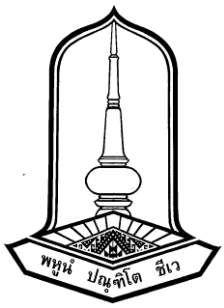

VERTEBRATE MICROREMAINS FROM THE EARLY CRETACEOUS SAO KHUA FORMATION, KHORAT GROUP IN PHU PHAN THONG FOSSIL LOCALITY AND THEIR BIOSTRATIGRAPHY

SUCHADA KHAMHA

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Palaeontology at Mahasarakham University

April 2018

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April 2018

The examination committee has unanimously approved this dissertation, submitted by Miss Suchada Khamha, as partial fulfillment of the requirements for the Degree of Doctor of Philosophy Program in Palaeontology, Faculty of Science, Mahasarakham University.

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Dean of Graduate School
April 28, 2018

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Suchada Khamha

ชื่อเรื่อง การศึกษาซากดึกดำบรรพ์ขนาดเล็กของสัตว์มีกระดูกสันหลังยุคครีเตเชียสตอนต้น จากหมวดหินเสาขัว (กลุ่มหินโคราช) ที่ค้นพบจากแหล่งซากดึกดำบรรพ์ภูพานทอง และการลำดับชั้นหินทางชีวภาพ

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บทคัดย่อ

จากการศึกษาตะกอนบริเวณแหล่งขุดค้นภูพานทอง หมวดหินเสาขัว พบความหลากหลายซากดึกดำบรรพ์ขนาดเล็กของสัตว์มีกระดูกสันหลังจำนวนมากประกอบด้วย ฉลามน้ำจืดไฮโบดอนท์ 7 ชนิด (*Egertonodus* sp., *Hybodus*sp., *Parvodus* sp., *IsanodusPaladeji*, *I. nongbualamphuensis*,*Lonchidionkhoratensis* and *Heteroptychoduskokutensis*) ปลากระดูกแข็ง 8 ชนิด (Cf. *Caturus*, (?*) Isanichthy* sp.*, Siamamia*sp., Cf.*Anomoeodus*, Cf.*Gyrodus*,*Ionocopus* sp., Cf. *Thaiichthys* และ Ginglymodi indet.) เศษกระดองเต่าฟันจระเข้ (วงศ์ Goniopholididae) และฟันไดโนเสาร์กินเนื้อ (Cf. *Dromeosaur*)

การค้นพบซากดึกดำบรรพ์ของสัตว์มีกระดูกสันหลังบริเวณแหล่งขุดค้นภูพานทอง เป็นการเพิ่มความรู้ ด้านความหลากหลายของจำนวนสิ่งมีชีวิตโบราณที่พบในหมวดหินเสาขัว *Isanodusnongbualamphuensis* ถูกตั้งขึ้นเป็นฉลามชนิดใหม่ ปลากระดูกแข็ง 2 สกุล Cf.*Gyrodus* และ*Ionocopus* sp.ได้ถูกค้นพบเป็นครั้งแรกในประเทศไทย ไดโนเสาร์กินเนื้อสกุล Cf. *Dromeosaur* ถูกพบครั้งแรกในหมวดหินเสาขัว แม้ว่าซากดึกดำบรรพ์ของเต่า และจระเข้จะไม่สามารถจัดจำแนกในระดับชนิดหรือสกุลได้ แต่ก็ช่วยบ่งชี้ถึงความหลากหลายและความสัมพันธ์ของกลุ่มสิ่งมีชีวิตในสภาพแวดล้อมโบราณที่ปรากฏในหมวดหินเสาขัว เมื่อเปรียบเทียบการเปลี่ยนแปลงของฉลามไฮโบดอนท์ที่ปรากฏในแต่ละหมวดหินพบว่า หมวดหินโคกกรวดฉลามไฮโบดอนท์มีจำนวนลดลง เนื่องจากไม่ปรากฏฉลามวงศ์ Lonchiidae เช่นเดียวกับในปลากระดูกแข็งซึ่งก็แสดงถึงความเปลี่ยนแปลงที่ลดลงอย่างชัดเจน จากการไม่ปรากฏของ Pycnodontiformes, Lepisosteiformes และ Caturidae เหตุการณ์นี้อาจมีสาเหตุมาจากการเปลี่ยนแปลงของสภาพแวดล้อมในช่วงยุคจูแรสสิกตอนปลายถึงครีเตเซียสตอนต้น เนื่องจากสภาพแวดล้อมมีความแห้งแล้งเพิ่มมากขึ้น ทำให้แหล่งที่อยู่อาศัยลดลงวิถีชีวิตในเชิงนิเวศของ Lonchiidae และปลากระดูกแข็งเหล่านี้ น่าจะถูกแทนที่โดยฉลามเฉพาะถิ่น ในขณะที่เต่า จระเข้ และไดโนเสาร์ไม่ได้รับผลกระทบจากการเปลี่ยนแปลงนี้ในแง่ของการกระจายตัวทางบรรพ

ภูมิศาสตร์ซากดึกดำบรรพ์ของฉลามไฮโบดอนท์ แสดงให้เห็นถึงความสัมพันธ์ที่ใกล้ชิดร่วมกับฉลามเชื้อสายยุโรป (*Lonchidionkhoratensis*, *Egertonodus* sp. และ *Parvodus* sp.) รวมถึงฉลามจากเอเชีย (*Heteroptychoduskokutensis* และ *IsanodusPaladeji*) โดยเฉพาะการค้นพบฉลามสกุล *Lonchidion* ในหมวดหินคลองมีน ภูกระดึงและเสาขัว แสดงให้เห็นถึงการกระจายตัวอย่างกว้างขวางของฉลามวงศ์ Lonchiidae ทั้งในอเมริกาเหนือ ยุโรป แอฟริกา และเอเชีย ซึ่งน่าจะแพร่กระจายเข้ามาในชายฝั่งทะเลของไทยในช่วงกลางยุคจูแรสสิก และอพยพเข้ามาตั้งถิ่นฐานในแหล่งน้ำจืดของประเทศไทยจนเกิดความหลากหลายสูงในยุคครีเตเซียสตอนต้น การค้นพบจระเข้สกุล *Theriosuchus* ในหมวดหินภูกระดึง (ยุคจูแรสสิคตอนปลาย) ก็ช่วยสนับสนุนความสัมพันธ์ที่ใกล้ชิดร่วมกับสิ่งมีชีวิตเชื้อสายยุโรป และยังชี้ให้เห็นว่ายุโรปและเอเชียเชื่อมต่อกันในช่วงเวลาดังกล่าว อย่างไรก็ตามในปลากระดูกแข็งยังไม่สามารถประเมินการกระจายตัวและความสัมพันธ์ที่ใกล้ชิดได้ เนื่องจากความสัมพันธ์ที่แน่ชัดของตัวอย่างที่พบในบริเวณแหล่งขุดค้นภูพานทองยังไม่ชัดเจน

จากการเปรียบเทียบความสัมพันธ์ของลำดับชั้นหินพบว่า แหล่งขุดค้นภูพานทองวางตัวอยู่ในหมวดหินเสาขัวตอนล่าง และจากความสัมพันธ์ของสิ่งมีชีวิตในชั้นหิน แสดงให้เห็นว่าภูพานทองน่าจะมีอายุอยู่ในช่วง Hauterivian ถึง Barremian ตอนต้น โดยอาศัยหลักฐานของซากดึกดำบรรพ์ ละอองเรณู หอยสองฝา และฉลามไฮโบดอนท์บางชนิด

คำสำคัญ: หมวดหินเสาขัว ซากดึกดำบรรพสัตว์มีกระดูกสันหลังขนาดเล็ก ฉลามไฮโบดอนท์ มีโซโซอิค ยุคครีเตเซียสตอนต้น

TITLE Vertebrate microremains fromthe Early Cretaceous Sao Khua Formation, Khorat Group in PhuPhanThongfossil locality and their biostratigraphy

CANDIDATE Miss Suchada Khamha

DEGREE Doctoral of Philosophy Program in Palaeontology

ADVISORS Assistant Professor Komsorn Lauprasert, Ph.D.

Professor Gilles Cuny, Ph.D.

UNIVERSITY MahasarakhamUniversity **YEAR** 2018

ABSTRACT

Sampling of sediments from PhuPhan Thong, NongBuaLamphu Province (Sao Khua Formation) showed a high diversity of vertebrate microremains consisting of seven taxa of hybodont sharks (*Egertonodus* sp., *Hybodus*sp., *Parvodus* sp., *Isanoduspaladeji, I. nongbualamphuensis, Lonchidionkhoratensis* and *Heteroptychoduskokutensis*), eight taxa of bony fishes (Cf. *Caturus,* (?*)Isanichthy* sp., *Siamamia*sp., Cf.*Anomoeodus,* Cf.*Gyrodus,Ionocopus* sp., Cf. *Thaiichthys*and Ginglymodiindet.), turtle (fragmentary shell plates)**,** crocodilians (two morphotypes of Goniopholididae teeth) and one taxon of theropod dinosaur (Cf. *Dromeosaur*).

The discovery of vertebrate microremains from PhuPhan Thong fossil locality increased our knowledge about the palaeobiodiversityof ancient faunas from the Sao Khua Formation. These included the discovery of a new hybodonts species, *Isanodusnongbualamphuensis,* thefirst recordsof cf.*Gyrodus* and *Ionoscopus* sp. in Thailand and a first record of the dinosaur,Cf. *Dromeosaur*in the Sao Khua Formation. Although turtle and crocodile remains were not identified at the generic and specific levels, these organisms could be used to better understand the palaeoenvironmentof the Sao Khua Formation. In term of evolution of the fish fauna, hybodonts of the KhokKruat Formation show a decline compared with the fauna of the Sao Khua Formation, mostly because of the disappearance of the Family Lonchiidae and there is a dramatic decline of bony fishes because of the loss of Pycnodontiformes, Lepisosteiformesand Caturidae. This faunal turn-over has been caused by changes in the palaeoenvironment during the Early Cretaceous, due to increasing drought environment,

causing habitat reduction.Lonchiidae and bony fishes seem to be replaced in the same ecological niches by endemic hybodont sharks in the KhokKruat Formation. On the contrary, turtle, crocodiles and dinosaurs were not affected.

From apalaeobiogeographical point of view, the hybodont fossils from the Sao Khua Formation displayed affinities with both European hybodonts (*Lonchidionkhoratensis*, *Egertonodus* sp. and *Parvodus* sp.) and Asian hybodonts (*Heteroptychoduskokutensis* and *Isanoduspaladeji*). The discovery of *Lonchidion* from the Khlong Min, PhuKradung and Sao Khua Formations confirms the wide distribution of the Family Lonchiidae, which was already known in North America, Europe, Africa and Asia. They probably reached the coast of Thailand during the Middle Jurassic and then penetrated and radiated in freshwater environments during the Barremian. The discovery of *Theriosuchus*from the PhuKradung Formation (Late Jurassic) also supports affinitieswith European faunas and also suggests that Europe and Asia has been connected at that time. The palaeogeographical affinities of bony fishes are not possible to assess because the exact affinities of the materials from PhuPhan Thong are unclear.

Concerning stratigraphic correlation,PhuPhan Thong is situated at the bottom of the Sao Khua Formation and biostratigraphic study indicates that PhuPhan Thong is Hauterivian to Early Barremian in age based on pollen, bivalve and some hybodontevidences.

Keywords: Sao Khua Formation, vertebrate microremains, hybodont, Mesozoic, Early Cretaceous

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CHAPTER 1

INTRODUCTION

1.1 Rational of study

Fossil vertebrates from the Mesozoic have been found in many parts of Thailand, most of them coming from Isan (in the Northeast part of the country). In this area, the fossils come from the Khorat Group and show an important diversity, including hybodont sharks, bony fishes, lungfishes, temnospondyl amphibians, turtles, crocodilians, pterosaurs and dinosaurs (Buffetaut and Suteethorn, 1998). However, these faunas, are mainly known from the study of macroremains whereas the microremains are still poorly known. The vertebrate microremains from the Khorat Group form a rich assemblage. Most of these fossils were obtained from three formations of the Khorat Group, i.e., the Phu Kradung, Sao Khua and Khok Kruat Formations.

Phu Phan Thong locality is situated along the Nong Bua Lamphu-Udon Thani road, Nong Bua Lamphu Province. Accrording to the lithology and stratigraphic position, Phu Phan Thong is referred to the Sao Khua Formation. This locality has yielded a rich assemblage of vertebrate microremains which includes at least various hybodont sharks, bony fishes and Pycnodontiformes, various small crocodiles and dinosaur remains, including a possible troodontid theropod. However this fauna has never been studied in details. Phu Phan Thong is a very interesting site partly because it lies on the lower part of the Sao Khua Formation and appears transitional between the faunas from the older Phu Kradung Formation and the sites situated lie on upper part of the Sao Khua Formation. Several sites from the Phu Kradung Formation (Chong Chat in Nong Bua Lamphu Province, Khok Sanam and Phu Noi in Kalasin Province), from the red beds facies of the Sao Khua Formation (Phu Phok in Sakhon Nakhon Province, Phu Wiang in Khon Kaen Province, Nong Sung in Mukdahan Province) and the Khok Kruat Formation (Lam Pao Dam in Kalasin Province, Khok Pha Suam in Ubon Ratchathani Province) have also yielded a rich

assemblage of vertebrate microremains, which allow a detailed comparisons between these sites. Such detailed comparisons will allow a better understanding of the differences observed between these different faunas, and to discuss the impact of possible environmental changes on the evolution of terrestrial palaeobiodiversity in Thailand at the Jurassic/Cretaceous boundary.

1.2 Objectives

1. To establish a list of the vertebrate microremains from the Sao Khua Formation and to study their taxonomy.

2. To differentiate the different fauna assemblages to understand the palaeoecology at the Early Cretaceous in Thailand.

3. To better understand the palaeogeography of the time.

1.3 Study areas

1.Study locality: the Sao Khua Formation, Phu Phan Thong fossil locality in Nong Bua Lamphu Province

2. Comparison localities;

2.1 Phu Kradung Formation: Phu Noi, Phu Num Jun and Khok Sanam in Kalasin Province, Chong Chat in Nong Bua Lamphu Province.

2.2 Sao Khua Formation: Phu Phok in Sakhon Nakhon Province, Phu Wiang in Khon Kaen Province.

2.3 Khok Kruat Formation: Lam Pao Dam in Kalasin Province, Khok Pha Suam in Ubon Ratchathani Province.

2.4 Khlong Min Formation: Mab Ching in Na Khon Sri Thammarat Province.

2.5 Equivalent to the Sao Khua Formation: Kut Island (Ko Kut) in Trad Province.

1.4 Significances of study

The results will improve our knowledge of the vertebrate palaeobiodiversity in Thailand during the mesozoic as well as will allow a better understanding of the evolution of the terrestrial palaeobiodiversity in Thailand at the Jurassic/Cretaceous boundary.

CHAPTER 2

LITERATURE REVIEW

The main aim of this researchis to identify the vertebrate microremains from Phu Phan Thong locality, Sao Khua Formation. The specimens from the Phu Kradung, Sao Khua and Khok Kruat Formations will be compared to study their adaptation and to understand the ecosystem in which they lived, in order to reconstruct the palaeoenvironment during Jurassic and Cretaceous. To achieve the research objectives as described above, related literatures and research articles have been reviewed for preliminary concerning;

2.1 Definition of the fossil vertebrate microremains and their significances

Fossils are the remains or indication of past life. They are generally the hard parts of animals that have been petrified, transformed from the shell or bone into stone. Vertebrate microremains or microfossils are vertebrate fossils generally not larger than four millimeters, and commonly smaller than one millimeter, the study of which requires the use of light or electron microscope. Fossils which can be studied with the naked eye or low-powered magnification, such as a hand lens, are referred to as macrofossils. Obviously, it can be hard to decide whether or not some organisms should be considered microfossils, and so there is no fixed size boundary (Mckenna *et al.*, 1994). Some vertebrate microremains come from a hard part of animals that was difficult to decay such as teeth, scale and some part of bone.

2.2 Morphological study

Vertebrate microremains mainly consist of a part of aquatic and terrestrial organisms, in order to identify specimens, their morphology will be study in detail.

2.2.1 Chondrichthyes

Sharks and rays belong to the Class Chondrichthyes (meaning

"cartilage fishes"), because they lack an internally ossified bony skeleton, having instead a special type of cartilage forming the braincase, jaws, gill arches, vertebrae and fin supports. The only hard bony tissues are developed in their defensive fin-spines, teeth and scales.

Shark remains are known mainly by isolated teeth which are found abundantly in many fossil localities. Skeletons are much rarer and have been preserved in only a few exceptional deposits such as in Eocene deposits of Monte-Bolca and the Green River limestones in Wyoming also in the Cenomanian and Santonian depositional environment of Lebanon and Campanian of Bavaria (Cappetta, 1987).

General Morphology

The general morphology of selachians varies strongly from group to group. Nectic sharks, the body is fusiform and very stream lined with a sharp snout and well deveiloped tail whearas pelagic sharks, the anal fin is reduced and an important size difference can be observed between the large pectoral and small pelvic fins. The benthic sharks, the lower lobe of the caudal fin is generally reduced and the anal fin is relatively well developed. There are possess 5 to 7 gill-slits opening laterally behind the head (Cappetta, 1987).

Dentition

The dentition of selachians is polyphyodont, teeth are replaced throughout their life. The teeth are also lyodont that is to say that they are not strongly anchored in the jaw cartilage. Selachians teeth consist of an enameloid-covered part, the crown and well-developed basal part. The root are anchored by connective tissue fiber in the covering the jaws (Vennemann *et al.*, 2001).

Most of the selachians of the past are therefore described on the basis of small scattered remains including the teeth and dermal denticles. The variation in shape morphology according to their position in the jaws makes the identification of isolated teeth quite difficult. In homodont dentition, teeth in the upper and lower jaws have the same morphology whereas in heterodont dentition, the teeth display different shapes according to their position in the jaws (Figure 2.1). The shape of shark teeth reflects the type of food that each species eats (Cappetta, 1987).

For definning the different categories of teeth on the jaw, I shall refer to the species *Carcharias taurus* which has been studied by Leriche (1950) and later by

Applegate (1965) (Figure 2.2). In the upper jaw, there are three well-developed anterior files and followed by a file of reduced (sometime distorted teeth). These are called intermediate teeth and followed by Seven files of lateral teeth, which have crowns slanted towards the rear. Fifteen of posterior teeth are followed, which have crowns reduced.

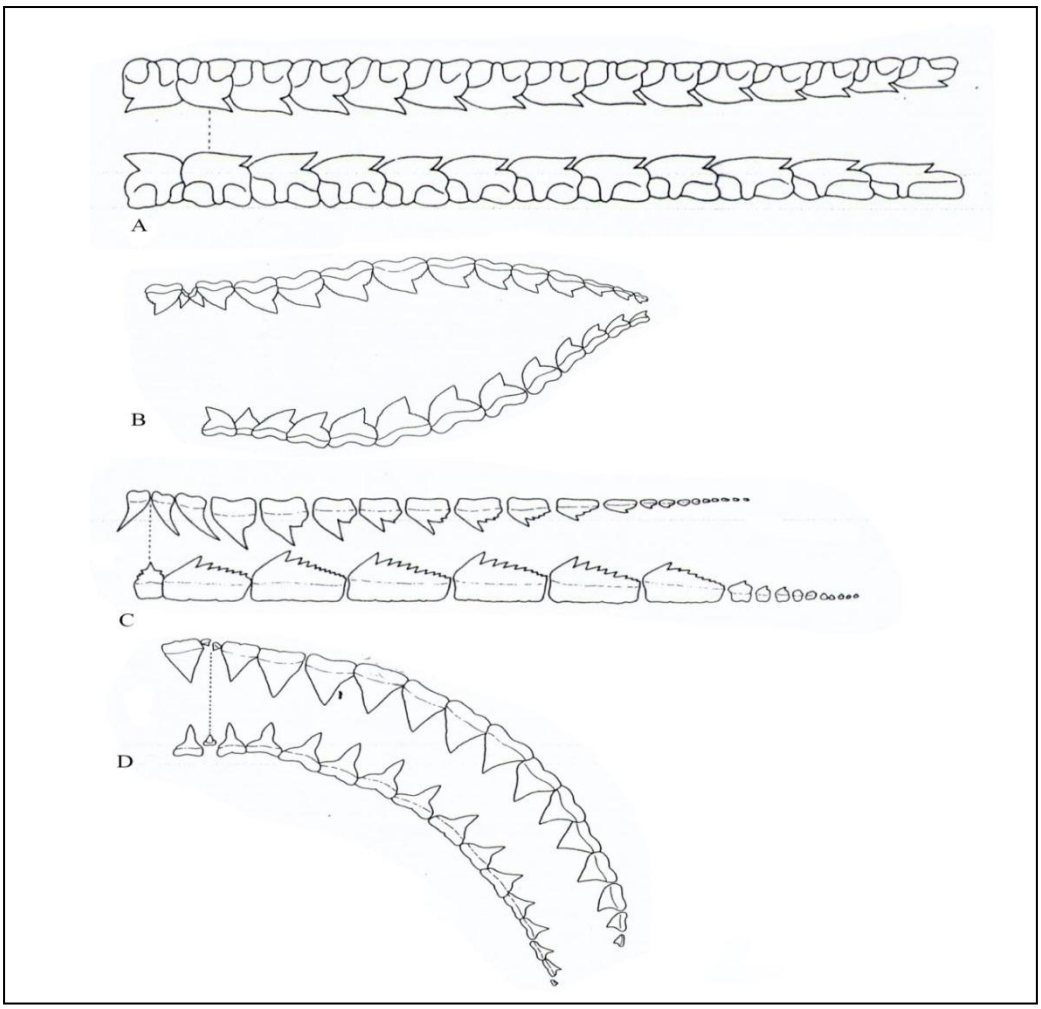

Figure 2.1 A-B; the homodont dentition. (A) cutting type of *Squalus acanthias*, (B) cutting type of *Galeocerdo cuvier*. C-D the heterodont dentition. (C) cutting-clutching sub-type of *Hexanchus griseus* and (D) cutting-clutching sub-type of *Pterolamiops*cutting type of *Galeocerdo cuvier*. C-D the heterodont dentition. (C) cutting-clutching sub-type of *Hexanchus griseus* and (D) cutting-clutching sub-type of *Pterolamiops longimanus* (Modofied from Bigelow and Schroeder, 1948)

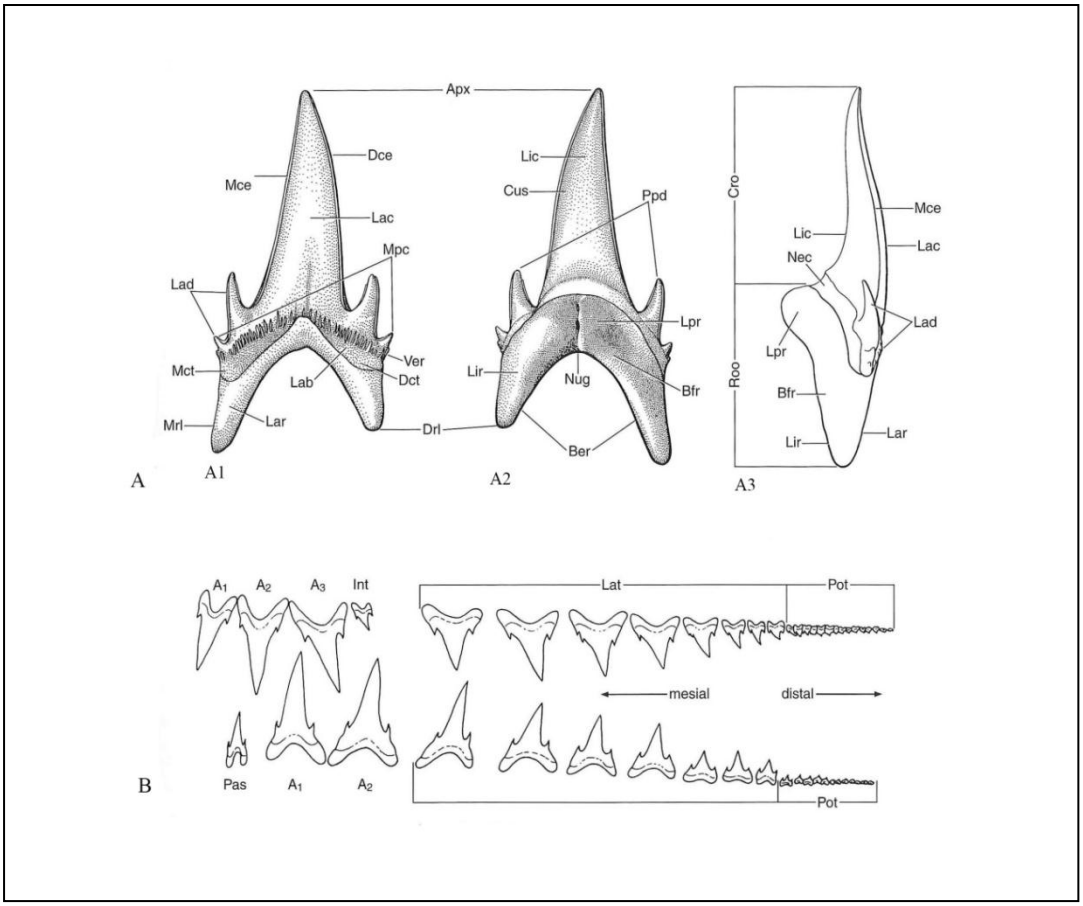

Figure 2.2 (A) shark tooth terminology (A_1) labial, (A_2) lingual and (A_3) mesial views. (B) the position of *Carcharias taurus*teeth (redrawn from Bigelow and Schroeder, 1948)

Abbrevvations used in Figure : $A_{1,2,3}$: anterior teeth, Apx: apex, Ber: basal edge of the root, Bfr: basal face of the root, Cro: crown, Cus: cusp, Dce: distal cutting edge, Dct: distal crown tongue, Drt: distsl root lobe, Lac; labial bulge of the crown, Lad: lateral cusplets, Lar: labial face of the root, Lir: lingual face of the root, Lpr: lingual protuberance of the root, Mce: mesial cutting edge, Mct: mesial crown tongue, Mpc: marginal pair of cusplets, Mrl: mesial root lobe, Nec: neck (lingual furrow), Nug: nutritive groove, Ppd: proximal pair of cuspletes: Roo: root, Ver: vertical ridges.

Dermal denticles

The sharks are protected by dermal denticles embedded in the skin. A dermal denticle arises in the dermis, anchored by a basal plate. Its point pushes up through the epidermis. A nerve and blood vessel growns through the plate into the soft tissue within the denticle, called the pulp cavity. Around there is a layer of one of nature's hardest substances, dentine. And this is covered by an even harder material, enameloid. The structure of a dermal denticles is thus very similar to that of a tooth. In modern sharkss, once a denticle reaches its full size, it stops growing, eventually fall out, and is replaced by another one. More primitive sharks possessed growing dermal denticles. Dermal denticles vary widely in shape and size between shark species and according to their position on the body (Figure 2.3) (Reif,1980).

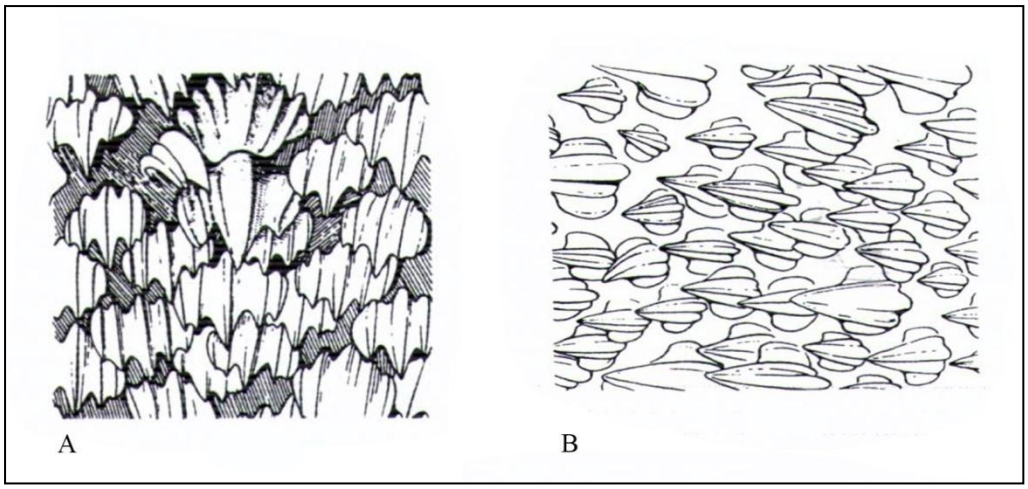

Figure 2.3 The dermal denticles various families of sharks. (A) *Carcharhinus leucas*, (B) *Scyliorhinus canicula* (Cappetta, 2012)

2.2.2 Osteichthyes

The osteichthyans (bony fish) today form the largest and most diverse group of vertebrates. They first appeared in the Silurian, some 420 mya when they were only a minor component of the ancient fish faunas. By the start of the Devonian Period all major groups of bony fishes had appeared, and before the end of Devonian, the first land animals had evolved from within the lobe-finned bony fishes (sarcopterygians).

The three major groups of bony fishes are ray-finned (Actinopterygii), the lungfishes (Dipnoi) and the predatory lob-finned. Aside from their differing physical features, especially their unique pattern of bones forming the skull and shoulder girdles, each group evolved unique tooth tissue types for specific feeding adaptation (Kardong, 2006). The primitive scales in actinopterygian are made of bone, dentine and ganoine (a kind of enameloid) (Figure 2.4). Primitive bony fishes teeth can be easily recognized because they are covered by two different enameloid tissue: ganoine at the base and acrodine at the top (Figure 2.5).

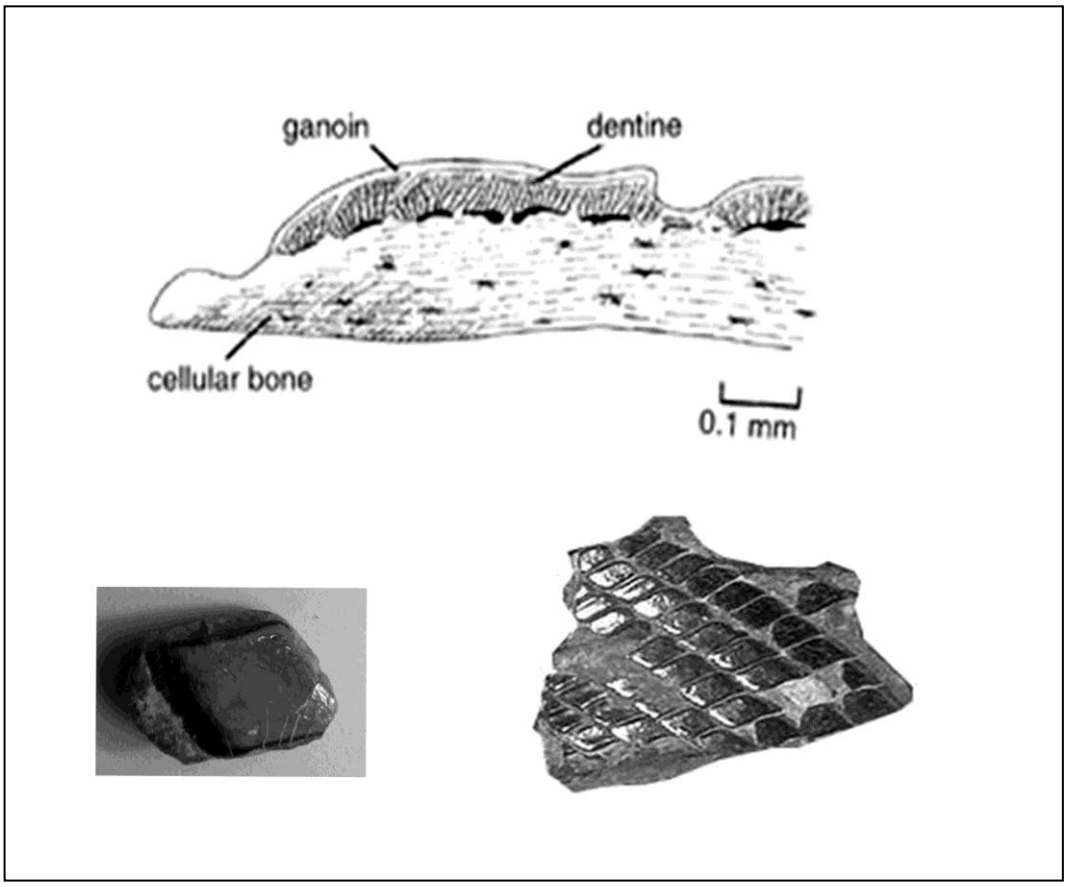

Figure 2.4 The bony fish scales (bony fishe scales from Phu Num Jun locality, Kalasin Province)

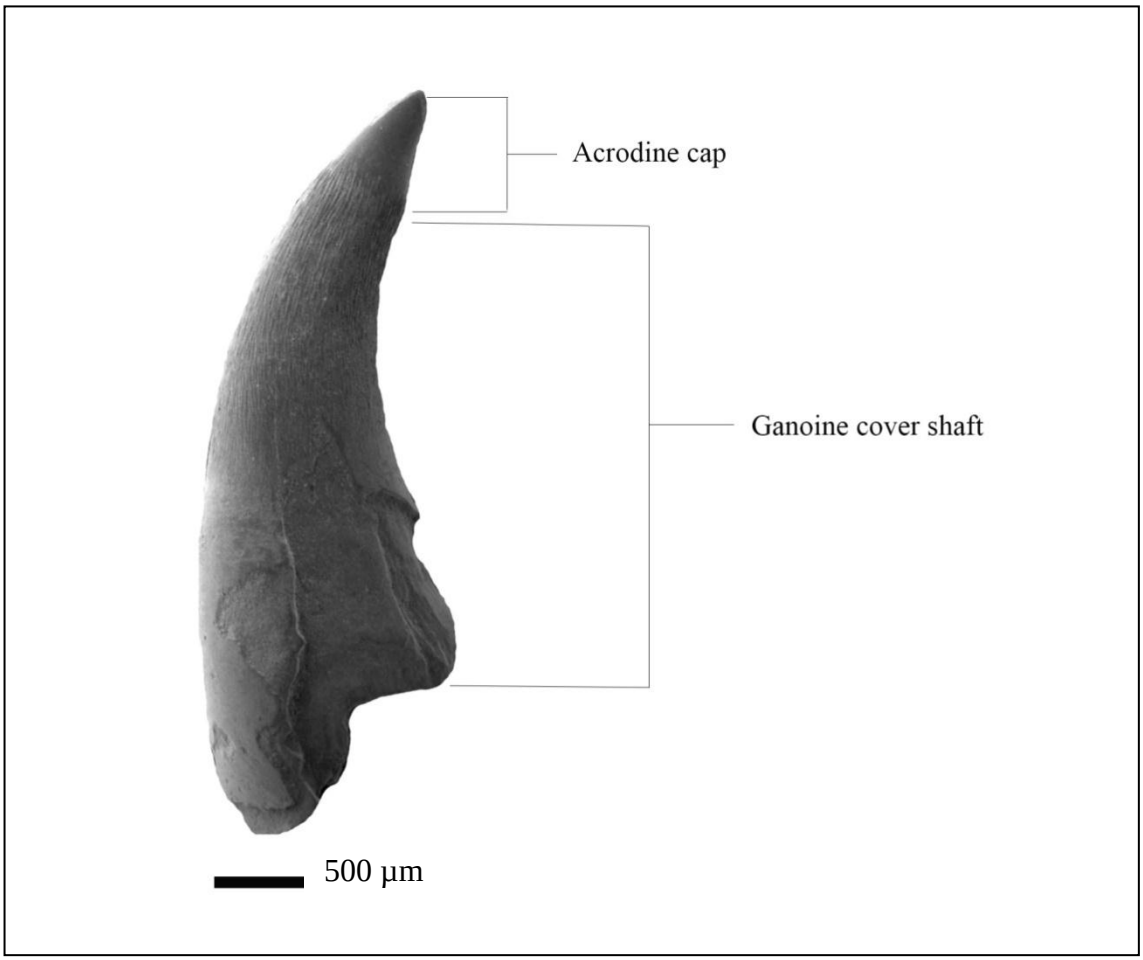

Figure 2.5 The detail of bony fish tooth, *Belonostomus* sp. from southern England (Sweetman *et al.*, 2014). Scale bar 500 µm

2.2.3 Reptilia

Subclass Anapsida

Three orders are included in the Anapsida : Protothyromorpha, Procolophonia and Pareiasauria. In this group temporal fenestrae are absent on their skull. The numerous specialized modification of Turtles (Testudines) justify their separation from Anapsida into a separate subclass, chelonomorpha. Order Protothyromopha assumes a key position because it contained the ancestors of most of the higher reptiles.

