortunately, there is no fossil evidence to determine the age of both the Kerum Formation and the Lanis Conglomerate thus far.

Age of Mangking Formation

The occurrence of the plant fossil *Gleochenoides* in the type section of the Mangking Formation indicates a broad age range of Jurassic to Early Cretaceous (Khoo, 1977). Two floral assemblages where reported from Locality 5201 and 5202 near Maran (Smiley, 1970), namely, the Upper Maran Florule which resembles the Ulu Endau flora, and the Lower Maran Florule which resembles the Panti flora. The lower and upper Maran floral assemblages indicate a Neocomian age (Early Cretaceous) for the Maran sandstone units, which was said to be equivalent to the Mangking Sandstone. Some pollen were found at the lower part of the Maran sandstone, indicating a probable Jurassic age at the base of the Maran sandstone. Although the details on pollen species and palynological age were not mentioned, Smiley (1970) concluded that the Mangking Formation is at least Late Jurassic to Neocomian in age. In 2005, Ainul et al. reported a palynomorph assemblage from an outcrop of the Mangking Formation located along the Tembeling River. The palynomorph assemblage, which closely resembles the *Stylosus* Assemblage, indicates that the Mangking Formation is ?Neocomian–Aptian in age (Ainul et al., 2005). Later in 2007, Uyop et. al. reported a palynopmoph assemblage from an outcrop interpreted as the Mangking Formation equivalent in Chenor–Maran area. The assemblage shows similarity to both *Stylosus* and *Speciosus* assemblages, therefore was assigned to a Valanginian–Hauterivian age (Uyop et al., 2007).

Towards the southern part of the Peninsular Malaysia, as mentioned above, the Ulu Endau Beds and the Panti Sandstone are correlatable to the Maran sandstone units by sharing similar plant fossil assemblages, therefore both units were dated as Late Jurassic to Neocomian in age. Another palynomorph assemblage was reported from Kluang, near Kampung Tanah Runtuh, and the fossil strata were dated to be Berriasian–Valanginian in age (Uyop et al., 2003).

Age of Temus Shale

The lower part of the Temus Shale was first dated to be Early Cretaceous based on the presence of freshwater bivalves *Trigonoides kodairai* and *Plicatounio* (Khoo, 1977). Later, the primitive angiosperm-like pollen *Clavatipollenites* was found in the Temus Shale, indicating that the formation is no younger than the Barremian (Shamsudin & Morley, 1994). *Clavatipollenites* is absent from the Mangking Sandstone, leading to the possibility that the Mangking Sandstone is pre-Barremian in age. Towards the south, the same primitive angiosperm pollen was also discovered from Felda Keratong area

(Uyop, 2002). Together with other species found, the strata were dated to be Barremian to Albian in age. A summary of age dating of the Mangking Sandstone and the Temus Shale is shown in Figure 2.2.

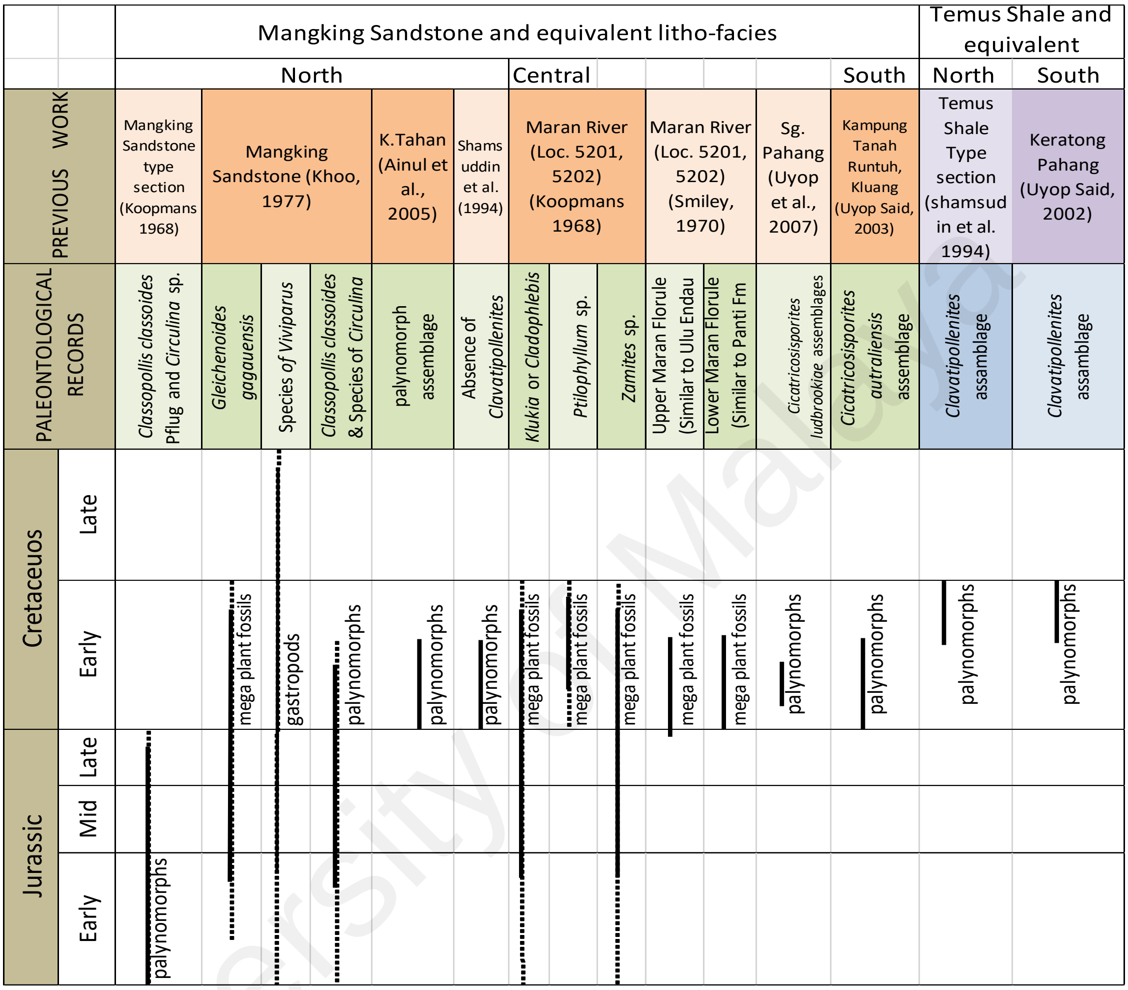


Figure 2.3 Paleontological record on all of the JK rocks based on previous studies.

The Khorat Plateau in the north

Towards the north in Southeast Asia region, thick terrestrial J–K redbeds are distributed in the northeastern part of Thailand, namely, the Khorat Group, extending themselves into southeastern and central Laos as the Vientiane Basin and the Savannakhet Basin (Racey, 2009; Ward & Bunnag, 1964). In terms of regional geological setting, these basins are situated on the Indochina Block.

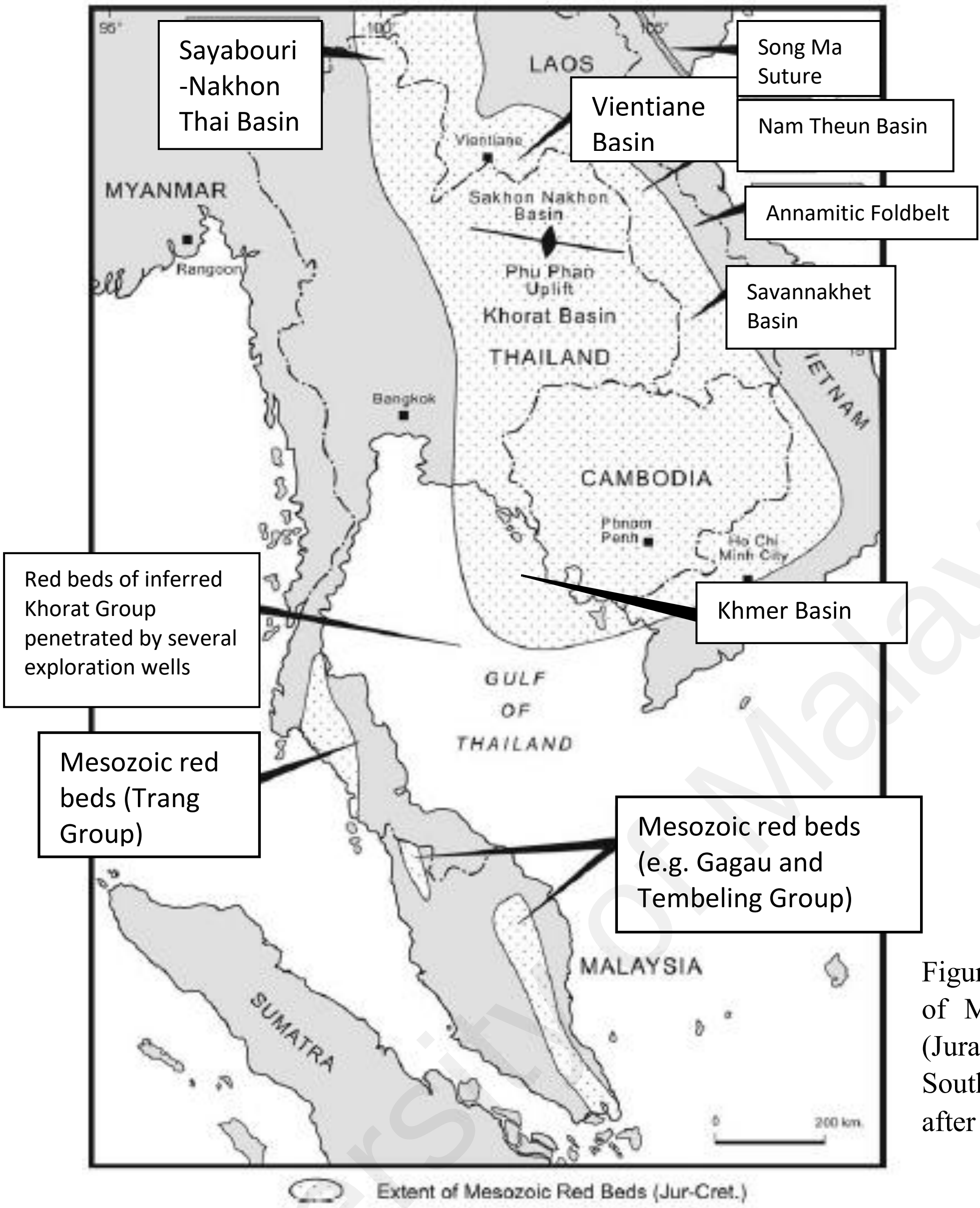


Figure 2.4 Regional map of Mesozoic Red Beds (Jurassic–Cretaceous) in Southeast Asia, modified after Racey (2009).

The Khorat Group is divided into five formations, from bottom to top, the Phu Kradung Formation, the Phra Wihan Formation, the Sao Khua Formation, the Phu Phan Formation and the Khok Kruat Formation. A summary of the lithology of the Khorat Group is shown in Figure 2.4.

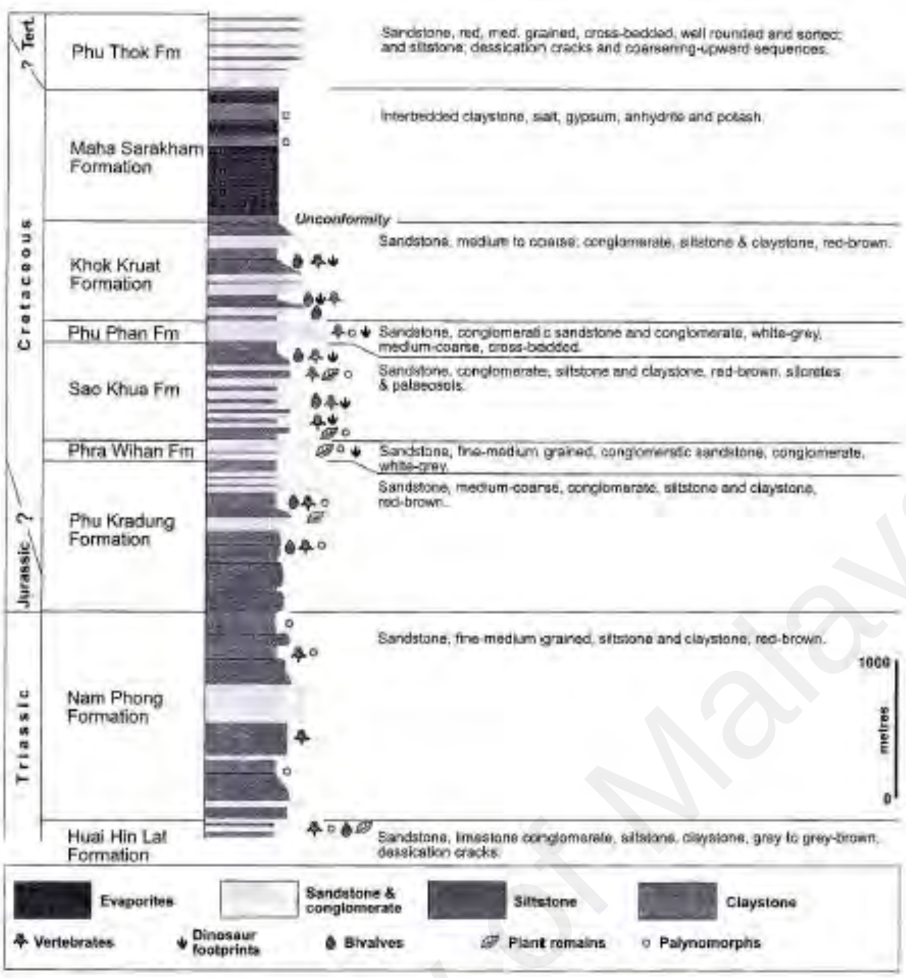


Figure 2.5 Composite stratigraphic column of the Mesozoic rocks of the Khorat Group, NE Thailand (Meesook, 2011).

Based on litho-facies analysis, depositional environment of the Phu Kradung Formation was interpreted to be an anastomosing river system under semi-arid to sub-humid palaeoclimate condition during the time of deposition. (Horiuchi et al., 2012). The formation yields some freshwater shark (Cuny et al., 2007), theropod, sauropod, crocodilian, and other vertebrate fossils (Buffetaut, 1983; Buffetaut & Rucha, 1986; Buffetaut & Suteethorn, 1998). An attempt was made to date the formation using its vertebrate fossil records (Buffetaut & Suteethorn, 1998), by comparing the *Sunosuchus,* Temnospondyls and euhelopodid sauropods found from the Phu Kradung Formation to those from China, and the comparison suggested a Jurassic age for the formation. Later, palynomorphs from the Phu Kradung Formation were obtained from both outcrops and borehole wells (Racey & Goodall, 2009). The presence of the palynomorph

Dicheiropollis estruscus in the Phu Kradong Formation (except at its basal part) in the Phu Horm-1 well, suggests that the base of the Phu Kradung Formation is latest Jurassic and the rest of the formation is Early Cretaceous (Berriasian–Barremian) in age (Racey & Goodall, 2009). Other palynomorphs *Classopollis* sp., *Cyathidites* sp. and *Ballosporites hians* Madler were found from the type section of the formation, supporting an Early Cretaceous age (Racey & Goodall, 2009).

The Phra Wihan Formation sits conformably on top of the Phu Kradung Formation (e.g. Meesook, 2011). The depositional environment of the Phra Wihan Formation was interpreted to be a high energy braided river system, which did not favour fossil preservation (Mouret et al., 1993). Palynological analysis was carried out with a palynomorph assemblage found near the base of the formation. The assemblage consists of an important index species, namely *Dicheiropollis etruscus*, indicating a Berriasian–early Barremian age for the formation (Racey & Goodall, 2009).

The overlying Sao Khua Formation consists mainly of floodplain deposits and low-energy meandering channels deposits (Buffetaut & Suteethorn, 1998; Meesook, 2011; Racey & Goodall, 2009). This formation yields the richest vertebrate fossils of the Khorat Group, including freshwater sharks (Cuny et al., 2007), dinosaurs and birds (Buffetaut & Suteethorn, 1998). The Sao Khua Formation was originally assigned to the Late Jurassic–Early Cretaceous based on palynological analysis (Racey et al., 1996). Later, a new assemblage of palynmorphs were obtained from the Phu Phan Thong and Hui Sai localities. The assemblage is dominated by *Dicheiropollis etruscuss*, *Corollina* spp. and other species which suggest an Early Cretaceous age. The absence of angiosperm pollen from the palynomorph assemblage confined the age range of the Sao Khua Formation from Berriasian to early Barremian (Racey & Goodall, 2009). Buffetaut (2005a) suggested that, since the Khok Kruat Formation was dated to be Aptian–Albian in age, the Sao Khua Formation is pre-Aptian. Later, an attempt of age dating for the Sao Khua Formation using a new species of bivalve, *Pseudohyria* (*Matsumotoina*) *somanai* was carried out (Tumpeesuwan et al., 2010). The new species is dated to be late Barremian because the preceding sole species of the subgenus *Pseudohyria (Matsumotoina)* occurred in the Sebayashi faunal association of the late Barremian (Tumpeesuwan et al., 2010). Tympeesuwan et al. (2010) hence suggested a late Barremian age for the Sao Khua Formation.

Overlying the Sao Khua Formation, the Phu Phan Formation was deposited in a high energy braided river system which carried a significant amount of quartz pebbles (Mouret et al., 1993; Racey & Goodall, 2009). There is no vertebrate body fossils found in this formation, and only some poorly preserved dinosaur footprints were found (Buffetaut et al., 2009). This is probably due to its powerful depositional environment which did not favour fossil preservation (Mouret et al., 1993). Palynological analysis assigned a long ranging age of Early Jurassic–Cenomanian to this formation (Racey et al., 1996). Since the underlying Sao Khua Formation was dated to be Late Barremian, and the overlying Khok Kruat Formation was dated to be Aptian–Albian, the Phu Phan Formation was suggested to fall within the interval of Barremian–Aptian (Racey & Goodall, 2009).

The Khok Kruat Formation is the upper most formation of the Khorat Group. An unconformity was found between the Khok Kruat Formation and the overlying Maha Sarakham Formation in both outcrop and a well log analysis (Meesook, 2000, 2011). The occurrence of a cutting dentition freshwater shark, *Thaiodus ruchae*, was taken as an important indication of Aptian–Albian age for the Khok Kruat Formation: the same species was reported from the Takena Formation in Tibet, that was dated to be Aptian–Albian based on foraminiferas (Cappetta et al., 2006; Cappetta et al., 1990).

A brief chronostratigraphic correlation between the Khorat Group and the Tembeling Group (and its equivalents) is shown in Figure 2.5. As mentioned above, out of the four formations of the Tembeling Group, only the Mangking Sandstone is relatively well dated based on palynological analysis. Several palynomorph assemblages were reported from Maran and other southern area, however the continuity and relationship of these rock units to the Tembeling Group is poorly constrainted.

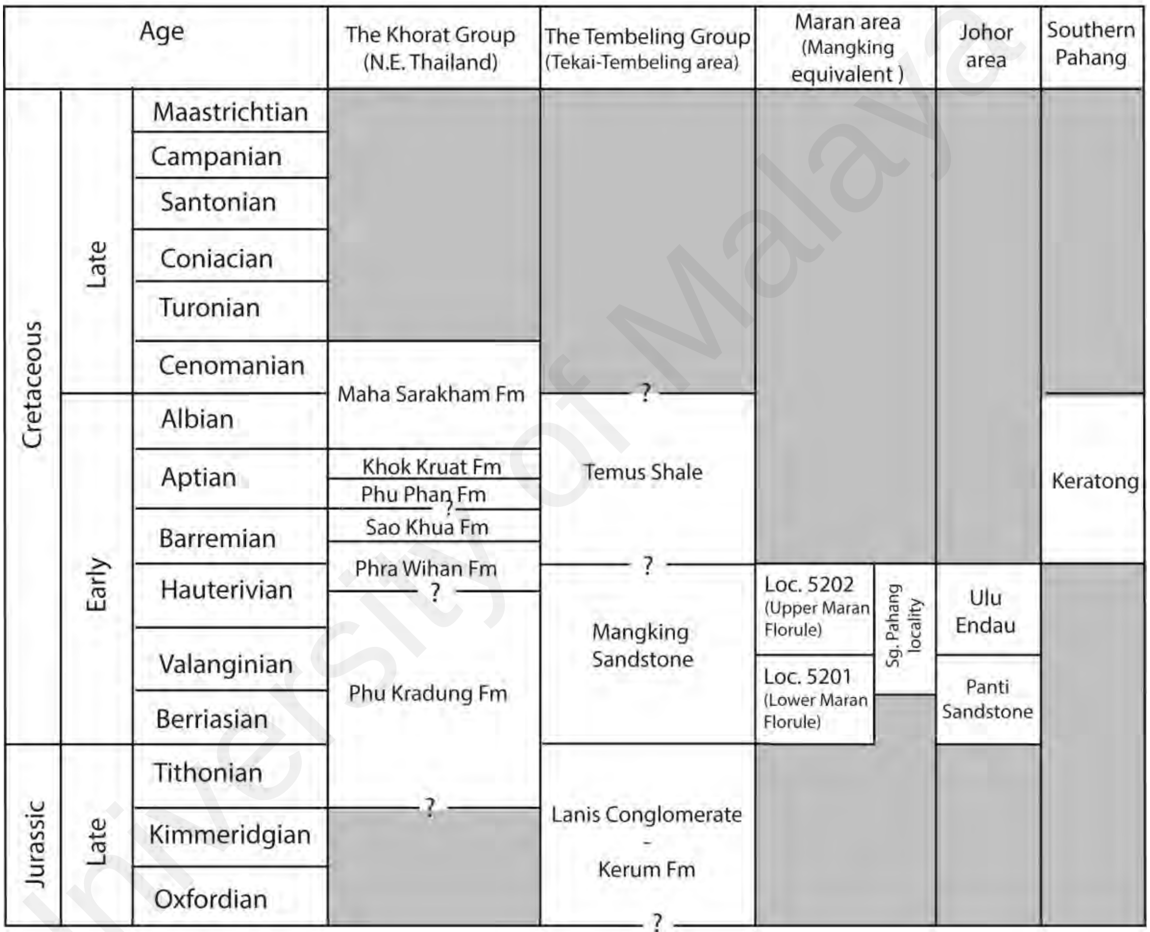


Figure 2.6 Chronostratigraphy correlation between the Khorat Group and the Tembeling Group (and its equivalents) (modified from Racey, 2009 and Khoo, 1983) .

The depositional environments of the formations of the Khorat Group are similar to those of the Tembeling Group (and its equivalents). A summary of the palaeoenvironments and palaeoclimates is shown in Figure 2.6.

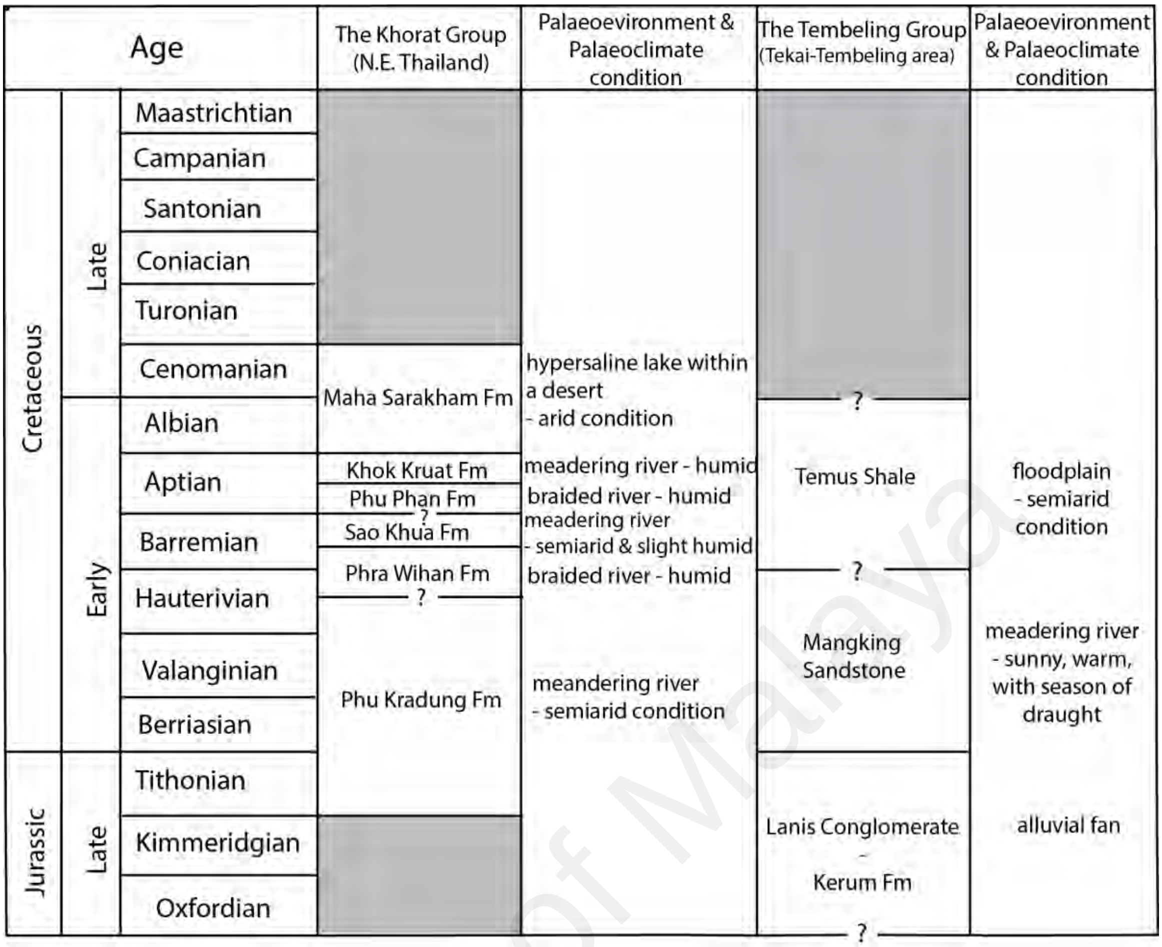


Figure 2.7 Brief summary of palaeonvironments and Palaeoclimates for the Khorat Group and the Tembeling Group based on the previous workers (Ahmad Jantan et al., 1991; Meesook, 2011; Shamsudin & Morley, 1994; Smiley, 1970)

Palaeogeography

Peninsular Malaysia is supposed to have been closer than today to the Khorat Plateau during the Early Cretaceous before the Malay Basin and the Gulf of Thailand's opened during the Tertiary (Hutchison, 2007). Tectonically, the Khorat Group is situated within a relatively broad and stable Indochina Terrane, while the Tembeling Group (and its equivalent) is situated in a former mountainous Island-arc terrane which is a southern extension of the Sukhotai Terrane (Mitchell, 1977; Sone & Metcalfe, 2010). A Cretaceous biogeographical relationship between the Khorat Plateau and Peninsular Malaysia is now suggested by the similarities of the fish faunas in Thailand and Malaysia.

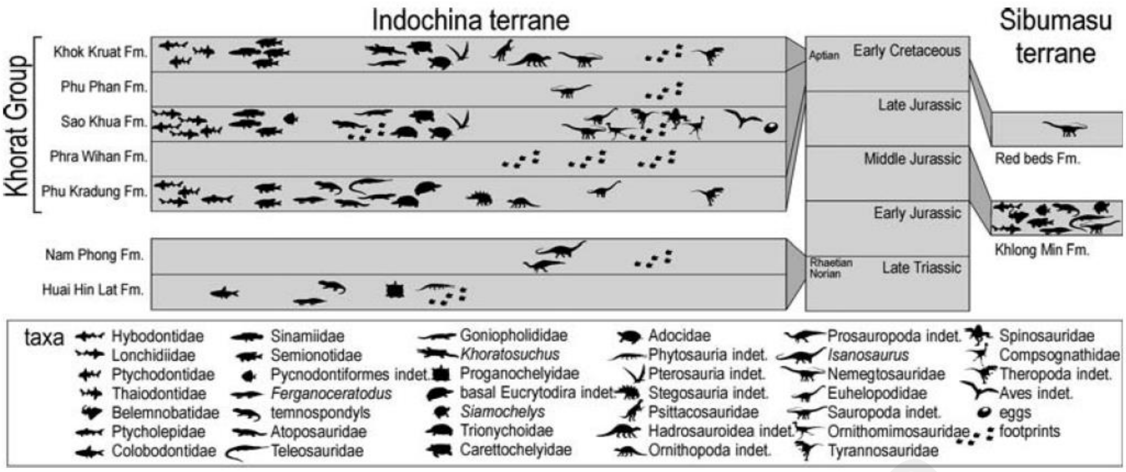
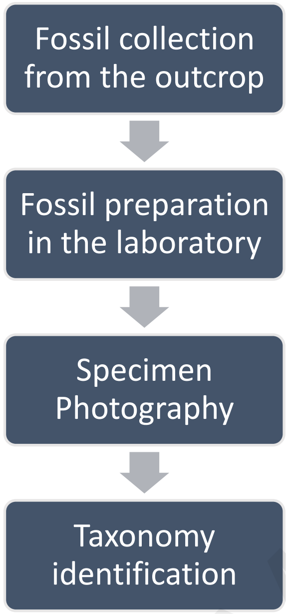


Figure 2.8 Distribution of main groups of vertebrates in the no-marine formations of Thailand. Figure produced by L. Cavin taken from Buffetaut et al., 2009.

The Khorat Group has yielded abundant vertebrate fossils over the past 40 year (Figure 2.7). Three out of the five formations, namely, the Phu Kradung Formation, the Sao Khua Formation and the Khok Kruat Formation, yield significant amounts of fossil fishes, especially hybodonts (Cuny et al., 2003; Cuny et al., 2005; Cuny et al., 2007). However, the main dating tools for the formations of the Khorat Group are palynomorphs and bivalves. The fossil fishes did not play a dominant role in dating the formations. The reason is that the non-marine fish faunas found in Thailand are strongly endemic (Fernandez et al., 2009). Their age ranges are not well-established yet due to limited correlations available with other fish faunas around the world. The age ranges of the rock units where they were found are still in debate, especially for the Sao Khua Formation. Therefore, the discovery of a fish fauna in Malaysia is significant in providing a new correlation to the Thai fish faunas. The correlation between fish faunas from the Tembeling Group equivalent and the Khorat Group provides a better age constraint for the Tembeling Group and also provides a better understanding of the diversification and distribution of endemic hybodont sharks in Southeast Asia during the Early Cretaceous.

CHAPTER 3 METHODOLOGY

Basically the project methodology is divided into four main parts,



Fossil collection from the outcrop

Rocks containing fossils were collected from the locality, labelled and transported back to the laboratory for further preparation.

Fossil preparation in the laboratory

Fossil preparation is the process of removing the matrix surrounding the specimens so that the characteristics of the specimens can be made clearly visible. The fossil preparation was done under Nikon SMZ645 stereo microscope (Figure 3.1).

Figure 3.1 Nikon SMZ645 stereo microscope used for fossil preparation.

First, an engraver was used to remove consolidated sediments around the specimens. Sharp tools including needles and blades were used to clean the matrix attached to the surface of the specimens, especially those stuck in the delicate structure on the surfaces. Plier was used to cut off some strongly cemented matrix at the edge of the rock samples. Chemical glue, both liquid and gel types were applied on the specimens to strengthen them and prevent them from breaking.

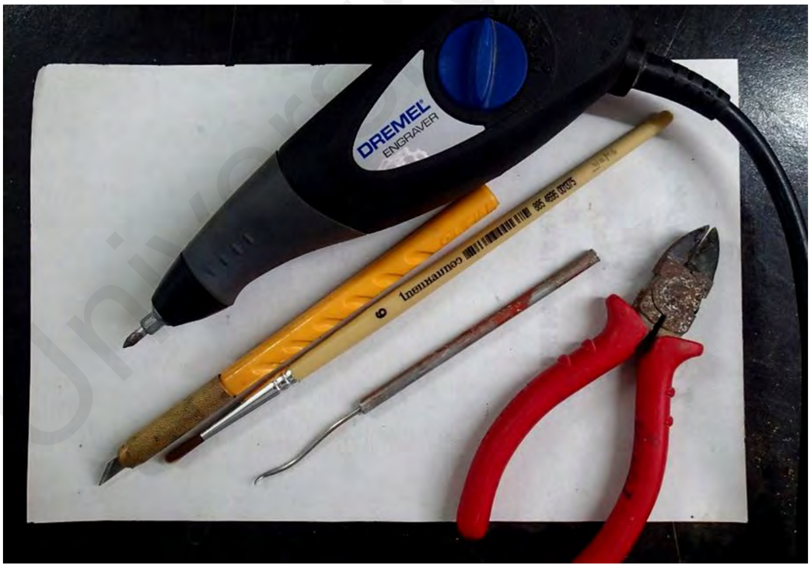


Figure 3.2 Dremel engraver, sharp tools and brush used for fossil preparation

Specimens were then categorised according to their characteristics and kept in containers.

Figure 3.3 Catogorise the specimens and keep them in containers.

Specimen Photography

Specimens in good condition were photographed using two methods.

The first method is a focus stacking method. Images at different depth of field were taken and combined to create a focus stack in which the whole specimen is in focus (Brecko et al., 2014). The camera used is a Nikon D300 DSLR (Digital Single Lens Reflex) camera with a resolution of 12 MP and equipped with a macro lens. The macro lens has a 105mm focal length, with a magnification of 1—2x aided by a tally convertor. The lightning source used were a Nikon fibre optic illuminator and a Nikon ring light. Setup of the photographic equipments used is shown in Figure 3.4.

Figure 3.4 Camera setup (image stacking method)

While taking images of different depth of field, the step size is determined by focusing the top and bottom of the specimens, and dividing the gap in between into an average of 8 steps. Images were aligned and stacked in the software CombineZP and Adobe illustrator.

The second method uses a JEOL JSM-7001F field emission Scanning Electron Microscope (SEM). to take micrograph of the specimens. Each specimen was first mounted on a metal stub by using carbon tape, then was coated with a thin layer of gold using a Leica EM SCD005 sputter coater. The gold coated specimens were then inserted into the sample chamber of the field emission SEM machine. A magnification range of x23 to x27 and an accelerating voltage range of 5.0 kV to 15.0 kV were applied. Image of the specimens could be viewed on the computer screen and micrograph were taken via the computer device.

Figure 3.5 A Leica EM SCD005 sputter coater; B Scanning Electron Microscope

Taxonomical Identification

Taxonomical identification was carried out by observing and documenting the characteristics of each specimen, comparing the differences and similarities with previously reported species and identifying the specimens based on their diagnostic characteristics.

CHAPTER 4 SYSTEMATIC PALAEONTOLOGY

4.1 Introduction & Terminology

More than 100 samples of fish remains were collected from the fossil locality in this study. Table 4.1 shows the number of specimens prepared for each taxon. They are mostly isolated teeth, bone fragments and scales. These specimens are labelled based on the horizons where they were collected, which are A1, A2, A3, B3 and B4 horizons.

Table 4.1 List of taxa and number of specimens for each taxon reported in this study.

		Species	**Number of Specimens**
Fish	**Chondrichthyes (Cartilaginous fish)**	*Heteroptychodus* cf. *steinmanni*	2
		Heteroptychodus kokutensis	31
		Isanodus nongbualamphuensis	21
		Hybodus sp. A	5
		Hybodus sp. B	2
		Isanodus? sp.	2
		Mukdahanodus trisivakulii	2
	Osteichthyes (Bony fish)	*Lepidotes* sp.	9
		Caturus sp.	14
		Semionotidae genus indet	1
Others		Turtle shell	3
		Crocodile tooth	1
		Bony fish scale	4

Generally, “fishes” are divided into two classes that are the Chondrichthyes and the Osteichthyes. The Chondrichthyes are cartilaginous fishes, which are commonly known as shark and rays. The Osteichthyes are bony fishes. This study reports micro-remains of both cartilaginous and bony fishes from the fossil locality in Pahang.

Skeletons of Chondrichthyes are hardly preserved as fossils because the cartilage is easily decomposed. Most of the time, only teeth can be found as fossilised. These teeth are more easily preserved as fossils because each tooth is capped by a layer of enameloid. The enameloid is one of the vertebrate hard tissue that present in fishes. It is hypermineralised by hydroxyapatite which appears as crystallites under microscopic observation. As a result, the mineralisation gives the enameloid a property of resistance to weathering or alteration (Burgess, 2000). The fossilised teeth of the Chondrichthyes bear diagnostic dental characteristics that are useful for taxonomic identification. Figure 4.1 illustrates the relationship of Chondrichthyes and Osteichthyes.

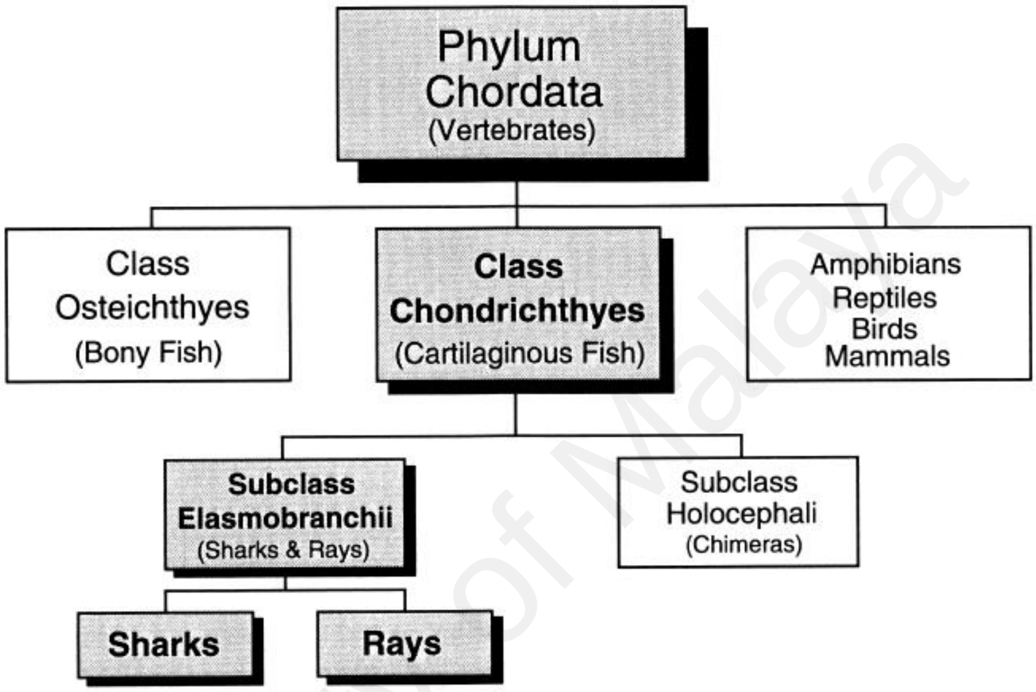


Figure 4.1 Phylogenetic relationship of the class Chondrichthyes (Welton & Farish, 1993).

Terminology

Upper and **Lower** teeth – Teeth from upper jaw and lower jaw.

Symphysis – Midline of each jaw where the left and right jaw cartilages meet.

Labial – Face of tooth toward the lips (outer face).

Lingual – Face of tooth toward the tongue (inner face).

Mesial – Side of tooth toward the jaw symphysis (midline).

Distal – Side of tooth toward the hinges of the jaw (corners).

Occlusal – Biting surface of the tooth.

Basal – Bottom of tooth.

Apical – Top of tooth.

Homodonty – All the teeth in the mouth are the same in shape and are approximately the same size.

Heterodonty – Contrary to homodonty, teeth vary in size and shape along the jaw, between the upper and lower jaws, between sexes, and between different maturity stages.

Crown – Pointed or rounded, enameloid-covered portion of an oral or rostral tooth, scale or denticle, supporting blades, cusplets and shoulders.

Cusp – Principal crown prominence.

Longitudinal ridges – Parallel or subparallel or anastomosing, raised, enameloid ridges found on occlusal crown faces.

Transverse ridges – Ridges developed in the enameloid on the apical surface of the crown and oriented transversely.

Marginal Area – Flattened and ornamented shelf-like surface surrounding the cusp on teeth.

incertae sedis – An open nomenclature used for a taxonomic group when its broader relationships are unknown or undefined.

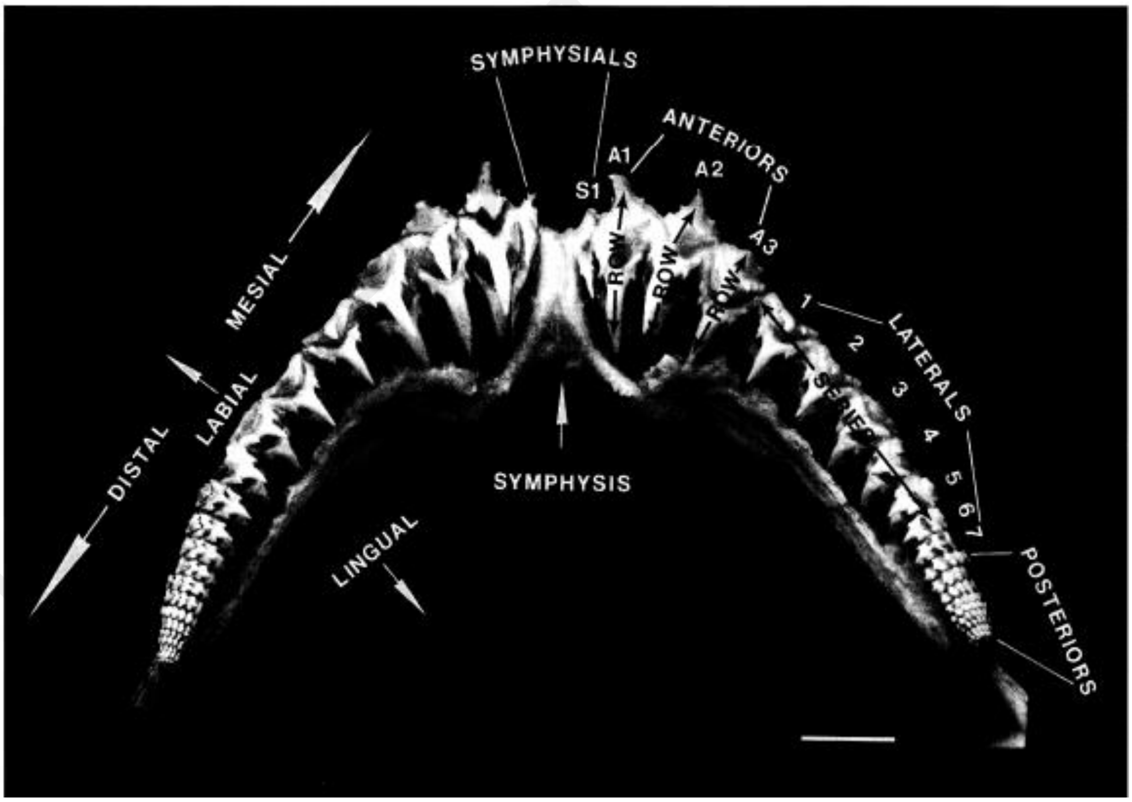


Figure 4.2 Tooth orientation (Welton & Farish, 1993)

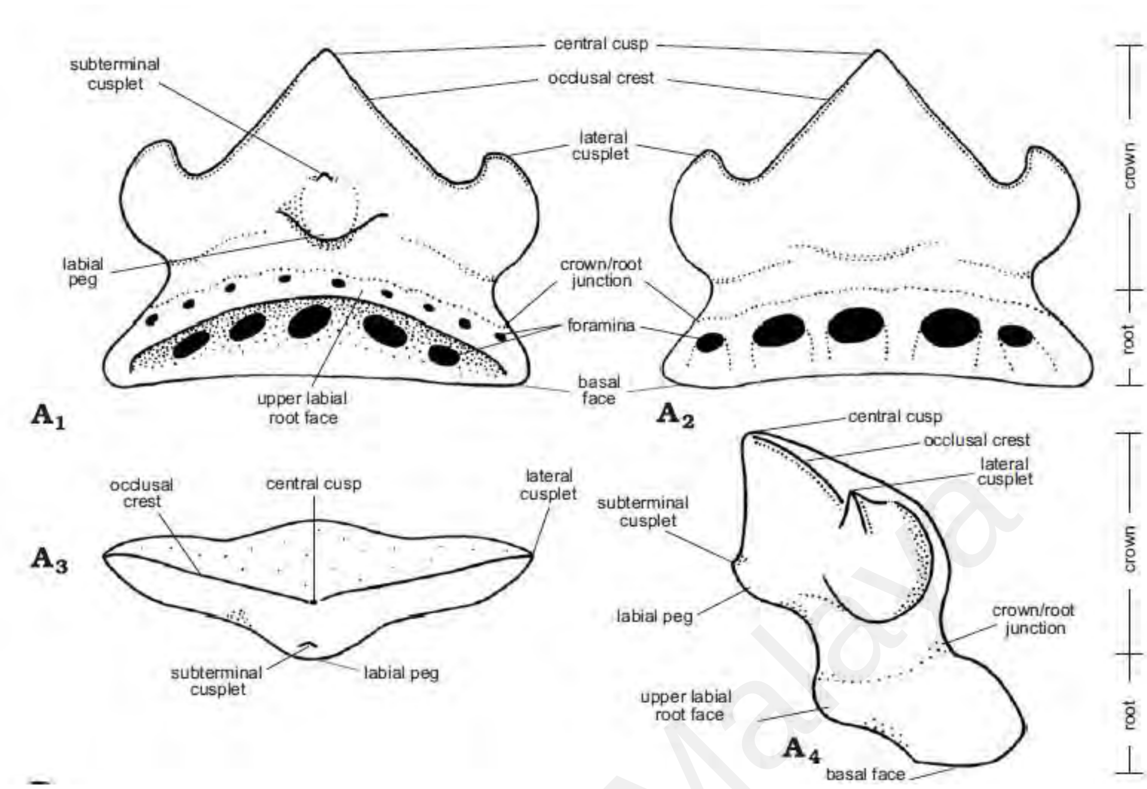


Figure 4.3 Diagrammatic illustration of *Lissodus sardiniensis* showing terminology of dentition (Fischer et al., 2010).