Subclass Chelonomorpha

Order Testudines (Testudinata, Chelonia, turtles)

Reptiles whose short body is enclosed between an arched dorsal shield (carapace) and a flat ventral plate (plastron). Carapace and plastron are formed from an outer epidermal keratinous layer over an inner bone plate (theca). The temporal roof may be emarginated from behind and/or below. There is a tendency to reduce the dermal elements of the skull. Teeth are absent, except in the oldest forms. The phalangeal formula is mostly 2 3 3 3 3 (Emil Kuhn-Schnyder and Hans Rieber, 1986).

Subclass Archosauria

A large group of active, diapsid reptiles (possessin a lower and upper temporal fenestrae) of medium to very large dimensions, with several bipedal line. Theskull is akinetic, mostly with an antorbital opening. Bipedalism in some groups led to profound modifications of girdles and limbs(Emil Kuhn-Schnyder and Hans Rieber, 1986).

Crocodylia

Among the new groups of reptiles that flourished in the Jurassic and Cretaceous times were the crocodilians, which are the largest of modern reptiles. They first appeared in the Late Triassic as lightly built terrestrialforms. They show heavily armored, elongated bodies with long snouts and powerfultails and limbs. The neck, trunk and tail are armored dorsally and sometime ventrally by bony plates (osteodermes) that are covered with thick keratinous skin (Zug *et al.,* 2001).
Teeth of crocodilians are like mammalian teeth, so-called thecodont, which mean they are set into sockets to which they are attached by ligaments. They are also excellent swimmers and can move surprisingly fast on land, where they generally adopt a semierect gait (Pough *et al.*, 2001; Zug *et al.*, 2001).

Dinosauria

From the middle Triassic to the end of the Cretaceous, the land was ruled by two orders of Archosauria: Saurischia and Ornithischia. The secret of their success was fast locomotion and efficient dentition. The dinosaurs are currently a focus of lively debate concerning whether they were cold or warm-blooded. In view of the variety of their anatomical and ecological characteristic, it can be conjectured that their thermophysiology was variable as well.

The two order Saurischia and Ornitischia differed mainly in the shape of the pelvis. The saurischian pelvis is triadiate, with the pubis directed forward. Ornithischian have a posteriorly pointing pubis that runs parallel to the ischium; in addition, they often have a forward directed process (tetraradiate type) (Emil Kuhn-Schnyder and Hans Rieber, 1986).

2.3 Geology of the Khorat Plateau

The Khorat Group in the Northeastern Thailand is a set of Continental sediments deposited during the Mesozoic Era. It is at least 4000 meter thick. It is not only restricted in Northeastern Thailand but also extends into Laos, Cambodia, Vietnam and Southwestern China (Racey *et al.,* 1994). In previous studies, the Khorat Plateau was said to encompass 9 formations, the Huai Hin Lat, Nam Phong, Phu Kradung, Pra Wihan, Sao Khua, Phu Phan, Khok Kruat, Mahasarakham and Phu Thok Formations in ascending order, ranging in age from the late Upper Triassic to the Upper Cretaceous based mainly on vertebrates, bivalves and palynomorphs (Meesook *et al.*, 2002). The main lithologies of the rocks are reddish brow to light gray sandstones, conglomeratic sandstones, siltstones, claystones and conglomerates. Evaporitic rocks are found in Mahasarakham Formation only. The rocks are interpreted as having been deposited by meandering and braided rivers in semi-arid conditions (Meesook, 2000). However, there is a gap between the Nam Phong and the Phu Kradung Formations, so that the latter does not belong to the Khorat Group as shown by Carter and Bristow (2003). The latter authors restricted the Khorat group to 5 formations on the basis of stratigraphical principles: the Phu Kradung, Pra Wihan, Sao Khua, Phu Phan, and Khok Kruat formations in ascending order. The age of the Khorat Group is thus considered as mostly Late Jurassic/Early Cretaceous. Only the Phu Kradung, Sao Khua and Khok Kruat Formations will be discussed here. For more in formation about the different formations of the Khorat Group, see Carter and Bristow (2003).

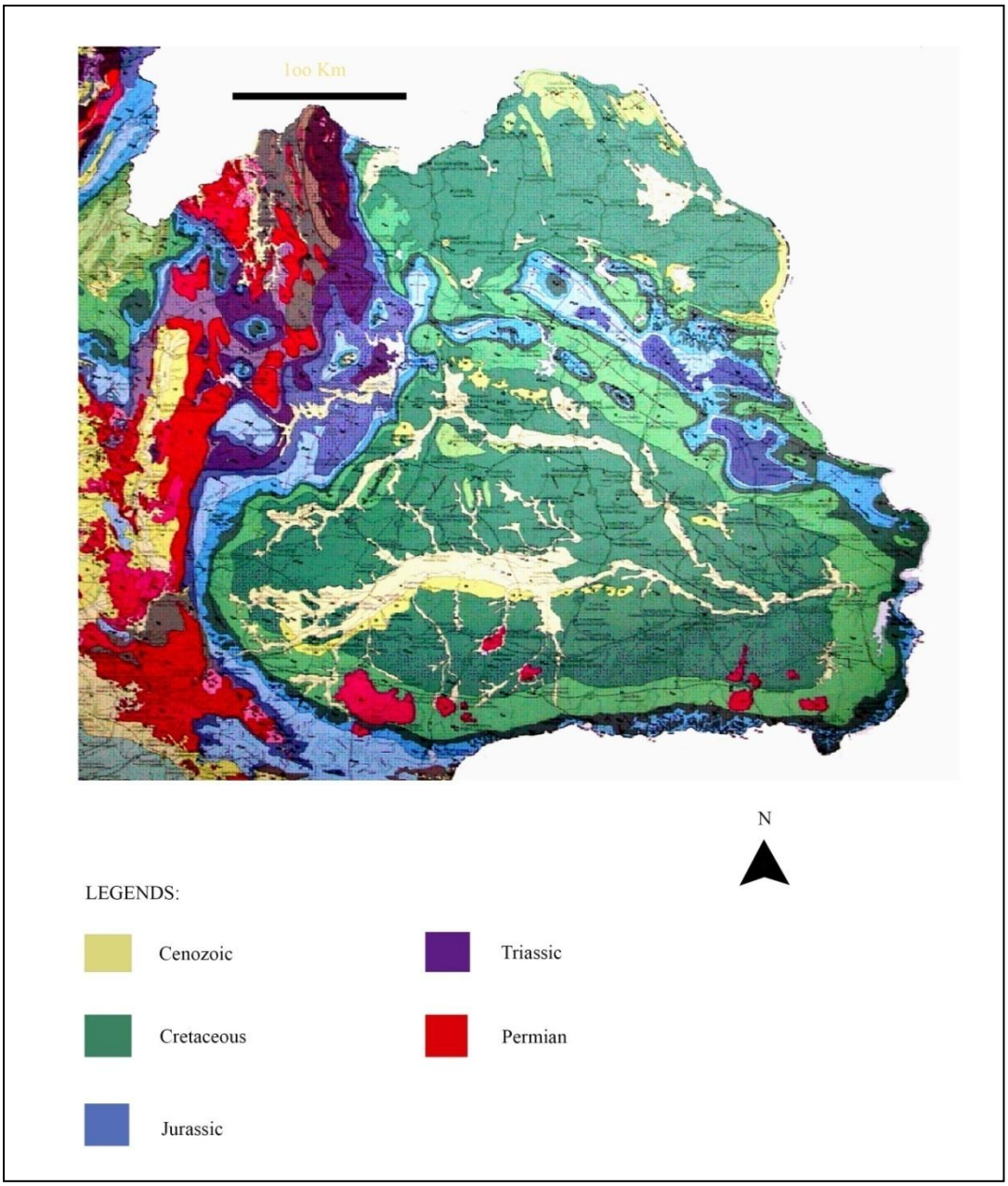

Figure 2.6 Geological map of the northeastern Thailand (Adapted after DMR, 1999)

2.3.1 Phu Kradung Formation

The Phu Kradung Formation is the lowest formation of the Khorat Group. According to age constraints provided by the overlying formationsand fossils evidence, the Phu Kradung Formation might be Late Jurassic or basal Cretaceous in age (Buffetaut and Suteethorn, 2007; Tong et al., 2009; Racey and Goodall, 2009; Cuny *et*

al., 2014) . It is about 1,1001 metres thick at the type section wich consists of maroon micaceous siltstone, sandstone, mudstone with intermittent calcreat and conglomerate. It was deposit in continental environment, mainly lake-dominated floodplain cut by meandering and occasionally braided river channels. The palaeoclimatology of this formation is interpreted as semi-arid condition (Meesook, 2000).

2.3.2 Sao Khua Formation

The Sao Khua formation can be observed thoughout the western, eastern and southern parts of the plateau and most parts of the Phu Phan Range along the NE-SE trending anticlinal axes. This formation contains various cycles of reddish brown mudstone, siltstone and fine to medium grained sandstones. The sandstones tend to be light gray in color. Lenses of fine-clast conglomerate with calcareous cement and mica content and including cross lamination and bedding appear in some sandstone beds. The evidences from fossil assemblages and stratigraphic correlation point to an Early Cretaceous age for this formation (Sattayarak *et al.*, 1991). Based on the freswater bivalve, *Pseudohyria (Matsumotoina) somanai* and pollen evidence, the Sao Khua Formation was not younger than Barremian-Aptian in age (Tumpeesuwan *et al*., 2010, Racey and Goodall, 2009). During this time, the sediment deposited in low-energy, meandering rivers and on extensive floodplain (Mouret *et al.*, 1993; Racey *et al.*, 1996). The deposition of sediments suggests that the prevailing braided river system has changed to the meandering river together with the changes from slightly humid to semi-arid palaeoclimate. The palaeoclimate at that time was more semi-arid than the Late Triassic-Jurassic, which contained many calcrete horizons and some bedded and nodule silcrete layer (Meesook, 2000)

The Sao Khua formation has yielded the most abundant and most diverse vertebrate fauna of the Khorat Group, comprisinga lot of isolated hybodont sharks, a numerousof isolated teeth and scales of bony fishes, shell fragment of turtles, crocodiles teeth, isolated teeth and fragment bones of dinosaurs (Buffetaut *et al.*, 2005; Cavin *et al.*, 2007; Cuny *et al.*, 2006; 2007).

2.3.3 Khok Kruat Formation

The Khok Kruat Formation is assigned to the top of the Khorat Group. It is separated from the basal anhydrite of the overlying unconformtably Mahasarakham Formation. However, it was rests conformably on the underlained Phu Phan Formation. It is about 430-700 metres. It mainly consists of reddish brown silstone, reddish brown maroon sandstone, mudstone and conglomerates (Meesook, 2000). The sediment were deposit in channel sandstones and floodplainsequences. This formation, paleoclimate had changed from humid to semi-arid. The occurrence of freshwater shark *Thaiodus ruchae* which is also found in the Aptian-Albian of Takenena Formation of the Lhasa block of Tibet, it was possible to suggests the Khok Kruat Formation as the Early Cretaceous (Aptian-Albian) in age (Cappetta *et al.*, 1990).

The Khok Kruat Formation has yielded a various vertebrate fossils including a number of freshwater sharks, isolated teeth of Ginglymodi, bone and teeth of crocodiles, diverse dinosaurs and pterosaurs (Cappetta *et al.,* 1990; Cuny *et al.,* 2003; 2006; 2007; Tong *et al.,* 2005; Lauprasert, 2007; Buffetaut *et al.,* 2003).

2.4 Stratigraphical framework

In this work, stratigraphical range based on the chart published by Gradstein *et al.*, (2004) (Figure 2.7).

Era	Sub-era Period Sub-period		Epoch		Age	Age (My)	Age abbr.
Cenozoic	Quaternary or Pleistocene				Holocene	0.01	Hol
					Pleistocene	1.81	Ple
	Tertiary	Neogene	Pliocene		Piacenzian	3.60	Pia
					Zanclean	5.33	Zan
			Miocene		Messinian	7.25	Mes
					Tortonian	11.61	Tor
					Serravallian	13.65	Srv
					Langhian	15.97	Lan
					Burdigalian	20.43	Bur
					Aquitanian	23.03	Aqt
		Paleogene	Oligocene		Chattian	28.4	Cht
					Rupelian	33.9	Rup
			Eocene		Priabonian	37.2	Prb
					Bartonian	40.4	Brt
					Lutetian	48.6	Lut
					Ypresian	55.8	Ypr
			Paleocene		Thanetian	58.7	Tha
					Selandian	61.7	Sel
					Danian	65.5	Dan
Mesozoic	Cretaceous		K2	Senonian	Maastrichtian	70.6	Maa
					Campanian	83.5	Cmp
					Santonian	85.8	San
					Coniacian	89.3	Con
					Turonian	93.5	Tur
					Cenomanian	99.6	Cen
			K1		Albian	112.0	Alb
					Aptian	125.0	Apt
					Barremian	130.0	Brm
				Neocomian	Hauterivian	136.4	Hau
					Valanginian	140.2	Vlg
					Berriasian	145.5	Ber
	Jurassic		Malm		Tithonian	150.8	Tth
					Kimmeridgian	155.7	Kim
					Oxfordian	161.2	Oxf
			Dogger		Callovian	164.7	Clv
					Bathonian	167.7	Bth
					Bajocian	171.6	Baj
					Aalenian	175.6	Aal
			Lias		Toarcian	183.0	Toa
					Pliensbachian	189.6	Plb
					Sinemurian	196.5	Sin
					Hettangian	199.6	Het
	Triassic		Tr3		Rhaetian	203.6	Rht
					Norian	216.5	Nor
					Carnian	228.0	Crn
			Tr2		Ladinian	237.0	Lad
					Anisian	245.0	Ans
			Tr1		Olenekian	249.7	Ole
					Induan	251.0	Ind

Figure 2.7 Stratigraphical chart with abbreviation, the data from Gradstein *et al.*, (2004)

2.5 Mesozoic vertebrate microremains in the Khorat Plateau

The Khorat Plateau has an excellent record of non-marine Mesozoic environments. Many localities in the northeastern part of the country have yielded abundant fossils, including plants, invertebrates and vertebrates (Figure 2.8). Concerning the vertebrates, a Thai-French cooperation on Mesozoic vertebrates from Thailand has resulted during the past 20 years in the discovery of many important sites and specimens, and in the publication of numerous papers on the topic. Among the main results of this cooperation are the discoveries of the earliest known tyrannosaur (*Siamotyrannus isanensis*, described in *Nature* in 1996), the earliest known sauropod dinosaur (*Isanosaurus attavipachi*, described in *Nature* in 2000), and the new Cretaceous sauropod *Phuwiangosaurus sirindhornae* (described in *Comptes Rendus de l'Académie des Sciences de Paris* in 1994). However, these faunas are mainly known from the study of macroremains whereas the microremains are still poorly known. During the part of this project most of the microremains especially freshwater sharks has been studied by Dr. Gilles Cuny. He mentions that Mesozoic sharks in Thailand (both in the Indochina and Sibumasu (Shan-Thai) terranes) represent at least 24species, many of which have not yet been named, distributed in 14genera (Cuny *et al.*, 2006; 2007; 2009; 2010; 2014) (Table 2.1). In addition, Cavin *et al*. (2009) and Deesri *et al*. (2013; 2014) described the bony fishes record from Late Jurassic-Early Cretaceous. They have been identified these materails on the basis of the mophotypes of the isolated teeth, scales and the articulated materials (Table 2.2).

Table 2.1 Mesozoic fossil record of hybodont sharks in Thailand (Cuny *et al.*, 2006; 2007; 2009; 2010; 2014)

Formations	Sites	Hybodont shark taxa
Indochaina Terrane		
Hauai Hin Lat	Chulabhorn Dam (Chaiyaphum)	Isolated dermal denticals
	Chong Chat (Nong Bua Lamphu), Phu Nam Jun (Kalasin), Wang Din So (Pitsanulok), Kham Phok (Mukdahan)	*Hybodus* spp.
	Phu Noi (Kalasin),	*Acrodus kalasinensis*
	Chong Chat (Nong Bua Lamphu), Wang Din So (Pitsanulok)	*Acrodus* sp.
	Phu Noi ,Sang Khae (Kalasin)	*Jiaodontus* sp.
	Chong Chat (Nong Bua Lamphu), Wang Din So (Pitsanulok)	*Acrodus* sp.
	Phu Noi (Kalasin),	*Acrodus kalasinensis*
Phu Kradung	Phu Noi, Khok Sanam (Kalasin)	*Lonchidion* sp A
	Phu Noi (Kalasin), Kham Phok (Mukdahan) NBL32 (Nong Bua Lamphu), Wang Din So (Pitsanulok)	*Lonchidion* sp B
	Kham Phok (Mukdahan), Sang Khae (Kalasin)	Cf. *Heteropthychodus kokutensis*
	Kham Phok (Mukdahan), Sang Khae (Kalasin)	Cf. *Heteropthychodus kokutensis*
	Kham Phok (Mukdahan), Sang Khae (Kalasin)	Cf. *Heteropthychodus kokutensis*
	Chong Chat (Nong Bua Lamphu)	*Heteropthychodus* sp.
	Kham Phok (Mukdahan), Khok Sanam (Kalasin), Wang Din So (Pitsanulok)	Hybodont dosal fin spines
Sao Khua	Phu Phan Thong, Phu Wat (Nong Bua Lamphu), Phu Noi (Sakhon Nakhon), Nong Sung (Mukdahan), Ko Kut (Trad)	*Hybodus* sp.A *Hybodus* sp. B
	Phu Phan Thong (Nong Bua Lamphu)	*Lonchidion khoratensis* *Parvodus* sp.
	Phu Phan Thong, Phu Wat (Nong Bua Lamphu), Phu Noi (Sakhon Nakhon), Ko Kut (Trad)	*Isanodus paladeji*

Table 2.1 Mesozoic fossil record of hybodont sharks in Thailand (Cuny *et al.*, 2006; 2007; 2009; 2010; 2014) (continue)

Formations	Sites	Hybodont shark taxa
Indochaina Terrane		
Sao Khua	Phu Phan Thong, Phu Wat, Huai Dua and Huai Lao Yang (Nong Bua Lamphu), Phu Wiang(Khon Kaen), Phu Kum Khao, Phu Mai Paw (Kalasin), Phu Phok, Phu Noi (Sa khon Nakhon), Non Liam (Chaiyaphum)	*Heteroptychodus kokutensis*
	Nong Sung (Mukdahan)	*Mukdahannodus trisivakulii*
	Phu Phan Thong (Nong Bua Lamphu),	Isolated dermal denticles
		Cephalic spine
	Phu Noi (Sa khon Nakhon)	Dorsal fin spines
Khok Kruat	Khok Pha Suam (Ubon Ratchathani), Sam Ran (Khon Kaen), Ban Khok Kruat, Ban Sapan Hin (Nakhon Ratchasima)	*Thaiodus ruchae*
	Khok Pha Suam (Ubon Ratchathani), Sam Ran (Khon Kaen), Ban Khok Kruat, Ban Sapan Hin (Nakhon Ratchasima)	*Thaiodus ruchae*
	Khok Pha Suam (Ubon Ratchathani)	*Khoratodus foreyi*
	Khok Pha Suam (Ubon Ratchathani)	*Acrorhizodus khoratensis*
	Khok Pha Suam (Ubon Ratchathani)	*Acrorhizodus khoratensis*
Sibumasu (shan-Thai) Terrane		
Formations	**Sites**	**Hybodont shark taxa**
Khlong Min	Mab Ching, Ao Min (Nakhon Sri Tammarat), Khong Thom (Krabi)	*Hybodus* spp.
	Ao Min (Nakhon Sri Tammarat), Ao Luk (Krabi)	*Asteracantus* sp.
	Ao Min (Nakhon Sri Tammarat)	*Lonchidion reesunderwoodi*
Huai Hin Fon	Pha Dang Zinc Mine	*Asteracantus* sp.

Table 2.2 Late Jurassic- Early Cretaceous of the bony fish taxa from Thailand (Cavin *et al.*, 2009; Deesri *et al.*, 2013; 2014)

Formations	Sites	Bony fish taxa
Phu Kra Dung	Khok Sanam, Phu Noi, Phu Nam Jun (Kalasin), Chong Chat (nong Bua Lamphu)	*Ferganoceratodus* sp.
	Khok Sanam (Kalasin)	Cf. *Ptycholepis*
	Phu Noi (Kalasin)	*Isanichthys lertboosri*
	Phu Nam Jun (Kalasin)	*Isanichthys palustris*
	Phu Nam Jun (Kalasin), Kham Phok (Mukdahan)	*Thaiichthys buddhabutrensis*
	Chong Chat (Nong Bua Lamphu)	Cf. *Thaiichthys*
	Khok Sanam (Kalasin)	Ginglymodi sp.
Sao Khua	Phu Phok (Sakhon Nakhon)	*Siamamia naga*
	Phu Phan Thong (Nong Bua Lamphu)	Cf. *Anomoeodus*
		Pycnodontiformes indet
	Phu Phan Thong (Nong Bua Lamphu), Nong Sung (Mukdahan)	
	Phu Phan Thong (Nong Bua Lamphu)	*Siamamia* sp.
	Phu Phan Thong (Nong Bua Lamphu)	Cf. *Carturus*
	Phu Phan Thong (Nong Bua Lamphu), Nong Sung (Mukdahan), Phu Wiang (Khon Kaen), Phu Phok (Sakhon Nakhon)	Ginglymodi indet.
Khok Kruat	Khok Pha Suam (Ubon Ratchathani), Lam Pao Dam (Kalasin), Sam Ran (Khon Kaen), Ban Saphan Hin (Nakhon Ratchasima)	Ginglymodi indet.
	Khok Pha Suam (Ubon Ratchathani)	*Siamamia* sp.

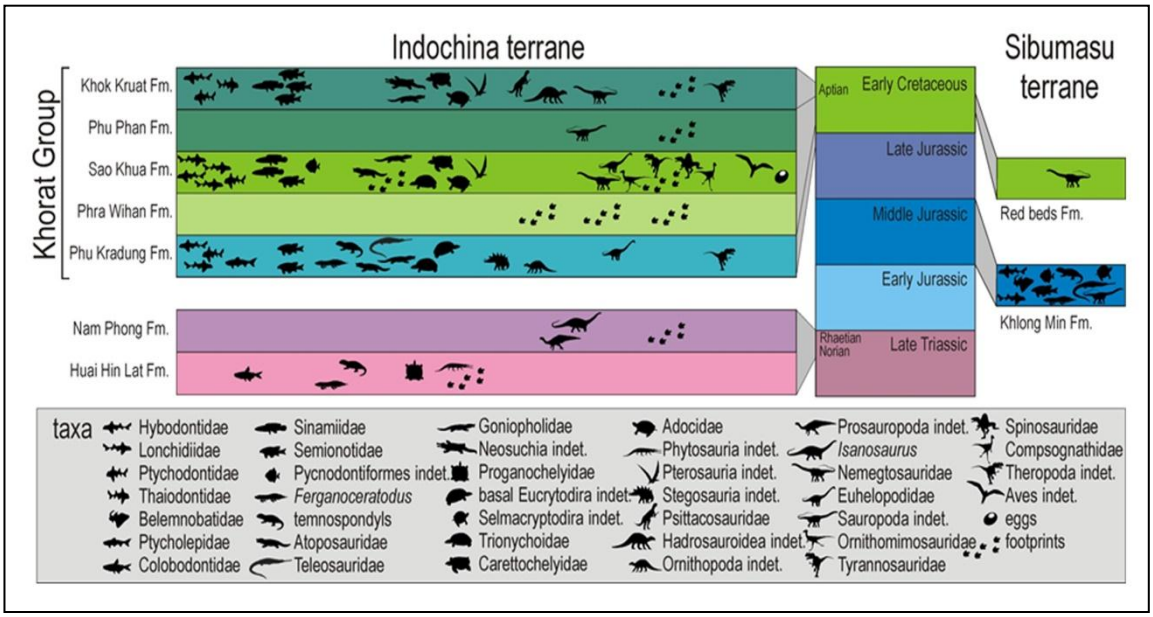

Figure 2.8 Distribution of main groups of vertebrate in the non-marine formations of Thailand. The Indochina Block comprises NE Thailand (Khorat Plateau). The Sibumasu (or Shan-Thai) Block includes western and southern peninsular Thailand (After Cavin, 2009)

CHAPTER 3

MATERIAL AND METHODS

3.1 Study site

The outcrop is located in Nong Bua Lamphu Province (northeastern part of Thailand), in the banks of the road between Udon Thani and Nong Bua Lamphu, near Phu Phan Thong hill. More than 450 kg of sediments in total were screen-washed using 0.5 and 1.7mm mesh-sized sieves.Stratigraphically, this fossilbed situated underlying the Phu Phan Formation, and overlying on Phra Wihan Formation, this indicating that Phu Phan Thong belong to the Sao Khua Formation. A new species of bivalue *Pseudohyria (Matsumotoina)somani*was described for the first time in the Sao Khua Formation, this genus was also occurs limited to the Late Barremain Formation of Japan and Korea. It was possible to suggest a Late Barremian age for the Sao Khua Formation (Tumpeesuwan *et al.*, 2010).

Figure 3.1 Phu Phan Thong locality, Nong Bua Lamphu Province in 1992 before improvement work of road 210 (Photograph by Paladej Srisuk)

Figure 3.2 Fossil bed of Phu Phan Thong locality (black line), Nong Bua Lamphu Province, during the improvement work of road 210 in 2003

Figure 3.3 Phu Phan Thong sediment wereprepared for screen washed at Sirindhorn Museum in 2003

3.2 Comparison localities and their geology

The comparison localities have been colleced the specimens. The first one, Mab Ching located in Nakhon Sri Thammarat Province, the southern part of Thailand. It belong to the Khlong Min Formation. The rest localities located on the Khorat Plateau. In the Phu Kradung Formation, comprises Phu Nam Jun, Phu Noi and Khok Sanam, all situated in Kalasin Province. In the Sao Khua Formation comprise Phu Wiang in Khon Kean Province, Nong Sung in MukdahanProvince and Phu Phok in Sakhon Nakhon Province. The youngest formation deposited in the Khorat Group, the Khok Kruat Formation contains Lam Pao Dam in Kalasin Province and Khok Pha Suam in Ubon Rachathani Province.

3.2.1 Mab Ching locality

Mab Ching locality located along a road near Ao Min village, Thung Song District, Nakhon Sri Thammarat Province in southern peninsula of Thailand. Lithology shows well-bedded calcareous silstones and sandstone interbedded with thin-bedded pale grey limestone and limestone lenses (Meesook *et al.*, 2002 and Cuny *et al*., 2009).

Figure 3.4 Outcrop of Mab Ching in 2006 during to collected the sediment sampling

3.2.2 Phu Nam Jun locality

Phu Nam Jun locality located on a small hill of Ban Dong Neau, Kuchinarai, Kalasin Province. It reveals a portion of the Khorat Group, namely the Phu Kradung Formation (Cavin *et al.*, 2004). The Phu Kradung Formation is Late Jurassic or Basal Cretaceous in age. The stratigraphic section studied in Phu Nam Jun is 4.5 meters thick. The slope of the fossiliferous beds dips about 12 degrees towards the southeast. Beds consist of mudstones, siltstones and sandstones represented by 70-80% clay and 20-30% silt. The color of the rock is maroon to purple at the top to brown-gray-green at the bottom. The lower stratum consists of sandstone with a grain size fine to medium. Roundness of the grains is rounded. The sorting is moderate. The fish remains are present throughout a 1 meter thick mudstone and sandstone layer.

Figure 3.5 Phu Num Jun locality in 2004 during the excavation, sediments consist of mainly mudstone, siltstone and sandstone

3.2.3 Phu Noi locality

Phu Noi locality sitated at Phu Phan Mountain Range in Kalasin Province, Northeastern Thailand. The outcrop belongs to the Phu Kradung Formation]of Khorat Group. The stratigraphic section in Phu Noi locality is 7 meters thick, the slope of the fossiliferous layer where the isolated fish scales were dispersed dips about 10 degree towards to northwest. Beds consist of maroon and reddish brown sandstones with greenish gray sandstones, very thin to thin bedded. The layer below consists of siltstone interbedded with mudstones, reddish brown to maroon and greenish gray, very laminated and mica rich. The lowest layer consists of greenish gray siltstone about 100 centimeters thick, interbedded with three layers of plant remains, which present iron oxidation (limonite). The sub articulated fish was found in this layer.

Figure 3.6 Phu Noi Locality in 2012 during the excavation sediments consist of mainly mudstone, siltstone and sandstone

3.2.4 Khok Sanam locality

Khok Sanamlocality located in the Phu Phan Mountain Range in Kam Muang district, Kalasin Province, Northeastern Thailand.Only a small outcrop can be observed on the surface. Sediments consist of siltstone interbedded with mudstones, reddish brown to maroon and greenish gray, very laminated and mica rich. There are referred to the Phu Kradung Formation.

Figure 3.7 Khok Sanam locality in 2004 during collected the sediment sampling, sediment consist of siltstone interbedded with mudstones, reddish brown to maroon and greenish gray

3.2.5 Chong Chat locality

Chong Chat locality, Nong Bua Lamphu Province is close to the contact between the Phu Kradung and Phra Wihan Formation. The stratigraphic section in this locality which is about 1.3 metersthick, consists of maroon mudstones interbedded with grayish white siltstones with poor sorting and scattering sand lenses.

Figure 3.8 The outcrop of Chong Chat locality in 2005 during the collected sediment sampling, sediment consists of maroon mudstones interbedded with grayish white siltstones

3.2.6 Phu Wiang locality

Phu Wiang locality, Khon Kaen Province. Fish scales kept in the Palaeontological Research and Education Centre (PRC)collection were studied. Buffetaut and Suteethorn have mentioned on a sauropod dinosaur from this area, *Phuwiangosaurus sirindhornae*. They refer the sediments to the Sao Khua Formation of

Khorat Group.