Class: Chondrichthyes Huxley, 1880
Subclass: Elasmobranchii Bonaparte, 1838
Order: Hybodontiformes Maisey, 1987
Family: *Incertae sedis*

Genus: *Heteroptychodus* Yabe and Obata, 1930

Type species. *Heteroptychodus steinmanni* Yabe and Obata, 1930

Discussion. *Heteroptychodus* was previously reported only from Asian countries, which are Thailand, Japan, Mongolia and Kyrgyzstan (Cuny et al., 2003; Nessov, 1997; Yabe & Obata, 1930). The type species reported by Yabe & Obata (1930) was first placed under the family Myliobatidae Bonaparte, 1838. Later, the genus was revised and placed under the family Ptychodontidae Jaekel, 1898 (Cappetta et al., 2006; Cuny et al., 2003; Cuny et al., 2006; Goto et al., 1996; Patterson, 1966) due to its similarity with the genus *Ptychodus*, by having numerous transverse ridges across its crown. Ptychodontidae, a family of hybodont shark, is originally defined by flattened crushing teeth with strong ridges or crests of enamel, and heterodonty dentition with an unpaired symphysial file in each jaw. In terms of dental arrangement, tooth size decreases posteriorly (Patterson, 1966). Contrary to *Ptychodus*, there is no report on any symmetrical symphysial tooth in *Heteroptychodus*. Later, Mutter et al. (2005) pointed out that the family Ptychodontidae lost a clear definition of synapomorphy upon the reporting of a new species *Ptychodus cyclodontis* which is remarkably homodont. Cuny et al. (2010) agreed with their argument and reclassified *Heteroptychodus* as family *incertae sedis*.

All teeth of *Heteroptychodus* reported previously were found isolated, leading to a hypothetical dental reconstruction of the genus. There are three types of teeth being described by Cappetta et al. (2006) and Cuny et al. (2003): bulging anterior teeth, less bulging lateral teeth and flat posterior teeth. The characteristics differentiating these teeth are summarised in Table 4.2. This dental reconstruction fits the gradient monognathic pattern that is common in hybodonts (Burgess, 2000; Welton & Farish, 1993).

Table 4.2 Characteristics of teeth from different dental position of *Heteroptychodus,* based on Cappetta et al (2006) and Cuny et al. (2003).

	Anterior	**Lateral**	**Very Lateral/ Posterior**
Symmetricity	Asymmetrical	Asymmetrical	Asymmetrical
Bulge development	Well-developed/ pronounced bulge, more angular	Moderately developed, less angular	No bulge
Bulge position	Not central	Not central	-
Crown shape	Regularly convex	Regularly convex	Almost flat

The modern shark *Heterodontus* provides an analogue of the possible hybodont dentition. *Heterodontus* is said to be a surviving member of the hybodont group (Burgess, 2000). Its teeth (Figure 4.4) are cuspidate anteriorly and becoming flat towards the posterior (Powter et al., 2010). Similarly, the teeth with well-developed bulges are interpreted as the anterior teeth of *Heteroptychodus*, whereas the relatively flat teeth are presumed to be the posterior teeth.

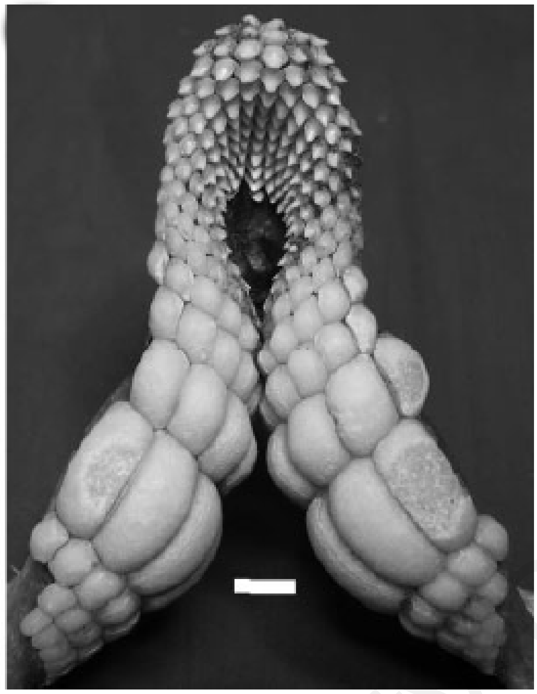


Figure 4.4 Jaw and teeth of a male adult *Heterodontus portusjacksoni*. Scale 10 mm (Reproduced from Powter et. al., 2010, fig. 6c).

Three species of *Heteroptychodus* have been reported so far. They are *Heteroptychodus steinmanni* Yabe & Obata, 1930, *Heteroptychodus kokutensis* Cuny, Laojumpon, Cheychiw, Lauprasert, 2010 and *Heteroptychodus chuvalovi* Nessov, Glückman and Mertiniene, 1991 The type species *H. steinmanni* was relatively well-studied and both anterior and posterior teeth were described by Cappetta et al. (2006), whereas for *H. kokutensis*, only lateral teeth were reported previously. Lateral teeth of *H. kokutensis* are generally flat without bulging, as seen in the Thai type species (Cuny et al., 2010b).

Heteroptychodus cf. *steinmanni* Yabe and Obata, 1930

(Figure. 4.5)

cf.
1930 *Heteroptychodus steinmanni* Yabe & Obata, 1930: Pl II, fig 6–8 (original description)
2003 *Heteroptychodus steinmanni* Yabe & Obata, 1993: Cuny et al., pp. 52, fig. 1G–K.
2006 *Heteroptychodus steinmanni* Yabe & Obata, 1993: Cuny et al., pp. 27, fig. 4A–H.
2006 *Heteroptychodus steinmanni* Yabe & Obata, 1930: Cappetta et al., pp. 551, fig. 6A–M.

Materials examined. Two isolated teeth, incomplete, no root preserved. Specimens B3001–B3002.

Description. The best preserved specimen, B3001, although slightly broken, measures 15 mm mesio-distally and 15 mm labio-lingually. Although the outline B3001 is not well preserved, it is observable to be labio-lingually broad and the crown has a sigmoidal outline. In occlusal view (Figure 4.5A), the surface of the crown is ornamented by 25 transverse ridges oriented mesio-distally. There is no marginal area on the crown. These transverse ridges are closely packed and parallel to each other. Labio-lingually oriented short ridges originate from the lingual side of each transverse ridge. These short ridges are non-branching and almost parallel to each other and they do not connect to the adjacent transverse ridges. The best preserved specimen B3001 (Figure 4.5B) is interpreted as an anterior tooth because its crown shows high convexity and its sigmoidal outline indicates the presence of a bulge.

Discussion. The species *Heteroptychodus steinmanni* was erected by Yabe and Obata (1930) based on a single isolated tooth from the Tatsukawa Formation of the Monobegawa Group located in Yanagidani province of Awa in Shikoku, Japan, and was dated to be Hauterivian (Cuny et al., 2005; Goto et al., 1996). Later, more *H. steinmanni* teeth has been reported from the Khok Kruat Formation of Thailand (Cappetta et al., 2006). Compared to the previously known occurrences, the Malaysian specimens clearly exhibit the main characteristics of *Heterptychodus,* and are especially similar to the specimens from Thailand (Cappetta et al., 2006), by having transverse ridges running from mesial to distal ends with numerous short ridges perpendicular to the transverse ridges. Also, the Malaysian specimens show a broader rather than longer parallelogram outline and sigmoidal outline, which are also important characteristics to be identified as *H. steinmanni*.

A well-preserved set of *H. steinmanni* has been reported from the Khok Kruat Formation, dated to be Late Jurassic to Aptian in age (Cappetta et al., 2006). A specimens identified as *H. steinmanni* has been reported from the Phu Kradung Formtion(Cuny et al., 2003), but the identification is questionable.

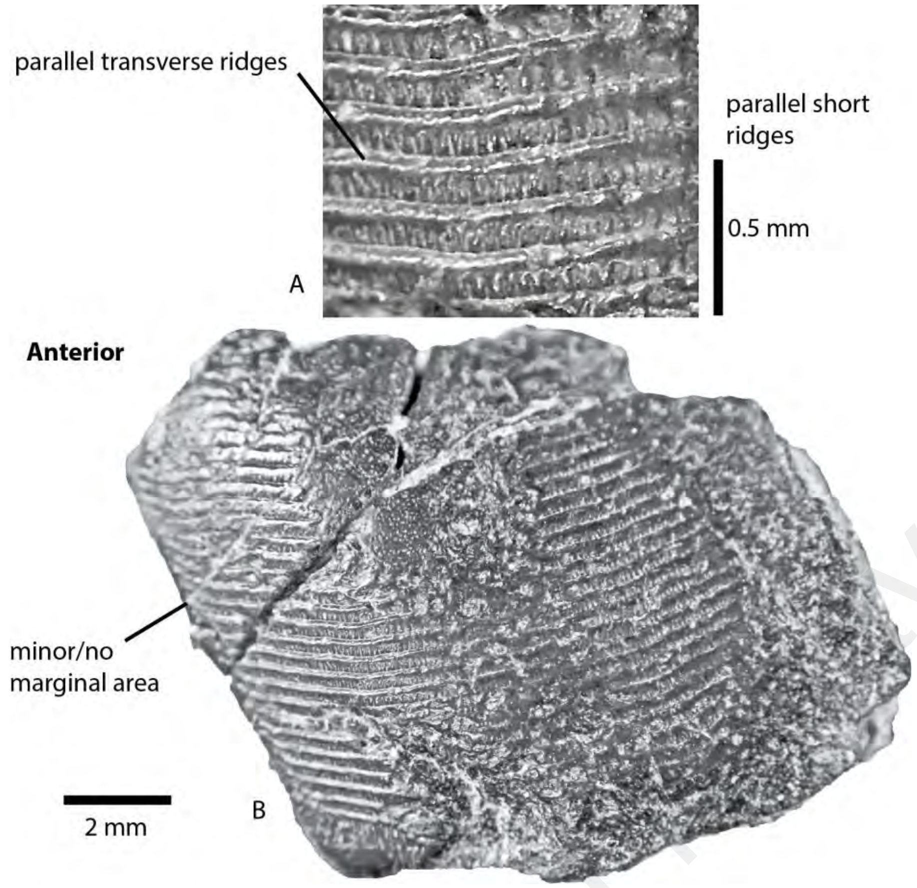


Figure 4.5 *Heteroptychodus steinmanni* from Pahang. Anterior tooth Specimen B3001 in A. Closed up observation; B occlusal view. Scare 2 mm.

Table 4.3 Dental characteristics of *Heteroptychodus steinmanni* (Malaysian specimens).

Dentition Arragement	**Anterior**	**Posterior**
Characteristics	**B3001**	**B3002**
Broken/complete	broken	broken
Outline/Shape	rhombic (broken)	?
Interlocking system	lingual side has a concave straight wall, concave at labial. Lingual edge is thicker than labial	
Traverse ridges Number	25	at least 12
Tranverse ridges parallel to each other / anastomosing	parallel	parallel
Short ridges pattern (braching/parallel)	parallel, not connecting tranverse ridge	parallel, not connecting tranverse ridge
Strong edge	yes	?
Stort ridges attaining basal/edge	basal	?
Crown Shape (flat/bulging)	bulky	flat
Bulging position	?	-
Marginal Area	not present	minor with ridges minor branching near mesio/distal edge
Sigmoidal curvature	strong sigmoidal	potentially sigmoidal due to abrasion observed at some part
Size	15mm MD, 15 mm LL	6.5 mm MD, 5.5 mm LL

MD – Mesial to distal

LL – Labial to lingual

Heteroptychodus kokutensis **Cuny, Laojumpon, Cheychiw & Lauprasert, 2010**

(Figures 4.6 – 4.9)

2010 *Heteroptychodus kokutensis* Cuny, Laojumpon, Cheychiw & Lauprasert, 2010: pp. 419, fig. 3A–L (original description).
2007 *Heteroptychodus sp.* Cuny, Laojumpon, Cheychiw & Lauprasert, 2010: Cuny et al., pp. 351, fig. 1.

Materials examined. 31 isolated teeth, no root preserved. Specimens B3003–3035, A3001–3002, A1001.

Description. Well preserved teeth show quadrilateral and elongated outline with sharp to rounded corners. All teeth are generally narrowed labio-lingually and slightly convex from labial or lingual view. Specimens size ranges from 3 mm to 8 mm labial-lingually, 6 mm to 16 mm mesio-distally. From occlusal view, surface of the crown bears 4 to 20 transverse ridges running from mesial to distal extremities. Secondary short ridges originated from the lingual side of each transverse ridge. In some of the specimens, these short ridges are non-parallel to each other. They tend to anastomose and connect adjacent transverse ridges to form a wavy pattern and pitted surface (Figure 4.8D–F). In some other specimens, the transverse ridges are parallel to each other. The labial surface is slightly concave and perpendicular to the occlusal surface, while the lingual surface is strongly concave, causing the occlusal surface to overhang its base. A narrow oblique surface is present in between the occlusal and labial surfaces of the crown. Both labial and lingual edges of the crown are sharp and angular. From mesial or distal view, the labial end is thicker than the lingual one. A very narrow marginal area is present near the lingual edge, occupied by short ridges with a branching and anastomosing pattern.

The anterior tooth (Figure 4.6A–I) is characterised by pronounced labio-lingually oriented bulge near the mesial third. Its mesial end extends obliquely beyond the bulge. Transverse ridges are curvy and form chevrons across the bulge. Short ridges at the tip of each chevron tend to connect the adjacent transverse ridges (Figure 4.6D). Towards the distal end of the crown, transverse ridges end abruptly with a clear boundary. Towards the mesial end, the transverse ridges gradually branch and end at the edge. The posterior tooth (Figure 4.8A–F) is characterised by a non-bulging convex surface. Although it has no bulge, some weakly developed chevrons are still present on the mesial third of the crown.

The juvenile teeth (Figure 4.9A–J) is much more elongate and narrow labio-lingually. The mesial end is often narrowing. In some smaller teeth, the distal end is also narrowing. Tooth size is generally smaller than the adult teeth, ranging from 3 mm to 8 mm mesio-distally, 1 mm to 3 mm labio-lingually. Up to 7 transverse ridges are present on the occlusal surface and only the relatively larger specimens have secondary short ridges generated from the transverse ridges. The anterior tooth bears small bulge near the mesial end with transverse ridges curved over the bulge. Beyond the bulge, the mesial end becomes angular to the crown and narrowing towards its extremity.

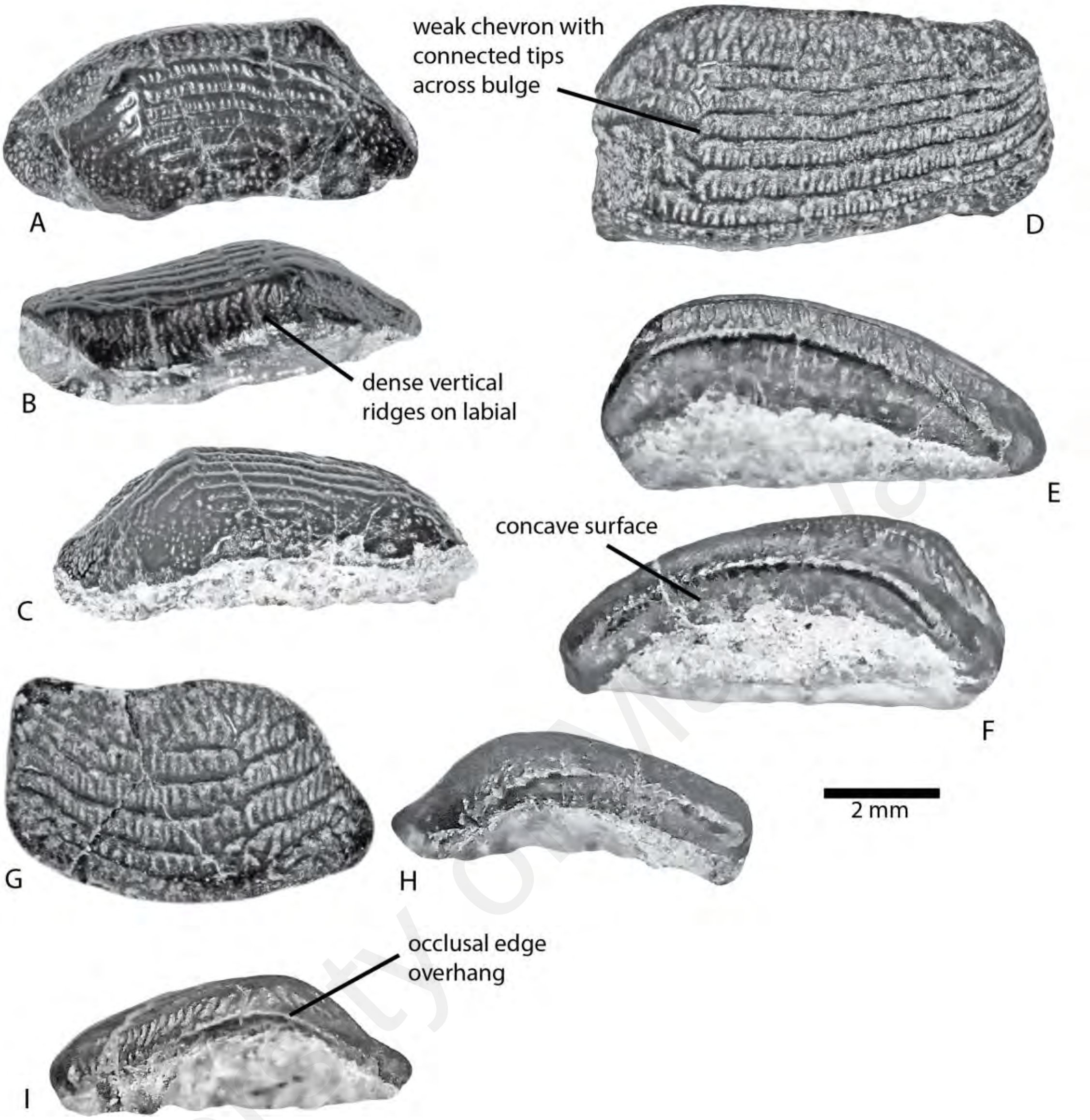


Figure 4.6 Anterior teeth of *Heteroptychodus kokutensis* from Pahang. Specimen A3001 in A occlusal view, B labial view, C lingual view; Specimen B3025 in D occlusal view, E labial view, F lingual view; Specimen B3026 in G occlusal view, H labial view, I lingual view. Scale bar 2 mm.

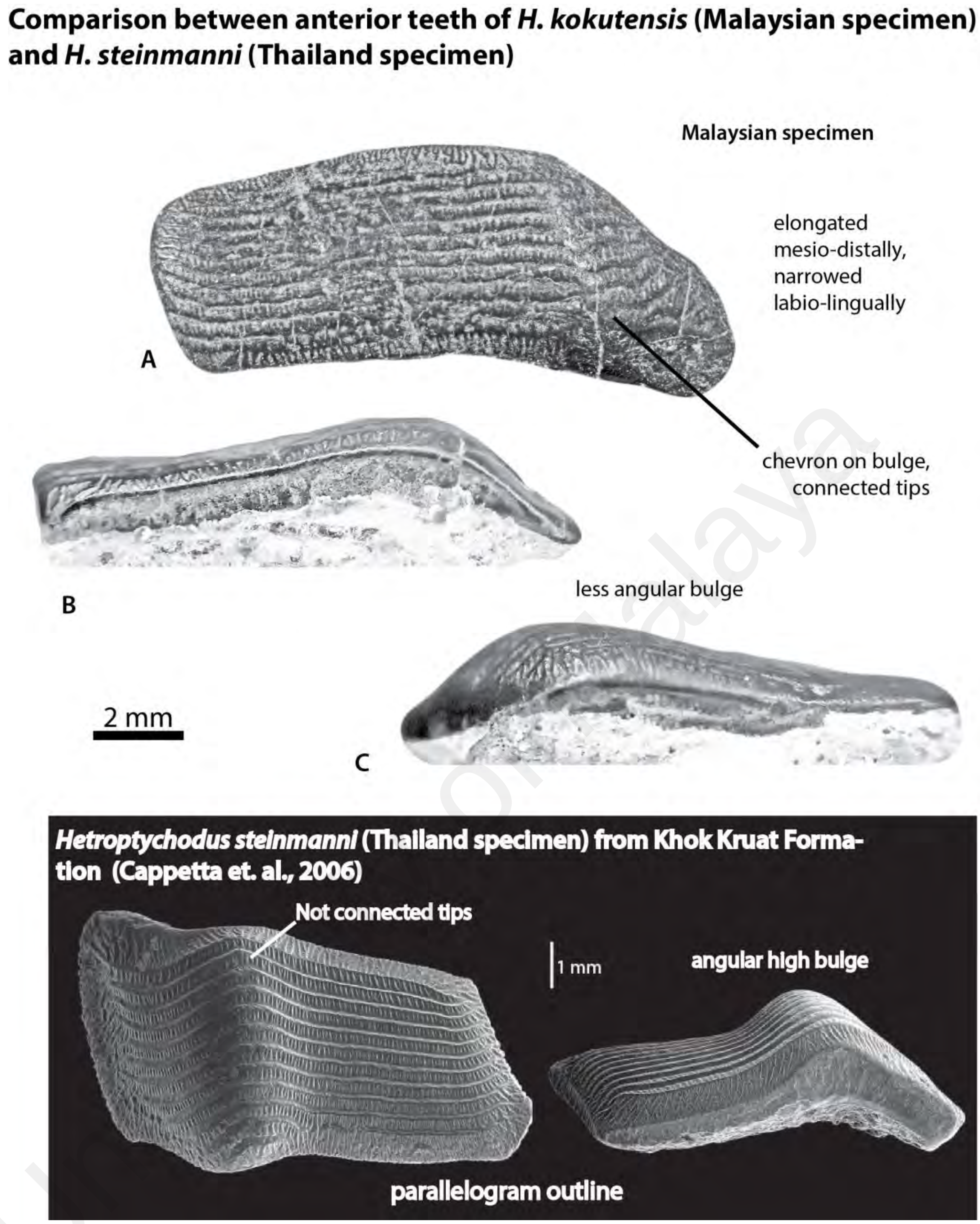


Figure 4.7 Comparison of *H. kokutensis* (Specimen B3010) with Thai *H. steinmanni*.