3.2.7 Phu Phok locality

Fish scales, dinosaur teeth, pterosaur and small lizard eggs have been found on a slope of the Phu Phan Mountain Range in Sakhon Nakhorn Province. It reveals a portion of the Khorat Group, namely the Sao Khua Formation (Lauprasert *et al.*, 2007). The outcrop consists of a reddish brown siltstone, 5 meters thick, showing a clear sorting of the sediments with scattered pebbles inside. In addition, Cavin *et al.*, (2007) described a new fish from this locality. It's referred to *Siamamia naga*.

Figure 3.9 The outcrop of Phu Phok locality in 2004 during collected the specimens on the surface, sediment consistreddish brown siltstone

3.2.8 Nong Sung locality

Nong Sung locality, Mukdahan Province is located along the road between Nong Sung and Nikhom Kham Soi. The outcrop consists of displaced blocks of the red sandstone which were set beside on the road during its constrction. The road is situated

below the Phu Phan Formation therefore these blocks should belong to the Sao Khua Formation (Cuny *et al*., 2009).

Figure 3.10 Nong Sung locality in 2007 during extracted specimens out from the blocks of sandstone

3.2.9 Lam Pao Dam

Spillway of Lam Pao Dam is located in Kalasin Province, the Khok Kruat Formation. It consists of conglomeratic sandstones with pebble grain of about 2 centimeters in diameter, purple to reddish brown, 10 centimeters thick. The overlying bed consists of reddish brown siltstone interbedded with sandstone with a grain size fine to medium. Roundness of the grain is sub-rounded.

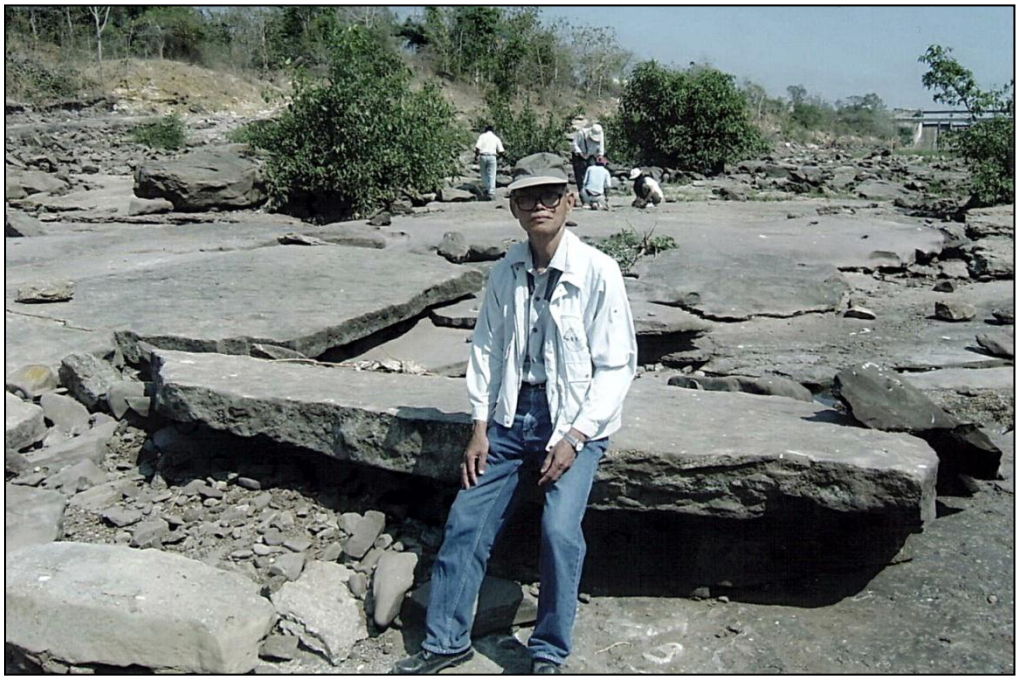

Figure 3.11 Sprillsway of Lam Pao Dam in 2006 during to extracted specimens out from the conglomeratic sandstones

3.2.10 Khok Pha Suam locality

Khok Pha Suam locality is located at Sri Chiang Mai district, Ubon Rachathani province. Sediments consist of grey and write clay interbedded in reddish brown and grey siltstone, overlying by a 30 centimeters thick layer of laterite. Based on the occurrence of the hybodont shark, *Thaiodus ruchae*.Cappetta *et al.*, (1990) suggested an Aptian-Albian age for the Khok Kruat Formation.

Figure 3.12 Khok Pha Suam locality in 2008 during the excavation, exposes the gray and write clay interbedded with reddish brown and gray siltstone

3.2.11 Kut Island (Ko Kut)

Kut Island (Ko Kut) is located in the eastern part of the Gulf of Thailand, South East of Chang Island, Trad Province. The outcrop near Ban Ao Kalang is a rocky beach where a series of predominantly red and grey sanstones and silstone. These series is approximatly 1 metres thick and the middle part there is bed of indurated, dark grey conglomerate sandstone (Cuny *et al.,* 2010). From the fossil evidence this locality was equivalent to the Sao Khua Formation.

Figure 3.13 Kut Island (Ko Kut) locality in 2015 during extracted specimens out from the blocks of sandstone.

3.3 Methods

3.3.1 Sediment collecting

For this study, the main sediments has been collected from Phu Phan Thong, Nong Bua Lam Phu Province, Sao Khua Formation and from other sites for comparison of their microvertebrate faunas. Sediments were sampled for screen washing, but the largest specimens were collected directly at the surface of the outcrop.

3.3.2 Screen washing of sediments to recover vertebrate microremains

This method aims at recovering vertebrate microremains, which are usually hardly noticeable by the naked eye (Mckenna *et al.*, 1994). Sediment from each locality (about 50-500 kilograms per site) was left in water for at least 24 hours before being

screen-washed. The sediment was screen washed under water using 0.5 mm mesh size sieves. The sediment was then dried under the sunlight. It was then dry sieved to separate a coarse fraction (more than 2-3 mm) from a fine one. Fossils were picked from the fine fraction under a binocular microscope, and with the naked eye from the coarse fraction.

The specimens from the comparative sites were investigated under a stereomicroscrope to categorize their teeth morphotype differences on the basis of shape (size and curvature) of crowns, ridge ornamentations and the presence of serration.

3.3.3 Scanning electron microscope

For scanning electron microscope, the vertebrate microremains were clean with ethanol and dried up. These specimens were coated with a thin layer of gold and examined with a JEOL JSM-T20 scanning electron microscope conducted in Faculty of Science, Mahasarakham University.

CHAPTER 4

SYSTEMATIC PALAEONTOLOGY

The following descriptions concern the vertebrate microremains from Phu Phan Thong (main study site) and comparison sites including Phu Noi, Chong Chat, Phu Num Jun, Phu Phok, Phu Wiang, Huai Lao Yang, Lam Pao Dam and Khok Pha Suam. These descriptions are based on the specimens housed in the Palaeontological Research and Education Centre (PRC), Mahasarakham University and the specimens from the collection of Sirindhorn Museum, Kalasin Province, including the specimens reported by Cuny *et al.*, (2003; 2006; 2007; 2009 and 2010) and Cavin *et al*., (2009). Here all vertebrate microremains material will be described.

4.1 Systematic description

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Order Hybodontiformes Patterson 1966

Family Hybodontidae Owen 1846

Subfamily Hybodontinae Owen 1846 *sensu* Maisey 1989

Genus *Egertonodus* Woodward 1916

***Egertonodus* sp.**

Occurrence: Sao Khua Formation; Phu Phan Thong (Nong Bua Lamphu province). Phu Kradung Formation; Phu Noi, Phu Din Dang (Sakhon Nakhon Province) and Nong Sung (Mukdahan Province).

Material: Phu Phan Thong 36 fragmentary crowns**,** Phu Noi 8 fragmentary crowns and Nong Sung 5 fragmentary crowns (n=49) (Figure 4.1).

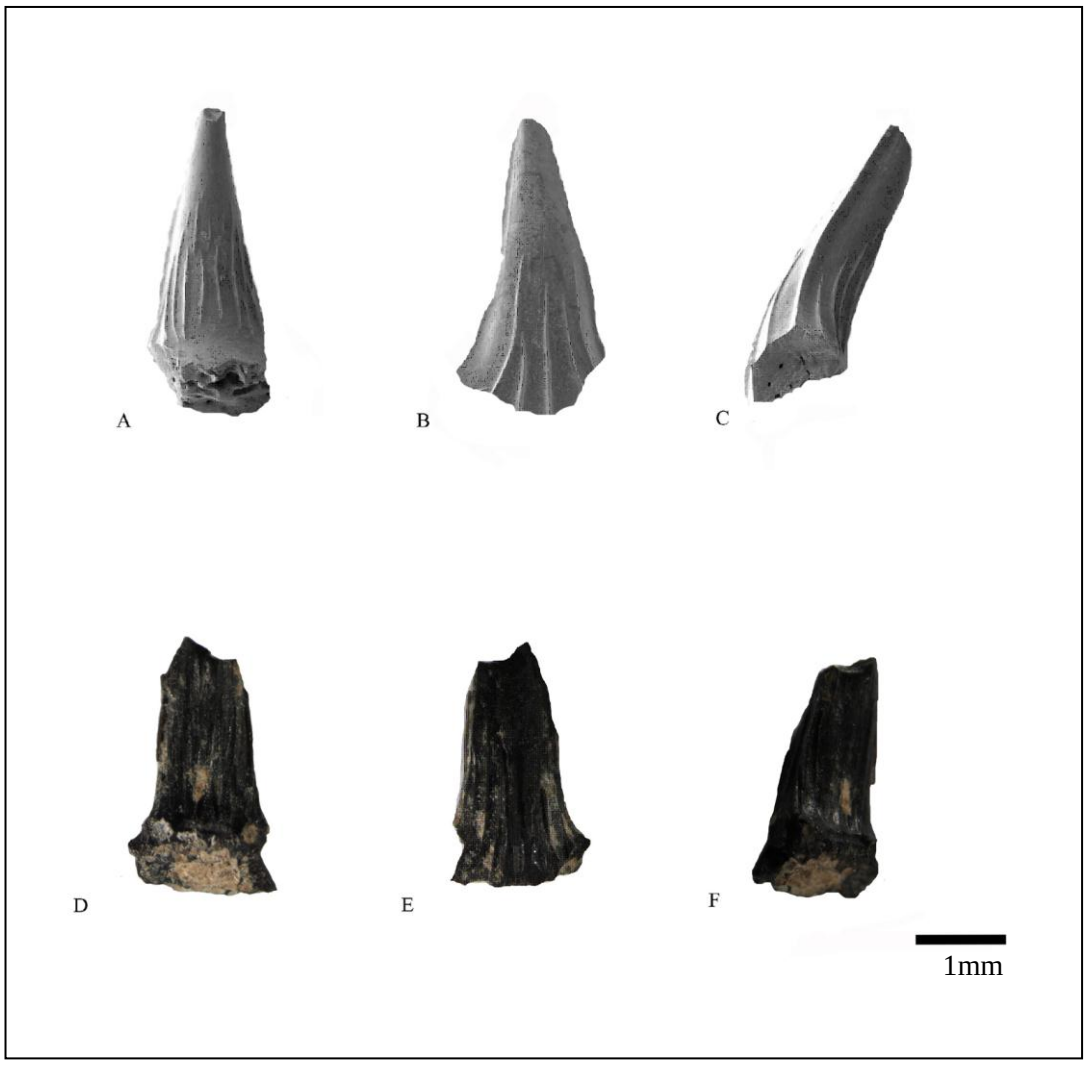

Figure 4.1 Main cusp of *Egertonodus* sp. A-C PPT75. (A) lingual, (B) labial and (C) mesial or distal. D-F PPT27. (D) lingual, (E) labial and (F)mesial or distal views. Scale bar 1 mm

Description

Only the central cusp is preserved in the recovered material. The maximum height of the isolated cusps (PPT75) without root is 5 mm. The cusps are slightly compressed labio-lingually with a sigmoid curve in mesial or distal view (Figure 4.1 C and F) and present a developed cutting edges. The lingual side is ornamented by numerous ridges, which do not anastomose and are longer than the labial side. The lingual and labial ridges start from the lower part of the crown but do not reach the apex.

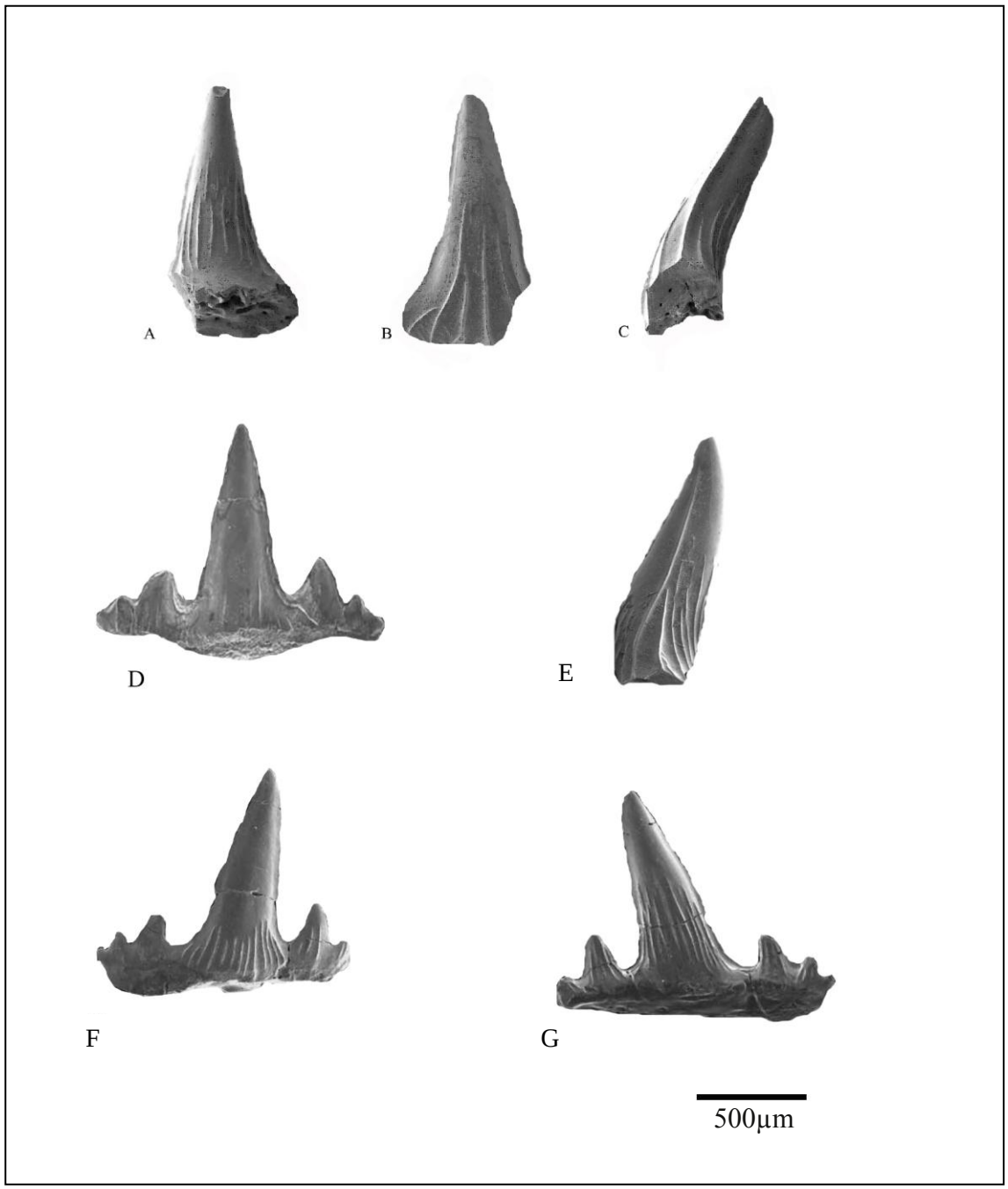

Figure 4.2 Comparison of *Egertonodus* sp. PPT85 with *Egertonodus basanus* (D-F; Bermudez-Rochas, 2009; G; Sweetman *et al.,* 2014). *Egertonodus* sp. PPT85. (A) lingual, (B) labial and (C)mesial or distal views. *Egertonodus basanus* MGM-11012C. (D) anterior tooth in labial view. MGM-10798C. (E) antero-lateral tooth in labial, (F) lingual views and (G) NHMUKPVP73425 mesial or distal views. Scale bar 500µm.

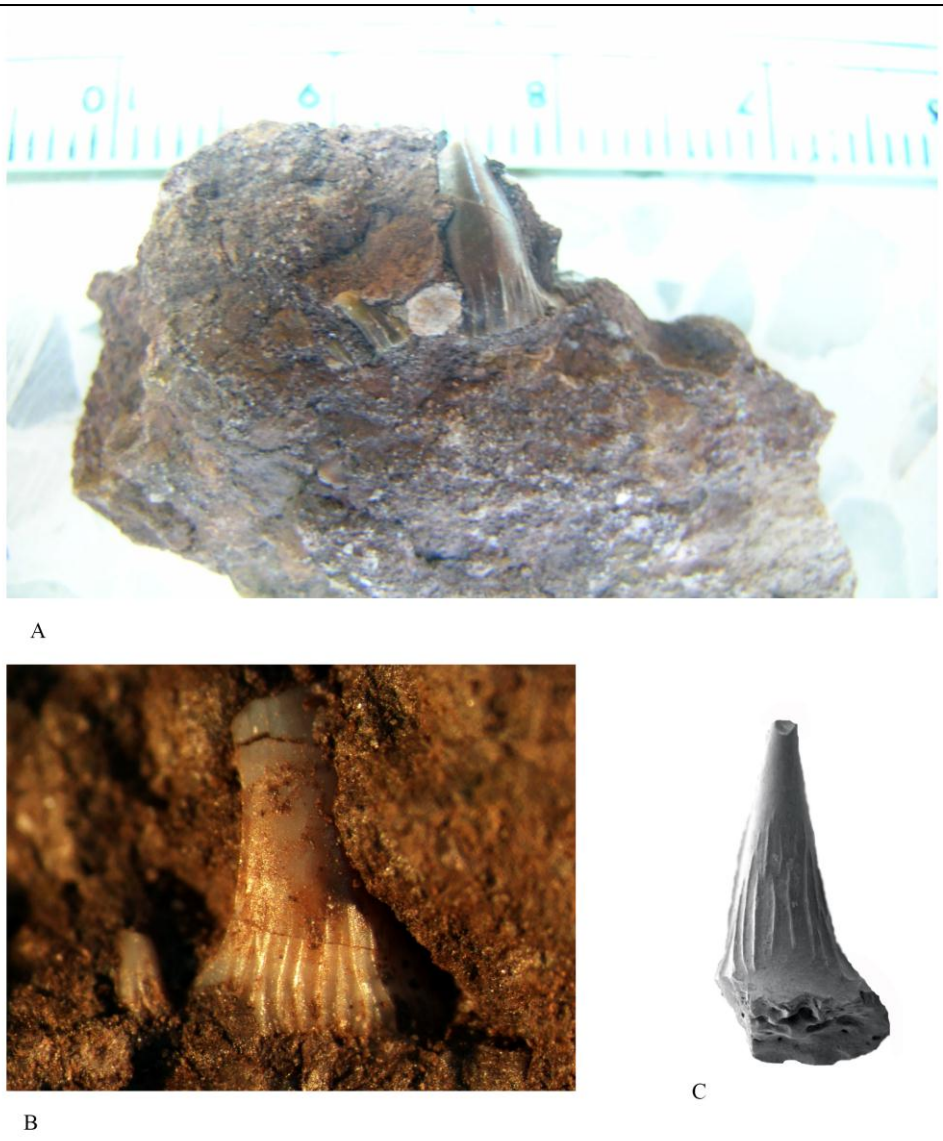

Figure 4.3 Comparison of *Egertonodus* sp. (PPT85) with the specimens from other localities of the Sao Khua formation. (A) tooth from Nong Sung (Mukdahan Province), (B) tooth from Phu Din Dang (Sakhon Nakhon) and (C) main cusp of PPT 85

Discussion

These teeth are different from other *Hybodus* spp. by a sigmoidally curved main cusp and an ornamentation make of short ridges that do not reach the top of the crown (Cappetta, 2012; Maisey, 1987; Ress, 2008). In a previous study, Cuny *et al*., (2006) described *Hybodus* sp. A from Phu Noi, Nong Sung and new site, Phu Din Dang which possess an ornamentation pattern and a sigmoidal curvature of the main

cusp similar to the teeth from Phu Phan Thong (Figure 4.3). He mention *Hybodus* sp. A should be considered as the genus *Egertonodus* rather than *Hybodus*. This study, I prefer to include Phu Phan Thong materials to genus *Egertonodus* based on their dental characters.

The main cusp teeth from Phu Phan Thong are quite similar to the anterior teeth of *Egertonodus basanus* from the Early Cretaceous of the Basque-Cantabrian in the north of Spain (Bermudez-Rochas, 2009; Figure 4.2) by the ornamentation ridges on the crown in labial and lingual side. Moreover, the sigmoidal curvature can be observed in Phu Phan Thong teeth alike in *Egertonodus basanus* from the Barremian of southern England (Sweetman *et al.*, 2014; Figure 4.2). Although Phu Phan Thong materials are quite similar to *Egertonodus basanus*, the assignment of Phu Phan Thong *Egertonodus* species is still unlikely because all the materials from this study preserve only main cusp. Therefore, made it difficult to identify the materials are belong to *Egertonodus basanus*.

***Hybodus* morphotype 4**

Occurrence: Sao Khua Formation; Phu Phan Thong and Phu Wat (Nong Bua Lamphu Province).

Material: Phu Phan Thong 78 fragmentary crowns**,** Phu Wat 12 fragmentary crowns (n=90) (Figure 4.4).

Description

The specimens show low crowned teeth with cusp and cusplets. The lingual and the labial side are ornamented by short ridges. The ridges on both side reach to the apex and are anastomosed in the upper part of the cusp. The largest tooth is 6 mm mesio-distally and 3 mm labio-lingually and one lateral cusplets flank the main cusp. Ten fragmentary teeth show a root preserved. On the labial side shows a single irregular row of foramina whereas on the lingual side, it shows a large foramina row at the base of the root and another smaller foramina row is above.

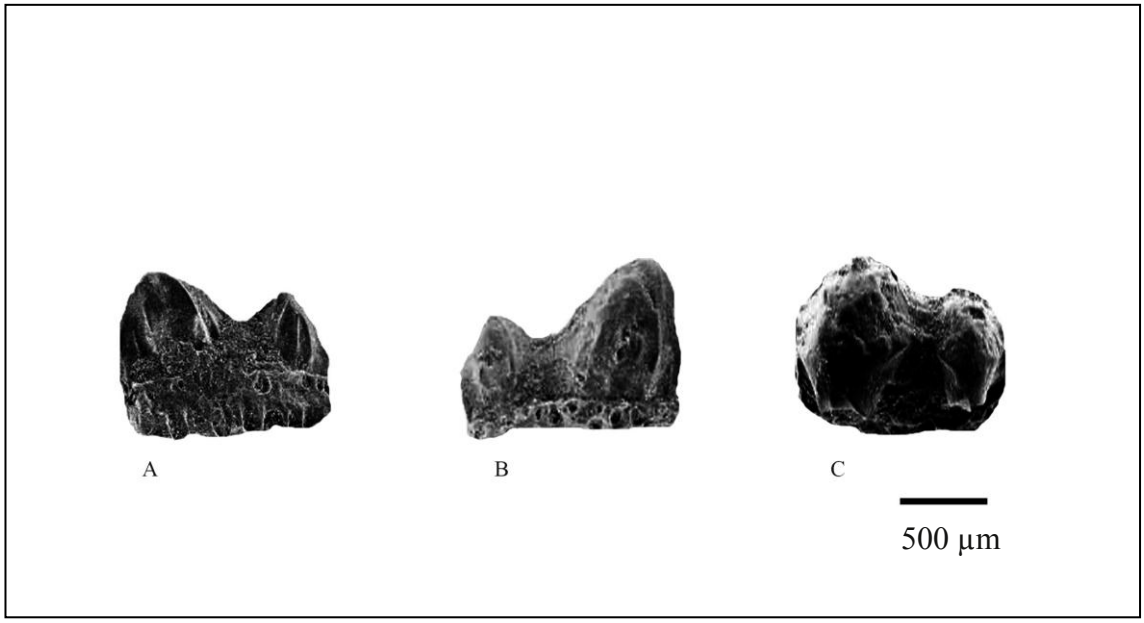

Figure 4.4 An incomplete tooth of *Hybodu*s sp. Morphotype 4, PRC-PT435. (A) lingual, (B) labial and (C) apical views. Scale bar 500 µm.

Discussion

Many isolated teeth from Phu Phan Thong have been ascribed to the genus *Hybodus* because they possess a circular cross-section of the cusps, lack a labial node (Delsate *et al.*, 2002; Underwood and Ress 2002) and the lingual face of the root shows a large foramina (Cappetta, 2012). The teeth from Phu Phan Thong are quite different from *Hybodus reticulatus* Agassiz, 1836, which is the type species for *Hybodus*. *H. reticulatus* displays teeth with a high and slender main cusp with well-developed cutting edges and ornamented by seldom branching vertical ridges which rarely reach the apex (Delsate *et al*., 2002; Cuny *et al.*, 2008). Currently, at least five different morphotypes of *Hybodus* have been also found in many sites from Thailand (Cuny *et al*., 2014; 2009; 2008; 2007; 2006) (Figure 4.5), many of which have not yet been named except *Hybodus aequitridentatus.* It can be classified in the Table 4.1.

The materials from this study are very similar to the teeth described by Cuny *et al.,* (2006) as *Hybodus* sp. B. This material can be easily separated from those of *Hybodus* morphotype 1 (Cuny *et al.,* 2014; Figure 4) and *Hybodus aequitridentatus* (Cuny *et al.,* 2008; Figure 4), because they are less densely ornamented on the labial and lingual side. Phu Phan Thong teeth were also different from *Hybodus* morphotype 2

(Cuny *et al.*, 2014; Figure 4) showing cusplets less compressed labio-lingually and being more heavily built. *Hybodus* morphotype 3 (Cuny *et al.*, 2009a; Figure 3) shows ornamentation ridges attaining the apex of cusp and cusplets that made them different from Phu Phan Thong materials (Cuny *et al.*, 2014; 2008; 2007; 2006).

Although the teeth of *Hybodus* sp. from Phu Phan Thong are quite different from other *Hybodus* without complete teeth at hand, it is very difficult to identify them at the species level. Therefore, I referred Phu Phan Thong materials to *Hybodus* sp. B until more complete teeth are found.

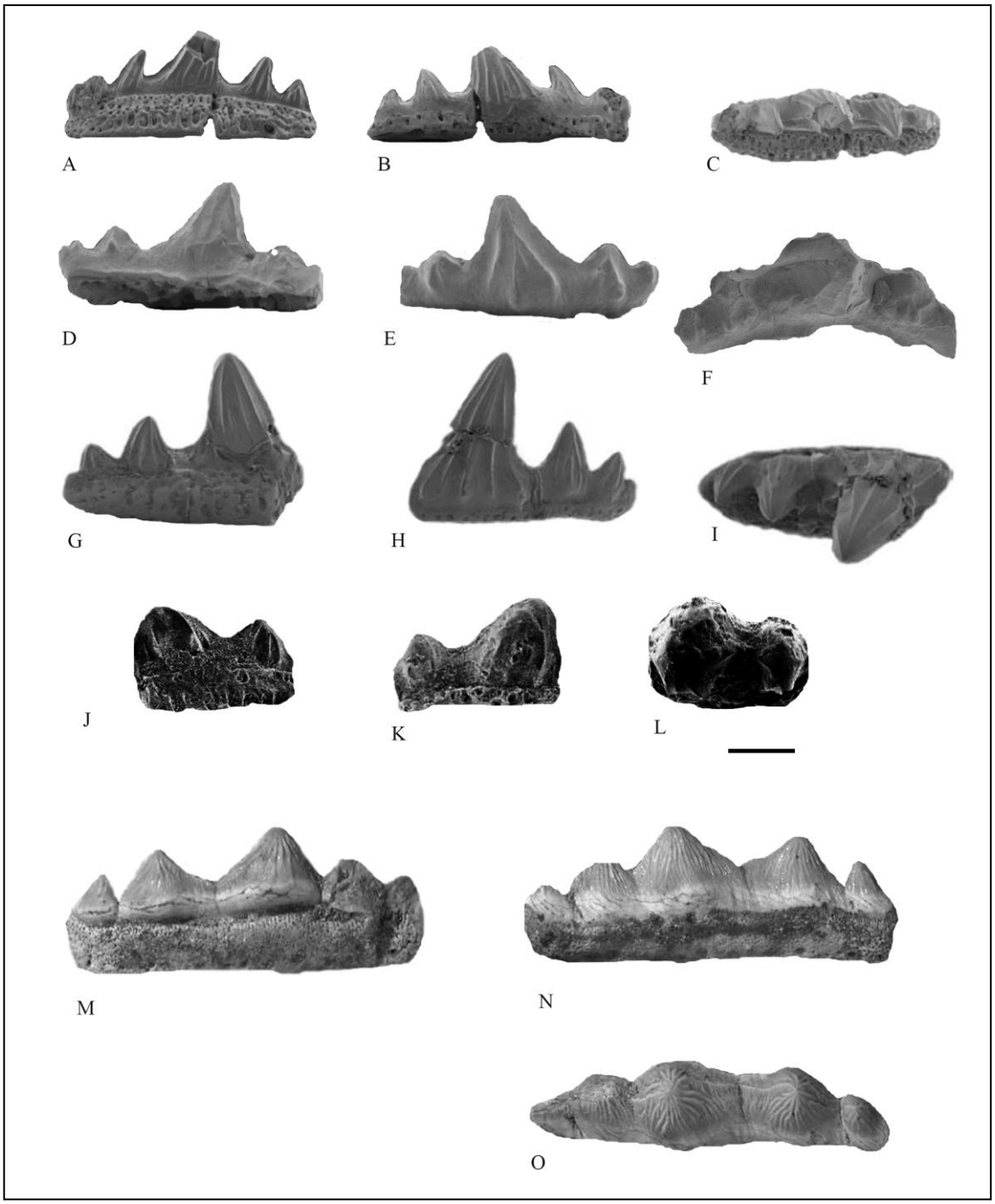

Figure 4.5 Five morphotypes of *Hybodus* sp. A-C: *Hybodus* sp. morphotype 1 (SM2012-1002). (A) lingual, (B) labial and (C)apical views. D-F *Hybodus* sp. morphotype 2. (D) lingual, (E) labial and F apical views. G-I *Hybodus* sp. morphotype 3 (SM-TF 9017). (G) lingual, (H) labial and (I) apical views. J-L *Hybodus* sp. morphotype 4 (PRC-PT435). (J) lingual, (K) labial and L:apical views. M-O *Hybodus aequitridentatus* (TF7644). (M) lingual, (N) labial and (O) apical views. Scale bar 500 μm

Table 4.1 Five different morphotypes of *Hybodus* found in Thailand

Morphotype	Age	Localities	Characteristics
1 (considered by Cuny *et al.*, 2014 as *Hybodus* sp.)	Late Jurassic-Early Cretaceous	- Chong Chat, Nong Bua Lamphu Province; - Wang Din So, Phitsanulok Province; - Phu Nam Jun, Kham Phok, Phu Noi, Kalasin Province (Phu Kradung Formation) - Kut Island, Trat Province (equivalent to the Sao Khua Formation)	- main cusp flanked by up to three cusplets - up to ten ridges per cusp - strong ridges on the crown start from the apex of the cusp and cusplets and almost reach the base of crown on both side, some teeth present anastomosed ridges on the lower part of the crown - moderately developed longitudinal crest
2 (considered by Cuny Cuny *et al.*, 2014 as aff. *Hybodus* sp.)	Late Jurassic-Early Cretaceous	- Phu Noi, Kalasin Province (Phu Kradung Formation)	- two pair of lateral cusplets - main cusp and cusplets are triangular in outline in labial and lingual view - three anastomosed ridges on labial and four on lingual face - forming a node at the base of crown
3 (considered by Cuny *et al.*, 2009 as *Hybodus* sp.)	Mid-Late Jurassic	- Kholng Min and Ao Min, Nakhon Sri Tammarat Province (Khlong Min Formation)	- main cusp flanked by two lateral cusplets - cusp and cusplets moderately compressed labiolingually, convex labial and lingual face - strong ridges on cusp and cusplets - some ridges reach the apex, some ridges are anastomosed, all of them do not reach the base of the crown, well developed cutting edges

Table 4.1 Five different morphotypes of *Hybodus* found in Thailand (continue).

Morphotype	Age	Localities	Characteristics
4 (materials from this study and *Hybodus* sp. B; Cuny *et al.*, 2006)	Berriasian-Barrimian ???	- Phu Phan Thong, Phu Wat, Nong Bua Lamphu Province, Phu Noi, Sakhon Nakhon Province (Sao Khua Formation)	- low crown, two pairs of lateral cusplets flank the maincusp, strong ridges on the lingual and the labial side which reach to the apex and anastomosed on the upper part of the cusp - up to five ridges per cusp and cusplets
H.aequitridentatus (Cuny *et al.*, 2008)	Aptian-Albian	- Khok Pha Suam, Ubon Ratchathani Province (Khok Kruat Formation)	- low, blunt cusp, two pairs of cusplest which almost the same size as the main cusp,densely ornamented by fine anastomosed ridges on labial and lingual side - moderately –developed longitudinal crest - lack of labial node at the base of the crown

Family Lonchidiidae Herman 1977

Genus *Lonchidion* Estes 1964

***Lonchidion khoratensis* Cuny *et al.*, 2006**

Occurrence: Sao Khua Formation; Phu Phan Thong (Nong Bua Lamphu Province).