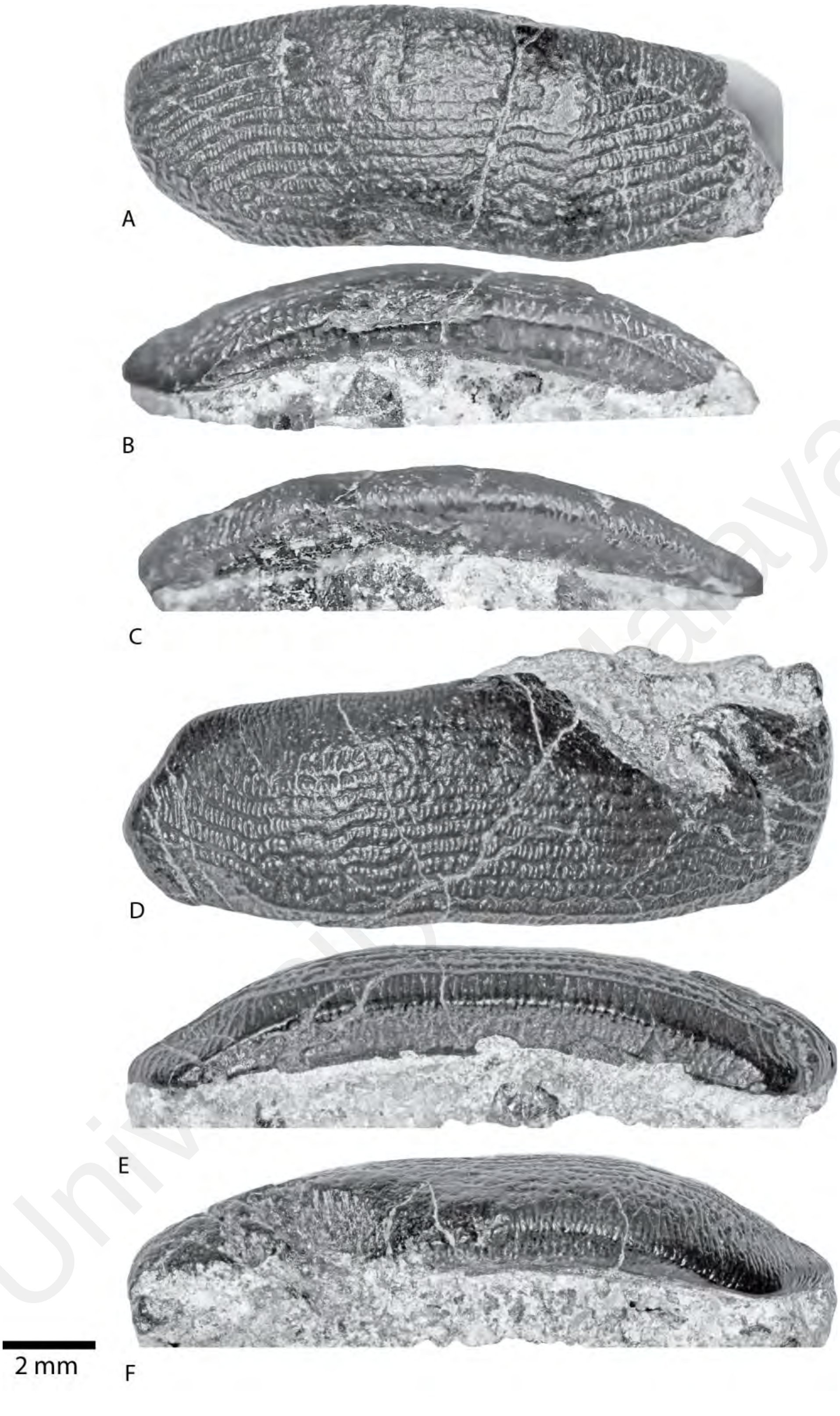


Figure 4.8 Posterior teeth of *Heteroptychodus kokutensis* from Pahang. Specimen B3014 in A occlusal, B labial, C lingual view; Specimen B 3008 in D occlusal, E labial, F lingual view. Scale bar 2 mm.

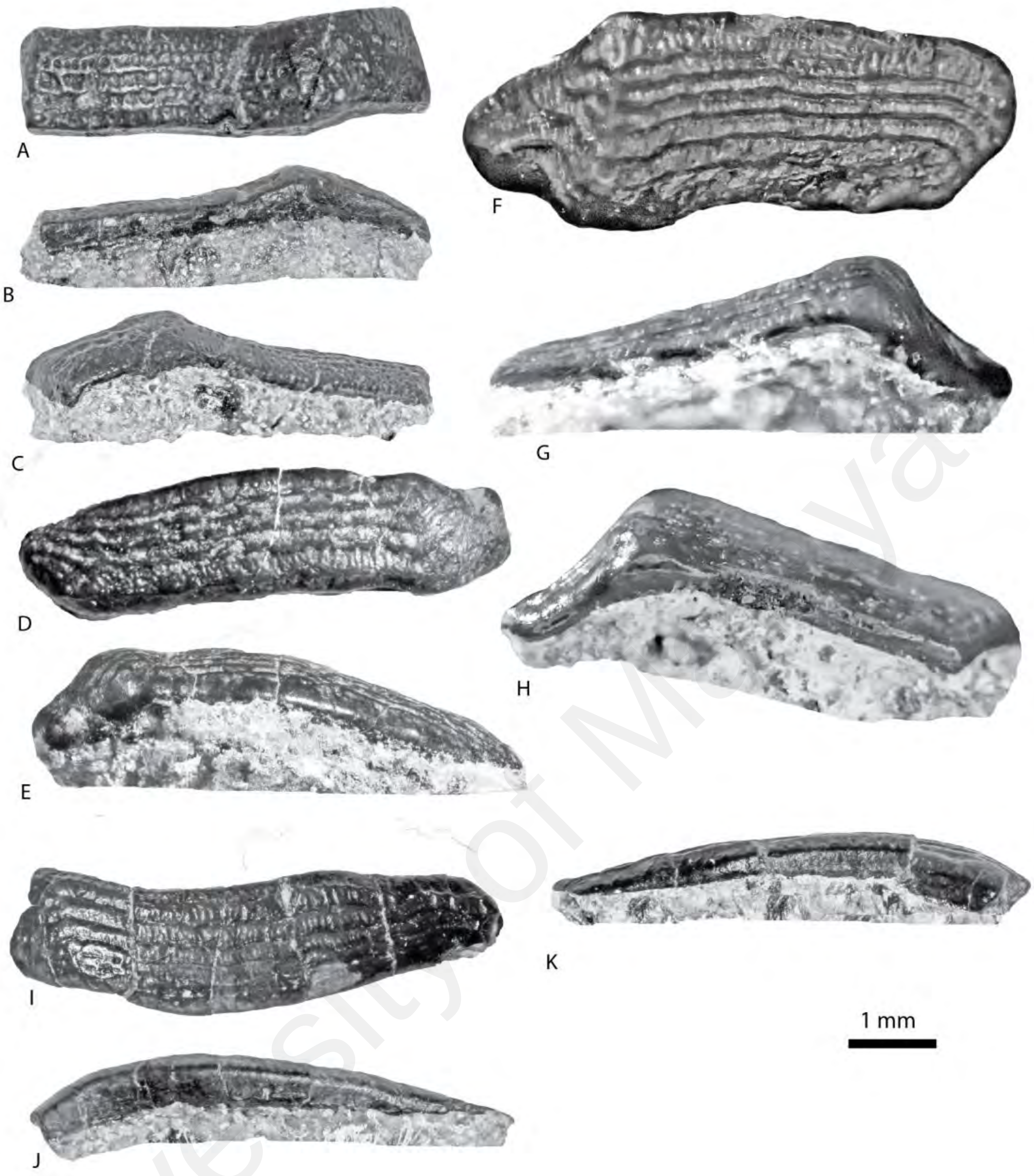


Figure 4.9 *Heteroptychodus kokutensis* from Pahang. B3028, anterior teeth in A occlusal, B labial , C lingual view; B3013 in D occlusal, E lingual view; B3029 in F occlusal , G lingual, H labial view. B3031, posterior tooth in I occlusal, J lingual, K labial view. Scale 1 mm.

Discussion. *Heteroptychodus kokutensis* is an endemic species known only from Kut Island and the Sao Khua Formation in Thailand so far (Cuny et al., 2010b; Cuny et al., 2014; Cuny et al., 2007). The Malaysian specimens possess the main characteristics of *H. kokutensis*. However, the Malaysian form also exhibits some unique features that are seen only in *H. steinmanni* and *H. chuvalovi*. This seems to blur the diagnostic characteristics of each species and complicate the identification of this Malaysian form. Comparison among these species is summarised in Table 4.4.

Table 4.4 Comparison of *Heteroptychodus kokutensis* (Malaysian specimens) with *H. kokutensis* from Thailand (Cuny et al., 2010), *H. steinmanni* (Cappetta et al., 2006) and *H. chuvalovi* (Cuny et al., 2008).

Characteristics	***H. kokutensis* (Malaysian)**	***H. kokutensis* (Thai type specimens)**	***H. steinmanni* (Thai specimens)**	***H. chuvalovi (Mongolian specimen)***
Outline	More elongated mesio-distally than labio-lingually	More elongated mesio-distally than labio-lingually	broader than long, roughly parallelogram-shaped	More elongated mesio-distally than labio-lingually
Pattern of mesio-distal oriented transverse ridges	Anastomose; Parallel; Mixture of anastomose & parallel	Anastomose only	Parallel only	Parallel to wavy
Presence of bulge in the anterior tooth	Low bulge near mesial third	No anterior tooth reported	High angular bulge near mesial third	No bulge.
Vertical ridges on labial & lingual faces	Present in some, absent in some.	Presence	Absence	Presence only on lingual face
Presence of Juvenile teeth, outline	Present, elongated	Absent	Present, rhombic	Absent
Presence of chevrons across the bulge	Present	Absent	Absent	Present

Firstly, all of the Malaysian specimens show typical *H. kokutensis* tooth morphology, which is elongate mesio-distally and narrow labio-distally. Specimens of *H. kokutensis* from Thailand are all flat without bulging and therefore were identified as lateral teeth. The first anterior tooth of *H. kokutensis* is reported here from Malaysian fauna. The anterior tooth of *H. kokutensis* from Malaysia is distinguishable from the anterior tooth of *H. steinmanni* because it has a low bulge, contrary to the high angular bulge in *H. steinmanni* (Figure 4.7). Measurements have been taken on both Malaysian and Thai anterior specimens. The Malaysian specimens show a higher ratio of mesio-distal length to bulge height, ranging from 6.4 to 8 as compared to 3.7 to 4.4 for the Khok Kruat specimens. These measurements suggest that the tooth morphology of *H. kokutensis* and *H. steinmanni* is well distinguishable.

Table 4.5 Comparison of mesio-distal length to bulge height ratio of anterior teeth of *Heteroptychodus steinmanni* and anterior teeth of *Heteroptychodus kokutensis.*

Specimen number	Mesio-distal length (mm)	Bulge Height (mm)	Mesio-distal length : Bulge height ratio
Malaysian specimens			
B3026	6	0.9	6.7
B3032	7	1.1	6.4
B3037	8	1	8
B3038	13	1	13
(Cappetta et al., 2006) measurement taken on hand specimens			
SDRC 11	8.8	2	4.4
SDRC 13	6.6	1.8	3.7

*Higher ratio indicates a gentler and lower bulge.

Secondly, though the specimens are quite consistent with elongated outline, the surface ornamentation is not as consistent. Some of the Malaysian specimens show typical surface ornamentation of *H. kokutensis*, which is anastomosing transverse ridges on the occlusal face with vertical ridges on the lingual and labial faces of the tooth.

However, some of the specimens exhibit surface ornamentation more similar to that of *H. steinmanni*, by having parallel transverse ridges and secondary short ridges not connecting to the adjacent transverse ridges. It is observable that the transverse ridges become wavy on some part of the crown, indicating that the ridges pattern could be subject to intraspecific variation and might not be a good indicator to differentiate *H. steinmanni* and *H. kokutensis*.

Thirdly, the transverse ridges become wavy and form chevrons across the bulge in all *H. kokutensis* specimens from Malaysia. This characteristic is absent in both *H. steinmanni* and *H. kokutensis*. In fact, it is the main characteristic of *H. chuvalovi* reported from Mongolia (Cuny et al., 2008). This intermediate pattern of surface ornamentation shows that there is a need to revise the diagnosis of each species under the genus *Heteroptychodus* as the current diagnosis could not draw clear boundaries among different species.

Generally, the *H. kokutensis* found in this study has a parallelogram outline. However, among the specimens found, there is a set of specimens that possess complete but weakly developed surface ornamentation of *H. kokutensis*, their size is smaller and their morphology is distinctively narrower labio-lingually. All of them possess a bulge near the mesial third which is similar to an anterior tooth (Figure 4.9). This bulging morphology recalls the juvenile teeth of *Heterodontus* — a modern day analogue to hybodont. Powter et al. (2010) demonstrated that the dentition of juvenile *Heterodontus portusjacksoni* has a higher proportion of cuspidate teeth compare to that of the subadults and adults. This leads to an interpretation that these Malaysian specimens that are equipped with bulges, are possible to be the juvenile teeth of *H. kokutensis*.

Juvenile teeth of *H. kokutensis* have never been reported elsewhere. Its presence in the Malaysian Fauna, if confirmed, suggests that *Heteroptychodus* was capable of reproducing in freshwater environment and the species might have lived in the freshwater for its whole life.

Most fossils found in the Pahang locality are in strongly abraded and fragmented condition, indicating that the teeth were transported and not preserved in situ in the original habitat. The current might have picked up both juvenile and adult teeth at different parts of the river system and gather them at one depositional site.

Table 4.6 Dental characteristics of *Heteroptychodus kokutensis* (Malaysian specimens).

Dentition Arragement	Anterior	Anterior	Anterior	Anterior	Anterior	Anterior	Anterior	Anterior	Anterior
Specimen	**B3009**	**B3010**	**B3019**	**B3012**	**B3021**	**A1001**	**B3026**	**B3025**	**A3001**
Broken/complete	Broken	Complete	Broken	Broken	Broken	Complete	Complete	Complete	complete
Outline/Shape	Elongated,	elongated, bulky, monolobate	elongated	elongated; monolobate	elongated	elongated, monolobate	rhombic to rectangular, monolobate	elongated, bulky	elongated, end lightly arched towards labial
Interlocking system	lingual side has a concave straight wall, concave at labial. Lingual edge is thicker than labial								
Traverse ridges Number	13	11	7	6	11	9	5	7	6
Tranverse ridges parallel to each other / anastomosing	parallel with minor degree of wavy ridges at some part	abraded, parallel	abraded	parallel	parallel	parallel	parallel	parallel	parallel
Short ridges pattern (braching/parallel)	parallel with minor degree of wavy ridges at some part	parallel, not connecting tranverse ridges	abraded	parallel, partly connecting tranverse ridges	parallel, partly connecting tranverse ridges	abraded	parallel not connecting tranverse ridges	parallel, not connecting tranverse ridges	parallel
strong edge	yes	yes	yes	yes	?	yes	yes	yes	yes
Stort ridges attaining basal/edge	edge	edge	?	basal	?	?	edge	edge	?
Crown Shape (flat/bulging)	bulge assymmetrically with Chevron transverse ridges across the bulge	bulge assymmetrically with Chevron transverse ridges across the bulge	bulge where transverse ridges curves over the bulge	bulging, transverse ridges over bulge not observable	bulging	gentle bulge at center, transverse ridges weakly bend across bulge	bulge assymmetricall y with Chevron transverse ridges across the bulge	bulge assymmetricall y with Chevron transverse ridges across the bulge	bulge
Bulging position	mesial third	mesial third	mesial third	?	mesial third	mesial third	mesial third	mesial third	mesial third
Marginal Area	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	?	relatively broad with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	no present	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	broader marginal area with pitted/branchi ng secondary ridge
Sigmoidal curvature	slightly sigmoidal/	slightly sigmoidal	slight arch	?	slight arch	slight sigmoidal	slight arch	slight arch	near mesial
Size	8mm MD, 5.5mm LL	13 mm MD, 5mm LL	10 mm MD, 4 mm LL	7.5 mm MD, 3mm LL	10 mm MD, 5 mm LL	12 mm MD, 4mm LL	6 mm MD, 4 mm LL	7 mm MD, 3 mm LL	7 mm MD, 3 mm LL

MD – Mesial to distal LL – Lingual to labial

Table 4.5 Continued

Dentition Arragement	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior	Posterior
Specimen	**B3008**	**B3017**	**A3002**	**B3022**	**B3016**	**B3023**	**B3024**	**B3003**	**B3011**	**B3006**	**B3014**	**B3005**	**B3020**
Broken/complete	Almost complete	Broken	Broken	Broken	Broken	broken	complete	Broken	Broken	Broken	Complete	Broken	Broken
Outline/Shape	elongated	elongated	?	elongated	?	?	parallelogram no bulge, overall flat	potentially elongated	elongated	elongated	elongated	elongated	elongated
Interlocking system	lingual side has a concave straight wall, concave at labial. Lingual edge is thicker than labial												
Traverse ridges Number	10	9	at least 8	10	Pitted surface	abraded pitted surface	20	11	7	at least 14	11	at least 13	13
Tranverse ridges parallel to each other / anastomosing	anastomosing	anastomosing	anastomosing	anastomosing	abraded	anastomosing	anastomosing	parallel with minor degree of wavy ridges at some part	parallel with minor degree of wavy ridges at some part	parallel to each other but slightly wavy	parallel with minor degree of wavy ridges at some part	abraded, parallel	parallel
Short ridges pattern (braching/parallel)	non parallel, connecting tranverse ridges	non parallel, connecting tranverse ridges	some are parallel, some are wavy and connecting transverse ridges	non parallel, connecting tranverse ridges	?	non parallel, connecting tranverse ridges	non parallel, connecting tranverse ridges	parallel, abraided	parallel, not connecting tranverse ridges	parallel, not connecting tranverse ridges	parallel, not connecting tranverse ridges	abraded	parallel, not connecting tranverse ridges
strong edge	yes	yes	?	yes	?	yes	yes	yes	yes	yes	yes	yes	yes
Stort ridges attaining basal/edge	basal	basal	?	basal	?	basal	?	basal	edge	basal	edge	abraded	edge
Crown Shape (flat/bulging)	flat	flat	flat?	flat	?	slight arch	flat	?	?	flat	flat	flat	flat, sightly concave
Bulging position	-	-	-	-	?	-	-	-	-	-	-	-	-
Marginal Area	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	?	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	?	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	minor with branching secondary ridges (near labial edge)	some marginal area with pitted surface due to abrasion	minor with branching secondary ridges (near labial edge)
Sigmoidal curvature	slight arch	slightly sigmoidal at one side (preservation?)	?	slight sigmoidal	potentially sigmoidal	slight sigmoidal	slight sigmoidal	slight arch	slight arch	slight arch	slight arch	?	slight concave
Size	15 cm MD, 6 mm LL	7mm MD, 4 mm LL	3mm LL, 4 mm MD	10 mm MD, 6 mm LL	4 mm MD, 3mm LL	7 mm MD, 5 mm LL	16 mm MD, 8 mm LL	6mm MD, 4.5 mm LL	6mm MD, 3 mm LL	6 mm MD, 3 mm LL	14mm MD, 5mm LL	4 mm LL, 7mm MD	9 mm MD, 5 mm LL

MD – Mesial to distal LL – Lingual to labial

Table 4.7 Dental characteristics of juvenile teeth of *Heteroptychodus kokutensis* (Malaysian specimens).

Dentition Arragement	**Anterior**	**Anterior**	**Anterior**	**Anterior**	**Anterior**	**Anterior**	**Posterior**	**Posterior**
Specimen	**B3027**	**B3028**	**B3029**	**B3035**	**B3030**	**B3032**	**B3031**	**B3033**
Broken/complete	broken	complete	complete	broken	complete	complete	complete	broken
Outline/Shape	narrow & elongated. Mesial end is narrowing than the other (monolobate)	rectangular with cornered ends at both extremities	elongated, bulge, one end narrowing	elongated, bulge, one end narrowing	elongated, both extremities are narrowing	elongated, both extremities are narrowing	elongated, the mesial (?) extremity narrowing to become a sharp tip	elongated
Interlocking system	concave at labial side, convex at lingual side							
Traverse ridges Number		4	6	3	5	5	6	7
Tranverse ridges parallel to each other / anastomosing	parallel	parallel, connected by secondary ridges forming anastomose	parallel	parallel	Yes from lingual most two ridges	parallel	6 main ridges running across from mesial-distal ends	parallel with minor degree of wavy ridges at some part
Secondary ridges pattern (braching/parallel)	parallel	anastomos, connecting tranverse ridges, forming pitted appearance	parallel	abraded	parallel	parallel	parallel	parallel, not connecting tranverse ridges
Ridges attaining to edge/basal part	edge	edge	edge	not observable	edge	edge	edge	attaning edge
flat/bulging	bulge, transverse ridges form chevrons	bulge, transverse ridges curved on bulge	bulge, transverse ridges curved on bulge	bulge, transverse ridges curved on bulge	bulge, transverse ridges curved on bulge	bulge, transverse ridges curved on bulge	flat	no bulging observed
Marginal area	No	branching secondary ridges (near labial edge)	no	smooth	no	no	no	some marginal area with only secondary ridges at labial side
Bulging position	near mesial	near mesial	near mesial	near mesial	near mesial	near mesial	-	-
Sigmoidal curvature	slight sigmoidal	slight sigmoidal	slight sigmoidal	slight arch	slightly arch	slightly arch	slight arch	slight arch
Size	3mm MD, 1 mm LL	8 mm MD, 3 mm LL	7mm MD, 3mm LL	4mm MD, 1 mm LL	6 mm MD, 1 mm LL	6 mm MD, 1 mm LL	6 mm MD, 2 mm LL	6mm MD, 3 mm LL

MD – Mesial to distal LL – Lingual to labial

Genus: *Isanodus* Cuny, Suteethorn, Khamha, Buffetaut & Philippe, 2006

Type species. *Isanodus paladeji* Cuny, Suteethorn, Khamha, Buffetaut, Philippe, 2006

Discussion. *Isanodus* was first reported from the Sao Khua Formation of Thailand (Cuny et al., 2006). Two species were erected under the genus *Isanodus*, namely *Isanodus paladeji* Cuny, Suteethorn, Khamha & Buffetaut, Philippe, 2006 and *Isanodus nongbualamphuensis* Khamha, Cuny & Lauprasert, 2015. Only *I. nongbualamphuensis* is found in Malaysia in this study.

Initially, *Isanodus* was placed in the family Lonchidiidae because it possesses the characteristics of the family, such as low cusp, low root and well developed labial protuberance. Moreover, *Isanodus* has moderately to strongly developed occlusal crest, which is a common feature shared by the genera *Lissodus*, *Lonchidion*, *Vectiselachos* and *Parvodus* in the family Lonchidiidae (Rees & Underwood, 2002). Cuny et al. (2006) compared *Isanodus* with *Lissodus nodosus* described by Duffin (1985) and suggested close similarity of these two genera based on similar heterodonty and presence of labial nodes. However, *Lissodus* was later excluded from the family Lonchidiidae due to its similarity to *Acrodus* (Rees, 2008). *Lissodus* has not been assigned to any family since then. Therefore, *Isanodus* was also removed from the family Lonchidiidae and placed in the family *incertae sedis* for now (Cuny et al., 2010b).

Isanodus is defined by having one longitudinal crest with up to one mesio-distal V-shaped ridge on the labial side, and up to four mesio-distal V-shaped ridges on the lingual side. It also has a labial peg, a pyramidal main cusp with a triangular base and well developed labial nodes on the mesial and distal parts of anterolateral and posterolateral teeth (Cuny et al., 2006).

The dentition of *Isanodus* was reconstructed based on *Lissodus nodosus* (Seilacher 1943) described in Duffin (1985) since they are interpreted to be closely related

(Cuny et al., 2006). Later, the dentition reconstruction was revised by Khamha et al. (2015).

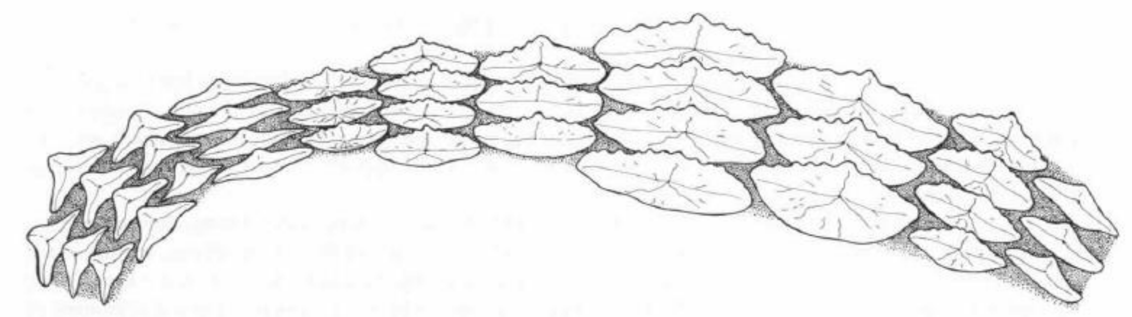


Figure 4.10 Reconstruction of the dentition of *Lissodus nodusus* (Seilacher) in occlusal view (Duffin, 1985), used as the basis for *Isanodus* dental arrangement.

Assumptions used for the dentition reconstruction of *Isanodus* are as below (Cuny et al., 2006; Khamha et al., 2016):

1. Non-gradient monognathic heterodonty.
2. A full series consists of four types of teeth, namely the anterior teeth, the anterolateral teeth, the posterolateral teeth and the posterior teeth.
3. Symmetrical crown on the anterior teeth, increasingly asymmetrical crown towards the posterior side.

However, these assumptions, when applied to the two species, *Isanodus paladeji* and *Isanodus nongbualamphuensis* respectively, lead to the inconsistencies below:

1. The revised *I. paladeji* by Khamha et al. (2015) has consistent crown height from anterior to posterior position. Whereas for *I. nongbualamphuensis*, the anterior and posterior teeth possess a high crown, whereas the anterolateral and the posterolateral teeth possess a low crown.
2. The revised *I. paladeji* has weaker longitudinal crest in the posterolateral and posterior teeth. Whereas for *I. nongbualamphuensis*, the longitudinal crest is weaker in the posterolateral tooth only.

3. The revised *I. paladeji* has a well-developed labial peg in the anterior tooth and a weakly developed one in the other teeth. Whereas for *I. nongbualamphuensis*, a labial peg is weakly developed in the anterior and posterior teeth and moderately developed in the anterolateral and posterolateral teeth.

The Malaysian forms provide a new hypothesis on the heterodonty pattern of the species, demonstrating a gradient monognathic heterodonty.

Isanodus nongbualamphuensis Khamha, Cuny & Lauprasert, 2015

(Figures 4.11–4.12)

2015 *Isanodus nongbualamphuensis* Khamha, Cuny & Lauprasert, 2015: pp. 5, fig. 3A–L

Materials examined. 23 isolated teeth, root not preserved. Specimens B3036–B3048, B4001–B4004, A3004–A3008, 001–004, A1005–A1006.

Description. The specimens are characterised by a triangular base and the pyramidal outline. The crown size ranges from 2 mm to 8 mm mesio-distally. A well-developed, bulky cusp is located mostly in the centre of the crown. One main ridge runs from mesial to distal ends across the crown, forming a longitudinal crest. Smaller ridges parallel to the longitudinal crest were developed at the lingual side of the cusp, with decreasing length towards the base of the crown. These ridges are kinked and are V-shaped on the cusp. The number of ridges ranges from one to three. Surfaces of the specimens are mostly abraded and do not show clear surface ornamentation. In the best preserved specimen (Figure 4.12), labio-lingually oriented short ridges perpendicular to the main ridges can be observed. The ridges tend to be anastomosed and form a pitted appearance. This specimen reveals that the surface ornamentation of all teeth is originally complex.

The presumed anterior tooth (Figure 4.11A–B) is characterised by a very high pyramidal crown with moderately developed labial peg. The tooth is elongated. A high cusp with narrow pointing apex is located at the center of the crown. No labial node is observed.

The presumed anterolateral teeth (Figure 4.11C–E) are characterised by a high crown with a bulky cusp at the center of the tooth. Due to poor preservation, it is unknown whether the specimens are symmetrical in outline. The apex of the crown is abraded, yet, it is observable that the main longitudinal crest and the secondary short ridges are moderately developed. Up to 10 well-developed labial nodes were observed in the best preserved specimen A3005. These nodes are located at the base of the crown and are pointing downwards.

The presumed posterolateral tooth (Figure 4.11F–H) has an elongated asymmetrical outline. The crown is high but relatively lower than the presumed anterior and anterolateral teeth. The cusp is bulky and well-developed, situated at the center of the crown. The mesial end is tapering and the distal end is often expanding. The main longitudinal crest is well-developed and up to four transverse ridges are present on the lingual side of the crest. The ridges form V-shape across the cusp and extend to the distal end. Labio-lingually oriented short ridges are well-developed from each of the transverse ridges. Labial peg is weakly developed. No labial node is observed.

The presumed posterior tooth (Figure 4.11I–K) is characterised by a low crown. It has an asymmetrical elongate outline, where the well-developed cusp is located near the mesial end. The best preserved specimen show a tapering mesial end. The tooth surface is ornamented by one weakly developed main crest and up to four transverse ridges running across the cusp and extending towards the distal side. No labial node is observed. A labial peg is weakly developed.

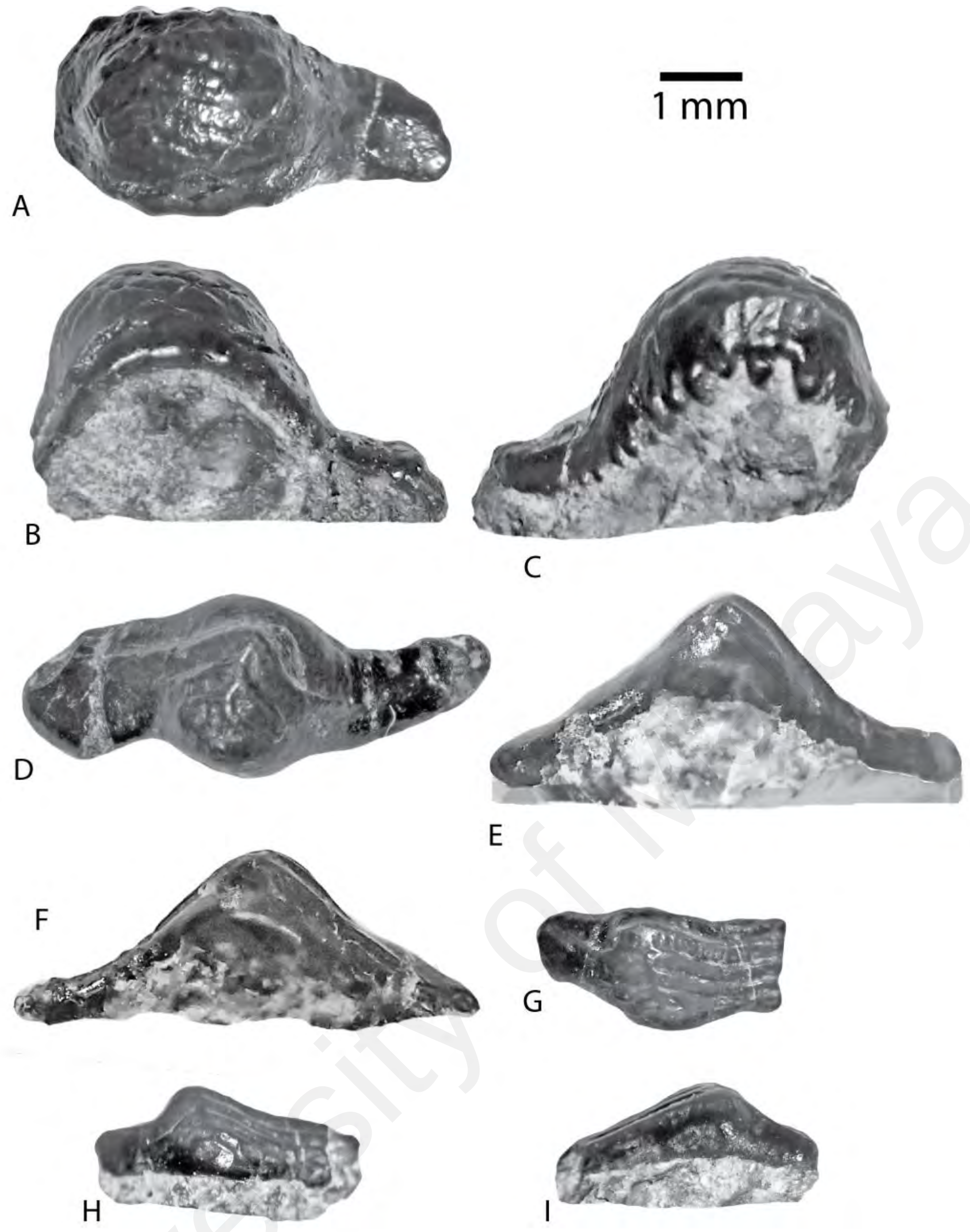


Figure 4.11 *Isanodus nongbualamphuensis* from Pahang. A3005, anterolateral tooth A occlusal, B lingual, C labial view; 001, posterolateral tooth in D occlusal, E labial and F lingual view; B3041, posterior tooth in G occlusal, H lingual, I labial view. Scale bar 1 mm.

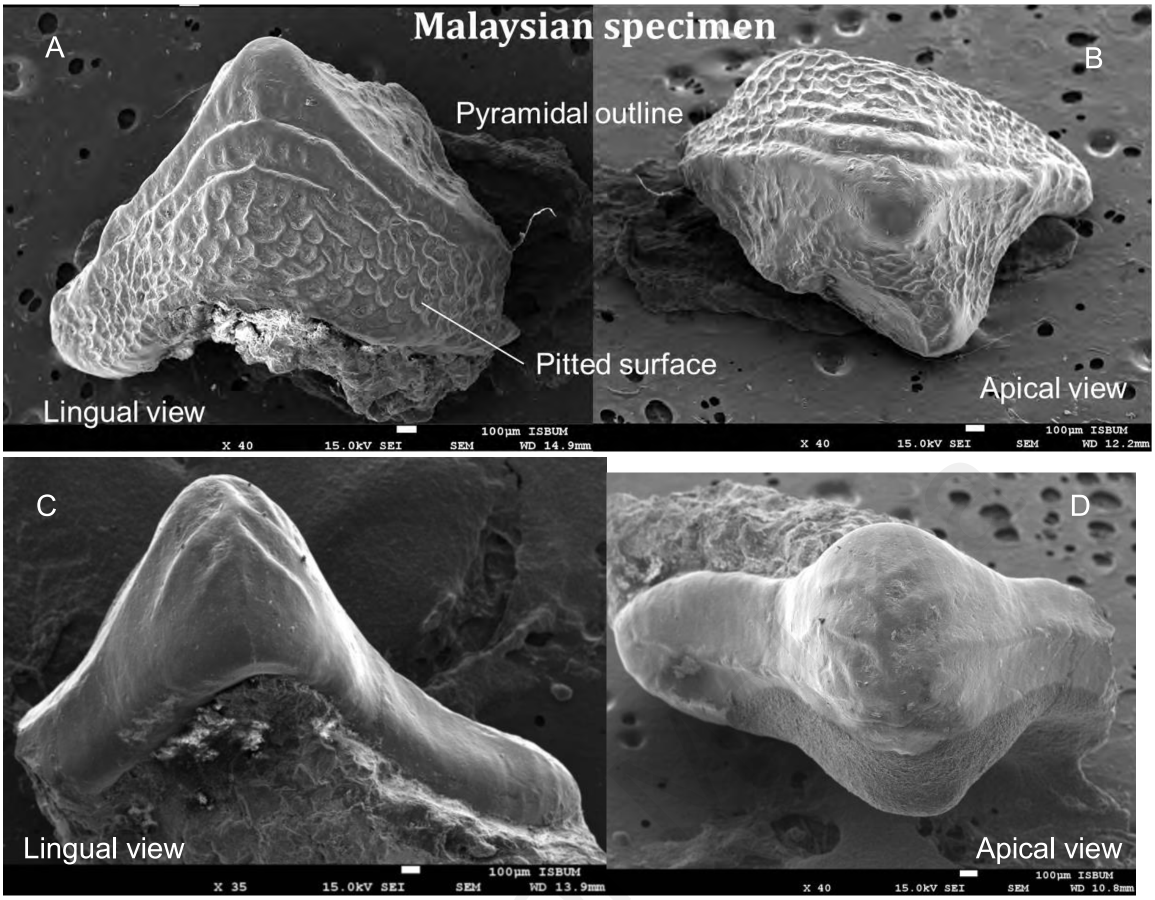


Figure 4.12 SEM images of anterior tooth of *Isanodus nongbualamphuensis* from Pahang. Specimen B3044, in A lingual, B apical view, showing unworn surface of the species. Sepcimen B3036 in C lingual, D apical view, showing worn surface.

Discussion. *Isanodus nongbualamphuensis* was erected by Khamha et al. (2016). It occurs in the Phu Phan Thong locality of north-eastern Thailand, which belongs to the Sao Khua Formation. The species is characterised by its complex surface ornamentation that is distinct from that of *Isanodus paladeji*. The surface ornamentation, which is mainly made of mesio-distal transverse ridges with secondary short ridges oriented perpendicular to them, is similar to the surface ornamentation of *Heteroptychodus.* Cuny (2008) suggested that *Isanodus* and *Heteroptychodus* are closely related. The Malaysian form exhibits a complex surface ornamentation that is identical to the type specimen of *I. nongbualamphuensis*, and therefore is identified to be conspecific. However, the Malaysian specimens generally possess much higher crowns compared to the Thai specimens.

A new dental reconstruction is suggested in this study because the Malaysian specimens demonstrate a gradient monognathic heterodonty, which is a more common heterodonty pattern as compared to non-gradient monognathic heterodonty.

This suggested dental reconstruction demonstrates decreasing crown height towards the posterior direction. Also, the crown becomes increasingly asymmetrical towards the posterior direction. Surface ornamentation are quite consistent in all teeth, except that the longitudinal crest is weakly developed in the posterior teeth.

Based on only isolated teeth and limited understanding on intraspecific variation of tooth characteristics, dentition of *Isanodus* are indeed highly hypothetical. Nevertheless, the new data from Malaysia provides a better understanding on the heterodonty pattern of *Isanodus*. Therefore, a revision for this genus should be carried out incorporating the new data in a near future.

Table 4.8 Dental characteristics of *Isanodus nongbualamphuensis* (Malaysian specimens).

I. nongbualamphuensis	**Anterior**	**Anterior**	**Anterior**	**Anterior?**	**Anterior**	**Anterior**	**Anterior**
Characteristic	**B3039**	**B3038**	**B3036**	**A3007**	**B3045**	**A3008**	**004**
Condition	Broken	Broken	Almost complete	Broken	Broken	broken	broken
Shape/outline (narrow, elongated/bulky)	bulky	bulky, triangular with one end broken, one end narrowing	narrow & elongated, with high cusp	bulky	bulky	elongated, high crown,with slight depression on both mesial & distal flanks	high crown
Triangular base	yes	yes	No	yes	?	?	yes
Cancave at labial edge, covex at lingual end	yes	yes	-	?	yes	yes	?
longitudinal crest (mesio-distal)	one main ridge from mesio to distal forming crest.			one main ridge from mesio to distal ends forming crest, abraded tip	one main ridge from mesio to distal forming crest.	one main ridge from mesio to distal ends forming crest, abraded tip	one main ridge from mesio to distal ends forming crest
Longitudinal ridges/tranverse ridges (mesio-distal)	3 small (short) ridges running across the bulge, decreasing in length towards lingual.	1 small ridges running across the bulge, decreasing in length towards lingual.	2 smaller ridges decreasing in length towards lingual side.	at least 2 ridges decreases in length towards lingual	3 smaller ridges at labial side extend to the one of the (mesio/distal) end.	no	1 small (short) ridges decreasing in length towards linguall.
Presence of labio-lingually oriented ridges	yes	no/weak	No	no	Yes from each longitudinal ridge	no	abraded
Is labio-lingually oriented ridges branching?	no	no	-	no	no, slight branching towards the basal	no	?
V-shape ridge (chevron) on labial side	yes	abraded/weak	yes	yes	yes	weakly	?
V shape ridge (chevron) fused together at the V-tips	yes	abraded/weak	Yes. V shape fused together at the tips	yes	yes	no	yes
Other surface ornamentation	smooth	smooth	smooth	smooth	no (smooth near the basal)	smooth	abraded
Crown shape (Symmetrical/Asymetrical)	?symmetrical	?	Symmetrical	?	symmetrical	?	asymmetrical
Labial node	no	labial node weakly developed, at least 3	No	no	**no**	no	no
Labial peg	no	no	no	no	no	no	yes
Size	2 mm MD, 2 mm LL	2 mm MD, 1 mm LL	3mm MD, 3.7mm H, 1.5 mm LL	2 mm MD, 1 mm LL	2 mm LL, 3 mm MD	3 mm MD, 2 mm LL	1.5 mm MD, 1 mm LL

MD – Mesial to distal LL – Lingual to labial

Table 4.8 Continued

I. nongbualamphuensis	Anterolateral	Anterolateral	Anterolateral	Anterolateral	Anterolateral
Characteristic	**A3004**	**A3005**	**003**	**002**	**005**
Condition	broken	almost complete	broken	broken	broken
Shape/outline (narrow, elongated/bulky)	bulky, elongated?	elongated, high crown, rounded cusp, one end narrowing	bulky	bulky , elongated?	bulky , elongated?
Triangular base	no	yes	?	?	?
Cancave at labial edge, covex at lingual end	yes	yes	yes	yes	yes
longitudinal crest (mesio-distal)	one main ridge from mesio to distal ends forming crest, abraded	one main ridge from mesio to distal ends forming crest, abraded tip	one main ridge from mesio to distal ends forming crest, abraded	one main ridge from mesio to distal ends forming crest	one main ridge from mesio to distal ends forming crest
Longitudinal ridges/tranverse ridges (mesio-distal)	3 ridges running from mesio- diatal extremities, no prominent main ridge	3 small (short) ridges decreasing in length towards linguall.	3 small (short) ridges decreasing in length towards linguall.	abraded	abraded
Presence of labio-lingually oriented ridges	weakly developed	yes	abraded	yes	yes
Is labio-lingually oriented ridges branching?	no branchiing.	yes	?	abraded	abraded
V-shape ridge (chevron) on labial side	very weakly developed	yes	?	abraded	abraded
V shape ridge (chevron) fused together at the V-tips	very weakly fused together	yes	abraded	abraded	abraded
Other surface ornamentation	no, smooth	smooth	abraded	abraded	abraded
Crown shape (Symmetrical/Asymetrical)	symmetrical	symmetrical?	?	?	?
Labial node	yes, weakly developed, 2	at least 10 moderate to well developed at the labial side	at least 3	at least 5	at least 5
Labial peg	no	no	weakly developed	no	no
Size	2 mm labial lingually, 4 mm mesio-distally	5 mm MD, 3 mm LL, 3 mm H	2.5 mm MD, 2 mm LL	3.5 mm MD, 2.5 mm LL	3.5 mm MD, 2.5 mm LL

MD – Mesial to distal LL – Lingual to labial

Table 4.8 Continued

I. nongbualamphuensis	Posterolateral	Posterolateral	Posterolateral	Posterolateral	Posterolateral	Posterolateral	Posterolateral
Characteristic	**001**	**B3037**	**B4003**	**A1005**	**B3046**	**B4004**	**B3040**
Condition	Complete	Complete	complete	broken	broken	complete	broken
Shape/outline (narrow, elongated/bulky)	elongated - triangular, with bulge, one end narrowing	elongated - triangular, with cusp, one end narrowing	elongated bulge, two end narrowing / wings	elongated, bulge, one end narrowing, the narrowing end is long	elongated, high crown, rounded cusp, one end narrowing	elongated - triangular, with bulge, monolobate, one end	elongated, high crown
Triangular base	yes	no?	yes	yes	yes	yes	?
Cancave at labial edge, covex at lingual end	yes	yes	yes	yes	yes	yes	?
longitudinal crest (mesio-distal)	one main ridge from mesio to distal ends forming crest,	one main ridge from mesio to distal ends forming crest	one main ridge from mesio to distal ends	one main ridge from mesio to distal ends	one main ridge from mesio to distal ends	one main ridge from mesio to distal ends	one main ridge from mesio to
Longitudinal ridges/tranverse ridges (mesio-distal)	3 small ridges running across the bulge, decreasing in length towards lingual.	3 small ridges running across the bulge, decreasing in length towards lingual.	3 ridges running across the bulge, ridges extending towards distal end	3 ridges running across the bulge, ridges extending towards distal end, one extended to mesial	3 small (short) ridges decreasing in length towards lingual.	2 small (short) ridges decreasing in length towards lingual.	2 small (short) ridges decreasing in length towards lingual.
Presence of labio-lingually oriented ridges	yes	yes	yes, strong	yes, weak	yes	no	abraded
Is labio-lingually oriented ridges branching?	yes	no	no	no	no	no	?
V-shape ridge (chevron) on labial side	yes	abraded	weak	yes	yes	yes	yes
V shape ridge (chevron) fused together at the V-tips	yes	abraded	no	no	yes	yes	abraded
Other surface ornamentation	smooth	smooth, some granule/discontinuous secondary ridges near labial edge	smooth	smooth	smooth	smooth	abraded
Crown shape (Symmetrical/Asymetrical)	bulge at the central. But mesio-distal extremities arch	bulge at the central. But mesio-distal extremities arch towards	assymetrical, bulge at center	asymmetrical	?	Asymmetrical, central bulge	?
Labial node	no	no	no	no	no	no	no
Labial peg	no	no	no	no	weakly developed	no	?
Size	6 mm MD, 3 mm LL	8 mm MD, 3 mm LL	7 mm MD, 3 mm LL	3 mm MD, 1 mm LL	3.5 mm MD, 2 mm LL	4 mm MD, 2 LL, 1.5 mm H	2 mm MD, 1.5 mm LL

MD – Mesial to distal LL – Lingual to labial

Table 4.8 Continued

I. nongbualamphuensis	Posterior	Posterior	Posterior	Posterior
Characteristic	**B3041**	**B4001**	**A3006**	**B3042**
Condition	Broken	Broken	broken	complete
Shape/outline (narrow, elongated/bulky)	narrow & elongated, with asymmetrical bulge. One of its end (mesio/distal) is narrowing than the other (monolobate)			
Triangular base	No	No	?	No
Cancave at labial edge, covex at lingual end	Yes	Yes	yes	yes
longitudinal crest (mesio-distal)	one main ridge from mesio to distal forming crest.	one main ridge from mesio to distal forming crest.	one main ridge from mesio to distal ends forming crest	one main ridge from mesio to
Longitudinal ridges/tranverse ridges (mesio-distal)	4 smaller ridges at labial side extend to the one of the (mesio/distal) end. It looks like a heteroptychodus, however, the narrowing end (mesio?) of the tooth has only one longitudinal main ridge extended on it.	2 smaller ridges at labial side extend to the one of the (mesio/distal) end.	3 ridges running across the bulge, ridges extending towards distal end	2 smaller ridges at lingual side extend to the one of the (mesio/distal)
Presence of labio-lingually oriented ridges	Yes on main crest only	Yes (abraded)	yes	no
Is labio-lingually oriented ridges branching?	no	non branching	no	-
V-shape ridge (chevron) on labial side	yes	yes	weak	abraided
V shape ridge (chevron) fused together at the V-tips	No	No	no	abraided
Other surface ornamentation	No	No	abraded	NO
Crown shape (Symmetrical/Asymetrical)	Asymetrical	Asymetrical	Asymmetrical	Asymmetrical
Labial node	No	no	no	no
Labial peg	no	no	no	no
Size	3mm mesio-distal, 1 mm labial-lingual	2mm mesio-distal, 1 mm labial-lingual	3,5 mm MD, 2 mm LL	4mm mesio-distally, 1.5 mm labial-lingually

MD – Mesial to distal LL – Lingual to labial

Isanodus? sp.