Material: 45 teeth (n=45) (Figure 4.6).

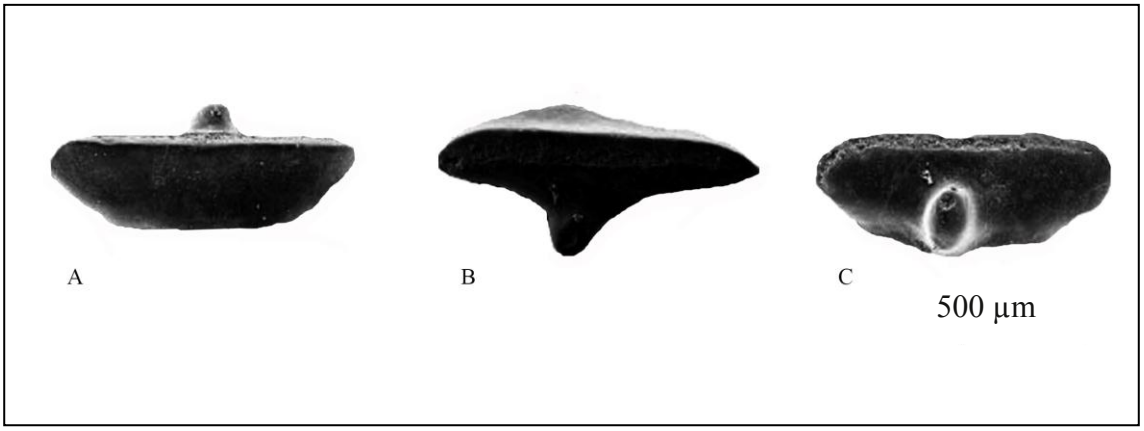

Figure 4.6 *Lonchidion khoratensis* tooth PPT-12. (A) lingual, (B) apical and (C) labial views. Scale bar 500 µm

Description

This shark has rather homodont teeth. The largest teeth (PPT12) measures 0.7 mm labio-lingually and 3 mm mesio-distally (Figure 4.6). There is a low crown without ornamentation, sharp longitudinal and cusplets are absent. The teeth are moderately elongated with a conspicuous, narrow labial peg. The posterior teeth are wider labio-lingually than the anterior ones. The lingual face of the crown is a slightly concave. No root has been found in our materials.

Discussion

These teeth belong to *Lonchidion* because they possess a narrow labial peg (Rees and Underwood, 2002). A smooth crown without any lateral cusplet has been found in three *Lonchidion* species: *L. humblei*, *L. breve* and *L. khoratensis* (Patterson, 1966; Duffin, 1985; 2001; Heckert and Lucas 2002; Huckert *et al.*, 2007; Cuny *et al.*, 2006 and Sweetman *et al.*, 2014). The teeth of *L. khoratensis* differ from those of *L.*

humblei and *L. breve* in presenting a more homodont dentition and lacking ascending ridges on the labial peg (Figure 4.7) (Heckert *et al.,* 2007 and Sweetman *et al.,* 2014). In addition, *L. khoratensis* teeth are slightly narrower than *L. breve*. So far, *Lonchidion* has been discovered from many localities. *Lonchidion* sp. A has been reported from Khok Sanam and NBL32 (Nong Bua Lamphu Province) in the Phu Kradung Formation. These teeth show a pair of lateral cuspletes, contrary to the teeth of *L. khoratensis.* Moreover, *L. khoratensis* can be separated from *Lonchidion* sp. B. from Wang Din So (Phitsanulok Province), Phu Noi (Kalasin Province), NBL32 (Nong Bua Lamphu Province), Kham Phok (Kalasin Province) in the Phu Kradung Formation (Cuny *et al*., 2014) and *L. resssunderwoodi* from Ao Min (Nakhon Si Tammarat Province) in the Khlong Min Formation by the absence of cusp and ornamentation on their crown (Cuny *et al.*, 2009).

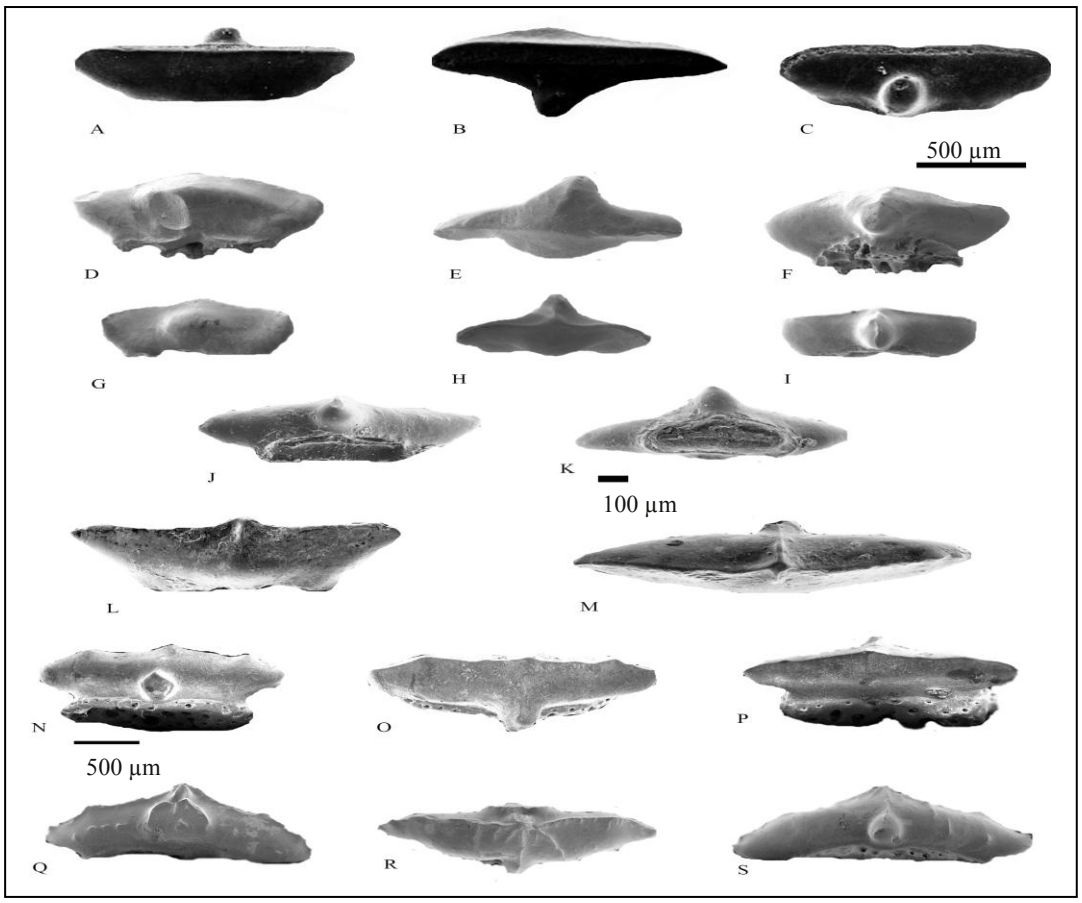

Figure 4.7 *Lonchidion khoratensis* tooth PPT-12 compared with *L. breve* from the Barremain Wessex Formation of southern England (Sweetman *et al.,* 2014), *L. humblei* from the upper Triassic of USA (Huckert *et al.,* 2007), *Lonchidion* sp. A and *Lonchidion* sp. B from the Phu Kradung Formation of Thailand (Cuny *et al.,* 2014). A-C *L. khoratensis*. (A) lingual, (B) apical and (C) labial views. D-F lateral tooth of *L. breve* (NHMUK PV P 73428). (D) lingual, (E) apical and (F) labial views. G-I anterolateral tooth of *L. breve* (NHMUK PV P 73429). (G) lingual, (H) apical and (I) labial views, scale bar 500 µm. J-K anterolateral tooth of *L. humblei* NMMNH P-26429a. (J) labial and (K) basal views. L-M lateral tooth of *L. humblei* NMMNH P-26429b. (L) lingual and (M) apical views, scale bar: 100 µm. N-P *Lonchidion* sp. A SM2012-1-105. (N) labial, (O) apical and (P) apico-lingual views. Q-S *Lonchidion* sp. B SM2012-1-107. (Q) labial, (R) apical and (S) lingual views, scale bar 500 µm

Genus *Parvodus* Rees and Underwood (2002)

***Parvodus* sp.**

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province).

Material: 26 teeth and 5 teeth with the root preserved (n=31) (Figure 4.8).

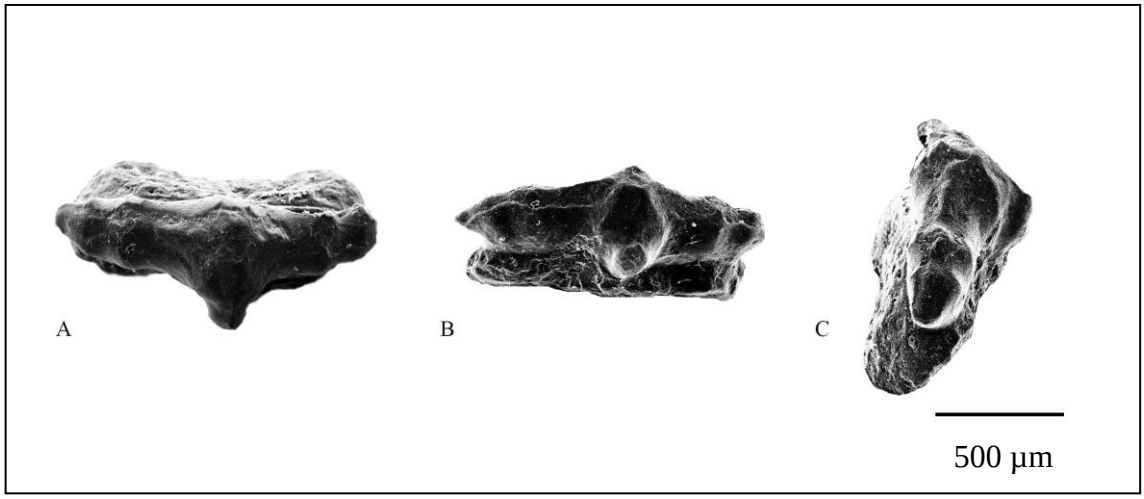

Figure 4.8 *Parvodus* sp. PPT-19. A-C: posterior tooth. (A) apical, (B) labial and (C) mesial or distal view. Scale bar 500 µm.

Description

The teeth are small with a low cusp and two pair of lateral cuspletes. The main cusp shows a pyramidal shape with a well-developed labial peg and a weakly labial node present at the base of crown. The longitudinal crest is moderately developed. The largest tooth with a root preserved (PPT-19) measures 1.5 mm mesio-distally and 0.5 mm labio- lingually and 1 mm in height including the root. The root is as high as the crown and the crown overhangs the root lingually. On its labial face, the root displays a small foramina row just under the crown whereas the lingual face is slightly concave with a row of small foramina and much larger foramina below, more randomly distributed

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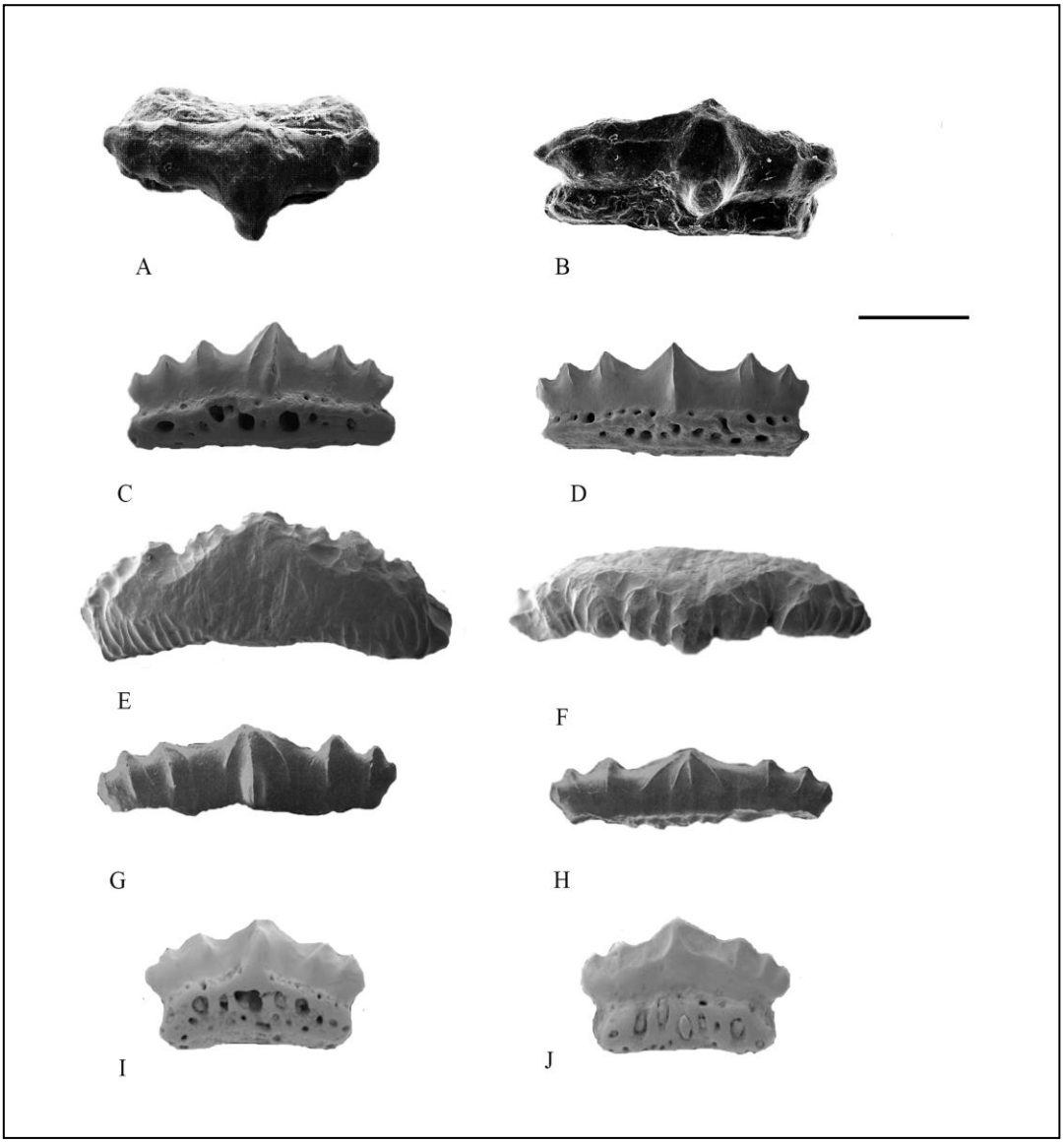


Figure 4.9 *Parvodus* sp. compared with *P. celsucuspus* (Ress *et al.*, 2013), *P. heterodon* (Sweetman *et al*., 2014), *P. rugianus* (Ansorege, 1990) and *P. pattersoni* (Rees and Underwood, 2008). A-B, posterior tooth of *Parvodus* sp. (A) apical, (B) labial views. C-D posterior tooth of *P. celsucuspus* CHVm03.640. (C) labial and (D) lingual views. E-F posterior tooth of *P. heterodon* NHMUK PV P73464. (E) lingual and (F) labial views. G-H *P. rugianus* (G) lingual and (H) labial views. I-J *P. pattersoni* 66524. (I) lingual and (J) labial views. Scale bar 500 µm

Discussion

This genus consists of five species, i.e., *Parvodus curvidens, P. pattersoni, P. rugianus, P. heterodon and P. celsucuspus* (Ansorge, 1990; Rees and Underwood, 2008; 2002; Rees *et al*., 2013 and Sweetman *et al*., 2014). The Phu Phan Tong *Parvodus* can be separated from all species by its absence of ornamentation. The Thai materials is also different from the four latter species by a moderately well-developed lateral cusplets (Figure 4.9). Although *Parvodus* sp. from Phu Phan Tong is quite different from other *Parvodus* species, the teeth at hand are not sufficient to define a new species.

Family *incertae sedis*

Genus *Isanodus* Cuny *et al.*, 2006

Type species *Isanodus paladeji* Cuny *et al.*, 2006

Emended diagnosis: non-gradient monognathic heterodonty showing four types of teeth: anterior, anterolateral, posterolateral, and posterior ones; main cusp pyramidal with a triangular base, labial peg present, ornamentation consisting of a longitudinal crest with up to one mesio-distal V-shaped labial ridge and up to four lingual ones, up to four labial nodes on mesial and distal part of anterolateral and posterolateral teeth, anterior and posterior teeth lack labial nodes, longitudinal crest is reduced in posterolateral teeth.

Isanodus paladeji

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province), Nong Sung (Mukdahan Province), Phu Noi (Sakhon Nakhon Province), Kut Island (Trat Province)

Material: 109 incomplete teeth, 22 teeth with a root preserved (n=131) (Figure 4.10).

Holotype: TF 7674 (posterior tooth).

Paratype: TF 7671 and TF 7679 (anterior teeth).

Referred material: PRC 241 (anterior tooth), PRC 242 (anterolaeteral tooth), PRC 243 (posterolateral tooth) and PRC 244 (posterior tooth).

Type locality: Phu Phan Thong (Nong Bua Lamphu Province).

Type stratum: Lower Sao Khua Formation, Khorat Group, Early Cretaceous.

Emended diagnosis: moderate heterodonty, anterolateral and posterolateral teeth small, narrow and elongated, labial nodes not well developed, labio-lingually oriented ridges not well developed, presumed posterolateral tooth and posterior teeth asymmetric.

Description

The teeth of this species show a moderate heterodonty and four types of teeth can be identified: anterior, anterolateral, posterolateral and posterior ones. A well preserved presumed anterior tooth (PRC 241) has the root preserved and measures about 2.5 mm mesio-distally, 1.5 mm labio-distally and is 2 mm high including the root. The crown shows a pyramidal shape with a triangular base and a well-developed main cusp as high as the root. The longitudinal crest is well developed. There are two V-shaped ridges parallel to each other on the lingual side. The labial peg is well developed at the base of the crown. The crown overhangs the root and is separated from the latter by a groove. The labial face of the root is concave. The root is straight under the crown, not being projected lingually. The presumed anterolateral tooth (PRC 242) is narrow and elongated mesio- distally, but the distal and mesial extremities of the crown are missing. It measures 3 mm mesio-distally, 0.5 mm labio-lingually and is 1 mm high including the root. The crown is arched in lingual or labial view and shows a well-developed longitudinal crest without lateral cusplets. On the lingual side, it presents two V-shaped ridges showing short perpendicular ridges on their lingual side. The labial peg is not well developed, but there are small, additional labial nodes at the base of the crown, up to three mesially and four distally. On the labial face, there is a short ridge starting from the apex but not reaching the base of the crown. The crown overhangs the root, which shows randomly distributed small foramina on its surface. The lingual side is straight under the crown and is not projected lingually.

The largest presumed posterolateral tooth (PRC 243) shows an asymmetric crown with a labial side more developed than the lingual one. It measures 3 mm mesio-distally, 0.6 mm labio-lingually and 2 mm in height, including the root. The crown is elongated mesio-distally with a high central cusp and the longitudinal crest is not well-developed. The lingual face is smooth. The labial peg is not well-developed. On the labial face, the tooth is ornamented by four small, short ridges originating from the apex but not reaching the base of the crown. The crown overhangs the root, the latter

showing randomly distributed small foramina on its surface. The root is as high as the crown and is slightly projected lingually.

The largest presumed posterior tooth (PRC 244) measures 2 mm mesio-distally, 1 mm labio-lingually and 1.5 mm in height, including the root. The tooth shows a well-developed longitudinal crest and is similar to the anterior one but with an asymmetric crown. There are up to two V-shaped ridges parallel to each other on the lingual side and one on the labial side. The root is as high as the crown and slightly projected lingually.

Discussion

The genus *Isanodus paladeji* was erected by Cuny *et al.*, (2006) based on four types of isolated teeth, i.e., anterior, anterolateral, posterolateral and posterior ones. According to these authors, *Isanodus* possesses a heterodont, clutching-grinding dentition with teeth possessing a labial peg, all characters that can be found in *Lissodus nodosus*, an European hybodont shark from the Triassic. However, new material, including presumed anterolateral and posterolateral teeth were recovered from Phu Phan Thong. These teeth show a shape and ornamentation equivalent to what can be seen on the presumed anterior (TF 7671) and posterior teeth (TF 7674) of *Isanodus paladeji*. In addition, new material of presumed anterior and posterior teeth were also discovered and can be compared with the presumed anterolateral (TF 7672) and posterolateral teeth (TF 7673) of *Isanodus paladeji*. This new material suggests a re-definition of the species *I. paladeji* is needed.

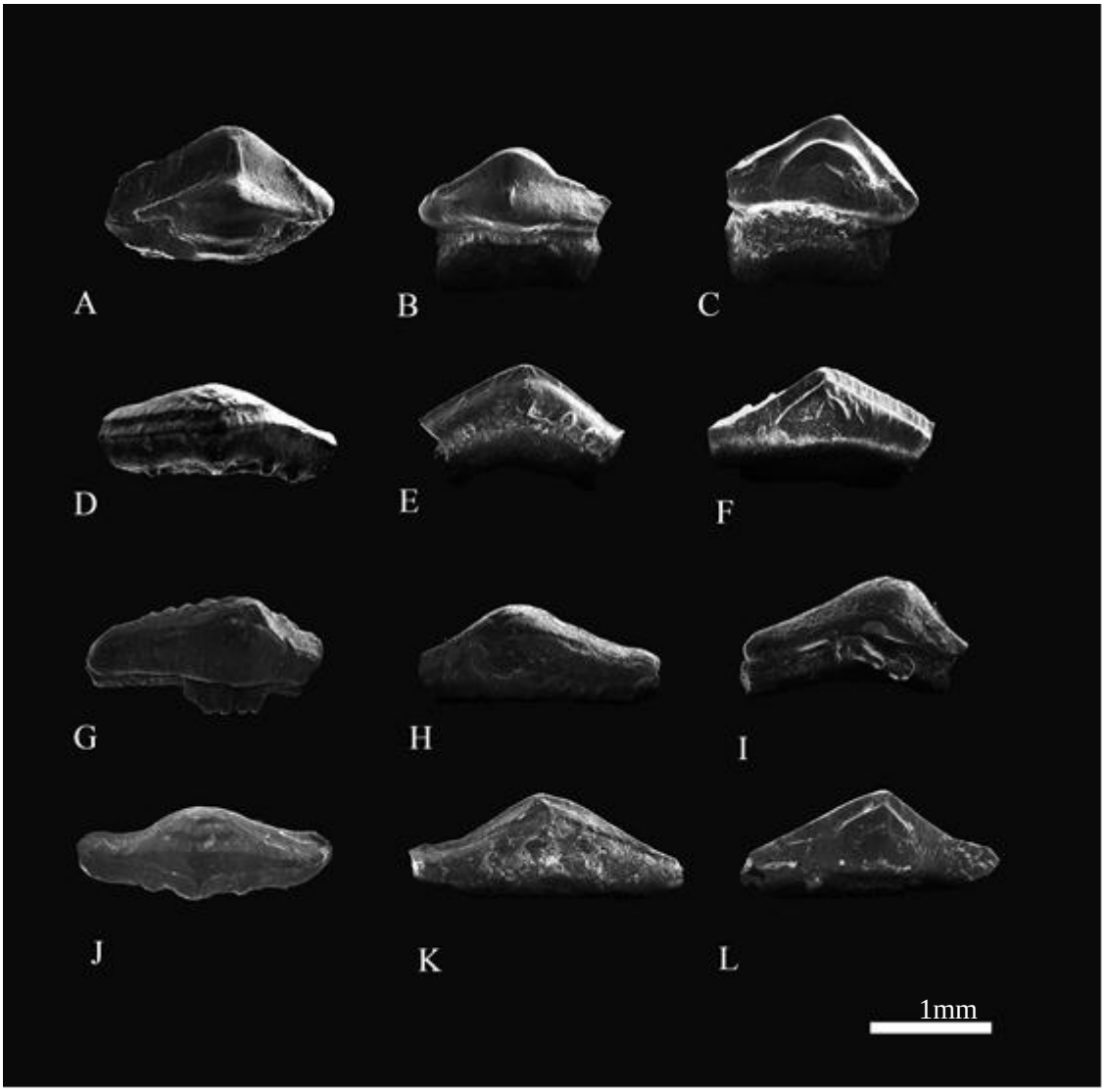


Figure 4.10 *Isanodus paladeji* A-C anterior tooth PRC241. (A) apical, (B) labial and (C) lingual views. D-F: anterolateral tooth PRC242. (D) apical, (E) labial and (F) lingual views. G-I: posterolateral tooth PRC243. (G) apical, (H) labial and (I) lingual views. J-L: posterolateral tooth PRC 244. (J) apical, (K) labial and (L) lingual views. Scale bar 1 mm

The new series of *Isanodus paladeji* teeth possess high main crowns in all types of teeth, whereas the original series showed low main crowns in the presumed anterolateral and posterolateral teeth. The presumed anterior, anterolateral and posterior teeth of the new series share the following combination of characters: well-developed

longitudinal crest and similarity in the pattern of V-shaped ridges on the lingual side (up to four ridges showing few weakly developed ridges perpendicular to them) whereas these characters disappear in the presumed posterolateral teeth. The presumed anterolateral (PRC 242) and posterolateral (PRC 243) teeth of the new series of *Isanodus paladeji* teeth possess a narrow and elongated crown mesio-distally, whereas their labial peg and labial nodes are not well developed. On the contrary, the former presumed anterolateral (TF 7672) and posterolateral teeth (TF 7673) show a wider crown. The root of both presumed anterior and anterolateral teeth is straight under the crown, whereas the one of both presumed posterolateral and posterior teeth is slightly projected lingually.

Isanodus nongbualamphuensis **Khamha *et al.*, 2015**

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province)

Material: 115 incomplete teeth and 12 teeth with a root preserved (n=127) (Figure 4.11).

Holotype: PRC 248 (posterior tooth)

Paratypes: PRC 245 (anterior tooth), PRC 246 (anterolateral tooth), PRC 247 (posterolateral tooth)

Referred material: TF 7672 (anterolateral tooth) and TF 7673 (posterolateral tooth) formerly identified as paratypes of *I. paladeji*

Type locality: Phu Phan Thong (Nong Bua Lam Phu Province)

Type stratum: Sao Khua Formation, Khorat Group, Early Cretaceous (Barremian)

Derivation of name: from Nong Bua Lam Phu province, where the type material was found

Diagnosis weakly heterodont, asymmetric crown, well developed labial nodes in anterolateral tooth, well developed V-shaped ridges on lingual side with short, stronglabio-lingually oriented ridges in presumed anterior, anterolateral and posterior teeth originating from the mesio-distal ridges.

Description

The teeth of *I. nongbualamphuensis* sp. nov. show four types of teeth: anterior, anterolateral, anteroposterior and posterior ones. A well preserved presumed

anterior tooth (PRC 245) lacks the root and measures 2 mm mesio-distally, 2 mm labio-lingually and is 1 mm high. The tooth shows a bulky crown and a well-developed main cusp, pyramidal in shape with a triangular base. The longitudinal crest is well developed. On the lingual side, there are four, well-developed V-shaped ridges and each ridge is ornamented by short ridges perpendicular to it. On the labial side, there are several short ridges originating from the middle of the crown and reaching the longitudinal crest. The largest presumed anterolateral tooth (PRC 246) measures 2 mm mesiodistally, 1.5 mm labio-lingually and is 2 mm high, but the root is not preserved. The tooth shows a bulky main cusp, pyramidal in shape with a triangular base. The longitudinal crest is well developed. The lingual side shows three well developed V-shaped ridges and each ridge is ornamented by short ridges originating from the top of each V-shaped ridge and reaching the following one. The labial side shows one V-shaped ridge, which is smaller than the ones on the lingual side. There are five well-developed labial nodes at the base of the crown.The largest presumed posterolateral tooth (PRC 247) mesures 2 mm mesiodistally, 1.5 mm labio-lingually and is 1.5 mm high including the root. This tooth is very similar to the anterolateral one but the pattern of ornamentation is not as well developed.

However, it shows a well-developed labial node at the base of the crown. The crown overhangs the root. The largest presumed posterior tooth (PRC 248) measures 3 mm mesio-distally, 1.5 mm labio-lingually and the crown is 1 mm in height, whereas the root is 0.5 mm high. The morphology of this tooth is very similar to the anterior one, but it is more elongated and it shows a more asymmetric crown. There is a well-developed longitudinal crest. There are four V-shaped, parallel ridges on the lingual side and each ridge is ornamented by short ridges. The labial peg is not well-developed. Some of the teeth show short, irregular ridges in the basal part of the lingual face of the crown. The crown overhangs the root and a long groove separates them on the labial side.

Discussion

The material described above does not belong to *Lissodus* because it shows a pyramidal cusp with a triangular base, ornamented with mesio-distal V-shaped ridges on the lingual side and it lacks lateral cusplets (Patterson, 1966; Duffin, 1985; 2001; Rees and Underwood, 2002). However, these characters are found in the genus

Isanodus (Cuny *et al.*, 2006). Comparison with *Isanodus paladeji* shows, however, several differences (Table 4.2). The new material shows a low main cusp. The ornamentation between the V shaped lingual ridges, made of labio-lingually oriented ridges, is more developed than on the teeth of *I. paladeji.* The labial peg in all types of *I. nongbualamphuensis* teeth is reduced in size, whereas only its presumed anterolateral and posterolateral teeth present well-developed labial nodes. On the contrary in the teeth of *I. paladeji*, the labial peg is always well-developed, whereas the labial nodes of the presumed anterolateral and posterolateral teeth are not well developed. The teeth previously considered as anterolateral and posterolateral teeth of *I. paladeji* show labio-lingual ridges together with a strong longitudinal crest, which are very similar to the presumed anterior and posterior teeth of *I. nongbualamphuensis*, although these characters are not well developed in the presumed posterolateral teeth. *I. nongbualamphuensis* sp. nov. should therefore encompasses the new presumed anterior and posterior teeth described here and the previously presumed anterolateral (TF 7672) and posterolateral (TF 7673) teeth of *I.paladeji*.

Table 4.2 Main character differences between the teeth of *Isanodus paladeji* and *Isanodus nongbualamphuensis*

Characters	***I. paladeji***	***I. nongbualamphuensis***
Dentition pattern	moderate heterodonty	weak heterodonty
Shape	narrow and elongate in anterolateral and posterolateral teeth	bulky teeth in all types
Crown shape	asymmetric in posterolateral and posterior teeth	asymmetric in all teeth
longitudinal crest	well-developed in anterior and anterolateral teeth	well-developed in anterior, anterolateral and posterior teeth
labio-lingually oriented ridges	not well developed	well-developed in anterior, anterolateral and posterior teeth. Not well-developed in posterolateral teeth
V-shaped ridges on the lingual side	moderately developed in anterior, anterolateral and posterior teeth	well-developed in anterior, anterolateral and posterior teeth
labial node in anterolateral teeth	moderately developed	well-developed
labial peg	well developed in anterior teeth, weakly developed in anterolateral, posterolateral and posterior teeth	weakly developed in anterior and posterior teeth, moderately developed in anterolateral and posterolateral teeth

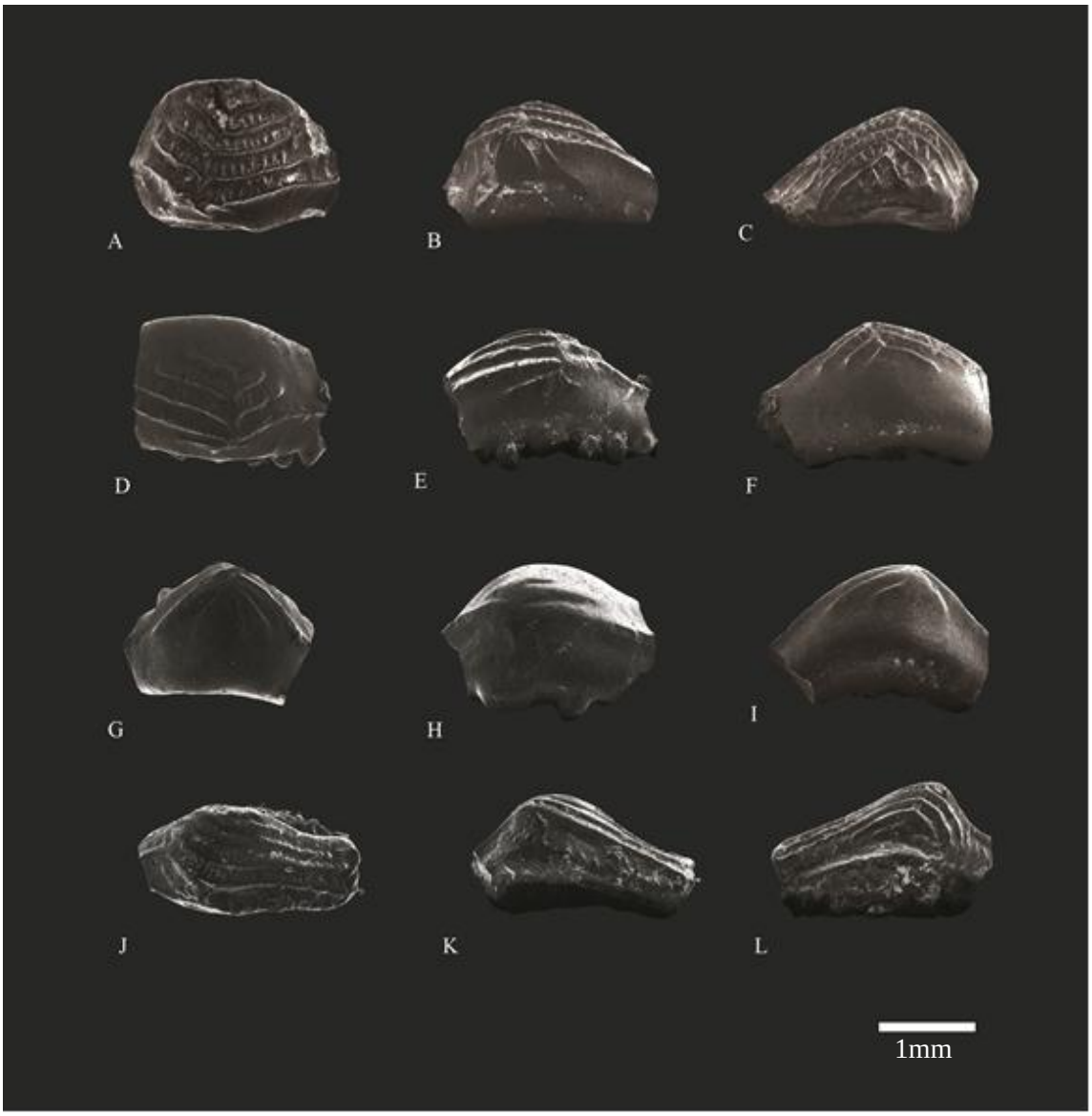


Figure 4.11 *Isanodus nongbualamphuensis* A−C: anterior tooth, paratype (PRC245). (A) apical, (B) labial and C: lingual views. D-F anterolateral tooth, paratype (PRC246). (D) apical, (E) labial and (F) lingual views. G-I posterolateral tooth, paratype (PRC247) (G) apical, (H) labial and (I) lingual views. J-L: posterior tooth, holotype (PRC248). (J) apical, (K) labial and (L) lingual views. Scale bar 1 mm

***Isanodus* sp. indet.**

Occurrence: Phu Phan Thong, (Nong Bua Lamphu Province).