(Figure 4.13)

Materials examined. Two isolated teeth. Root not preserved. Specimen A3015, A3016.

Description. The specimens show elongated outline with tapering mesial and distal parts. The crown base is wider than the upper part of the crown. The mesio-distal measurement is 3 mm long in both specimens, while the labio-lingual length is 2 mm. A main cusp is located at the centre of the crown, showing a central expansion and a bulky outline. The crown surface is smooth without any surface ornamentation, except a moderately developed longitudinal ridge running from the mesial to distal extremities. A labial peg is well-developed in the centre of the crown shoulder on the labial face, with a weakly developed ridge connecting it to the apex of the cusp. The occlusal surface slopes gently towards the crown base. Specimen A3015 possess three well developed labial nodes located at the base of the crown. The labial nodes are located on both the mesial and distal sides. Specimen A3016, however, has five well developed labial nodes are observed, in which four are located at the distal side, and one located at the mesial side, resulting in an asymmetrical crown. On the lingual side, both specimens possess three weak to moderately developed lingual nodes, distributed constantly at the base of the crown.

Discussion. The Malaysian specimens share similarities with the specimens of *Isanodus*, by having one longitudinal crest running from the mesial to distal extremities on the occlusal surface, with a low centralized low cusp and a triangular base. However, this Malaysian form is lacking in the V-shaped surface ornamentation that defines *Isanodus*. Identical specimens were reported from the Sao Khua Formation of Thailand (Khamha et al., 2016), identified as *Isanodus* sp.. But the Malaysian specimens suggest that this form is distinguishable from *Isanodus* by its smooth surface ornamentation and moderately developed lingual nodes, which are not present in *Isanodus*. Additionally, labial peg in *Isanodus* is much wider and weaker than in this Malaysian form.

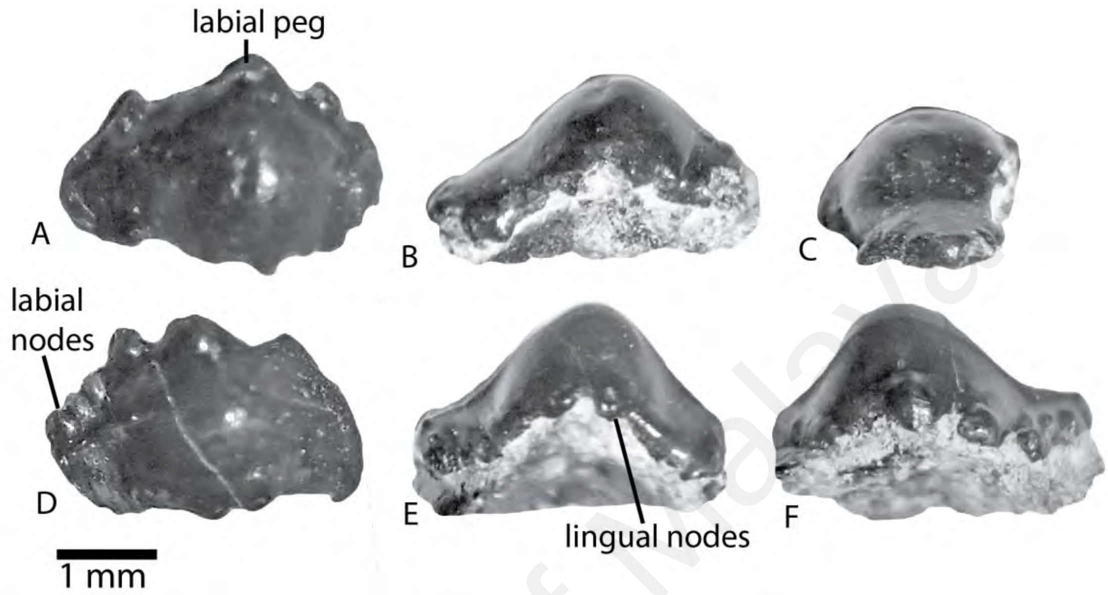


Figure 4.13 *Isanodus*? sp. from central Pahang. Specimen A3015 in A occlusal, B lingual, C mesial view; specimen A3016 in D occlusal, E lingual, F labial view. Scale 1 mm.

Compared to *Lissodus* Brough,1935, this Malaysian form shares similarities with *Lissodus* by having a similar crown shape, centralized cusp, moderate occlusal crest, strong labial peg and gently sloping occlusal surface. They, however, differ in surface ornamentation, as there are always some weak folds observed in *Lissodus* (Duffin, 1985; Rees & Underwood, 2002), and the lingual or labial nodes in most of the *Lissodus* species are not present or weakly developed. In *Lissodus nodosus* and *Lissodus leiodus,* nodes are only observed on the labial side and are weakly-developed (Duffin, 1985; Rees & Underwood, 2008).

As compared to *Lonchidion* Estes, 1964, the Malaysian form is clearly different from *Lonchidion* as the latter has a more gracile crown shape, and the crown base is always narrower than the upper part of the crown. In *Lonchidion*, the occlusal crest and crown shoulder are much stronger compared to the Malaysian form. Both *Lonchidion* and the Malaysian form possess labial peg, but the labial or lingual nodes in *Lonchidion* are either absent or weakly developed. A summary of comparison is shown in Table 4.9.

Table 4.9 Comparison of the Malaysian form with Lissodus, Lonchidion, Vectiselachos and Isanodus (based on Duffin (1985), Rees & Underwood (2002), Khamha et al., (2015), Cuny et al., (2006)).

Characteristics	**Malaysian form**	***Lissodus***	***Lonchidion***	***Vectiselachos***	***Isanodus***
Heterodonty	Not conclusive	Strong, monognathic	Moderate, mononagthic	Strong, monognathic	Weak-Moderate, mononagthic
Dentition type	Grinding?	Gasping-crushing	Cutting-crushing	Crushing	Clutching-grinding
Crown-shape	Low, wide, base is wider than upper part	Low, wide, base is wider than upper part	Gracile, base is narrower than upper part	Bulky	Low, wide, base is wider than upper part
Central cusp	Low-moderate	Low-moderate	Low-moderate	Minutes	Low-moderate
Lateral cusplets	Lacking	Non or Up to two pairs, minute	Up to three pairs, minute	Lacking	Lacking
Occlusal crest	Weak to Moderate	Moderate	Strong	Strong	Moderate – strong
Labial peg	Strong, lower in position	Strong, wider, lower in position	Strong, not supported by root	Weak, triangular	Weak
Crown shoulder	Occlusal surface slope gentle towards crown	Occlusal surface slopes gently towards crown	Moderate – strong	Strong	Occlusal surface slopes gently towards crown
Ornamentation	smooth	Numerous, weak folds	None to a few, weak folds	Moderate-strong Folds/granulae	Moderate to strong folds
Crown-root junction	-	Incised	Root larger	Crown larger	Crown overhang
Root-shape	Not preserved	Small, fairly low	Moderately large	Small, thin	Small, fairly low, projected lingually
Circular foramina at crown-root junction	Not preserved	Single row	Irregularly placed	Irregularly placed	Irregularly placed

*yellow box indicates similar characteristics.

The Malaysian form is probably closely related to *Lissodus* and *Isanodus*. So far, it is not possible to identify this form up to the genus level until more specimens are made available.

Since this Malaysian form is closely similar to *Isanodus*, which is currently put under a family *incertae sedis* (Cuny et al., 2010b), this form is assigned to a family *incertae sedis* as well.

Table 4.10 Dental characteristics of *Isanodus*? sp. (Malaysian specimens).

Characteristics	**A3015**	**A3016**
Outline	elongated with narrowing mesial and distal ends, central expension, bulky	elongated with narrowing mesial and distal ends, central expension, bulky
Cusp	one main cusp	one main cusp
Surface ornamentation	smooth, slight scar/depression on the apex of the cusp	smooth, no scar nor depression
Labial node	3 well developed	5 well developed (4 located at mesial/distal end; 1 located at another side)
Lingual node	at least 3, moderately developed. Two symmetrically located at base of the cusp, granulated edge	3 moderately to weakly developed. Granulated edge
Labial peg	1, central of the crown	1, central of the crown
Ridges connect labial peg with apex of cusp	yes	yes
Longitudinal crest	yes, weakly developed	yes, moderately developed
Crown symmetry	asymmetrical	asymmetrical
Size	3 mm MD, 2 mm LL, 1 mm H	3 mm MD, 2 mm LL, 1.5 mm H

MD – Mesial to distal LL – Lingual to labial H – Crown Height

Genus *Mukdahanodus* Cuny, Cavin & Suteethorn, 2009

Type species. *Mukdahanodus trisivakulii* Cuny, Cavin, Suteethorn, 2009

***Mukdahanodus trisivakulii* Cuny, Cavin & Suteethorn, 2009**

(Figure 4.14)

2009 *Mukdahanodus trisivakulii* Cuny, Cavin & Suteethorn, 2009: pp. 517, fig. 2A–J

Materials examined. Two nearly complete isolated teeth, root not preserved. Specimens A2001, A3019.

Description. Each of the teeth has a labio-lingually compressed and mesio-distally elongated, blade-shape outline (Figure 4.14). The mesiodistally oriented occlusal cutting edge is ornamented by strong seration. Each denticle of the serration is separated at its apex by a short groove. A relatively deeper groove is located near the centre of the occlusal edge. A horizontal pointing main cusp is located at the distal and mesial extremities. Up to five small accessory cusplets are located beneath the main cusp, with a decreasing size towards the base. The labial and lingual faces of the crown are smooth without ornamentation.

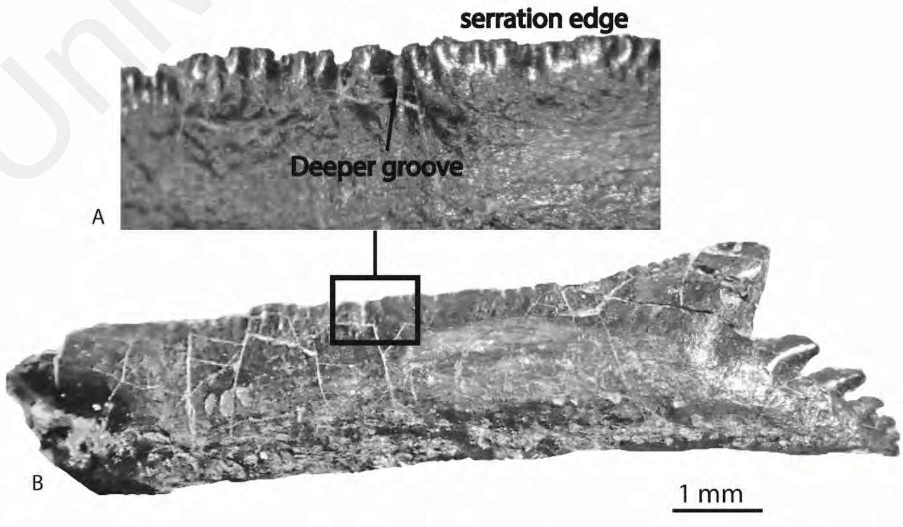


Figure 4.14 *Mukdahanodus trisivakulii* from central Pahang. Specimen A2001 in A. closed up view of the occlusal cutting edge; B. labial view. Scale 1 mm.

Discussion. *Mukdahanodus trisivakulii* is a highly specialised species, previously only found in the Sao Khua Formation of Thailand (Cuny et al., 2009). The Malaysian specimens are identical to the type specimen from Thailand by having the same serrated cutting edge at its occlusal face, low crown, horizontally pointing main cusp at the mesial and distal extremities, and small accessory cusplets below the main cusp. Tooth size measured 11 mm mesio-distally and 2 mm in height. However, there are a few differences between the Malaysian and Thai specimens. The Malaysian specimens possess a stronger serration and up to five small accessory cusplets, while the Thai specimens show relatively faint serration with up to four cusplets beneath the main cusp. Moreover, there is a notch interrupting the occlusal cutting edge in the Thai specimens, whereas the Malaysian specimens do not have notch, instead, there is only a relatively deep groove located on the occlusal cutting edge. Considering that there were only eleven specimens reported in Thailand previously, these minor differences are probably intraspecific variation that were not observable due to lack of specimens. Therefore, the species diagnosis should be revised to include the variations observed in the Malaysian specimens.

So far, only four species of hybodont with serrated dentition were ever reported (Cuny et al., 2009), namely, *Priohybodus arambourgi* d'Erasmo, 1960, *Pororhiza molimbaensis* Casier, 1969, *Thaiodus ruchae* Cappetta, Buffetaut, Cuny & Suteethorn, 1990 and *Mukdahanodus trisivakulii* Cuny, Cavin & Suteethorn, 2006. Cuny et al. (2009) interpreted *M. trisivakulii* as a euryhaline species, that is, lived in marine environment but spent some time of their life in freshwater environment. It is also believed to have been replaced by another species with similar dentition, *Thaiodus ruchae* Cappetta, Buffetau & Suteethorn, 1990, during the Late Cretaceous as *Mukdahanodus trasivakulii* was found only in the Sao Khua Formation whereas *T. ruchae* was found only in the Khok Kruat Formation. These two species with a cutting dentition are interpreted to have been preying on other fishes, such as *Heteroptychodus*. The presence of both *Heteroptychodus* and *Mukdahanodus* in the same rock unit in Malaysia supports this interpretation.

Table 4.11 Characteristics of *Mukdahanodus trisivakulii* (Malaysian specimen)

Characteristics	A2001	A3018
Complete/broken	almost complete	broken
Outline	compressed labio-lingually, elongated mesio-distally, blade-shape	compressed labio-lingually, elongated mesio-distally, blade-shape , slight depress on the labial/lingual face
Ornamentation	smooth on lingual/labial surface	smooth on lingual/labial surface
One serrated occlusal cutting edge from mesial to distal	yes strong serration	moderate to faint seration
Horizontal pointing main cusp (mesial/distal/both)	both mesial and distal extremities	both mesial and distal extremities
Serration on cusp	no	no
Cusplets beneath main cusp	5 cusplets at one mesio/distal end, another end broken	yes but broken tips, number of cusplets is uncertain
Cusplets decreasing size towards base	yes	yes
Notch/deep groove interrupting cutting edge	deep grove off center	deep grove off center
Size	11 mm MD, 2 mm H	10.5 mm MD, 2 mm H

MD – from mesial to distal H – height

Family: Hybodontidae OWEN, 1846

Genus: *Hybodus* Agassiz, 1837

Type species. *Hybodus reticulatus* Agassiz, 1837

Remarks. *Hybodus* is a cosmopolitan genus reported from many continents across the globe, including Europe, Asia, North America and Africa. Many of them were found in freshwater deposits of Late Jurassic to Late Cretaceous age (Cuny et al., 2010b; Goto et al., 1996; Kirkland et al., 2013).

***Hybodus* sp. A**

(Figure 4.15)

Materials examined. Five isolated teeth, mostly with broken tips and root not preserved. Specimens B3077–B3081, A3009–A3011.

Description. The specimens show high conical cusp with sharp pointed apex, with a height ranging from 2 mm to 6 mm, though in most specimens, the apexes are either abraded or broken. Also, most of the specimens show only one narrow high cusp due to poor preservation. Only one specimen (Figure 4.15A) possess three small cusplets flanking the main cusp. The lower two-third of the labial face is ornamented by numerous longitudinal ridges. These striations do not attain the apex.

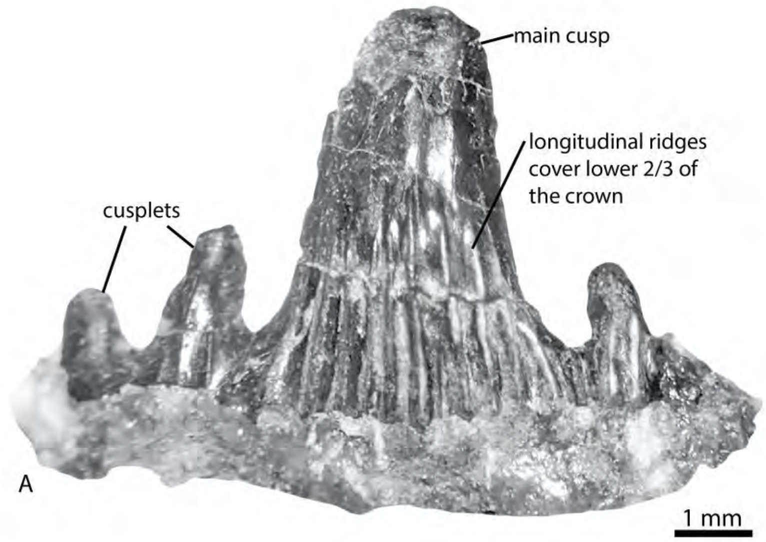


Figure 4.15 *Hybodus* sp. A from central Pahang, Specimen A3011 in labial view. Scale 1 mm.

HYBODUS sp. B

(Figure 4.16)

Materials examined. Two isolated teeth, root not preserved. Specimen A3009, A3010.

Description. The specimens show a high conical cusp with sharp pointed apex, tooth height ranges from 1 mm to 3 mm. Apex is well preserved. The largest specimen shows a crown compressed labio-lingual and ornamented by numerous longitudinal ridges on all faces. Some of the ridges cover two-third of the crown and some of them attain the apex. In the smaller specimens, all ridges attain the apex.

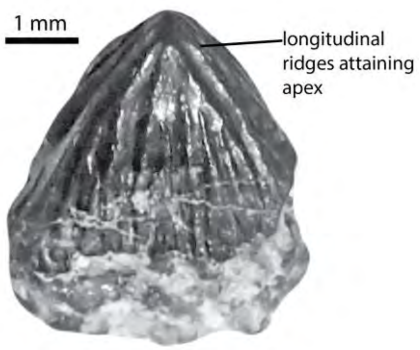


Figure 4.16 *Hybodus* sp. B from central Pahang, Specimen A3009 in labial view. Scale 1 mm.

Discussion. Compared to the lectotype of the type species, *Hybodus reticulatus* Agassiz, 1837 described by Maisey (1987), the Malaysian specimens show the characteristics of *Hybodus* in having a similar tooth morphology. However, Patterson (1966) stated that strong parallelism and convergence occur along the evolution of shark teeth, and the degree of heterodonty within species is poorly understood. Maisey (1987) supported that it is taxonomically unreliable to identify *Hybodus* up to the species level if the identification is only based on teeth or fin spines, because there are similar teeth occurring in different species. Therefore, the Malaysian specimens, even though having similar dental morphology to the lectotype specimens, can only be identified up to the genus level since there are only incomplete and isolated teeth. There are two specimens among the Malaysian *Hybodus* that are considerably different from each other, which the *Hybodus* sp. B having lower crown with striation attaining the apex. The *Hybodus* sp. B is similar to *Hybodus* sp. reported from the Phu Kradung Formation (Cuny et al., 2014) and Kut Island (Cuny et al., 2010b).

Table 4.12 Dental characteristics of *Hybodus* sp. (Malaysian specimens).

Characteristics	B3078	B3079	B3080	B3081	A3009	A3010	A3011	B3077
complete/broken	broken	broken	broken	almost complete	complete without root	broken	almost complete	broken
shape/outline	shape pointed	shape pointed?	shape pointed?	shape pointed	shape pointed, compressed LL	shape pointed	shape pointed	shape pointed
longitudinal ridges on	labial face	labial face	labial face	labial face	on all faces	on all faces	labial face	labial face
ridges attain 2/3 od the crown	yes	yes	yes	yes	some yes, some attaining apex	attaining apex	yes	yes
cusplets	1 main cusp	1 main cusp	1 main cusp	1 main cusp	1 main cusp	1 main cusp	1 main cusp with at least 3 cusplets	1 main cusp
size	4 mm H, 3 mm MD/LL	2 mm H, 2mm MD/LL	2.5 mm MD/LL; 2.5 mm H	4.5 mm H, 1.5 mm MD	2 mm LL, 4 mm MD, 3 mm H	1 mm LL/MD, 1 mm H	8 mm MD, 6 mm H	2 mm H, 2mm MD/LL

MD – Mesial to distal LL – Lingual to labial H – Crown height

Class: Osteichthyes Huxley, 1880
Subclass: Actinopterygii Klein, 1885
Order: Semionotiformes Arambourg and Bertin, 1958
Family: Semionotidae Lehman, 1966

Genus: *Lepidotes* Agassiz, 1832

Type species. *Lepodotes gigas* Agassiz, 1832

2009 *Lepidotes* Agassiz, 1832:Cavin & Suteethorn: pp. 131, fig. 5
2010 *Lepidotes* Agassiz, 1832: Cuny et al., pp. 420, fig. 4A–C
2013 *Lepidotes* Agassiz, 1832: Brinkman et al., pp. 202, fig. 10.4B

Remark. *Lepidotes* is a cosmopolitan genus, occurs during the Jurassic.

***Lepidotes* sp.**
(Figure 4.17)

Materials examined. Nine isolated teeth. Specimen B3071–B3076, A3012–A3014.

Description. The specimens show a button shaped crown with a circular to elliptical outline in apical view. Some of the specimens possess slightly pointed apex (Figure 4.17A–C) and a slightly mesial-distally compressed crown, while some specimens show a flat occlusal surface with no compression (Figure 4.17D–F). The crown surface is smooth without ornamentation. A depression is observed in some specimens. The tooth neck is observable near the base of the crown. Tooth size ranges from 1.5 to 6 mm labio-lingually and mesio-distally, crown height ranges from 1 to 5 mm.

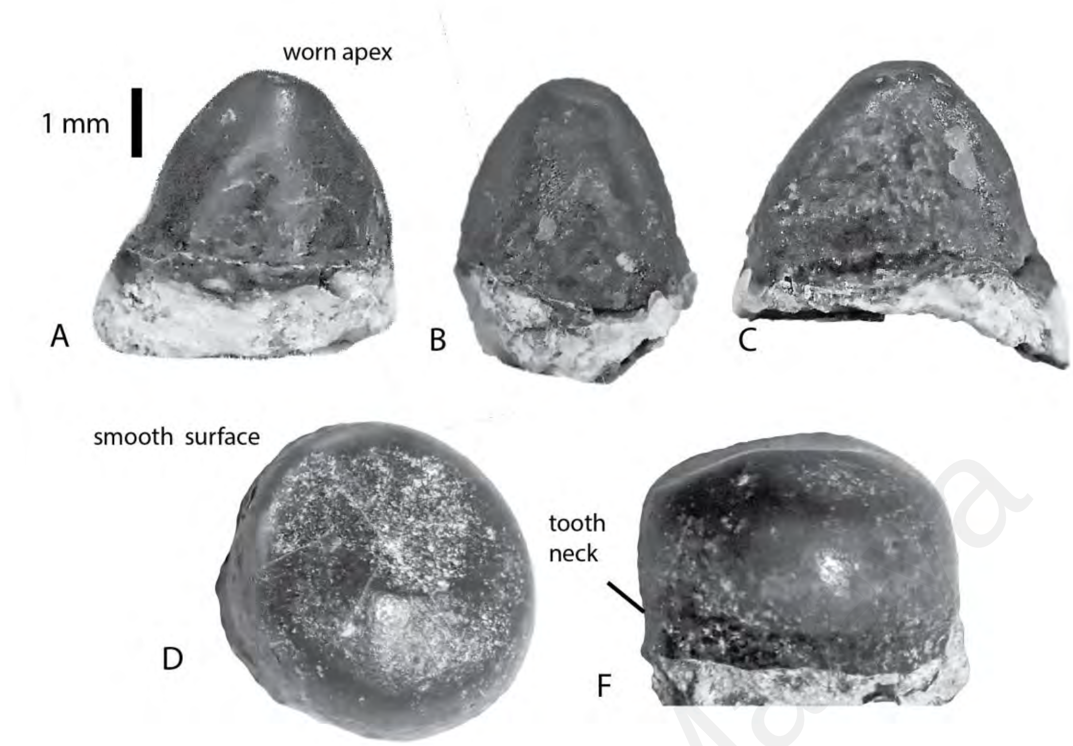


Figure 4.17 *Lepidotes* sp. from central Pahang. Specimen B3075 in A labial, B mesial, C lingual view; specimen A3013 in D occlusal, F mesial view. Scale 1mm.

Discussion. These specimens possess identical tooth morphology and tooth size, indicating a homodont dentition. Button-like tooth specimens identified as *Lepidotes* sp. have been reported from the Kut Island (Cuny et al., 2010b), the Sao Khua Formation and the Khok Kruat Formation, Thailand (Cavin et al., 2009). Also, similar button shape teeth were reported from Early Cretaceous to Late Cretaceous freshwater deposits in North America (Brinkman et al., 2013; Garrison et al., 2007). All of these specimens show similar tooth morphology and characteristics. Due to the lack of complete fossilised skeleton, these *Lepidotes* specimens can only be identified up to the genus level.

Table 4.13 Dental characteristics of *Lepidostes* sp. (Malaysian specimens).

Characteristic	B3071	B 3075	B3072	B3074	B3076	A3012	B3073	A3014	A3013
complate/broken	complete, no root preserved	complete, no root preserved	complete, no root preserved	almost complete, no root preserved	complete, no root preserved	complete, no root preserved	complete, no root preserved	complete, no root preserved	complete, no root preserved
Shape	button shape, rounded cap, compressed mesial distally	button shape, slight pointing apex, abraded	button shape, slight pointing apex, abraded	button shape, apex abraded , compressed mesial distally	button shape, apex abraded	button shape, slight pointing apex, abraded mark at apex (biological),	button shape, slight pointing apex, abraded apex, compressed	button shape, slight pointing apex, compressed	button shape, flat apex
Ornamentation	smooth surface	generally smooth with scars	generally smooth with scars	smooth surface	smooth surface with monir scar	smooth surface	smooth surface	smooth surface	smooth surface
tooth neck (depression near base of the crown)	yes	yes	yes	yes	yes	yes	yes	yes	yes
size	4 mm MD, 4.5 mm LL; 4 mm H	4.5 mm LL, 4 mm MD , 5 mm H	3.75 mm MD, 4 mm LL, 5 mm H	1.5 mm LL, 1 mm MD, 1 mm H	6 mm LL/MD, 4 mm H	5.5 LL, 4 mm MD, 4 mm H	5.5 LL, 4 mm MD, 4 mm H	5 mm MD, 6 LL, 4.5 H	5.5 MD, 7mm LL; 4 mm H

MD – Mesial to distal LL – Lingual to labial H – Crown Height

Semionotidae genus indet.

(Figure 4.18)

2010 Semionotidae Woodward, 1890: Cuny et al., pp. 417, fig. 2K–O
2010 Semionotidae Woodward, 1890: Cuny et al., pp. 618, fig. 2. 11–12

Materials examined. One complete isolated tooth. Specimen B4005.

Description. The specimen shows an elliptical and disc-like outline in occlusal view. A papilla is located near the centre of the crown, showing a rounded tip, which could have undergone some degree of abrasion. The marginal area surrounding the papilla is flat and wide, ornamented by some irregular granules. The tooth edge is surrounded by granules. The tooth measures 2.5 mm mesio-distally, 4 mm labio-lingually, 1 mm in height.

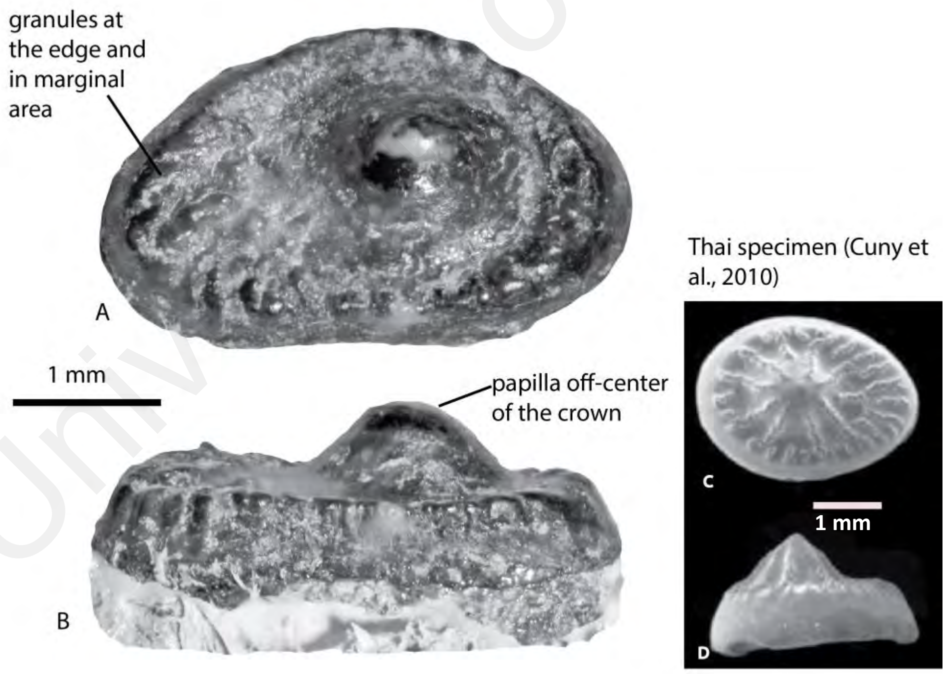


Figure 4.18 Semionotidae genus indet. from Pahang, Specimen B4005 in A occlusal view, B labial/lingual view. Scale 1 mm. Compared with Thai specimen in C apical, D labial/lingual view (Cuny et al., 2010b).

Discussion. A similar tooth morphology was reported in the freshwater specimens found in the Sao Khua Formation, identified as indeterminate actinopterygian tooth (Cuny et al., 2006), the Kut Island, identified as Semionotiformes indet (Cuny et al., 2010b), and Southern Tunisia, identified as Semionotidae indet (Cuny et al., 2010a). Its occurrence is only restricted to the Early Cretaceous so far.

Table 4.14 Dental characteristics of Semionotidae genus indet. (Malaysian specimen).

Characteristics	B4005
Complete/broken	complete
Shape	disc like with a papilla off center of the crown
Bulge	rounded tip
Marginal area (wide/narrow?)	wide
Ornamentation	marginal area ornamented by granules, edge surranded by granule
Size	2.5 mm, 4 mm (MD/LL) ; 1 mm H

MD – Mesial to distal LL – Lingual to labial H – Crown Height

Family: Caturoidae Owen, 1860

Genus: *Caturus* Agassiz, 1843

Type species. *Caturus furcatus* (Agassiz, 1833)

1996 *Caturus* Agassiz, 1834: Thies & Mudroch, Plate 2, fig.9–10
2014 *Caturus* Agassiz, 1834: Knoll & Lopez-Antonanzas, pp. 2, fig.1F–G
2007 *Caturus* Agassiz, 1834: Thies, Mudroch & Turner, pp. 82, fig.3a–c

***Caturus* sp.**

(Figure 4.19)

Materials examined. 14 isolated teeth. Specimens B3083–B3095, A1003.

Description. The specimens measure 0.5 mm to 2 mm mesio-distally and up to 6.5 mm in height. They have an arrow-like acrodin cap with a sharp pointing apex. In some of the specimens, the acrodin cap is compressed labio-lingually, while in other specimens, the acrodin cap is not compressed. Two strong cutting edges are present on both sides of the acrodin cap, running from the tip towards the base of the cap. The acrodin cap has a smooth surface without ornamentation. The lower part of the tooth, namely the tooth shaft, is covered by dense regular striation from tooth neck to the bottom of the shaft.

Discussion. The presence of cutting edges on both sides of the arrow-shaped acrodin cap is a characteristic shared by several genera, including *Caturus*, *Ionoscupus*, *Melvius*, *Calamopleurus*, *Pachyamia* and *Tomognathus* (Bogan et al., 2013; Bryant, 1987; Cavin & Giner, 2012; Chalifa & Tchervov, 1982; Everhart, 2009). However, the degree of sharpness of the cutting edges differ among these genera. Among all, the Malaysian form is most similar to *Caturus*. *Caturus* is characterised by an elongated acrodin cap, strong labio-lingual compression, sharp anterior and posterior keel and circular base (Grande & Bemis, 1998; Thies & Mudroch, 1996; Thies et al., 2007). However, most of the previously described *Caturus* specimens have no striation on the ganoine shaft, except for a specimen identified as *Caturus* sp. found in the coal layers of the Bathonian (Middle Jurassic) of southern France (Knoll & Lopez-Antonanzas, 2014), and some were also found in the Sao Khua Formation in Thailand. The specimens from southern France and Thailand are similar to the Malaysian specimens. *Caturus* is more commonly reported from marine deposits, although a few were reported from non-marine deposits, which includes middle Cenomanian to early Turonian lagoon or estuarine deposits in Canada (Cumbaa et al., 2006), early Barremian lacustrine deposits in Spain (Poyato-Ariza, 2005) and the abovementioned coastal swamp deposits in southern France (Knoll & Lopez-Antonanzas, 2014).

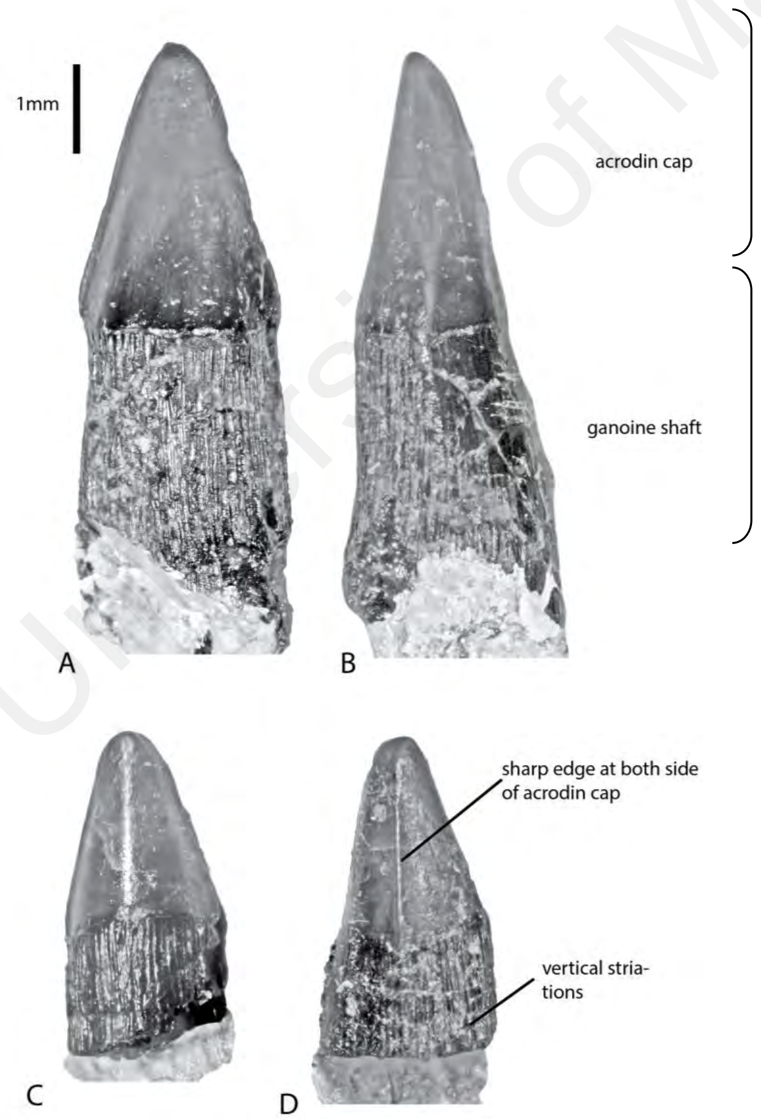


Figure 4.19 *Caturus* sp. from central Pahang, Specimen B3094 in A labial, B mesial view; Specimen 3090 in C labial, B mesial view. Scale 1 mm.

Table 4.15 Dental characteristics of *Caturus* sp. (Malaysian specimens).

Characteristics	B3083	B3084	B3085	B3086	B3087	B3088	B3089	B3090	B3091	B3092	B3095	B3093	B3094	A1003
complete/broken	broken lower part	broken lower part	broken lower part	broken lower part	broken lower part	complete	broken lower part	complete	broken lower part	broken lower part	almost complete	broken lower part	complete	complete
compressed MD/LL	no	no	LL, slight arched lingually	LL, slight arched lingually	LL, slight arched lingually	LL	no	MD	no	MD	LL	strongly compressed LL	slight arch lingually	slight arch lingually
size	1. 5 mm MD, 1 mm LL; 2 mm H	0.5 mm MD, 1.5 mm H	1 mm MD, 2.5 mm H	1.5 mm LL, 2 mm MD, 2.5 mm H	2 mm MD, 1.5 mm LL, 3 mm H	1 mm MD, 3.5 H	1.5 mm MD, 2 mm H	2 mm LL, 1.5 mm MD, 3.5 mm H	1 mm MD, 2.5 mm H	3 mm LL, 2 mm MD, 1.5 mm H	0.5 mm MD, 2.5 mm H	1 mm LL, o.5 mm MD, 2 mm H	2 mm MD, 1.5 mm LL, 6.5 mm H	
abraided mark	yes	yes	no	no	no	no	yes	yes	yes	yes	no	no	no	no
arrow like acrodin cap with sharp tip	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
strong edge	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
striated ganoine shaft	yes	?	?	?	?	yes	?	yes	?	yes	yes	?	yes	yes
colour	black	black	black	whitish colour	dark grey	translucent acrodin cap	whitish colour	black	black	black	translucent cap	black	translucent cap	translucent cap

MD – Mesial to distal LL – Lingual to labial H – Crown Height

CHAPTER 5 DISCUSSION

5. 1 Comparison of the Malaysian fish fauna with that of the Khorat Group.

Out of nine taxa of the Malaysian fish fauna, four are endemic species which are only known from the Khorat Group and the Tembeling Group equivalent so far. The four of them are *Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis*, *Isanodus*? sp. and *Mukdahanodus trisivakulii*.

A summary of fish faunas from the Phu Kradung Formation, the Sao Khua Formation, The Khok Kruat Formation and Ko Kut (Sao Khua equivalent) together with the Malaysian fish fauna is listed in Figure 5.1.

Formation	Khok Kruat	Sao Khua	Ko Kut (Sao Khua equivalent)	Phu Kradung	The Tembeling Group equivalent
Hybodus sp.	■	■	■	■	■
Thaiodus ruchae	■				
Acrorhizodus khoratensis	■				
khoratodus foreyi	■				
Heteroptychodus steinmanni	■	?		■	?
Heteroptychodus kokutensis		■	■		■
Mukdahanodus trisivakulii		■			■
Lonchidion Khoratensis		■			
Parvodus sp.		■			
Isanodus paladeji		■	■		
Isanodus nongbualamphuensis		■			■
Isanodus sp. (*Isanodus* ? sp. in this study)		■	■		■
Caturus sp.		■			■
Lepidotes sp. (button-shaped teeth)		■	■		■
Semiontidae genus indet.		■	■		■
Acrodus sp.				■	
Lonchidion sp.				■	
Acrodus kalasinensis				■	
Jaiodontus sp.				■	
Heteroptychodus cf. *kokutensis*				■	

Figure 5.1 Comparison of fish faunas from the Khorat Plateau and Malaysia.

Comparison shows that all nine taxa found in this study also occur in the Sao Khua Formation. The Malaysian fish fauna do not share much similarity with that of the Khok Kruat Formation and the Phu Kradung Fromation, except for the common presence of *Hybodus* sp.. Although the occurrence of *H*. cf. *steinmanni* in the Malaysian fish fauna might indicate a linkage with the fish faunas of the Khok Kruat and the Phu Kradung Formation, the specimens are not in good condition to affirm species identification. Therefore the Malaysian fish fauna is most closely related to that of the Sao Khua Formation.

Age range of the four endemic taxa shared between the Sao Khua fish fauna and the Malaysian fish fauna, namely, *Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis*, *Isanodus*? sp. and *Mukdahanodus trisivakulii*, is thus referable to the age of the Sao Khua Formation where these taxa were first found.

5.2 Age range of the Sao Khua Formation

As mentioned in Chapter 2, age range of the Sao Khua Formation has been debated in the past few decades. The formation was confined to Early Cretaceous mainly based on the presence of *D. etruscus* in the palynomorph assemblage found in the formation, and was refined to Berriasian to early Barremian based on the absence of angiosperm pollen (Racey & Goodall, 2009). However, negative evidence is not reliable to conclude the age range of a rock unit. Later, a new species of bivalve, *Pseudohyria* (*Matsumotoina*) *somonai*, was reported from the Sao Khua Formation and suggested a late Barremian age for the formation (Tumpeesuwan et al., 2010).

The subgenus *Pseudohyria* (*Matsumotoina*) was previously found in Korea, China and Japan. It is one of the subgenus included in both the Sebayashi faunal association (Kozai et al., 2005) and the second trigonioidid assemblages (Sha, 2007). The Sebayashi faunal association consists of the Yunoki fauna, the Sebayashi fauna, the Kitadani fauna, the Sengoku fauna, the Nakdong fauna and the Hasandong fauna. All these faunas are said to be coeval with each other (Kozai et al., 2005), based on the common occurrence of some index species, including *Nippononaia ryosekiana* and *Hayamina matsukawai*. *Pseudohyria* (*Matsumotoina*) was only found in the Kitadani, the Sengoku, the Nakdong and the Hasandong faunas. The Sebayashi faunal association was assigned to the upper Barremian because the Yunoki fauna from the Monobegawa Group was restricted to upper Barremian by marine fauna found at the uppermost part of the Yunoki Formation.

On the other hand, Sha (2007) divided the trigonioidid non-marine bivalves into seven assemblages based on their occurrences across Asian countries. Among all, *Pseudohyria* (*Matsumotoina*) was placed in the second trigoniodid assemblage. This assemblage was also characterised by the index species *Nippononaia ryosekiana*,. However, its age was based on its occurrence in the Sebayashi Formation. The Sebayashi Formation is overlaid by the Sanyama Formation containing Albian ammonites and underlaid by the Ishido Formation with Barremian ammonites (Sha, 2007). Therefore, the age range of the second trigonioidid assemblage was assigned to the upper Barremian to lower Albian, mainly Aptian.