Morphotype 1

Material: 10 incomplete teeth without the root preserved, including PRC 249 (n=10) (Figure 4.12).

These teeth are different from those of *Isanodus paladeji* and *Isanodus nongbualamphuensis* sp. nov. The largest tooth (PRC 249) measures 2 mm mesio-distally, 1.2 mm labio-lingually and is 1.5 mm high. The tooth shows a bulky main cusp, pyramidal in shape with a triangular base. The longitudinal crest is not well developed. The lingual side shows a V-shaped ridge without any labio-lingual ridges. The labial side is smooth and shows six well-developedlabial nodes at the base of the crown. The thickness of the crown, the pyramidal main cusp with a triangular base and the presence of labial nodes indicate that they could represent posterolateral teeth of the genus *Isanodus*. However, the teeth of *Isanodus* sp. morphotype 1 are thicker than those of the posterolateral teeth of the two other species and their exact taxonomic status is difficult to determine without finding more material.

Morphotype 2

Material: One tooth with the root preserved (PRC 250) (n=1) (Figure 4.12).

The tooth of *Isanodus* sp. morphotype 2 (PRC 250) mesures 2.5 mm mesio-distally, 0.5 mm labio-lingually and is 1 mm high including the root. The root is as high as the crown. The latter shows an upright, strong central cusp flanked with small lateral cusplets. The longitudinal crest is well developed. The lingual side shows two V-shaped ridges, the apexes of which are linked by a labio-lingual ridge. The labial side is smooth. The tooth also presents two labial nodes and well developed labial peg, which are diagnostic characters for *Isanodus paladeji*. However, it shows lateral cusplets, a character absent in the other *Isanodus* spp.. This character is more reminiscent of lateral teeth of *Lissodus,* like *L. minimus,* but the teeth of the latter species does not possess labial nodes at the base of the crown (Duffin, 2001). It is thus probable that this tooth represents a new species but more material is warranted to test this hypothesis.

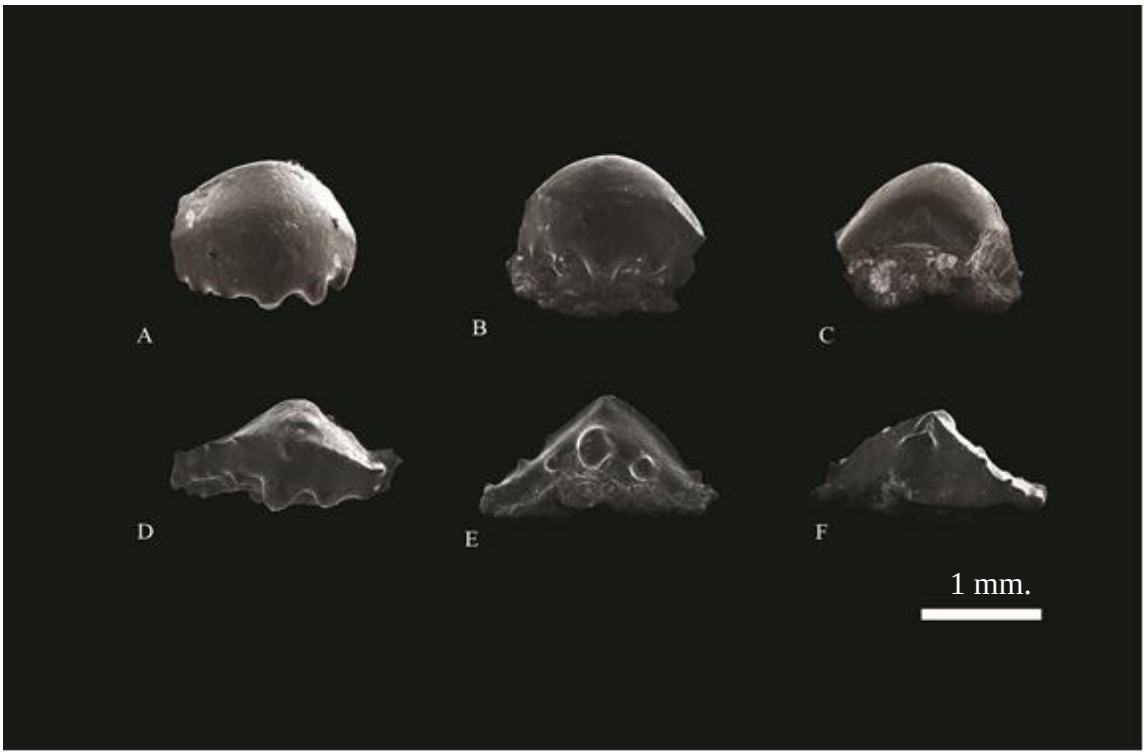


Figure 4.12 *Isanodus* sp. morphotype 1 (PRC 249) presumed posterolateral tooth. (A) apical, (B) labial and (C) lingual views. D-F: *Isanodus* sp. morphotype 2 (PRC 250) presumed anterolateral tooth. (D) apical, (E) labial and (F) lingual views. Scale bar 1 mm

Discussion

Isolated teeth of *Isanodus paladeji* have been found in many sites in the Sao Khua Formation: Phu Phan Thong (Nong Bua Lam Phu Province), Nong Sung (Mukdahan province), Phu Noi (Sakhon Nakhon Province) and Kut Island, Trat province (Cuny *et al.*,2006; 2007 and 2010), but *I. nongbualamphuensis* sp. nov. is so far only present in Phu Phan Thong locality. *I. Nongbualamphuensis* shows a weaker monognathic heterodonty than *I. paladeji.* The two species share a pyramidal main cusp with a triangular base, the presence of a labial peg and V-shaped ridges on the lingual side of the crown, which suggests they belong to the same genus. In both species, the lingual V-shaped ridges are not as well developed on the posterolateral teeth than on the other ones. *I. paladeji* shows small and weakly developed labial nodes in its narrow presumed anterolateral and posterolateral teeth, whereas the corresponding teeth of *I.*

nongbualamphuensis sp. nov. present more developed labial nodes and a lower crown. The possession of larger nodes in *I. nongbualamphuensis* served probably to stabilize the large grinding teeth while processing hard-shelled preys. On the contrary, *I. paladeji* might have preyed on softer preys. It should be noted, however, that the number of teeth recovered for each species in Phu Phan Thong is quite similar (109 teeth for *I. paladeji* and 115 teeth for *I.nongbualamphuensis),* which would suggest a sexual heterodonty. One "species" would then be the male or the female of the other "species" and vice versa. Neverteless, sexual heterodonty has not yet been demonstrated in hybodont sharks and the fact that *I. paladeji* has been recovered in several locations whereas *I. nongbualamphuensis* is restricted to Phu Phan Thong seems to argue against this hypothesis. It would indeed be difficult to explain why one of the two sexes would have a larger geographic distribution than the other. This is why it has been decided in this work to erect two different species. It is acknowledged, however, that if future discoveries demonstrate that these two species possess the same geographic distribution, the possibility that they represent the same species will have to be considered as more probable. The pattern of ornamentation in some teeth of *I. paladeji* and *I.nongbualamphuensis* is quite similar to the one observed in the genus *Heteroptychodus,* suggesting these two genera are closely related. Teeth of *Isanodus* were recently found on Kut Island (Cuny *et al.,* 2010). However, the teeth recovered on this island are larger than the teeth found at Phu Phan Tong. Some teeth show a strong and asymmetric crown with a dense ornamentation and numerous labial nodes, which is different from what can be observed on the teeth of *I. paladeji* and *I. nongbualamphuensis* sp. nov.. These characters, at first sight, could suggest that the material from Kut Island represents a species different from the teeth recovered at Phu Phan Tong (C. Laojumpon, pers. com.). If confirmed, this would indicate that this genus was abundant and diversified in the Lower Cretaceous of Thailand. In addition, *Isanodus* sp. was also found in Malaysia recently, which might lead to a new revision of the genus.

Family *incertae sedis*

Genus *Heteroptychodus* Yabe and Obata 1930

***Heteroptychodus kokutensis* Cuny *et al.*, 2010**

Occurrence Phu Phan Thong, (Nong Bua Lamphu Province), Phu Mai Paw, (Kalasin Province), Phu Noi (SaKhon Nakhon Province) and Kut Island (Trad Province).

Material: 110 fragmentary teeth (n=110) (Figure 4.13)**.**

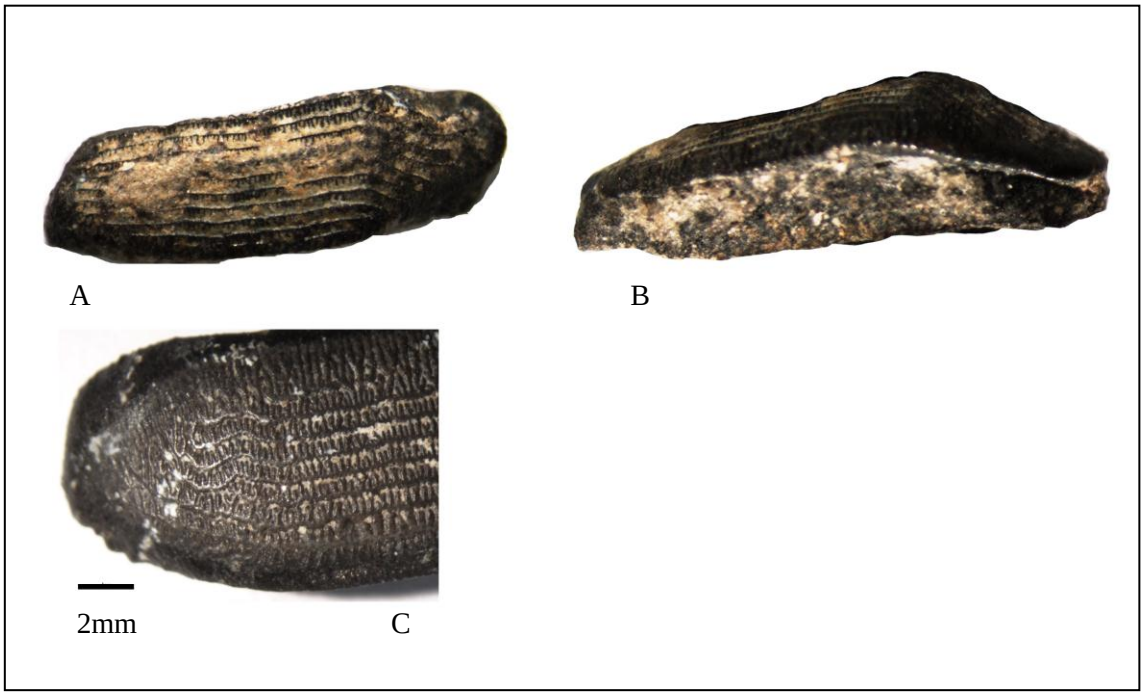


Figure 4.13 *Heteroptychodus kokutensis* (PRC-PT55) A-B tooth. (A) apical, (B) lingual Views and (C) PRC-PT58 tooth in apical view. Scale bar 2 mm

Description

The tooth with its root preserved (PRC-PT55) measures 12 mm mesio-distally, 4 mm labio-lingually and 6 mm in height including the root, which higher than the crown. The crown is elongated mesio-distally, almost flat and ornamented by tightly packed parallel ridges running mesio-distally. Numerous short and strong perpendicular ridges run labio-lingually between the main ridges. The marginal area of the tooth is ornamented with fine, radiating, branching ridges. The labial and lingual sides of the tooth are ornamented by ridges running from the base of the crown to the apical surface.

The crown overhangs the root labially and lingually. The root is perforated by a multitude of randomly distributed foramina and shows a well-defined row of enlarged foramina under the crown on the labial side whereas the enlarged foramina are located near the base of the root on the lingual side.

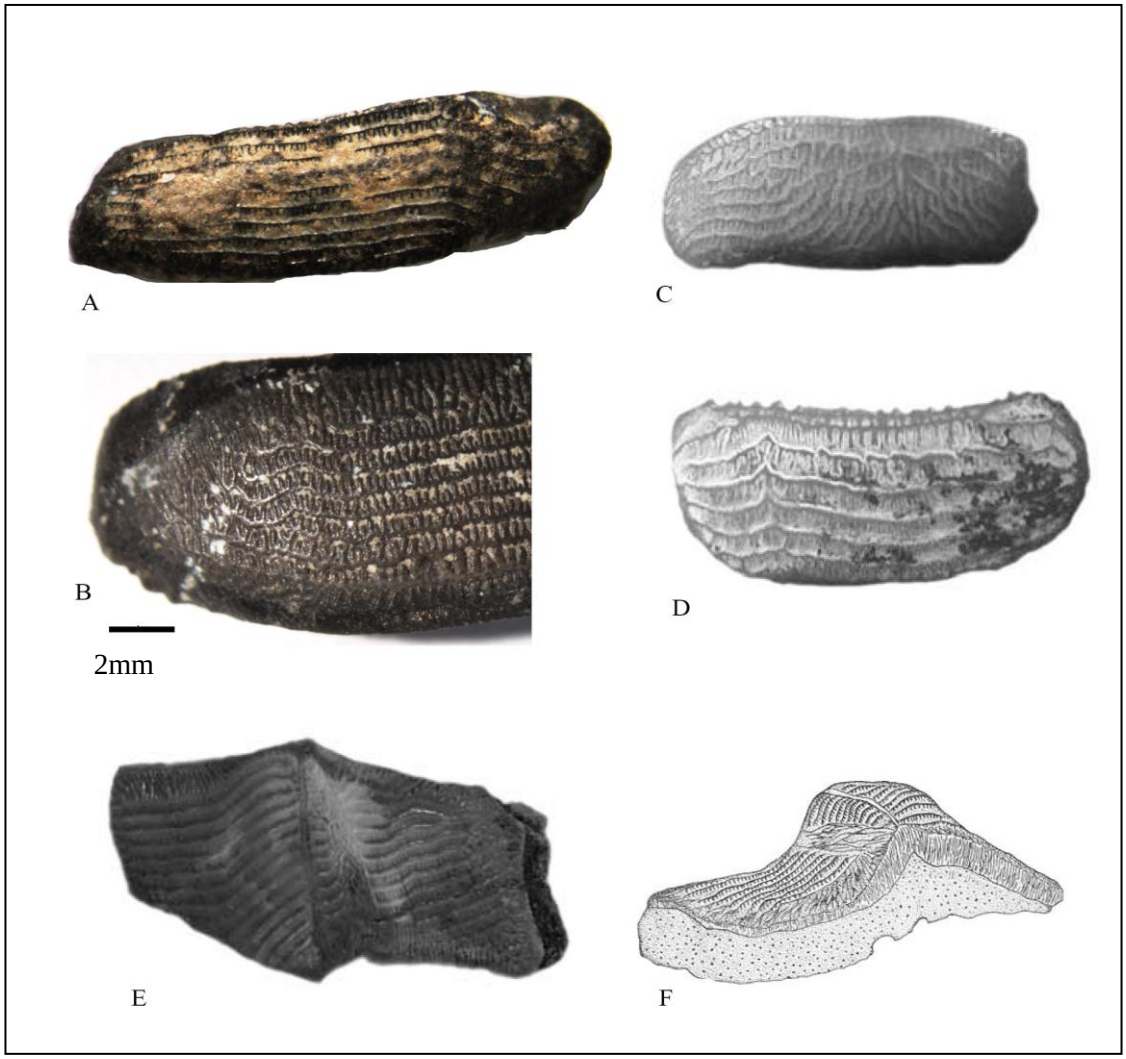


Figure 4.14 *Heteroptychodus kokutensis* compared with *H. chuvalovi* (115/12178, 114/12178) from the Aptian of Mongolia and *H. steinmanni* (TF 7679) from Khok Kruat formation, Aptian-Albian of Thialand (Cuny *et al.*, 2008). A-B *H. kokutensis* (PRC-PT55). (A) apical, (B) PRC-PT58 in apical views, (C) *H. chuvalovi* (115/12178) in apical and (D) *H. chuvalovi* (114/12178) in apical views, (E) Pathological tooth of *H. steinmanni* (TF 7679) in apical and (F) drawing of disto-lingual views. Scale bar 2 mm

Discussion

The specimens are low crowned and the ornamentation pattern of these teeth is similar to the one of the type species *Heteroptychodus steinmanni* (Yabe and Obata, 1930). *Heteroptychodus kokutensis* is different from *H. steinmanni* in possessing more asymetric teeth, narrow labio-lingually, elongated mesio-distally. In addition, anterior teeth of *H. steinmanni* show a well- developed bulge in the central part of the crown. Moreover, *H. kokutensis* separates from *H. chuvalovi* by having stronger labio-lingual ridges and lacking chevron-shaped mesio-distal ridges (Figure 4.14).

In the Phu Kradung Formation, hybodont fragmentary crowns also resemble *Heteroptychodus kokutensis*. The teeth are elongated mesio-distally and none of them display a well-developed bulge in the central part of the crown while *H. steinmanni* present these characters. Therefore, the teeth from the Phu Kradung Formation should not belong to *H. steinmanni,* but they should be considered as *H. kokutensis* on the basis of the above diagnostic characters. On the contrary, all hybodont materials from the Khok Kruat Formation were identified as *H. steinmanni* (Cuny *et al.,* 2003 and 2006). Interestingly, both *Heteroptychodus* species are present in the Sao Khua Formation. *H. steinmanni* has been reported from all localities whereas *H. kokutensis* has been reported only from Phu Wat and Phu Phan Thong. A competition between the two species of *Heteroptychodus* may have therefor been possible, and only *H. steinmanni* survived into the Khok Kruat Formation.

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Klein, 1885

Order Pycnodontiformes Lehmen, 1966

Cf. *Gyrodus*

Occurrence: Phu Phan Tong (Nong Bua Lamphu Province) 40 teeth; Phu Noi (Sakhon Nakhon Province) 2 isolated teeth.

Material: 32 isolated teeth and 10 incomplete vomerine dentitions (n=42) (Figure 4.15).

Figure 4.15 Cf. *Gyrodus* tooth. (A) PRC-PT44 in apical, (B) PPT135 in apical and (C) fragment of a vomerine PRC-PT32 in apical views. Scale bar 1 mm

Description

The tooth materials can be referred to two morphotypes as follow:

Morphotype 1 (Figure 4.15 A): The teeth are low, blunt, and oval shaped in apical view. They show no ornamentation. The largest crown (PRC-PT44) is 1 mm wide and 5 mm long and shows an elongated pedicle covered with ganoid, as high as the acrodine cap.

Morphotype 2 (Figure 4.15 B): The teeth are sub-circular shaped. The largest specimen (PPT135) is 3 mm long and 3.5 mm wide. The tooth shows a low crown with a groove which are ornamented by stronger tubercles. The teeth are much broader and shorter than morphotype 1

Ten fragmentary vomerine dentitions of pycnodont have been found as well. The largest specimen (PRC-PT32) is 7 mm long with four main rows of teeth. Teeth in the lateral row and the intermediate row (between the medial and lateral rows) are sub-circular to oval in shape and irregular in size. Their outline is quite similar to morphotype 2. The medial row consists of four bean shaped teeth, the three largest teeth showing a low crown with a narrow groove or central depression and ornamented by small tubercles similar to what have been described in morphotype 2 whereas the smallest tooth in this row is a smooth crown similar to morphotype 1.

Discussion

These vomerine material from Phu Phan Thong show bean-like and sub-circular teeth suggesting that they have a pycnodont affinity. Isolated teeth are quite similar to pycnodont ones from the Lower Cretaceous of Spain (Kriwet, 1997) and especially when compared with the genus *Gyrodus, Tepexichthys, Micropycnodont,* and *Mesturus* (Poyato-Ariza and Wenz, 2002). Phu Phan Thong teeth resemble *Gyrodus* more than the other three genera because *Mesturus* possesses only sub-circular teeth on prearticular while the other three genera also possess oval shaped teeth on prearticular. *Tepexichthy* consists of three rows on prearticular dentition while four rows were found in *Gyrodus* and *Micropycnodont* (Poyato-Ariza and Wenz, 2002). However, *Gyrodus* shows a deeper groove and stronger tubercles on the prearticular teeth than *Micropycnodont* (Everhart, 2007).

Pycnodont materials, Cf. *Gyrodus*, have been reported since 2009 in Thailand by Cavin *et al* (2009). He described materials from the Klong Min Formation (Late Jurassic) in the southern Thailand. Phu Phan Thong materials were compared with his vomer teeth and many similar characters were found (Figure 4.16). However, it is still difficult to identify all materials without a more complete dentition. Thus, all Phu Phan Thong pycnodont materials were referred to cf. *Gyrodus*, which is known from the Late Jurassic and Early Cretaceous (Kriwet, 2005; Fabre, 1982).

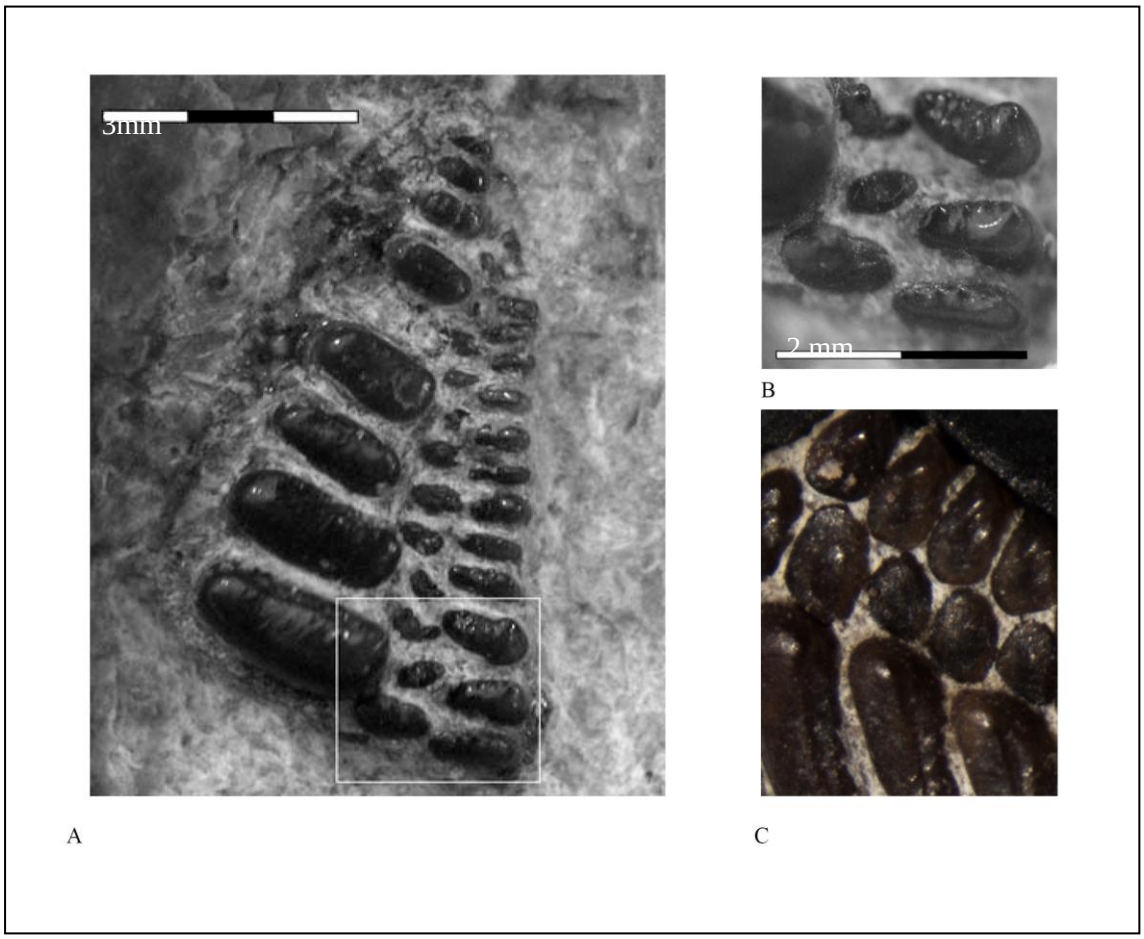


Figure 4.16 A-B Prearticular teeth of Cf. *Gyrodus* (TF8033) from Khlong Min Formation (Late Jurassic) of Thailand (Cavin *et al*., 2009). (A) complete dentition, scale bar 3 mm; (B) close-up view of the outlined area, scale bar 2 mm; (C) close-up view of Cf. *Gyrodus* (PRC-PT32) from Phu Phan Tong. Scale bar 2 mm

Cf. *Anomoeodus*

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province)

Material: 26 isolated teeth (morphotype1=11 and morphotype2 =15) and 5 incomplete vomerine dentitions (n=31) (Figure 4.17).

Description

Morphotype 1: The teeth are blunt, and oval shaped in apical view. The largest specimen (PPT130) is 4 mm length, 1 mm width and 0.5 mm hight. The tooth shows a low crown with a narrow curved groove dividing the crown in a narrow

anterior and a broader posterior part. The broad part slope posteriorly. It shows small faint tubercles around the groove.

Morphotype 2: The isolated teeth are circular or sub-circular in shaped with a central rounded cusp and radiating anastomosing ridges. The largest crown (PRC-PT135) is 2 mm hight and 3 mm in diameter.

Incomplete vomerine dentitions (PPT22) consist of four rows of teeth. The medial row is composed of five oval or sub-oval shaped teeth. The teeth show tuberculated ornamentation around the margin of the teeth. On the three larger teeth, they present a well-developed longitudinal crest while the two smaller teeth of the medial row are lacking it. The intermediate row shows four oval shaped teeth. They display a groove with faint tubercles whereas the teeth in the two lateral rows show a groove without tubercles.

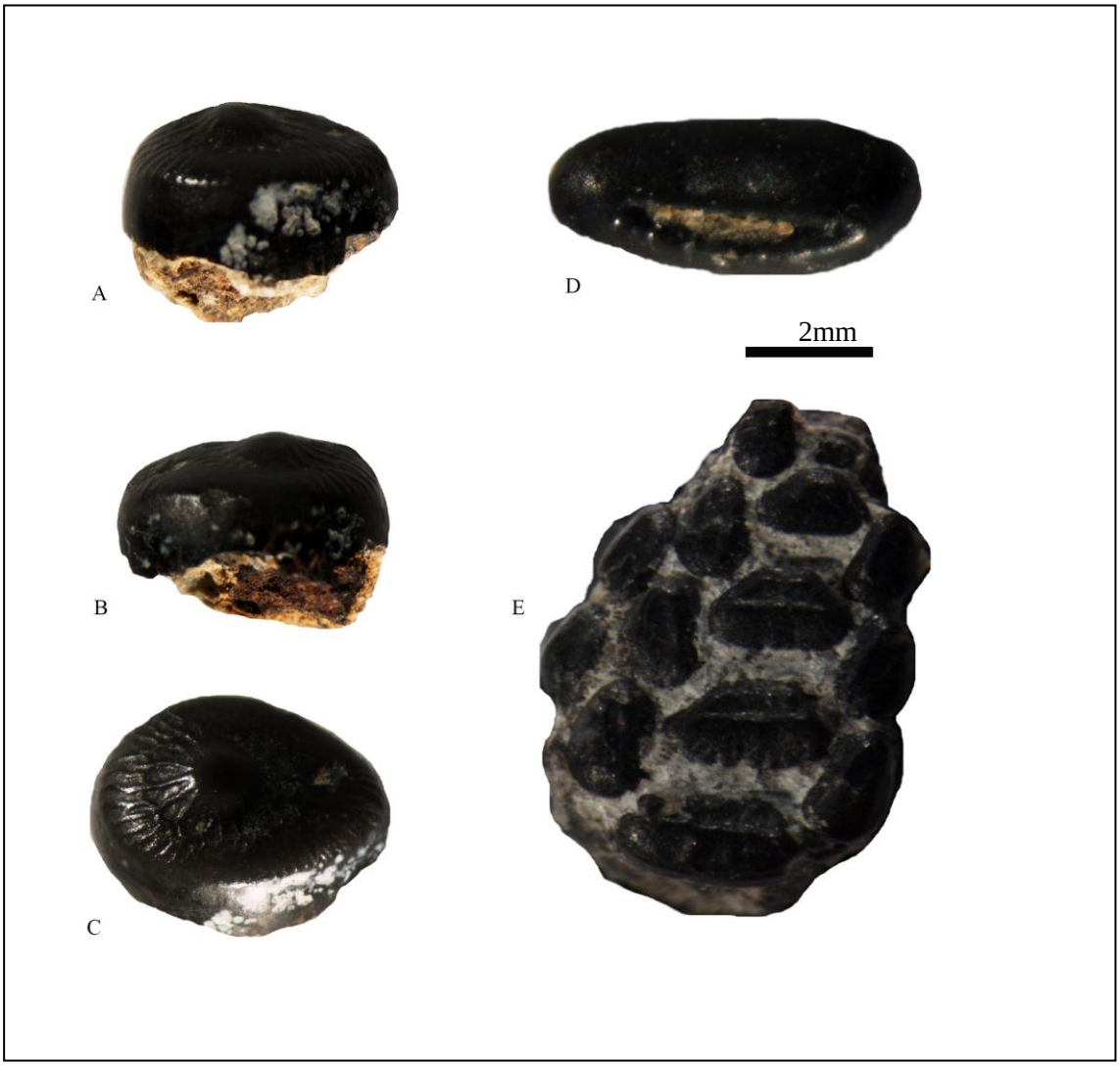


Figure 4.17 Pycnodontiformes *fam. Indet.* A-C PRC-PT135 tooth. (A) and (B) mesial or distal; (C) apical views, (D) PRC-PT135 tooth in apical view and (E) incomplete vomerine dentitions (PPT22) in apical view. Scale bar 2 mm

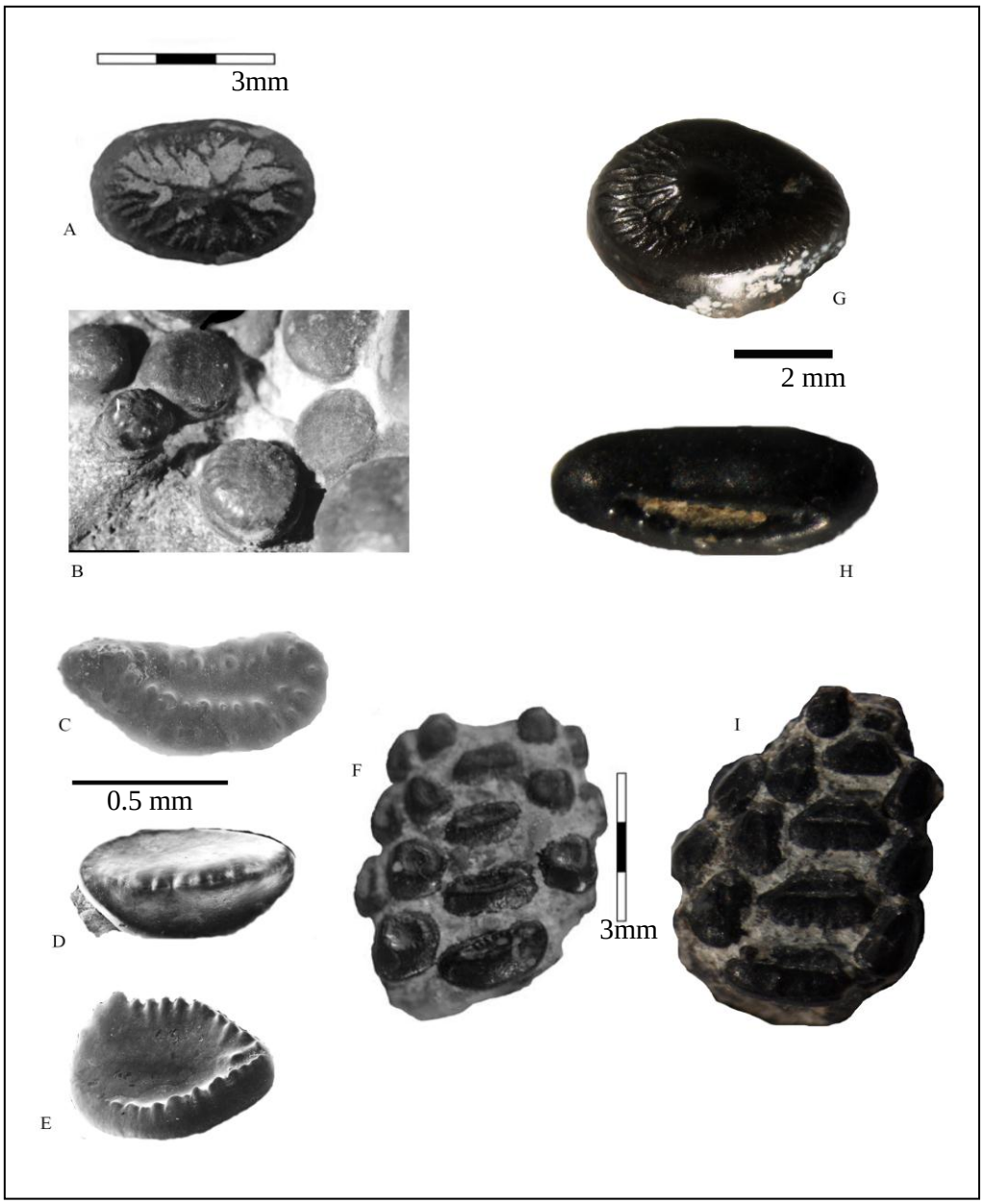


Figure 4.18 (A) cf *Anomoeodus* (TF 8037, Cavin *et al.*, 2009) tooth from Phu Phan Thong in apical view, scale bar: 3 mm. (B) lateral tooth of *Macromesodon* sp. from the Kimmeridgian of Germany (Kriwet, 2005); (C) *Anomoeodus* sp. from the Iberian of Spain in apical view. D-E *Nursallia* sp. from Turonian bone-bed of USA (Kriwet, 2005) in apical view. (D) specimen 3, (E) specimen 2, scale bar 0.5 mm. (F) cf *Anomoeodus* (TF 8034, Cavin *et al.*, 2009) in apical view. (G-I) Pycnodontiformes *fam. indet* from Phu Phan Thong in apical view, scale bar 2 mm

Discussion

The morphotype 1 is similar to actinopterygian teeth from southern Tunisia (Cuny *et al,* 2010). It has also been reported by Cuny *et al.*, (2006) from Kut Island. These specimens were reported as cf. *Anomoeodus* by Cavin *et al.* (2009). Rounded tooth morphology 1 is similar to the Ginglymodi-like teeth but they can be separated by the ridges ornamenting the acrodine cap. This characteristic has been found in some pycnodont i.e., *Anomoeodus*, *Macromesodon* and *Coelodus* sp. (Kriwet, 2005; Poyato-Ariza and Cartany, 1999). The Morphotype 2 is quite similar to *Anomoeodus* sp. from Mosquerella Formation (Cenomanian) of Spain (Kriwet, 2005) and they are also similar to the median row of vomerine teeth of cf. *Anomoeodus* from the same locality (Figure 4.17) (Cavin *et al.*, 2009). In addition, the occurrence of a well-developed longitudinal crest which tubercles on the median row of ovoid teeth of the vomerine dentition is resembling *Nursiallia* sp. from the Turonian bone bed of Colorado and Cenomanian of Spain (Kriwet, 2005), whereas Thai specimens possess stronger tubucles ornamentation around the margin of teeth. With no articulated skeleton remains at hand, the affinities of this specimen are still unclear. It is difficult to regard this material as belonging to a single taxon based only on isolated teeth.