Other than *Pseudohyria* (*Matsumotoina*), a summary of bivalve assemblages of the Khorat Group was mentioned by Tumpeesuwan (2010). The Sao Khua Formation consists of several other species of bivalves, including *Trigonioides* (*Diversitrigonioides*) sp. cf. *T.* (*D.*) *diversicostatus*. The species *T. (D.) diversicostatus* was included in the trigonioidid assemblage by Sha (2007), which was dated to be Aptian to Cenomanian. If using this species to date the Sao Khua Formation, the outcome is contradicting the age constrained by using *Pseudohyria* (*Matsumotoina*) alone.

The age range of one species might not represent the age range of a faunal association or assemblage, because all species are taken into account to determine the age range of an association. The age range of *Pseudohyria* (*Matsumotoina*) might be longer or shorter than that of the faunal association or assemblage. Thus, age dating by correlating only one species to a faunal association or assemblage could result in a bias. Therefore, it is still questionable whether the Sao Khua Formation is constrained to the upper Barremian.

Apart from bivalves, isolated spinosaurid teeth were also found in the Sao Khua Formation and the Khok Kruat Formation (Buffetaut et al., 2009; Buffetaut et al., 2005b, pp. 575-581, pp. 575-581). A summary of the spinosauridae occurrence (Bertin, 2010) stated that most of the spinosaurid were found in formations of late Early Cretaceous to Late Cretaceous, mainly Aptian. In South America, spinosaurids were found in formations of early Cenomanian to Santonian age; In Europe, spinosaurids were found in formations of Valaginian to early Barremian, and late Barremian to pre-mid Aptian age; whereas in Africa, spinosaurids were reported from formations of Aptian to Cenomanian age. In Asia, spinosaurids were found in formations of late Barremian to early Aptian, Albian to Santonian age. Spinosaurids were most abundant during the late Early Cretaceous. This implies that the spinosaurids in Malaysia and Thailand are most probably late Early Cretaceous in age.

5.3 Age of Malaysian fish fauna

Similarity of the Malaysian fish fauna to the Sao Khua fish fauna suggests that both faunas are most likely coeval. However, there are remarkable changes of depositional environment of the underlying Phra Wihan Formation and the overlying Phu Phan Formation (see Chapter 2. Literature Review), in which the species might have existed but not preserved as fossils, or, the species might have migrated to another province which was more suitable for living. Therefore, the age range of the Sao Khua Formation might not be the total age range of the endemic species, which are *Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis*, *Isanodus*? sp. and *Mukdahanodus trisivakulii*.

In addition, the changes of environment from meandering river to braided river (and vice versa) in the vertical succession of the Sao Khua Formation indicates that the meandering river and the braided river environments were laterally adjacent to each other according to Walther's law of correlation of facies. The fishes might have migrated towards a low energy environment in the downstream area during the deposition of the Phu Phan Formation.

In both case, it is possible that the age range of the Sao Khua Formation is a local vertical range (teil zone) instead of the total vertical range of these species. Owing to this possibility, the age range of these species might extent from upper Barremian and up to lower Aptian.

The occurrence of *Heteroptychodus steinmanni* is restricted to Asia, including Japan and Thailand. It was found in Hauterivian deposits in Japan, and in the Phu Kradung, the Sao Khua and the Khok Kruat Formation in Thailand. Its known age range is from Berriasian to Aptian. *Hybodus* and *Lepidotes* are cosmopolitan genera which are found worldwide. They have a long age range from the Middle Triassic to Maastrichtian, and from the Early to Late Jurassic, respectively.

Caturus is a genus commonly found in European countries. It is mostly found in marine deposits. However, the Malaysian form has a distinct tooth characteristic that is not found in any marine *Caturus* specimens. Similar specimens were reported only from Thailand and southern France, therefore the age range in the stratigraphic column by which these specimens were reported are referred in this study. Hence, the age range of this *Caturus* sp. is Bathonian (Middle Jurassic) to early Aptian.

Overall, the overlapping ranges of most of the nine taxa delineates an assemblage zone of upper Barremian to lower Aptian (Figure 5.2). This Malaysian assemblage zone can be correlated to that of the Sao Khua Formation (Figure 5.3).

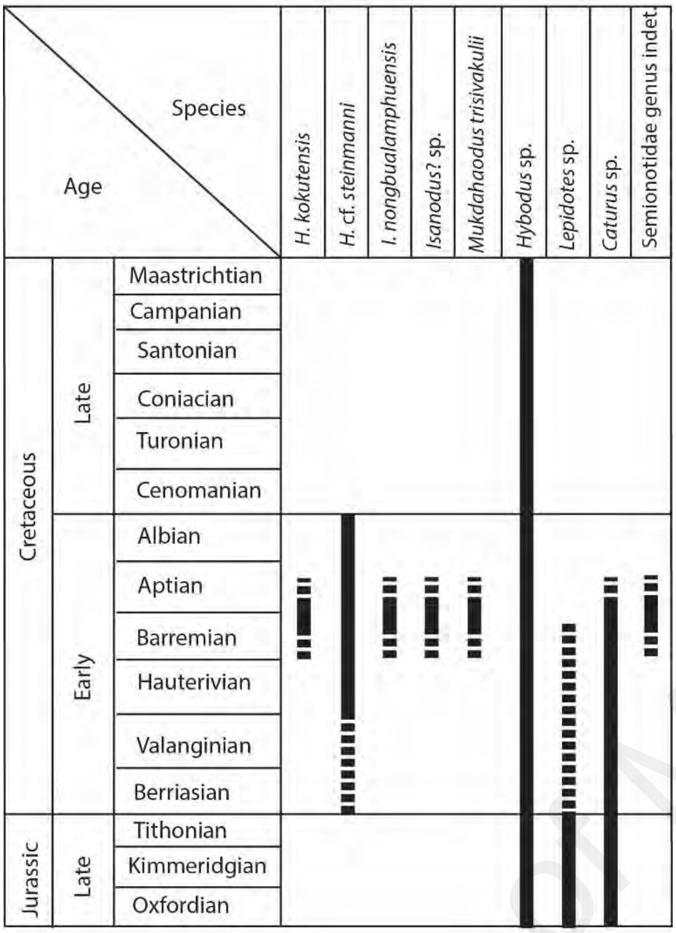


Figure 5.2 Age range of each taxon of the Malaysian fish fauna.

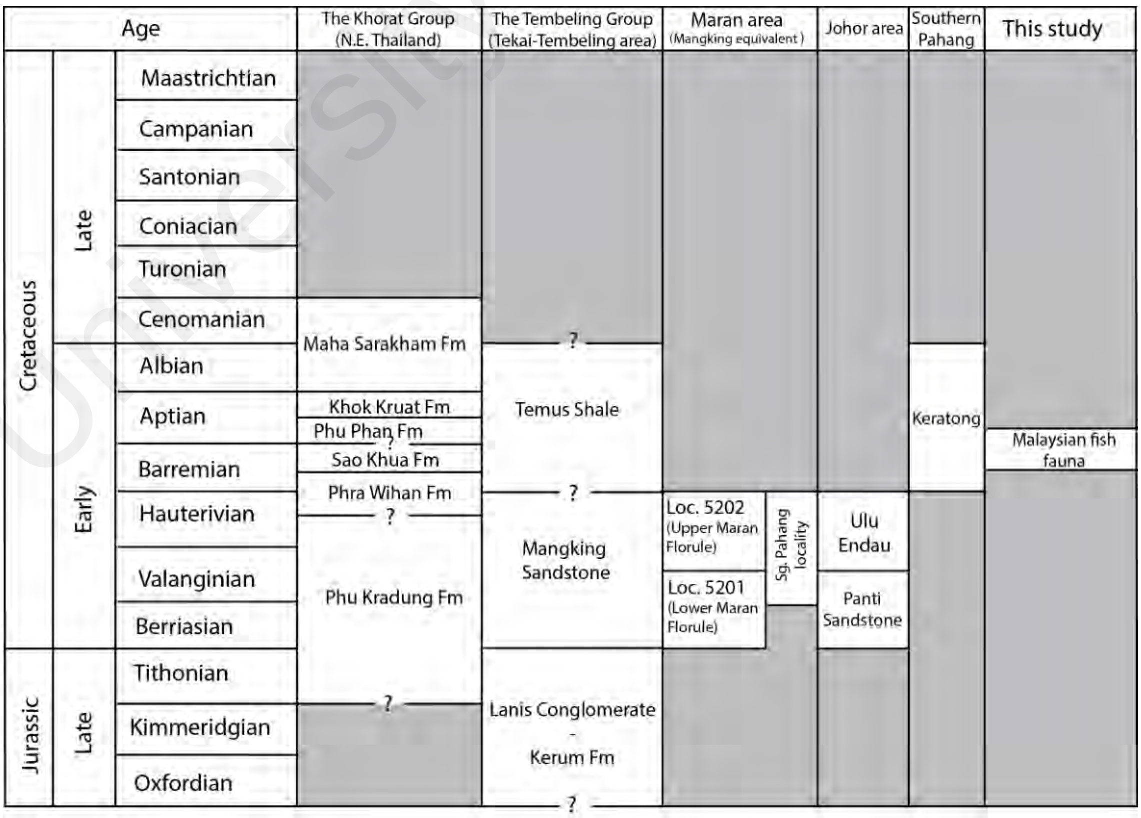


Figure 5.3 Chronostratigraphical correlation of the Malaysian fish fauna with the Tembeling Group equivalents and the Khorat Group.

5.4 Worldwide distribution

The Malaysian fish fauna and the Sao Khua Formation fish fauna are imprinted with strong endemism as shown in Figure 5.4. A biogeographical correlation between the Late Jurassic – Cretaceous non-marine vertebrate assemblages from Thailand and other Asian countries were carried out using taxonomic distinctness analysis and Raup & Crick's taxonomic similarity coefficient (Fernandez et al., 2009). Result of the analysis showed very limited connection between the Sao Khua assemblage with the others, suggesting a rather poor pathway within the continent for non-marine faunal exchange during the Early Cretaceous, and that the Indochina block faunas were isolated during the deposition of the Sao Khua Formation. As opposed to the strong endemism of the Sao Khua faunal assemblage, the Phu Kradung assemblage and Khok Kruat assemblage show better linkage with the others from the mainland (Fernandez et al., 2009). Strong linkage between the Malaysian fish fauna and the Sao Khua fish fauna suggests a possible connected pathway for faunal interchange between the Khorat Plateau and Peninsular Malaysia at least during the late Barremian to early Aptian. Even though the Peninsular Malaysia was supposedly a more mountainous and marginal terrane compared to the Khorat Plateau, there was probably no geographic barrier between these two provinces for the fishes to disperse.

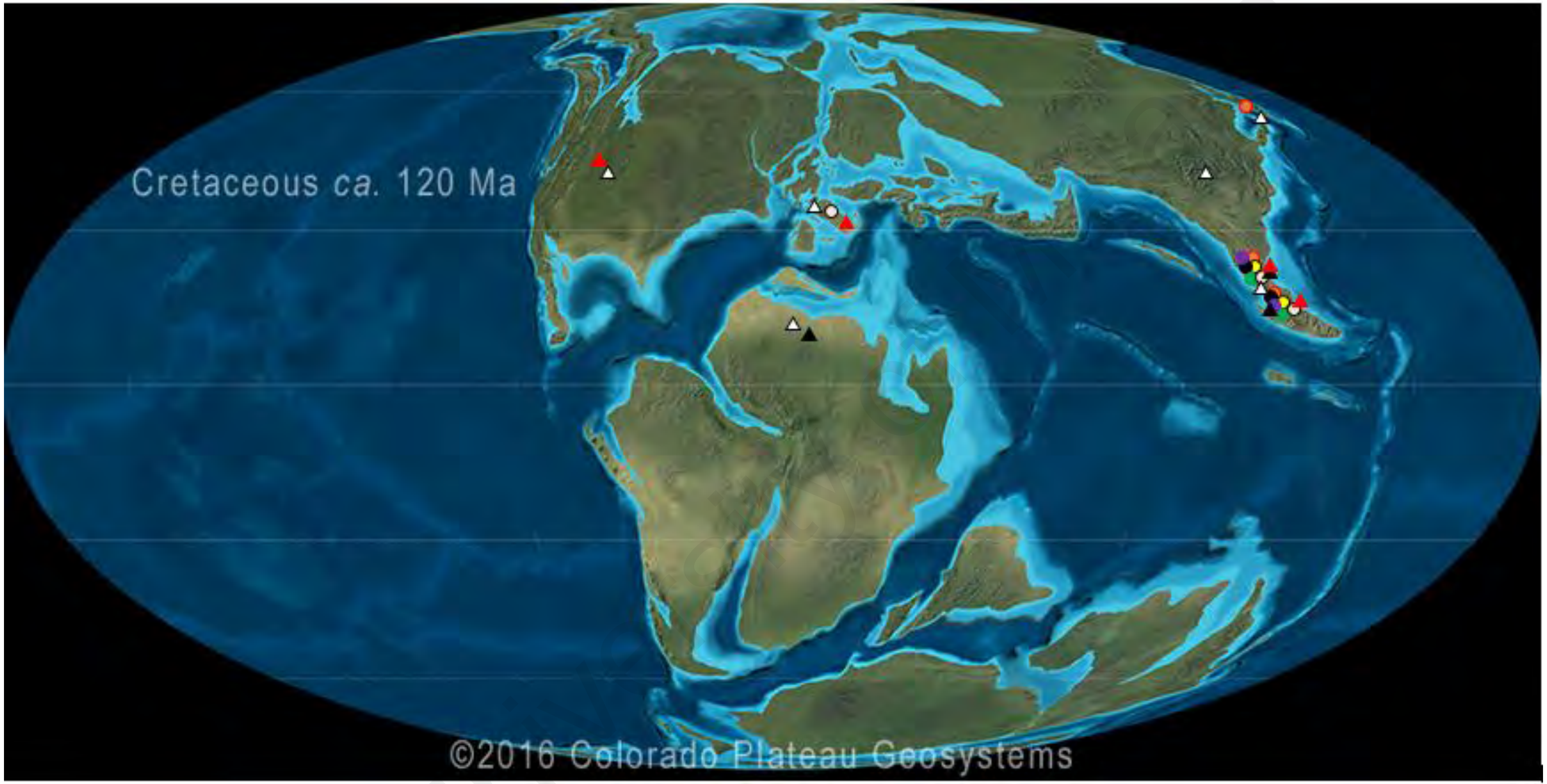


Figure 5.4 Distribution of each taxon of the Malaysian fauna on Cretaceous world map created by to Ron Blakey (https://www2.nau.edu/rcb7/).

Heteroptychodus steinmanni ●
Heteroptychodus kokutensis ●
Hybodus sp. △
Isanodus nongbualamphuensis ●
Isanodus? sp. (equivalent to *Isanodus* sp. in Thailand) ●
Mukdahanodus trisivakulii ●
Caturus sp. (striated shaft) ○
Semionotidae genus indet (button-shaped teeth) ▲
Lepidotes sp. ▲

Table 5.1 Summary of distribution of each taxon and age range of the formations where they were found based on Yabe & Obata (1930), Cuny et al. (2003, 2006, 2007, 2009, 2010), Knoll et al. (2014), Khamha et al. (2015).

Taxa	**Distribution**	**Age range of the formations**
Heteroptychodus steinmanni	Japan Thailand	Hauterivian (Lower Cretaceous) Berriasian to Aptian
Heteroptychodus kokutensis	Thailand	upper Barremian
Isanodus nongbualamphuensis	Thailand	upper Barremian
Isanodus? sp.	Thailand	upper Barremian
Mukdahanodus trisivakulii	Thailand	upper Barremian
Hybodus sp.	cosmopolitan	Middle Triassic to Maastrichtian (Upper Cretaceous)
Caturus sp.	southern France Thailand	Bathonian (Middle Jurassic) upper Barremian
Lepidotes sp.	cosmopolitan	Jurassic
Semionotidae genus indet	southern Turnisia Thailand	pre-Aptian upper Barremian

The Phu Kradung Formation, the Sao Khua Formation and the Khok Kruat Formation bear three distinct fish faunas (Figure 5.2). The age range of the different species of freshwater hybodonts are short and could potentially become a good dating tool. Presence of the Malaysian fish fauna provides a clue for a possible migration of the Sao Khua Formation fish fauna towards the southern part. More palynomorphs or inverterbrate fossils are needed to date the Tembeling Group and its equivalent, only then the age range of this fish fauna could be better established.

CHAPTER 6 CONCLUSION

This study identifies nine taxa from the Early Cretaceous Malaysian fish fauna, namely

1. *Heteroptychodus* cf. *steinmanni*
2. *Heteroptychodus kokutensis*
3. *Isanodus nongbualamphuensis*
4. *Isanodus*? sp.
5. *Mukdahanodus trisivakulii*
6. *Hybodus* sp.
7. *Lepidotes* sp.
8. *Caturus* sp.
9. Semionotidae genus indet.

Specimens examined in this study reveal some intraspecific variations in some endemic species of Southeast Asia, especially in providing more information on the heterodonty pattern of these species. They are *Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis*, *Isanodus*? sp. and *Mukdahanodus trisivakulii*. This taxonomic study indicates a need to revise the diagnosis of *Heteroptychodus* and *M. trisivakulii*, and the dental reconstruction of *Isanodus*.

The specimens of *Heteroptychodus kokutensis* found in Malaysia consist of both anterior and posterior teeth. This is the first report of anterior teeth for this species. Also, the first finding of juvenile teeth of *H. kokutensis* in this study implies that the species was able to reproduce in freshwater. Specimens of *Isanodus nongbualamphuensis* found in Malaysia demonstrates a gradient monognathic dentition, which is in contradiction with the non-gradient monognathic dentition suggested by the previous workers based on Thai specimens. *M. trisivakulii* found in Malaysia reaveals some intraspecific variations from the Thai type specimen. The Malaysian form has 5 instead of 4 lateral cusplets and a groove instead of a notch interrupting the occlusal cutting edge. These variations shall be included in the revised diagnosis of the species. On the contrary to the abovementioned endemic species, the cosmopolitan genera *Hybodus* and *Lepidotes* cannot be identified up to species level based on information of teeth alone.

The bony fishes, *Lepidotes* sp., Semionotidae genus indet. and *Caturus* sp. cannot be identified up to species level based on information of teeth alone. *Caturus* sp. found in the Malaysian fish fauna bears a different shaft ornamentation compare to typical *Caturus* teeth. The genus *Caturus* is commonly found in marine deposits in European coutnries. Its occurrence in a freshwater environment in Malaysia implies that the genus at least spent part of its life living in a freshwater environment in Southeast Asia. Even though these bony fishes could not be identified up to species level, they are of help in the biostratigraphic correlation between the Malaysian and Thai fish faunas.

The Malaysian fish fauna is very similar to Thai fish faunas. Comparing the Malaysian fauna with those of the Phu Kradung Formation, the Sao Khua Formation and the Khok Kruat Formation, it shows closest relationship with the Sao Khua Fauna. Out of nine taxa, seven are in common only with the Sao Khua Formation but are absent from the Phu Kradung and Khok Kruat formations.

Based on an assemblage zone correlation, the age range of the Malaysian fauna is interpreted as late Barremian to early Aptian. The similarity between the Malaysian and Thai faunas implies a possible pathway for freshwater faunal exchange between Peninsular Malaysia and the Khorat Plateau during the Early Cretaceous.

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APPENDIX A

Abstract of poster presentation at the 12th Symposium on Mesozoic Terrestrial Ecosystem held at Shenyang, China, on 18th August 2015.

First Cretaceous fish fauna from Malaysia: Preliminary report

Teng. Y. H. [1], Sone M. [1], Hirayama R. [2], Komatsu T. [3], Yoshida M. [4]

1. Department of Geology, University of Malaya, Kuala Lumpur 50603, Malaysia; yuhe_e@hotmail.com
2. School of International Liberal Studies, Waseda University, Tokyo, Japan
3. Faculty of Science, Kumamoto University, Japan
4. Graduate School of Science, the University of Tokyo, Japan

An assemblage of isolated fossilized fish was found from the Early Cretaceous fluvial/lacustrine red-beds of Pahang, and this is the first confirmation of Cretaceous fossil fishes in Peninsular Malaysia. Some 80 specimens, mostly of teeth, have been collected from this locality. So far as identified, a total of six fish taxa are present; that is, three genera of sharks (*Heteroptychodus*, *Isanodus*, and *Hybodus*) and three forms of ray-finned fishes (*Lepidotes*, *Caturus*?, and one indeterminate actinopterygii). *Heteroptychodus* and *Isanodus* are, so far known, endemic to the Early Cretaceous of Asia. This assemblage reasonably suggests a non-marine occurrence, as species of *Heteroptychodus* and *Isanodus* have previously been found in brackish/fresh water sediments. On the other hand, *Caturus* is common in the marginal nearshore deposits of the Jurassic (–early Cretaceous) age; hence, the Malaysian *Caturus*? needs verification. The newly found Malaysian fish fauna shows close similarities to the Early Cretaceous fresh-water faunas of the Khorat Group in Thailand; most closely to that of the Sao Khua Formation (Barremian–Aptian). Further study will be focused on paleobiogeographic affinities of the Malaysian fishes with other Asian faunas.

Keywords: Early Cretaceous, Malaysia, sharks, actinopterygii

APPENDIX B

Abstract of poster presentation at National Geoscience Conference 2015 at Kota Bharu, Kelantan, on 31st July 2015.

PRELIMINARY STUDY OF THE CRETACEOUS FISH FAUNA FROM PAHANG, PENINSULAR MALAYSIA

Teng Yu He[1*], Masatoshi Sone[1], Ren Hirayama[2], Toshifumi Komatsu[3], Masataka Yoshida[4]

[1]Department of Geology, University of Malaya, Kuala Lumpur 50603, Malaysia

[2]School of International Liberal Studies, Waseda University, Tokyo, Japan;

[3]Faculty of Science, Kumamoto University, Japan;

[4]Graduate School of Science, the University of Tokyo, Japan.

yuhe_e@hotmail.com

Mesozoic non-marine sediments, the so-called Jurassic–Cretaceous red beds, are widely distributed in Peninsular Malaysia. Recently, an assemblage of isolated fossilised fish teeth was discovered from the Cretaceous red beds of Pahang, Peninsular Malaysia. A total of six taxa were identified; that is, three genera of cartilaginous fish (Heteroptychodus, Isanodus, and Hybodus) and three forms of bony fishb(Lepidotes, Caturus?, and one indeterminate actinopterygian form). Elsewhere, the species of Heteroptychodus and Isanodus have previously been found in brackish/fresh water sediments of the Early Cretaceous, suggesting a non-marine origin of the present fish fauna, although Caturus is common in marginal nearshore environments of Jurassic (–early Cretaceous). This fossil record provides a paleo-geographical implication as it appears similar to the Early Cretaceous fresh-water faunas of the Khorat Group in Thailand, most closely to that of the Sao Khua Formation.