Order Amiiformes Hay, 1929

Family Caturidae Owen, 1860

***Caturus* sp.**

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province), Mab Ching (Nakhon Sri Thammaarat Province).

Material: 45 isolated teeth (n=45) (Figure 4.19)

Description

The teeth are quite high and slender. They are made of two parts. The upper acrodine cap is light coloured, while the ganoine cover at the base of the crown is darker. The acrodine cap is smooth and shows an arrow-like shape with two acute cutting edges. These cutting edges are well developed from the base of the lateral side of the acrodine cap and attain the apex. The ganoine sheath shows a rod-like shape and is ornamented by fine parallel ridges that cover the whole ganoine sheath part.

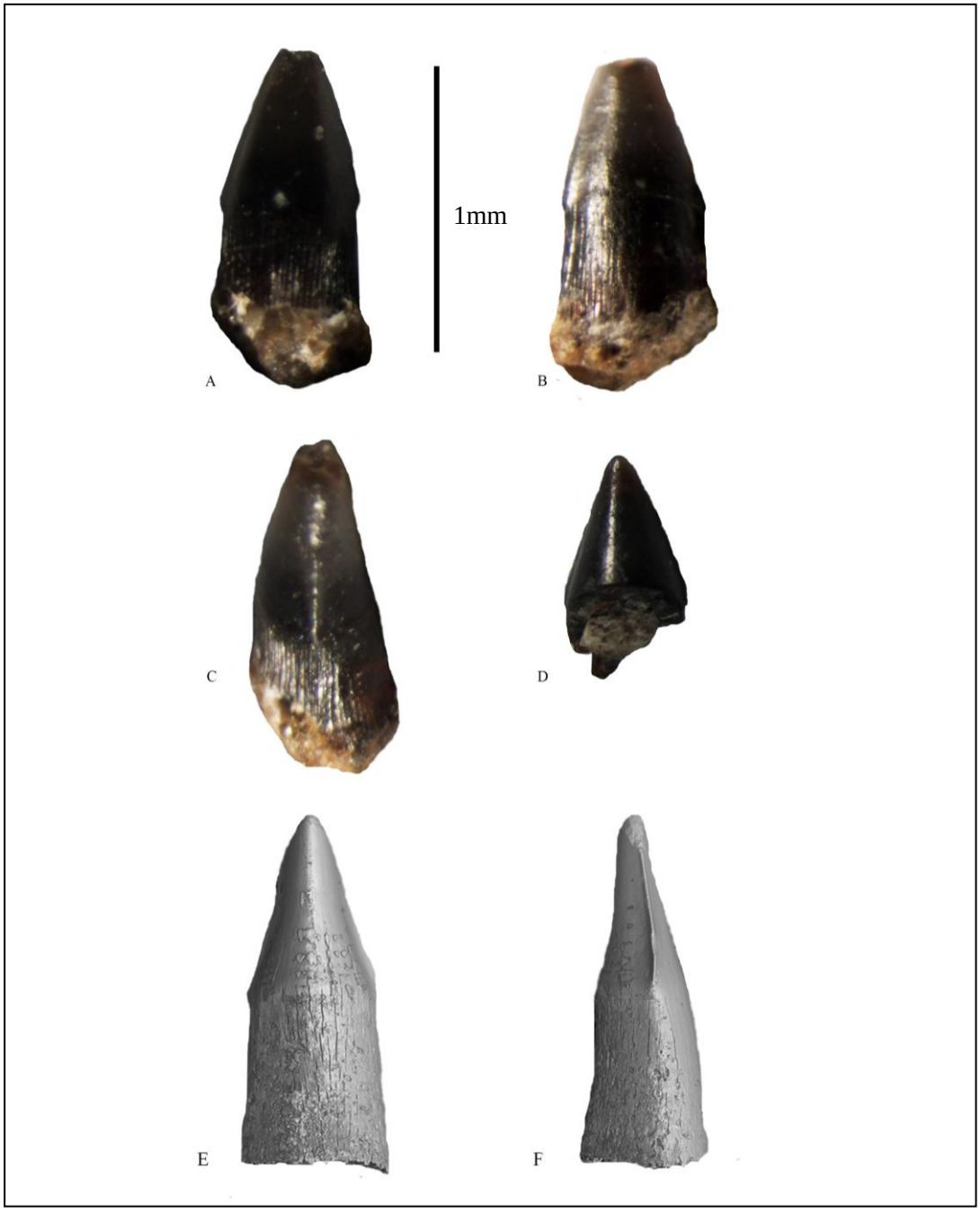


Figure 4.19 A-C *Caturus* sp. (PPT61) tooth . (A) labial, (B) lingual and (C) mesial or distal views, (D) acrodine cap of *Caturus* sp. (PPT 67). E-F *Caturus* sp. the Berriasian, of Cherves-de-Cognac in France (Pouech *et al.*, 2015). (E) lingual and F: mesial or distal views. Scale bar 1 mm

Discussion

Phu Phan Thong material is distinguished from other actinopterygians teeth by their arrow-like shape excepted *Caturus* sp, *Ionoscopus* sp. and *Callopterus* sp. which possessed arrow-like teeth. However, the two latter genera show weaker cutting edges running along the margin of the mesial and distal sides of the acrodine cap whereas *Caturus* sp. and the Thai material show stronger cutting edges. This character is diagnostic for the genus *Caturus* (Cuny *et al.*, 1991; Mudroch and Thies, 1996; Kriwet, 1997) and might indicate that Phu Phan Thong materials belong to *Caturus*.

Phu Phan Thong materials display similar shape to the teeth of *Caturus* sp. from the Berriasian of Cherves-de-Cognac in France (Pouech *et al.*, 2015). However, *Caturus* sp. from France shows less ridges on the ganoine sheath than Thai material (Figure 4.19). Therefore, Phu Phan Thong materials should belong to a new species. However, their taxonomic status is unmanageable based in only isolated teeth. During the late Jurassic, *Caturus* have been found only the marine habitats (Schaeffer and Patterson, 1984; Grande and Bemis, 1998; Kriwet, 20005) and expanded to lagoon and lacustrine environments during the Cretaceous time such as the Wealden and Purbeck Formation (Klug and Kriwet, 2013) as well as in the Phu Phan Thong sediment.

Subdivision Halecomorphi Cope, 1872

Order Ionoscopiformes Grande and Bemis, 1998

Family Ionoscopidae Lehman, 1966

Genus *Ionoscopus* Costa, 1853

***Ionoscopus* sp.**

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province).

Material: 38 fragmentary teeth (Figure 4.20).

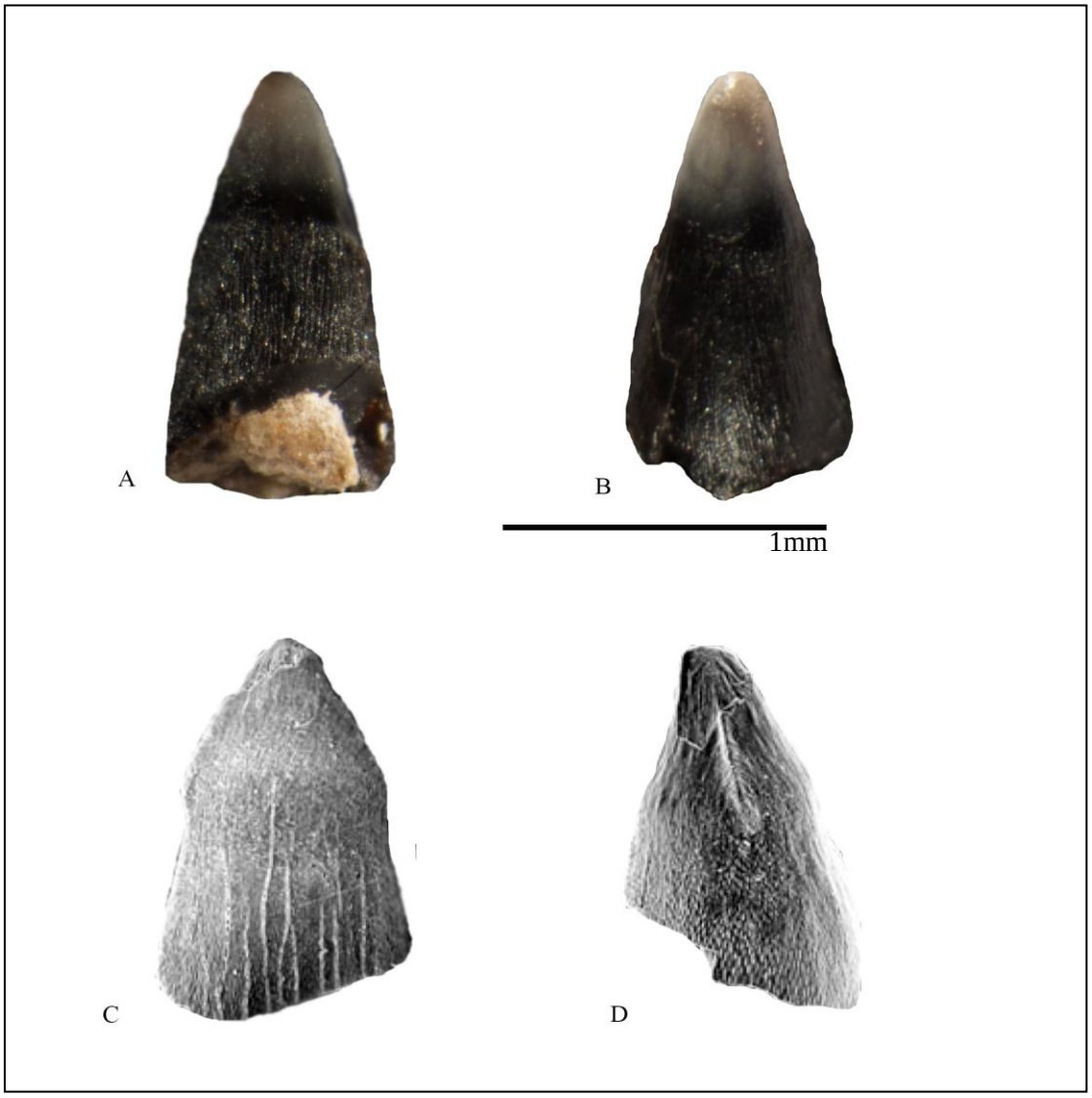


Figure 4.20 A-B: *Ionoscopus* sp. (PPT102) from Phu Phan Thong. (A) lingual and (B) labial views. C-D *Ionoscopus* sp. (MPZ 2012/790) from the Late Jurassic of Spain (Klug and Kriwet, 2013). (C) labial and (D) lateral views. Scale bar 1 mm

Description

The specimens are conical in shape with a circular cross-section at the base of the teeth. These specimens are relatively straight, high and slender. The largest tooth is 1 mm high and 0.5 mm in diameter. The acrodine cap is smooth without any ridges. They possess weakly developed cutting edges on the mesial and distal side. They do not reach the ganoine part. The ganoine sheath is ornamented by anastomosed ridges on the

whole of the labial and lingual sides. These ridges are running from the base of the ganoine sheath to the top of it.

Disscusion

The teeth of *Ionoscopus* sp. are almost as same as the *Caturus* ones. They can be separated by the fact that the teeth of *Ionoscopus* are stouter than the ones of *Caturus*. Their cutting edges on the acrodine cap are also weaker than on the *Caturus* teeth. The acrodine cap of the *Caturus* teeth is more compressed labio-lingually than the *Ionoscopus* one. These specimens are close to the *Ionoscopus* sp. from the Kimmeridgiam of Germany (Mudroch and Thies, 1996) (Figure 4.20), and similar to the teeth from the Late Jurassic of Switzerland (Muller, 2010) and Spain (Klug and Kriwet, 2013). The record of teeth similar to *Ionoscopus* is on the other hand the first of this kind in Thailand.

Subclass Actinopterygii Klein, 1885

Superdivision Ginglymodi Muller, 1844 (*sensu* Grande 2010)

Ginglymodi like-teeth

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province), Phu Wiang (Khon Kaen Province), Phu Phok (Sakhon Nakhon province), Khok Pha Suam (Ubon Ratchathani Province), Phu Kum Khao (K4), Lam Pao Dam and Phu Mai Paw, (Kalasin Province).

Material: 120 teeth (n=120); morphotype 1 (n=56), morphotype 2 (n=38**),** morphotype 3 (n=4) and morphotype 4 (n=22**)** (Figure 4.21)**.**

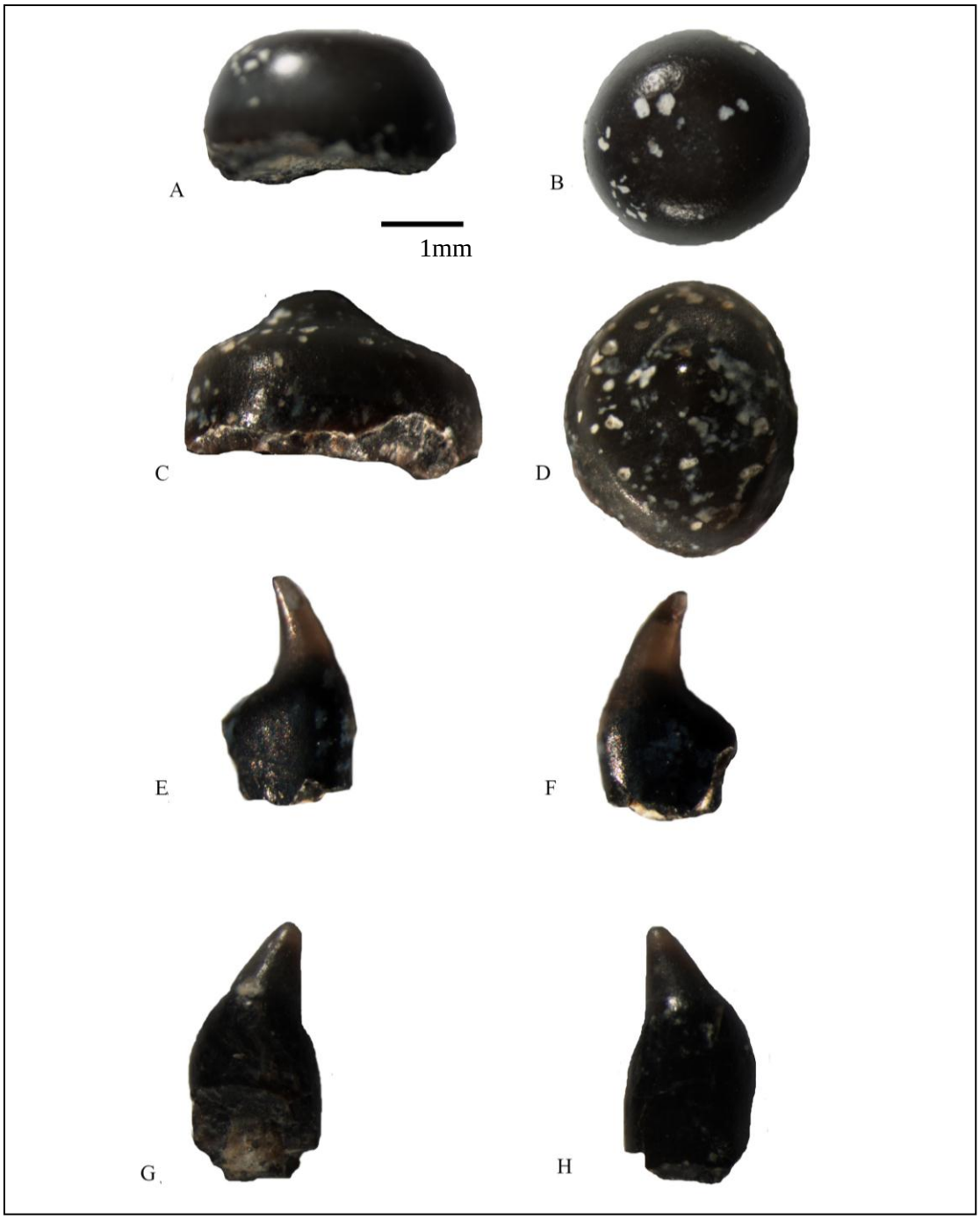


Figure 4.21 Ginglymodi like-teeth. A-B: morphotype 1. (A) mesial or distal and (B) apical views. C-D: morphotype 2 crushing teeth. (C) mesial or distal and (D) apical views. (E-F) morphotype 3 pharyngeal teeth in mesial or distal view, (G-H) morphotype 4 in mesial or distal view. Scale bar 1 mm

Description

Four morphotypes of teeth materials can be classified, i.e.,

Morphotype 1 (Figure 4.21 A-B): The largest specimen is 2 mm in diameter and 0.5 mm high. The specimens are button shaped and rounded. The acrodine cap and ganoine sheath are smooth without ornamentation.

Morphotype 2 (Figure 4.21 C-D): The largest specimen is 3 mm in diameter and 0.5 mm high. These specimens are a crushing teeth and circular or subcircular cross section. Most of the teeth are represented by the acrodine cap only and it shows a small button in the middle of the apical surface with a smooth cylindrical base.

Morphotype 3 (Figure 4.21 E-F): The largest specimen is 2 mm in height and 0.5 mm in diameter. The teeth are high, smooth and compressed laterally. They are hook or claw-shaped.

Morphotype 4 (Figure 4.21 G-H): The largest specimen is 2 mm in height and 1mm in diameter. The teeth are smooth and rounded in section. The ganoine sheath part is bulged with a curved conical acrodine cap.

Discussion

The specimens belonging to morphotype 1 are similar to the button-shaped crushing isolated teeth that were found in Phu Wiang, Phu Mai Paw, Phu Phok and Phu Kum Khao (K4) in the Sao Khua Formation and also in Lam Pao Dam and Khok Pha Suam in the Khok Kruat Formation (Cavin *et al.,* 2009). The materials are similar to the palatal teeth of Ginglymodian fish from Teruel in Spain which are rounded or ovoid in shape with a smooth surface. Some materials show small button at the surface of the acrodine cap (Estes and Sanchiz, 1982).

The teeth of morphotype 2 are similar to teeth like those of *Isanichthys palustris* (Figure 4.22) showing a conical shape and no ornamentation. They were found in Phu Nam Jun and Phu Noi, Phu Kradung Formation, Kalasin Province (Deesri *et al.*, 2014). However, Phu Phan Thong specimens were found only as isolated teeth and are poorly preserve. It is difficult to decide whether the teeth belong to *Isanichthy palustris* or not.

The teeth of morphotype 3 are similar to the pharyngeal teeth of ginglymodian fish that were found in the Late Jurassic of Cuba (Thies, 1989) and the

Kimmeridgian of Germany (Mudroch and Thies, 1996). However, these hook shaped pharyngeal teeth are also found in pycnodontid fishes (Kriwet, 1999), so it is difficult to decide whether our isolated pharyngeal teeth belong to Ginglymodian or Pycnodontiformes. I refer isolated teeth of morphotype 3 to Ginglymodian because these teeth are more compressed in labio-lingually than in Pycnodontiformes.

The teeth of morphotype 4 are quite similar to the teeth of *Thaiichthys* cf. *buddhabutensis* (TF 8026; Deesri, 2014) and *Thaiichthys buddhabutensis* (KS12-262) (Cavin *et al.*, 2013) by a rod shaped teeth with a less bulged base and curved conical apex (Figure 4.23). Their taxonomic status is rather difficult to identify based on isolated teeth. However, according to the dentary teeth of *Thaiichthys*, it should be appropriate to refer the Phu Phan Thong material as Cf. *Thaiichthys* for the time being until completed jaw will be discovered.

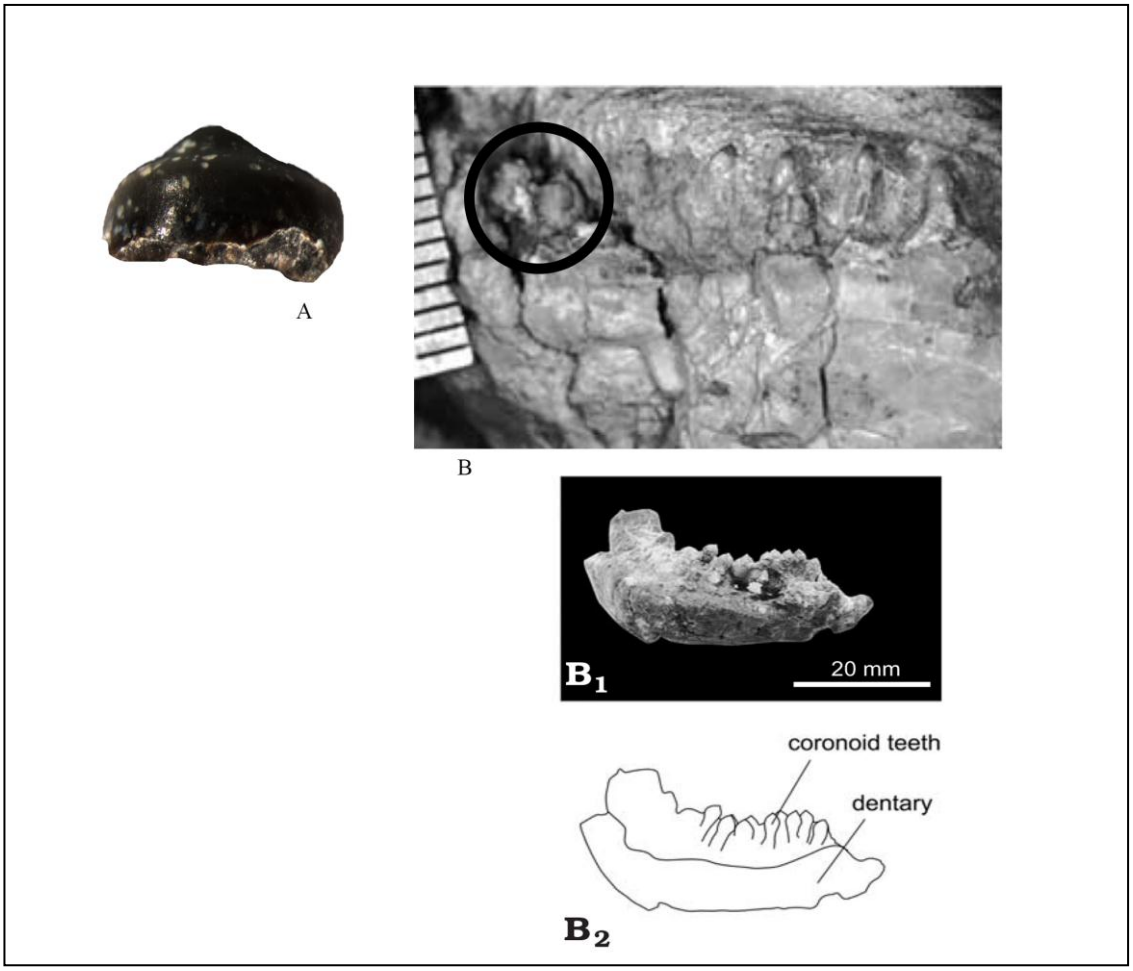


Figure 4.22 Tooth morphotype 2 compared with the teeth of *Isanichthys lertboosri* (KS34-281) from the late Jurassic of Thailand (Deesri *et al.*, 2014). (A) Phu Phan Thong tooth morphotype 2 in mesial or distal view; (B) *Isanichthys lertboosri* (KS34-281) teeth on the dentary; (B_1) *Isanichthys lertboosri* (KS36-2) and ($B_{2)}$ *Isanichthys lertboosri* (KS36-2) line drawing. Scale bar: 20 mm

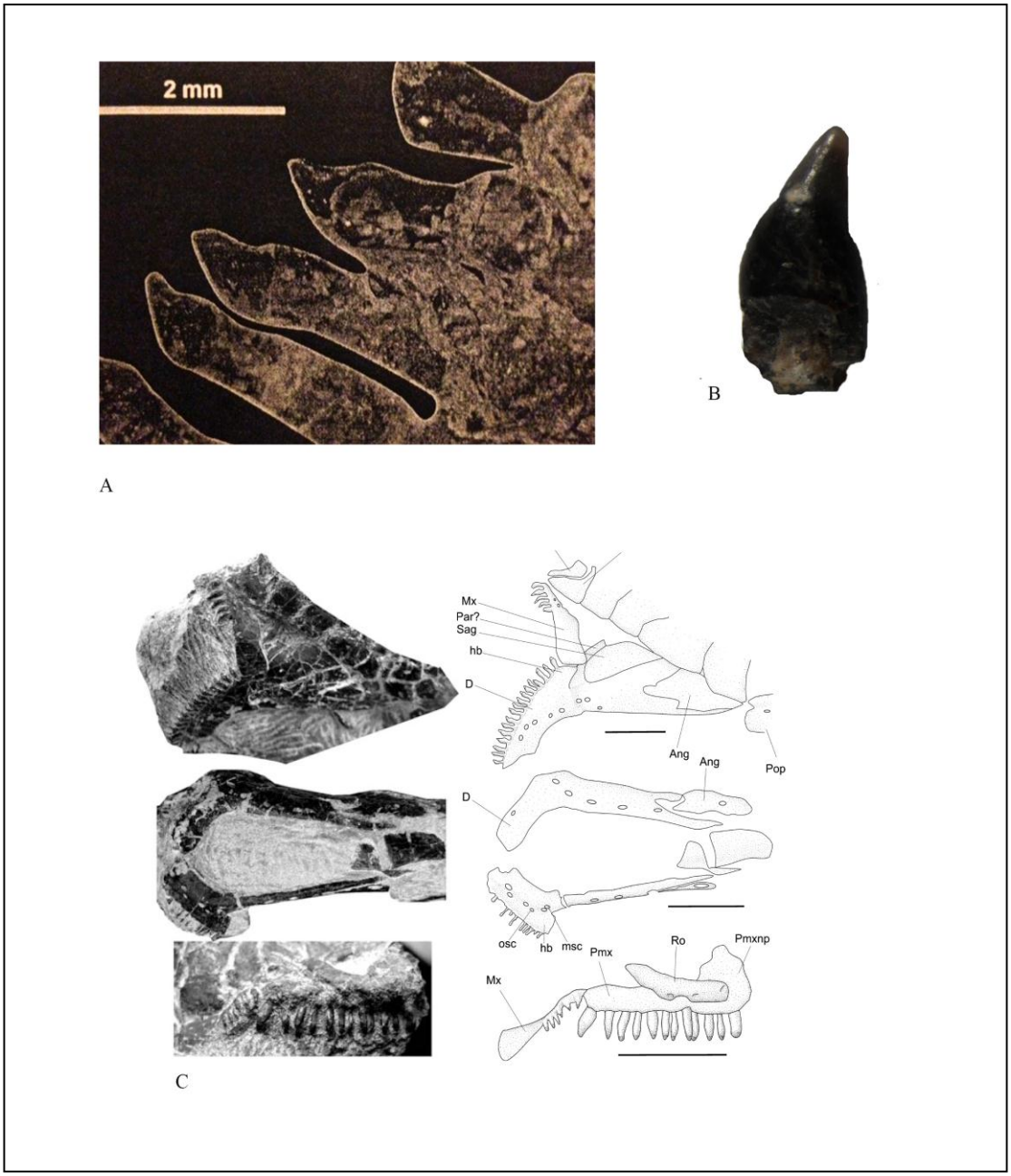


Figure 4.23 Tooth morphotype 4 compared with *Thaiichthys* cf. *buddhabutensis* (TF 8026; Deesri *et al.*, 2014). (A) dentary with teeth of TF 8026, (B) tooth of morphotype 4 in mesial or distal view and (C) jaw *of Thaiichthys buddhabutensis* (KS12-262) from Phu Num Jun, the Phu Kradung Formation (Cavin *et al.*, 2013). Scale bar 2 mm

Holostei *sensu* Grande 2005

Semionotiformes *sensu* Olsen and McCune 1991

Semionotidae *gen. indet.*

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province), Phu Wiang (Khon Kaen Province), Phu Phok (Sakhon Nakhon province), Khok Pha Suam (Ubon Ratchathani Province), Phu Kum Khao (K4), Lam Pao Dam and Phu Mai Paw, (Kalasin Province).

Materials: 250 fragmentary scales (Figure 4.24).

Description

Numerous fragmentary scales have also been found. The largest well preserved scale is 14 mm in length. These scales are rhomboid or traprezoid in shape with rounded corners. They are made of a bony plate covered by ganoine. The ganoine is smooth but sometime it shows small pits on the surface.

Discussion

Although ganoid scales are abundant and common found among the microremains of Phu Phan Thong. They are difficult to identify when found isolated. However, Deesri (2013) studied the shape and micro-ornamentation study of fish scales from Phu Phan Thong locality. These scales show many tubercles or holes on the surface with large size holes only along the lateral edge whereas the center of the scale is lacking tubercles. This pattern is similar to some scales of *Siamamia naga* from Phu Phok locality and located in the same formation. The some scales from this study are also showed the same characters. Based on the similarity of shape, the some scales from Phu Phan Thong might belong to *Siamamia*.

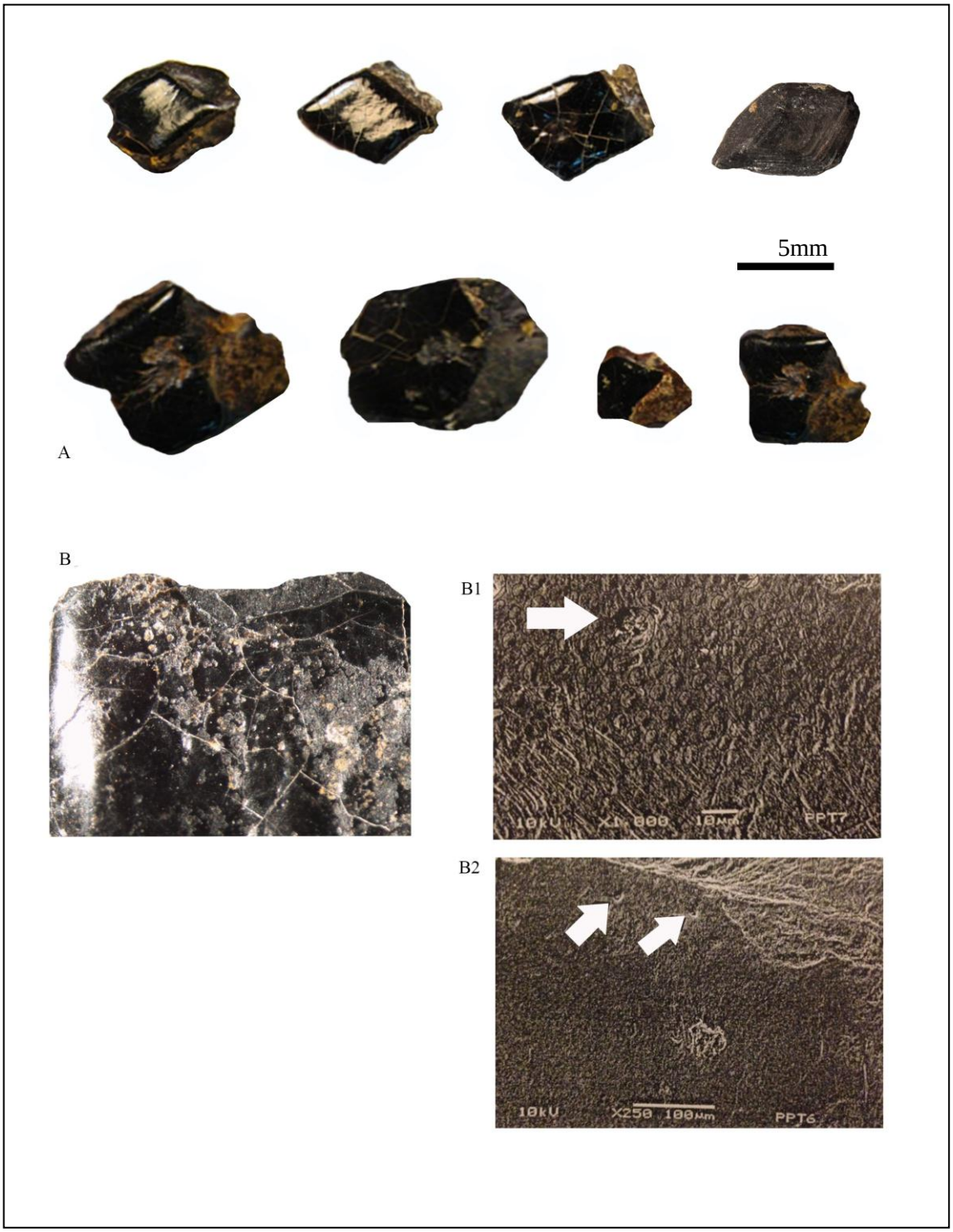


Figure 4.24 (A) Isolated bony fish scales from Phu Phan Thong locality. Scales bar 5 mm; (B) the lateral edge of Phu Phan Thong scales, (B_1-B_2) Scanning electron shows a large hole only along the lateral side. Scale bare 100 µm

Superorder Crocodylomorpha Hay, 1930 (*sensu* Walker, 1970)

Order Crocodylia Gmelin, 1789

Goniopholididae *gen. indet.*

Occurrence: Dan Lung, Dan Kerng (Mukdahan Province), Khok Sanam, Phu Noi, Khok Kong, Phu Phak (Kalasin Province), Phu Phan Thong (Nong Bua Lamphu Province), Nong Sung (Mukdahan Province), Phu Wiang, Phu Pratu Tee Ma, Ban Samran (Khon Kaen Province), Phu Phok (Sakhon Nakhon Province), Khok Pha Suam (Ubon Ratchathani).

Material: 50 fragmentary teeth (n=50) (Figure 4.25).

Description

Two tooth morphotypes can be separated.

Morphotype 1 (Figure 4.25 A-C): The teeth of this morphotype are rather abundant. The crown of this morphotype is robust and conical in shape with a circular cross-section at the base of the crown. The largest tooth is 3 mm height and 2 mm in diameter. The surface of the crown is ornamented with fine parallel ridges on the labial and lingual side. The carinae start from the base of the crown to the apex.

Morphotype 2 (Figure 4.25 D-E): Fourteen incomplete isolated teeth have been found. The crowns of these teeth are relatively high and show a conical shape. The largest crown is 5 mm height and 3 mm in diameter. All apexe of these crowns are broken. The base of crown is circular in cross-section. The teeth are curved lingually.

Discussion

The specimens of the two mophotypes are similar in shape and ridge ornamentation to the teeth of the family Goniopholididae based on their well-developed carinae (Owen, 1841; Salisbury et al., 1999; Averianov, 2000; Schwarz, 2002). Moreover, they are also close to the genus *Goniopholis* sp. from the Rabekke Formation of Denmark (Schwarz et al, 2009). These mophotypes were also found in the Phu Kradung and Khok Kruat Formations showing the same slender shape and the mesio-distal compression at the base of their crowns (Buffetaut and Ingavat., 1980, 1983, 1984; Lauprasert, 2007). The appearance of morphotype I, therefore, can be used to confirm the existence of the family Goniopholididae in Phu Phan Thong and also shows

that this crocodilian was relatively widespread in the Khorat Group of Thailand. However, it is difficult to identify the isolated teeth to generic level.

Figure 4.25 Goniopholididae *gen. indet.* A-C: morphotype 1. (A) labial or lingual, (B) mesial or distal (C) apical views. D-E morphotype 2. (D) mesial or distal and (E) labial or lingual views. Scale bar 3 mm

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Superfamily Testudinoidea Batsch, 1788

Testudinoidea *fam. indet.*

Occurrence: Khok Sanam, Phu Noi, Khok Kong, Phu Phak, Phu Kum Khao, Ban Na Krai, Phu Mai Paw (Kalasin Province), Chong Chat, Phu Phan Thong (Nong Bua Lamphu Province), Dan Lung, Dan Kerng, Nong Sung (Mukdahan Province), Phu Wiang, Phu Wat, Ban Samran (Khon Kaen Province), Phu Phok (Sakhon Nakhon Province), Khok Pha Suam (Ubon Ratchathani).

Material: 98 isolated plate fragments (n=98) (Figure 4.26).

Description

Only fragmentary plates have been found no larger than 5 cm. some of them show a smooth surface and some materials ornamented by small pits or ridges randomly distributed on the surface.

Figure 4.26 Turtle shell plate fragment from Phu Phan Thong locality

Discussion

Although the turtle shell plates are abundant in the Phu Phan Thong sediment, they are fragmentary and of small size. The incompleteness of these plates does not allow a precise identification.

Superoder Saurischia Seeley 1888

Order Theropoda Marsh 1881

Cf. *Dromaeosaurus*

Occurrence: Phu Phan Thong (Nong Bua Lamphu Province).

Material: 32 fragmentary teeth and one complete crown (PPT 16) (n=33) (Figure 4.26).

Description

All materials found from Phu Phan Thong are very small teeth, not more than 8 mm height. The complete one is 8 mm in height with a basal length of about 5 mm labio-lingually. The crown is strongly curved distally and compressed labio-lingually with well-developed mesial and distal serrated carinae. The serration are oriented perpendicular of the carinae. The serrated anterior carina originates from the upper half of the crown and reaches to the apex whereas the serrated posterior one starts from the base to the top of the crown. No root has been preserved.

Discussion

General morphology of these teeth is quite similar to *Dromaeosaurus* morphotype A from the late Cretaceous (Campanian) of Canada (Sankey *et al,* 2002). They have the same size and the same development of the serration on the mesial and distal side, although Phu Phan Thong specimens are more recurved distally than the specimens from Canada. These teeth are also quite similar to the Dromaeosauridae teeth from the late Jurassic of France (Vullo *et al.,* 2014). They share a D-shaped cross-section and well-developed serration. However, it is difficult to identify these teeth to species level with only few complete specimens in hand.

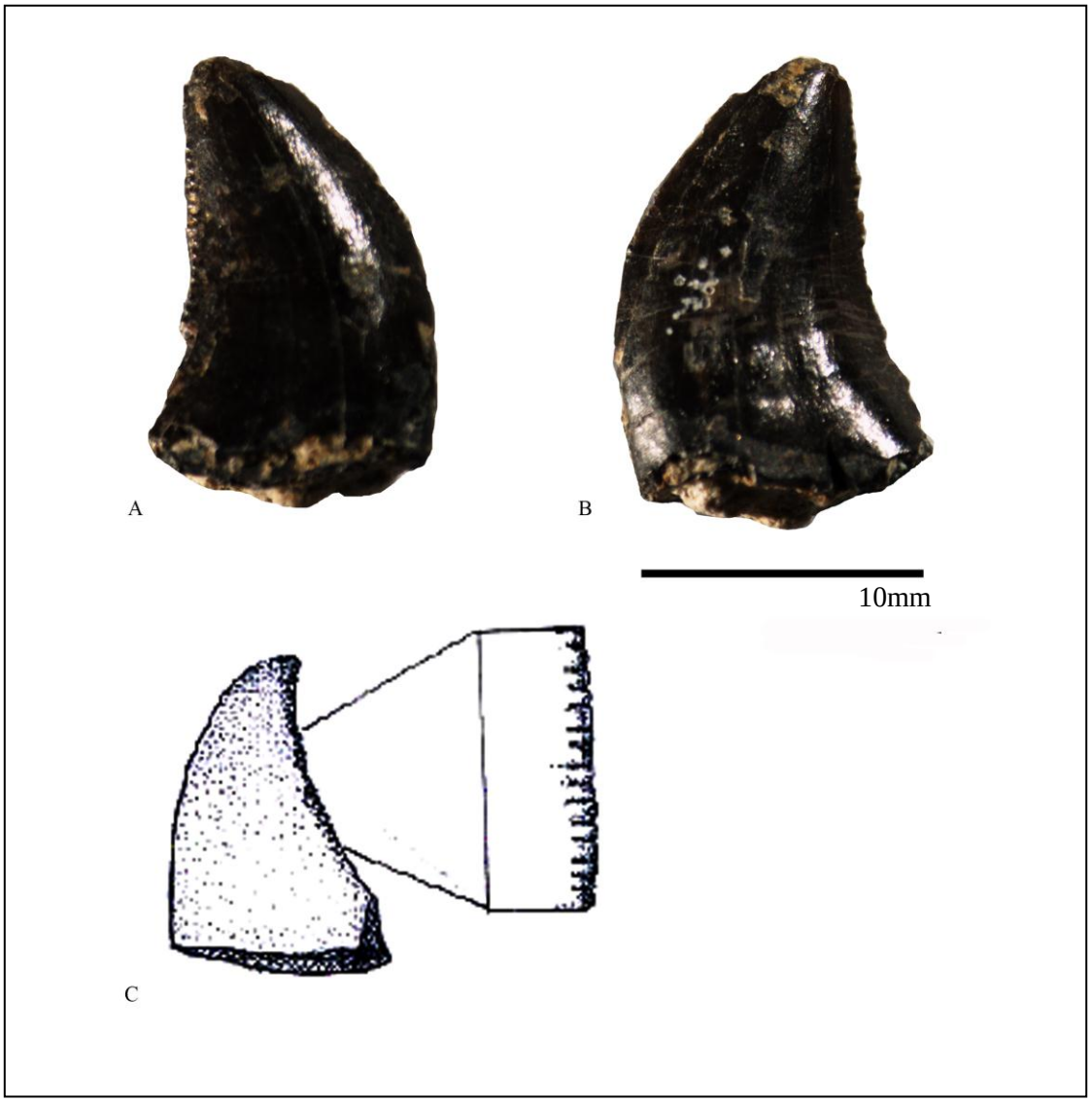


Figure 4.26 Cf. *Dromaeosaurus* (PPT 16) in A-B: labial or lingual views and C: details of distal serration. Scale bare 10 mm

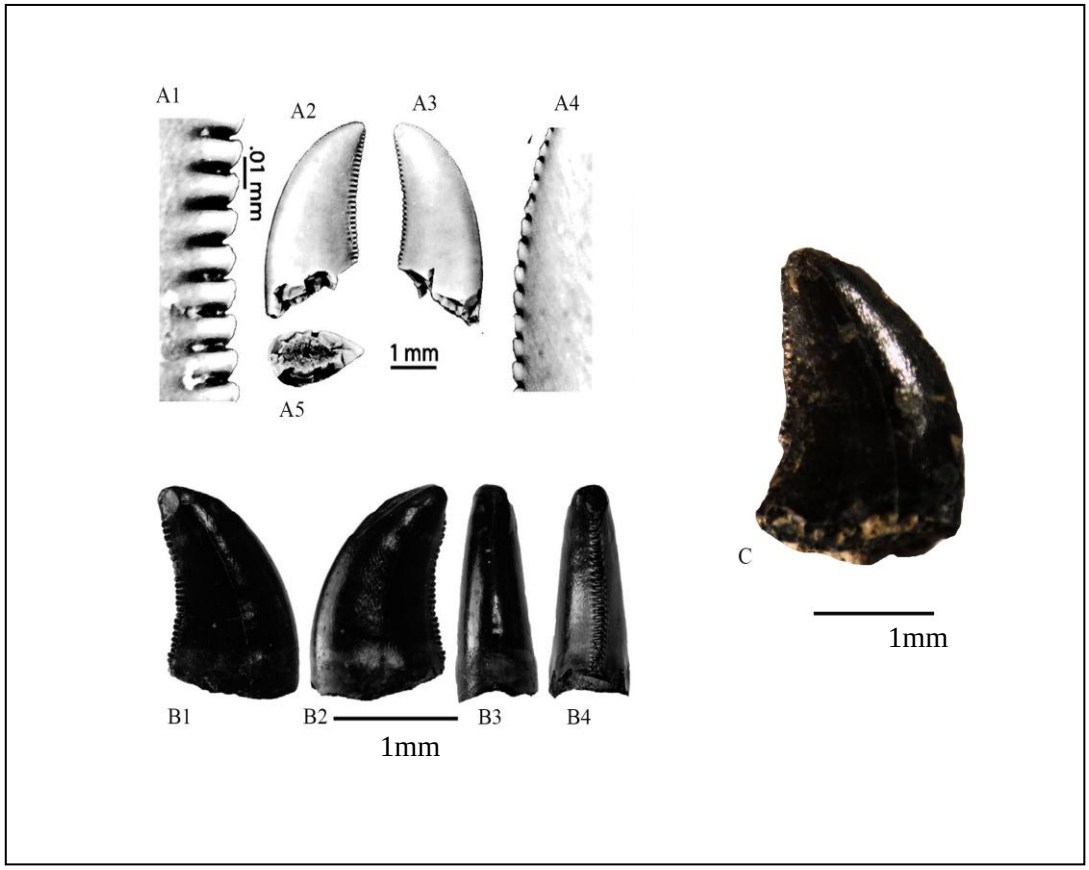


Figure 4.27 Dromaeosauridae teeth. A1-A5 *Dromaeosaurus* morphotype A from the late Cretaceous (Campanian) of Canada (Sankey *et al.*, 2002). (A1) detail of serration in distal, (A2, A3) labiolingual, (A4) mesial views and (A5) D-shaped cross section tooth, scale bar 1 mm. B1-B4 the Dromaeosauridae tooth from the late Jurassic of France (Vullo *et al.*, 2014). (B1, B2) labiolingual, (B3) mesial and (B4) distal views and (C:) Cf *Dromaeosaurus* from Phu Phan Thong, scale bar 1 mm

4.2 Diversity of vertebrate microremains from Phu Phan Thong in comparison with other sites from the Sao Khua Formation

Diversity of vertebrate microremains from Phu Phan Thong and other three localities from the Sao Khua Formations were compared (Table 4.3) i.e., Phu Phok (Sakon Nakhon Province), Phu Wiang (Khon Kean Province) and Nong Sung (Mukdahan Province). Isolated teeth of nine hybodont species were described from the Sao Khua Formation: *Egertonodus* sp., *Hybodus* sp., *Parvodus* sp., *Isanodus paladeji*, *I.*

nongbualamphuensis, Lonchidion khoratensis, Heteroptychodus kokutensis, H. steinmanni and *Mukdahanodus trisivakulii*. Except for the last two taxa, the rest are only found in Phu Phan Tong locality, which shows the highest diversity of hybodont shark faunas when compared with Phu Phok, Phu wiang and Nong Sung (Sao Khua Formation). This high diversity could be due to a wide range of diets. *Parvodus* sp. was probably an opportunistic feeder while the grinding dentition of *Heteroptychodus kokutensis,* indicates more durophagous sharks. *Isanodus paladeji* and *I. nongbualamphuensis* with a clutching-grinding dentition represents another type of durophagous shark. *Egertonodus* sp. and *Hybodus* sp. probably fed on softer prey. Three bony fish taxa are known in all the above localities of the Sao Khua Formation. All localities have yielded a button-shaped crushing teeth referable to a ginglymodian while softer prey feeder like *Siamamia* were found in three localities; Phu Phok, Phu Phan Thong and Nong Sung whereas *Caturus* sp., Cf. *Anomoeodus,* Cf. *Gyrodus, Ionocopus* sp, Cf. *Thaiichthys* and *I. lertboesi* (?) were found only in Phu Phan Thong locality. It seem likely that ginglymodians were the most common and widely distributed fish in the of Sao Khua whereas *Caturus* sp., Cf. *Anomoeodus*, Cf. *Gyrodus, Ionocopus* sp., Cf. *Thaiichthys* and *I. lertboesi* (?) were limited in both distribution and abundance. Although it is very doubtedly to identify the genus and species level of bony fishes on the basis of isolated teeth, these aquatic faunas represented an important and diverse component of the freshwater ecosystems of the Sao Khua Formation.

The materials from Phu Phan Thong showed numerous microremains with high diversity of hybodonts and bony fishes. On the contrary, semi-aquatic faunas (tuetles, crocodiles) and terrestrial faunas (dinosaur) showed less diversity than other localities of the Sao Khua Formation. The abundance of hybodonts and bony fishes species probably suggested a perennial aquatic habitat, stable substrate and abundant food resource that are optimum condition for aquatic habitat (Brenchley and Harper, 1998; Cappetta, 1987). All hybodonts and bony fishes were preserved *in situ* while most remains of turtle, crocodile and dinosaur should be transported from other habitats based on the presence of many bone fragments, and disarticulated material. This reason suggested that these assemblages were slightly long way transported under high energy condition.

Table 4.3 Diversity of vertebrate microremains from Phu Phan Thong in comparison with other sites from the Sao Khua Formation

Taxa	Phu Phan Thong	Phu Phok	Phu Wiang	Nong Sung
Sharks				
Egertonodus sp.	x	-	-	x
Hybodus sp. morphotype	x	-	-	-
Heteroptychodus	-	x	x	-
steinmanni	x	-	-	-
H. kokutensis		-	-	-
Parvodus sp.	x	-	-	-
Isanodus paladeji	x	-	-	-
I. nongbualamphuensis	x	-	-	-
Lonchidion khoratensis	x	-	-	x
Mukdahanodus	-	-	-	x
trisivakulii				
Bony fishes	x	x	x	x
Ginglymodi like-teeth	x	x	-	x
Siamamia sp.	x	-	-	-
Cf.*Carturus*	x	-	-	-
Cf. *Anomoeodus*	x	-	-	-
Cf. *Gyrodus*	x	-	-	-
Ionocopus sp.	x	-	-	-
Cf. *Thaiichthys*	?	-	-	-
I. lertboesi				

Table. 4.3 Diversity of vertebrate microremains from Phu Phan Thong in comparison with other sites from the Sao Khua Formation (continue)

Taxa	Phu Phan Thong	Phu Phok	Phu Wiang	Nong Sung
Turtle				
Isanemys srisuki	-	x	-	-
Plate, bone fragment	x	x	x	x
Crocodiles			x	-
Goniopholis	-	-	-	-
phuwiangensis	-	x	x	x
Siamosuchus	-	x	x	x
phuphokensis				
Theriosuchus grandinaris	-	-	-	-
Teeth, bone fragments	x	x	x	x
Dinosaurs				
Phuwiangosaurus	-	-	x	-
sirindhornae	-	x	x	-
Siamosaurus suteethorni	-	x	x	x
Siamotyrannus isanensis	-	-	-	-
Cf. *Dromaeosaurus*	x	-	-	-

Table 4.4 List of fossil faunas from the Late Jurassic to Early Cretaceous of Thailand

Taxon	**Khlong Min Formation**	**Phu Kradung Formation**	**Sao Khua Formation**	**Khok Kruat Formation**
Hybodont Sharks				
Family *incertae sedis*	-	*Heteroptychodus kokutensis*	*H. kokutensis*	-
			H. steinmanni	*H. steinmanni*
Thaiodontidae	-	-	-	*Thaiodus ruchae*
	-	-	-	*Khoratodus foreyi*
Family *incertae sedis*	-	-	*Mukdahanodus trisivakulii*	-
	-	-	-	*Acrorhizodus khoratensis*
Bony fishes				
Lepisosteiformes	-	*Thaichthys*	-	-
	-	*buddhabutrensis*		
	-	Cf. *Thaichthys*	Cf. *Thaichthys*	-
	-	*Isanichthys palustris*	-	-
	-	*I. lertboesi*	*I. lertboesi*(?)	-
	-	*Khratichthy gibbus*	-	-
Sarcopterigii	*Ferganoceratodus martini*	*Ferganoceratodus martini*	-	-
	-	Ptycholepis	-	-
Caturidae	Cf. Caturus	-	Cf. Caturus	-
Ginglymodi	-	Ginglymodi sp. A	-	-
	Ginglymodi teeth	Ginglymodi teeth	Ginglymodi teeth	Ginglymodi teeth
Ionosopidae	-	-	*Ionoscopus* sp.	-
Ptycnodontiformes	Cf. *Gyrodus*	-	Cf. *Gyrodus*	-
	-	-	Cf. *Anomoedus*	-
	-	Ptycnodontiformes *fam.*indet	Ptycnodontiformes *fam.*indet	-
Sinamiidae	-	-	*Siamamia naga*	-
Semionotiformes	Scales, vertebrae	Scales, vertebrae	Scales, vertebrae	Scales, vertebrae

Table 4.4 List of fossil faunas from the Late Jurassic to Early Cretaceous of Thailand (continue)

Taxon	**Khlong Min Formation**	**Phu Kradung Formation**	**Sao Khua Formation**	**Khok Kruat Formation**
Turtles				
Chengyuchlydae	-	Chengyuchlydae	-	-
Trionychidae	-	*Basilochelys macrobios*	*Kizylkumemys khoratensis*	*K. khoratensis*
Carettochelydae	-	-	Carettochelydae	-
Adocidae	-	-	*Isanemys srisuki*	-
	-	-	-	*Shachemys* sp.
Xinjingchelyidae	-	*Phmoichelys trirakhupti*	-	-
Crocodiles				
Pholidosauridae	-	*Chalawan thailandicus*	-	-
Goniopholididar	-	-	*"Goniopholis" Phuwiangensis*	-
	Goniopholis indet	-	-	*Goniopholis* sp
Atoposauridae	-	-	*Theriosuchus grandinaris*	-
	-	Atoposauridae	-	-
Neosuchia	-	-	-	*Khoratosuchus jintasakuli*
Teleosauridae	*?Peipisuchus*	*?Peipisuchus*	-	-
Dinosaur				
Nemegtosauridae	-	-	*Phuwiangosaurus sirindhornae*	*Phuwiangosaurus sirindhornae*
	-	-	-	Nemegtosaurid
Spinosauridae	-	-	*Siamosaurus suteethorni*	*Siamosaurus suteethorni*
Metriacanthosauridae	-	-	*Siamotyrannus isanensis*	-
Stegosauridae	-	-	-	*Psittacosaurus sattayaraki*
	-	Stegosaurus	-	-
Theropoda	Theropod	Theropod	Cf.*Dromaeosaurus*	Theropod

Table 4.4 List of fossil faunas from the Late Jurassic to Early Cretaceous of Thailand (continue)

Taxon	**Khlong Min Formation**	**Phu Kradung Formation**	**Sao Khua Formation**	**Khok Kruat Formation**
Dinosaurs				
Euhelipodidae	-	Euhelipodidae	-	-
Iguanadontidae	-	-	-	Iguanadontid
Ornithopoda	-	Ornithopoda	-	-
Mamenchisauridae	-	*Mamenchisaurus* sp.	-	-

4.3 Comparison vertebrate fossil faunas from the Late Jurassic to Early Cretaceous

In the term of aquatic habitat, eight species of hybodont sharks were found from the Khlong Min and Phu Kradung Formations (?Late Jurassic) while fourteen species were found in the Sao Khua and Khok Kruat Formations (Early Cretaceous). Obviously, numbers of species diversity of hybodonts rose up from the Late Jurassic to early Cretaceous as well as numbers of endemic species. Only one taxon (*Acrodus Kalasinensis*) was found in the Phu Kradung Formation while five endemic taxa (*Isanodus paladeji*, *I. nongbualamphuensis*, *Lonchidion khoratensis*, *Heteroptychodus kokutensis* and *Mukdahanodus trisivakulii*.) was only found in the Sao Khua Formation and four endemic taxa (*Hybodus aequitridentatus, Thaiodus ruchae, Khoratodus foreyi* and *Acrorhizodus khoratensis*) was only found in the Khok Kruat Formation.

Comparing among the Phu Kradung, Sao Khua and Khok Kruat Formations, the highest diversity of hybodont sharks appeared during the Sao Khua Formation (9 taxa) where those of the Phu Kradung and Khok Kruat Formations were 7 taxa and 5 taxa, respectively. Obviously, the diversity of hybodont sharks somewhat steady during the Phu Kradung –Sao Khua Formations and swiftly decreased in the Khok Kruat Formation with disappearance of a huge interesting family, Lonchidiidae. This family appeared in Thailand in the Late Jurassic Khlong Min Formation and found until the Early Cretaceous Sao Khua Formations and then wiped out in the Khok Kruat Formation. Palaeoenvironments during the Phu Kradung–Sao Khua Formations seemed appropriate for surviving of freshwater hybodont sharks, especially the family Lonchidiidae. After that all Lonchidiids were replaced by specialized endemic hybodont sharks, that is, *Hybodus aequitridentatus*, *Thaiodus ruchae*, *Khoratodus foreyi* and *Acrorhizodus khoratensis* in the Khok Kruat Formation. Similar phenomenon of endemic fauna replacement had been observed in the Early Cretaceous of South America and Africa where endemic hybodont sharks were found in freshwater or shallow coastal water (Cuny *et a*l., 2014). The presence of endemic hybodont sharks and the absence of widely distribute hybodont sharks as the family Lonchidiidae during the Khok Kruat Formation may suggest a lack of connection between Europe and Southeast Asia during the Early Cretaceous (Cuny *et a*l., 2008), which resulted in

overlapped niches and high competitions of Thai hybodont sharks during the gap between the Sao Khua–Khok Kruat Formations.

The highest diversity of bony fishes was observed in the Phu Kradung Formation (10 taxa) while those of the Sao Khua and Khok Kruat formation were 9 taxa and 2 taxa, respectively. The data presented here are strongly affected by specimen biases. Actually, numerous disarticulated remains of bony fishes such as isolated teeth, scales and vertebrae were also found in the Sao Khua and Khok Kruat Formations. However, it is quite uncertainty to identify of bony fishes based on these microremains whereas hybodont sharks can be identified their status on the basis of isolated teeth and cephalic spines. At present, several complete bony fish were observed and identified in the Phu Kradung Formation (Cavin and Suteetorn, 2006; Cavin *et al*., 2009; Deesri *et al*., 2014; Deesri *et al*., 2016). The climate changes during the Late Jurassic to Early Cretaceous probably increased dry areas and decreased wet areas in the Khorat Plateau (Meesook, 2002). Consequently, habitat fragmentation and/ or loss could be the reason to explain why diversity of aquatic faunas during the Late Jurassic to Early Cretaceous in the Khorat Group was declined (Table 4.4).

Cappetta (2012) reported that, at the present, at least thirteen genera of hybodonts were described from the Triassic, twelve genera from the Jurassic and twenty five genera from the Cretaceous. The results of this study show that Thailand also yields a diverse fauna of freshwater hybodont sharks. The Khlong Min and Phu Kradung Formations yielded 41.6% of the Jurassic hybodont sharks whereas the Sao Khua and Khok Kruat Formations yielded 40% of the Cretaceous hybodont sharks. Base on this evidence can be made in the succession of hybodonts within the Late Jurassic- Early Cretaceous.

CHAPTER 5

STRATIGRAPHIC CORRELATION OF PHU PHAN THONG WITH OTHER FOSSIL LOCALITIES OF THE SAO KHUA FORMATION

Three fossil localities from the Sao Khua Formation were studied in order to correlate them with Phu Phan Thong, i.e., Huai Lao Yang (Nong Bua Lamphu Province), Phu Pratu Tee Ma and Phu Noi, which are situated in Phu Wiang district (Khon Kaen Province) (Figure 5.1). These three localities were chosen for comparison with Phu Phan Thong because Huai Lao Yang locality is close to the contact with the Phra Wihan Formation like Phu Phan Thong locality. On the other hand, Phu Pratu Tee Ma and Phu Noi localities are closer to the contact with the Phu Phan Formation. Therefore, they can be used as representatives of the upper Sao Khua Formation.

5.1 Geological Setting of Phu Phan Thong Locality

Phu Phan Thong hill is situated on road 210 between Udon Thani and Nong Bua Lamphu. Based on its lithology this locality was interpreted as belonging to the Sao Khua Formation (Chonglakmani *et al.*, 1985; Meesook, 2000). It is close to Huai Lao Yang Locality, which is about 1 km north to Phu Phan Thong (Figure 5.1). Both sequences are near the boundary between the lowermost horizon of the Sao Khua Formation and the uppermost horizon of the underlying Phra Wihan Formation. The lithology of Phu Phan Thong were studied and compared with other sites of the Sao Khua Formation (Phu Pratu Tee Ma and Phu Noi).

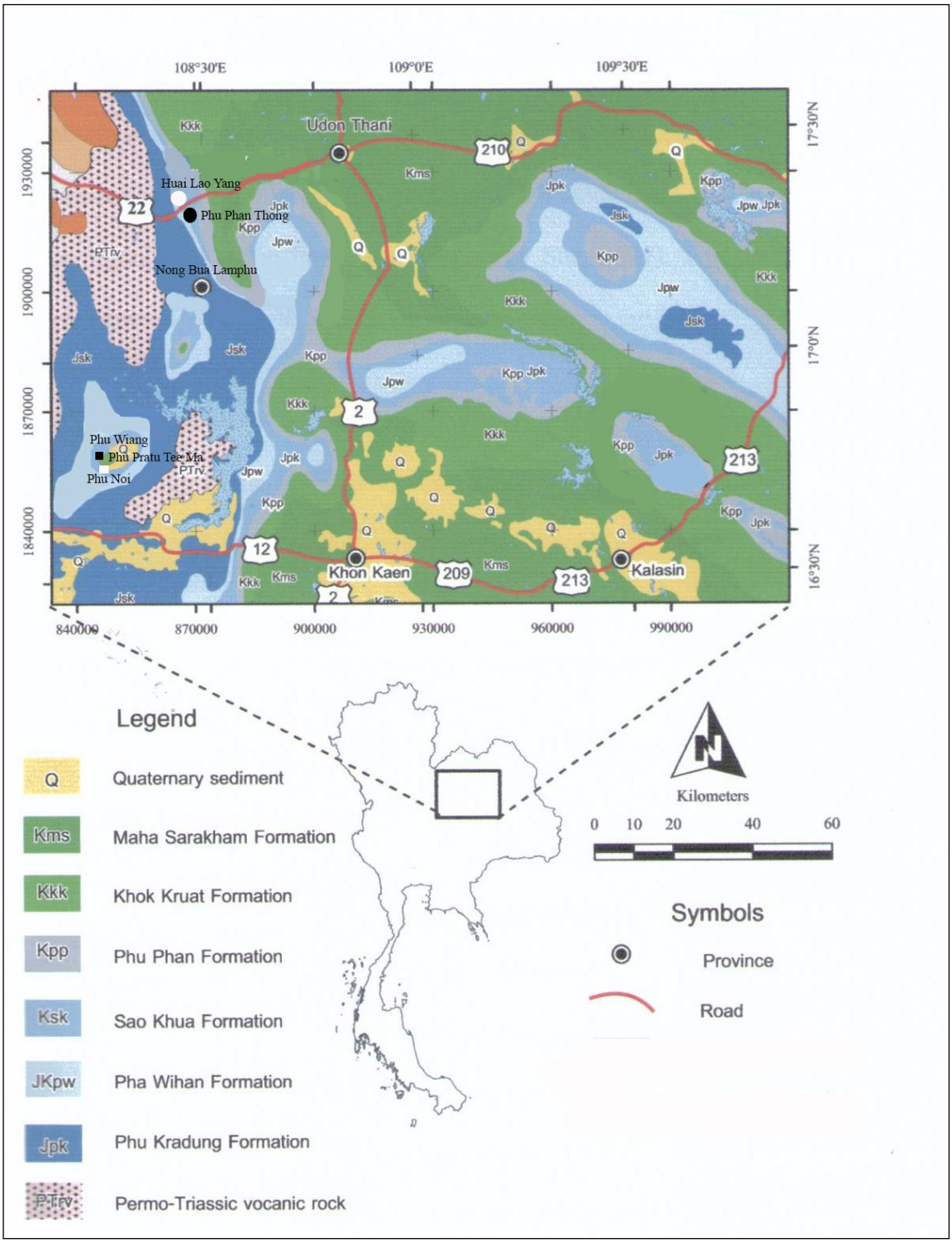


Figure 5.1 Geological Map of study localities, black circle (●) is Phu Phan Thong, white circle (◯) is Huai Lao Yang, black square (■) is Phu Pratu Tee Ma and white square (□) is Phu Noi localities (Modified from Tumpeesuwan, 2010)

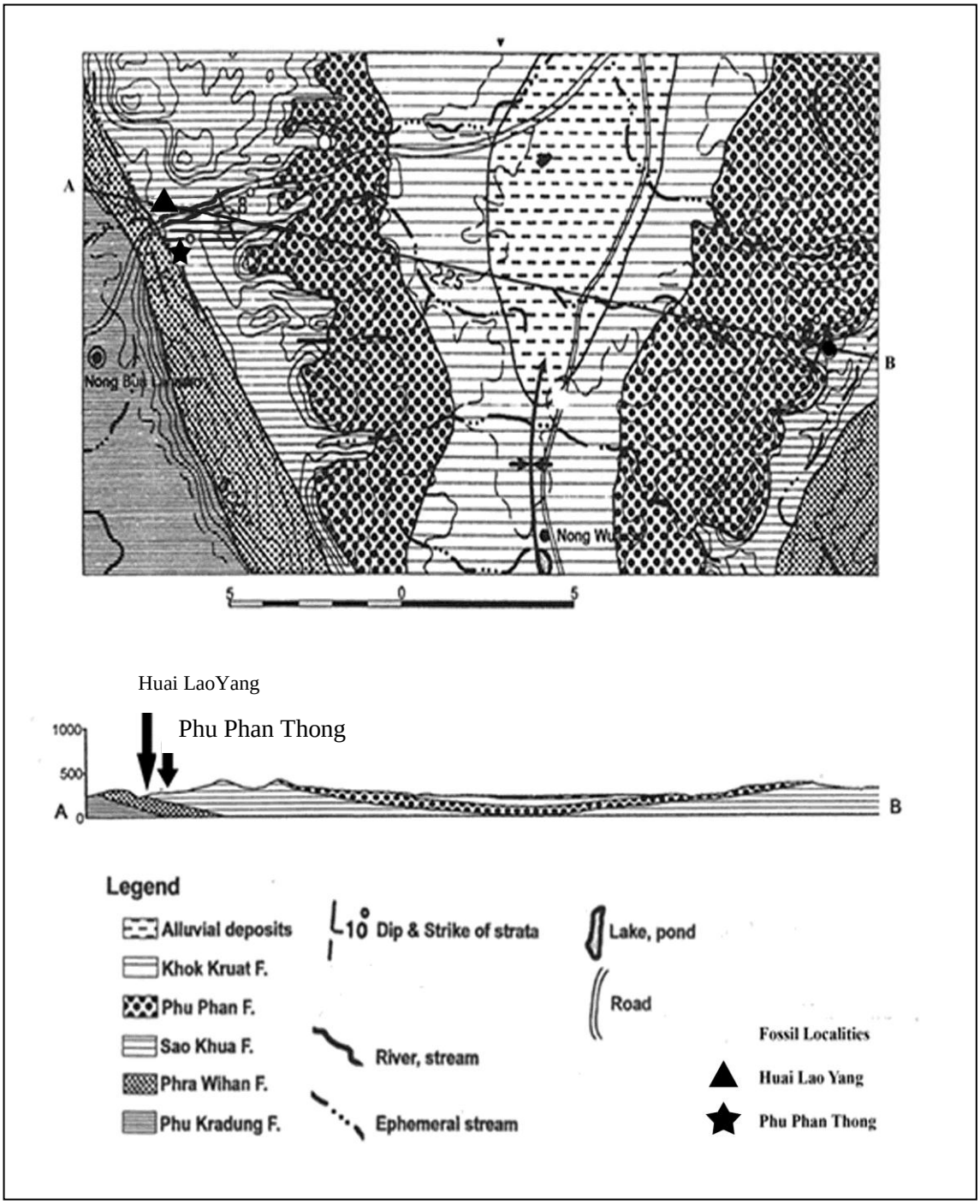


Figure 5.2 Geological map with a geological section of Phu Phan Thong (★black star) and Huai Lao Yang Localities (▲black triangle), Nong Bua Lamphu Province (Modified from Tumpeesuwan, 2010).

5.2 Stratigraphy of fossil excavation sites in the Sao Khua Formation

5.2.1 Phu Phan Thong Locality, Nong Bua Lamphu Province (study site)

UTM coordinates: 238031E 1889913N UTM Zone 48Q

Topographic Map: Map sheet 5443 II CHANGWAT NONG BUA LAMPHU

Location: Phu Phan Thong hill, Ban Phu Phan Thong

Accessibility: road 210 between Udon Thani and Nong Bua Lamphu

Stratigraphy: The columnar section was studied, taken at an outcrop along road 210 (Figure 5.3), has a total thickness of nearly 10 m. The lowermost part of this section contacts with the massive sandstone of the Phra Wihan Formation. The lowest layer of Phu Phan Thong is approximately 1.2 m in thickness. It is made of light grey, very fine-grained siltstone. The overlying bed is a shell bed in very fine-grained sandstone about 1 m in thickness, followed by a 0.8 m thick layer of mudstone changing upward to greyish-red and calcareous siltstone,. The next layer is a 3 m thick sandstone bed with medium sized grains, greyish-red in colour. Then, it is covered by a light grey, calcareous sandstone layer, and conglomeratic sandstone with abundant vertebrate microremains, about 2 m thick. The uppermost part of this section consists of yellowish-grey sandstone, fine to medium-grained containing some clasts, approximately 2 m thick (Figure 5.4). All fossils from this locality are fragmented. It means that they were transported under high energy flow and deposited in a low energy area.

Fossil content

Hybodont sharks: *Hybodus* sp. morphotype 4 (PRC-PT 435, PPT78), *Egertonodus* sp. (PRC-PT2, 75), *Heteroptychodus kokutensis* (PRC-PT55, PPT98), *Parvodus* sp.(PRC-PT223, PPT19), *Isanodus paladeji* (PRC-PT 241-243), *Isanodus nongbualamphuensis* (PRC-PT 246-248), *Lonchidion khoratensis* (PRC-PT294,PPT12), (Cuny *et al.*, 2007, 2006 and Khamha *et al.*, 2015)

Bony fish: Ginglymodi indet. (PPT120-138), Pycnodontiformes (PRC-130-135, PPT22), Cf. *Caturus* sp. (PPT61-67) and fragmented scales (PRC-PT725-768), (Cuny *et al.*, 2007, 2006: Deesri *et al*., 2014; 2013)

Turtle: fragmented plates (PRC-PT 133-195)

Crocodile: Goniopholididae teeth (PRC-PT 1194-1196)

Dinosaur: Dromaeosaurinae (PPT 16, Khamha *et at*., 2015)

Pollen: *Dicheiropllis etruscus*, *Cicatricosisporite* sp., *Corollina* sp., *Concavissimisporites punctatus* (Racey *et al.*, 2009)

Bivalves: *Koreanaia (Eokoreanaia)* sp., *Yunnanoconcha* sp., *Sinonaia* sp. and *Nakamuraria* sp. (Tumpeesuwan, 2010)

Figure 5.3 Outcrop of Phu Phan Thong locality showing the fossil bed (black lines are boundaries between fossil bed abd underlying beds), Nong Bua Lamphu Province, during the improvement work of road 210 in year 2003, where approximately 10 tonnes of sediments were sampled for screen-washing at Sirindhorn Museum, Kalasin Province

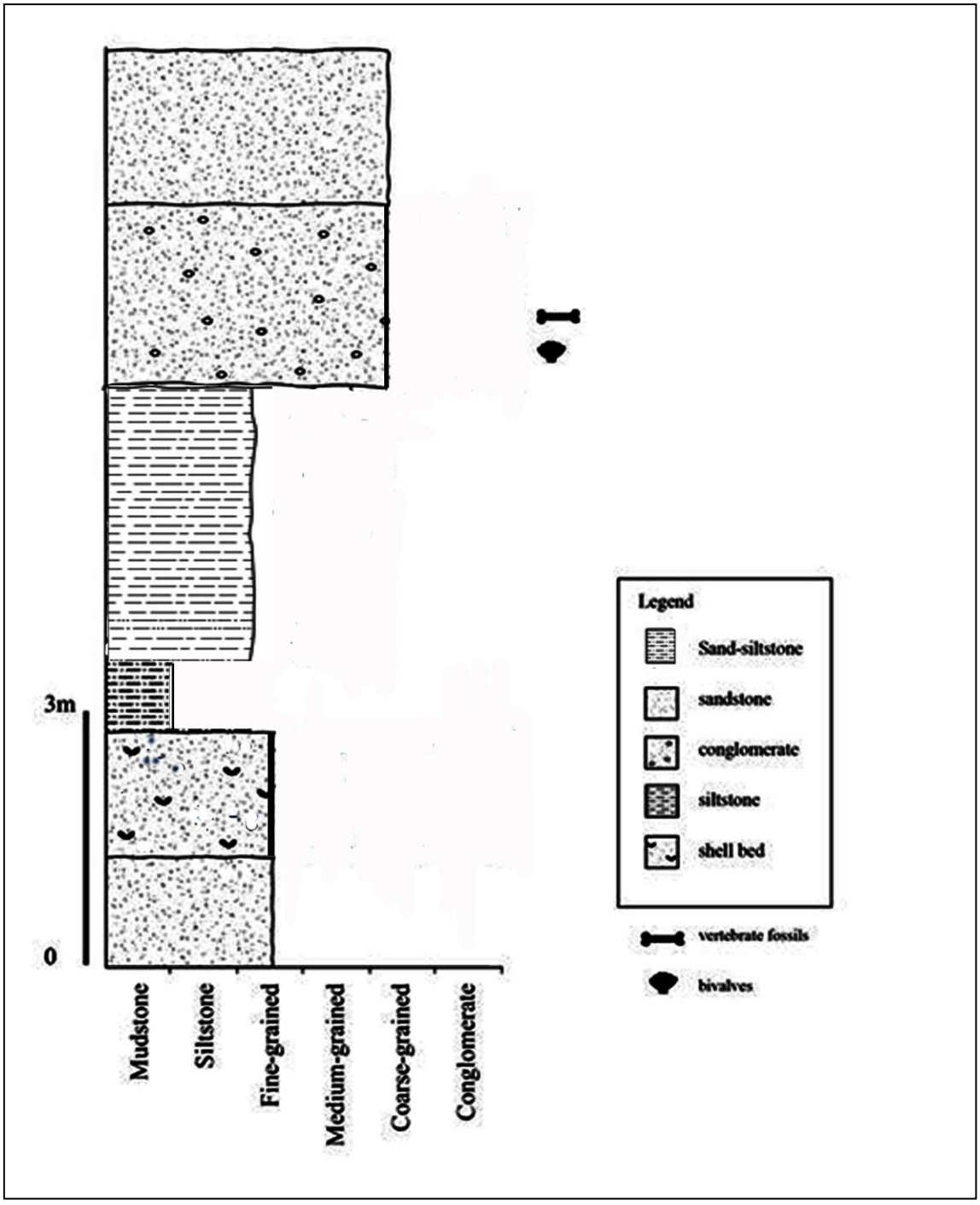


Figure 5.4 Lithologic columnar section of Phu Phan Thong, Nong Bua Lamphu Province.

5.2.2 Huai Lao Yang Locality

UTM coordinates: 224602E 1891955N UTM Zone 48Q**.**

Topographic Map: Map sheet 5443 II CHANGWAT NONG BUA LAMPHU**.**

Location: Soil pit near Huai Lao Yang Water station.

Acessibility: From Nong Bua Lamphu, between km 82 and km 83 of road 210 before to reach Ban Phu Phan Thong (Figure 5.5). The locality is about 0.5 km from Ban Phu Phan Thong.

Lithology: The lowest layer of Huai Lao Yang is made of a siltstone approximately 0.5 m in thickness. The overlying layer is a shell bed. It is 0.6 m in thickness and consists of red brown mudstone-silstone with numerous internal molds of bivalve, followed by a laminated, very fine to medium-grained sandstone with numerous burrows, which is about 0.2 m thick. Then, it is covered by a 4.8 m thick red brown mudstone-silstone. The top bed is 0.2 m thick of medium-grained sandstone with mud pebbles (Tumpeesuwan, 2010) (Figure 5.6).

Fossils content:

Hybodont sharks*: Hybodus* sp. (PRC-HLY 6-8, 25,176) *Heteroptychodus kokutensis* (PRC-HLY 179, 276)

Bony fish: scales and fragmented bone (PRC-HLY 277-312)

Pterosaur: teeth (PRC-HLY 783-788)

Turtle: fragmented plates (PRC-HLY 1003-1220)

Dinosaur: theropod teeth (PRC-HLY 769-782)

Trace fossils: coprolites (PRC-HLY 789-831)

Bivalves: *Koreanaia (Eokoreanaia)* sp., *Yunnanoconcha* sp., *Sinomania* sp. and *Nakamuraria* sp. (Tumpeesuwan, 2010)

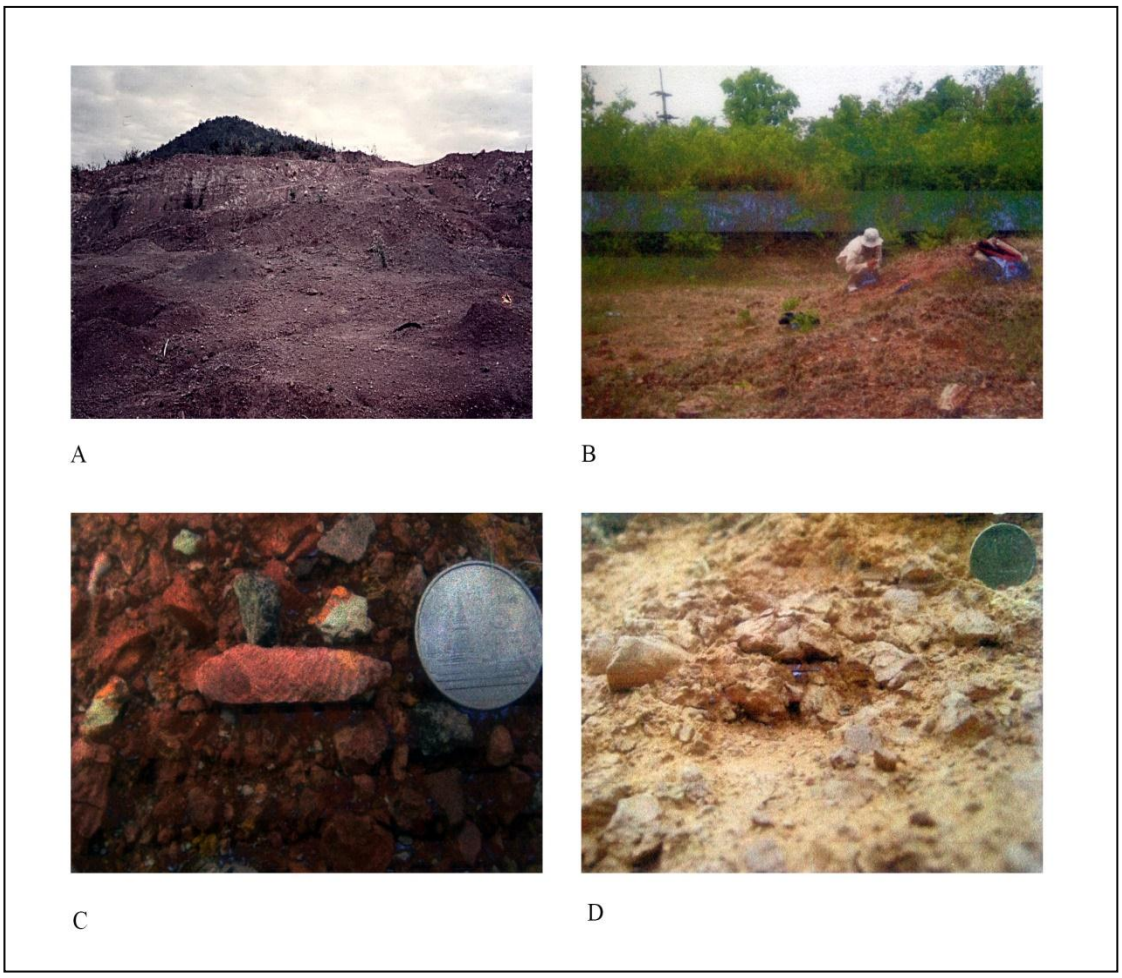


Figure 5.5 Huai LaoYang locality, Nong Bua Lamphu Province. A; Outcrop of Huai Lao Yang (1990) during the collection of specimens (photograph by Paladej Srisuk); B, C and D: Outcrop of Huai Lao Yang shell bed on the red mudstone-siltstone surface (Photograph from Tumpeesuwan, 2010)

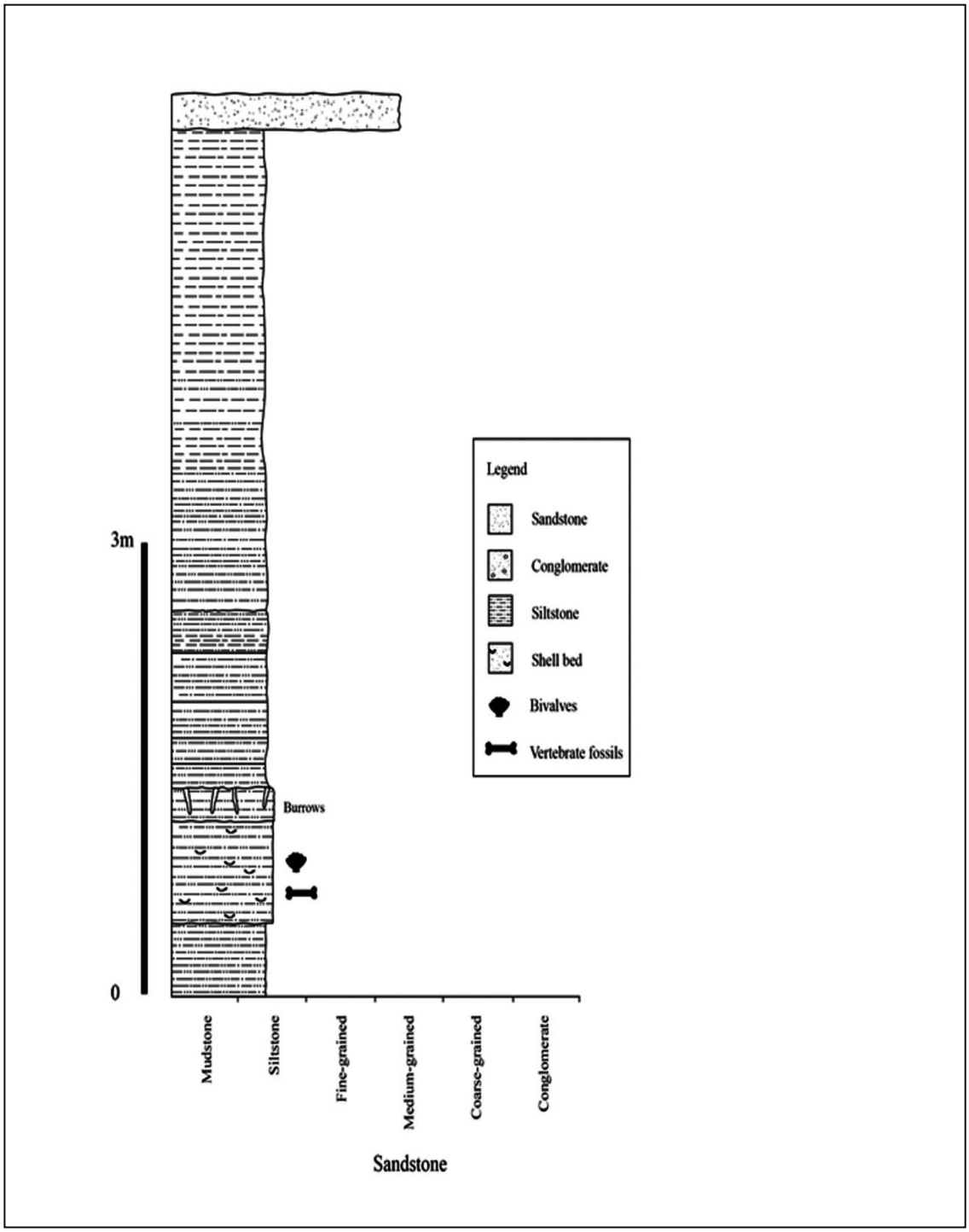


Figure 5.6 Lithologic columnar section of Huai Lao Yang, Nong Bua Lamphu Province (Modified from Tumpeesuwan, 2010)

5.2.3 Phu Noi Locality (Phu Wiang District, Khon Kaen Province)

UTM coordinates: 204068E 1842249N UTM Zone 48Q

Topographic Map: Map sheet 5442 II AMPHOE PHU WIANG

Location: Phu Noi, (Phu Wiang district) (Figure 5.7)

Accessibility: At Ban Muang Kao, take the road to Huai Bong Weir and walk across Huai Bong to the locality. Section was made at an outcrop exposed from the southern foot to the top of Phu Noi hill. Thickness of the section is about 30 m. (Figure 5.10)

Lithology and sedimentary structure: The section exposes 4 cycles of fining-upward sequence; the lowest cycle is a 2 m thick alternation of fine-, very-fine and medium fine grained sandstone with bivalve fossils. It is overlaid by a 18.5 m thick laminated fine-grained sandstone and siltstone beds, some beds of which contain burrows. The third cycle starts with 0.4 m of conglomerate is sandstone bed with bivalve fossils and hybodont teeth and lime nodules. This shell bed is overlaid by a 3 m thick fine-grained, cross-bedded sandstone. The second cycle is a shell bed. It is made of mud-nodules and siltstone. The last cycle is made of 0.2 m mud-nodule conglomerate. Then it is overlaid by 0.3 m of medium-grained, cross-bedded sandstone and 1.5 m of red siltstone. The top of the section is approximately made of 3 m of cross-bedded conglomerate and chert pebbles of the Phu Phan Formation (Figure 5.11) (Tumpeesuwan, 2010).

Fossils content:

Bivalves: *Pseudohyria (Matsumotoina) somanai, Nippononaia* sp. cf. *N. mekongensis* and *Trigonioides (Diversitrigonioides)* sp. cf. *T (D.) diversicostatus* (Tumpeesuwan *et al.,* 2010)

Hybodont sharks: *Heteroptychodus steinmanni* (Tumpeesuwan *et al.,* 2010)

A

B

Figure 5.7 (A) Upper shell bed of Phu Noi (Pw-M-5/2); (B) Cross bedded conglomerate of Phu Phan Formation on the top hill (black line) (Photograph from Tumpeesuwan, 2010)

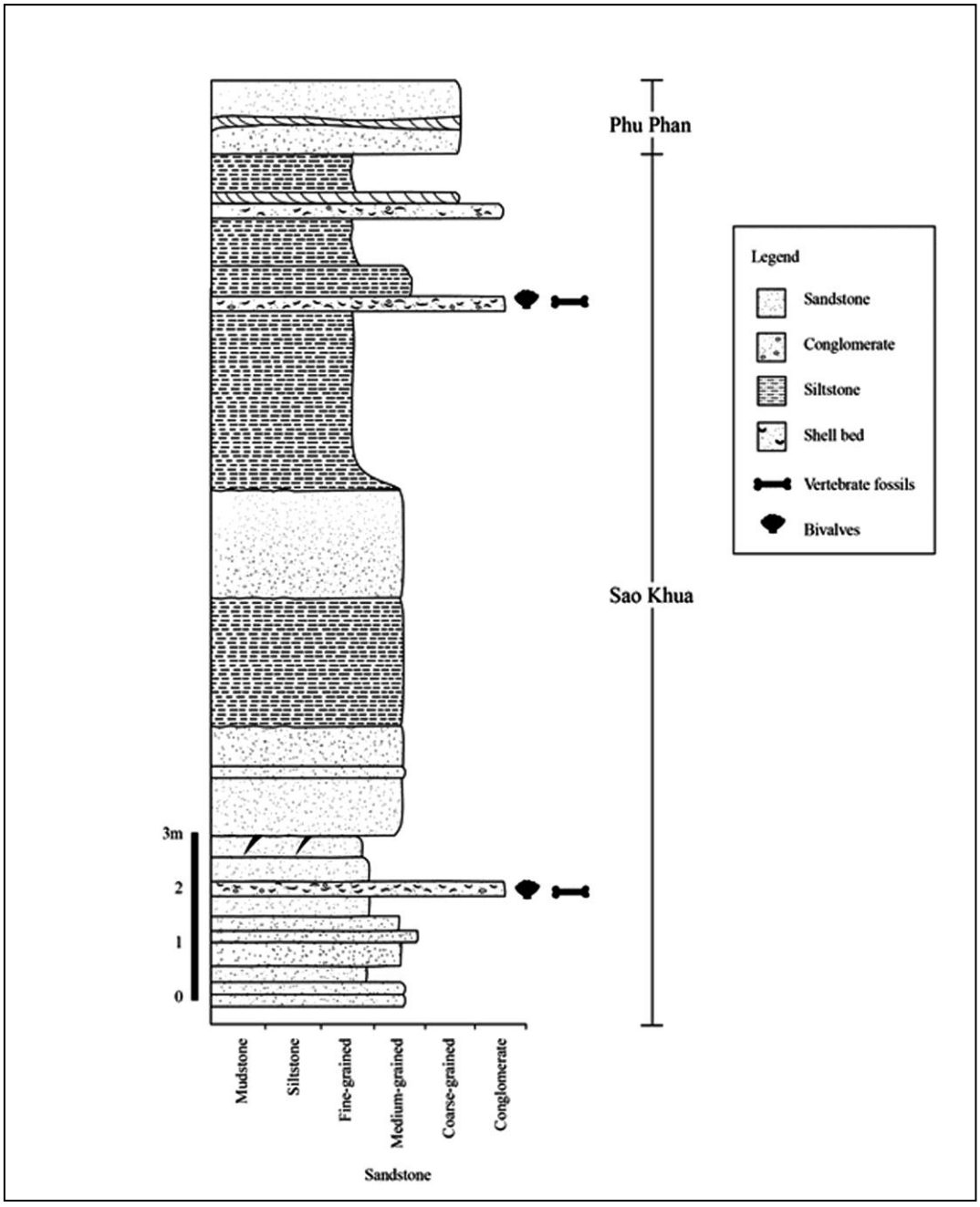


Figure 5.8 Lithologic columnar section of Phu Noi, Phu Wiang, Khon Kaen Province (Modified from Tumpeesuwan, 2010)

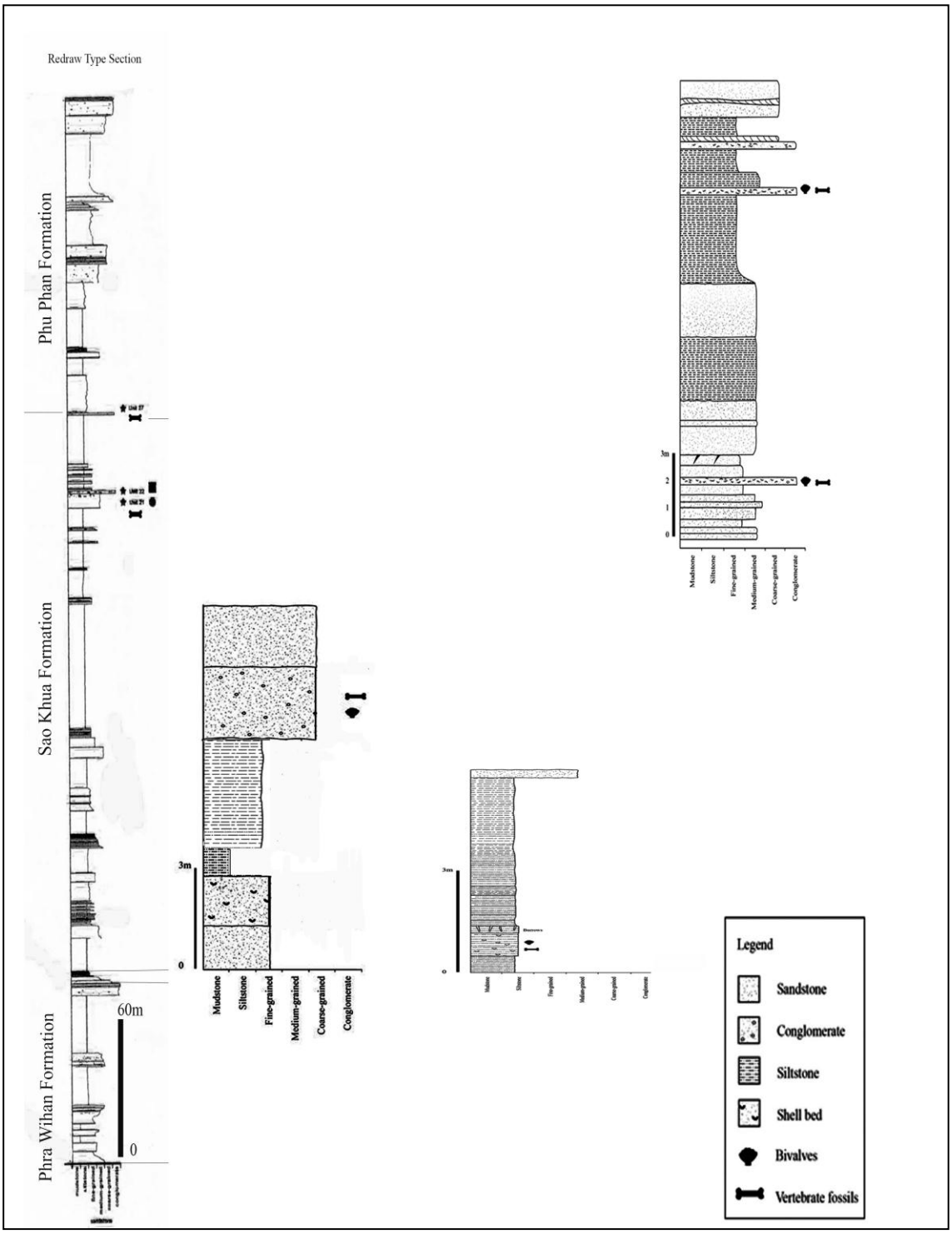


Figure 5.9 Lithologic columnar sections of four fossiliferous sites (Phu Phan Thong and Huai Lao Yang, Nong Bua Lamphu Province, Phu Pratu Tee Ma and Phu Noi, Phu Wiang, Khon Kaen Province) of the Sao Khua Formation and their relative position in the formation (Modified from Tumpeesuwan, 2010)

5.3 Stratigraphic correlation of Phu Phan Thong Locality in the Sao Khua Formation

Lithologic columnar sections of Phu Phan Thong, Huai LaoYang and Phu Noi localities were correlated to each other. According to this field observation, Phu Phan Thong is located nearby to the type section of the Sao Khua Formation (Huai Sao Khua), which is situated at Km 35.2-41.5 of highway 210 between Udon Thani and Nong Bua Lamphu province. Based on a stratigraphic survey, this study showed that the Phu Phan Thong section is in contact with the massive sandstone of the uppermost horizon of the Phra Wihan Formation. Ward and Bunnag (1964) mentioned flaggy beds of quartzitic sandstone at the base of the Sao Khua Formation type section. This depositional features fit well with our observation at the Phu Phan Thong locality. It is therefore assumed that Phu Phan Thong should belong to the lower part of the Sao Khua Formation (Figure 5.9).

Correlation of Phu Noi shell bed with the type section of the Sao Khua Formation (Fig 5.9) showed that it is in the uppermost horizon of the Sao Khua Formation because it is in contact with the lower part of the Phu Phan Formation. Therefore, it should be concluded that they belong to the upper part of the Sao Khua Formation.

5.4 Biostratigraphic correlation of Phu Phan Thong Locality in the Sao Khua Formation

Fossil assemblages found at Phu Phan Thong locality are diversified when compared with other Sao Khua localities (Table 5-1). Most of the geological ranges of these fossils are wide. However, there are some specimens with a narrower geological range such as pollen, bivalves, hybodont sharks. They are used for correlating the position of this locality.

Table 5.1 Distribution of the different taxa in the Phu Phan Thong, Haui Lao Yang and Phu Noi localities (Racey and Goodall, 2009; Tumpeesuwan, 2010; Cavin *et al.*, 2009; Deesri *et al.*, 2014; 2013; Cuny *et al.*, 2007; 2006; Khamha *et al.*, 2015)

Site	Hybodonts							Pollen				Bivalves				
	Hybodus sp.	*Egertonodus* sp	*Lonchidion* sp	*Parvodus* sp.	*Heteroptychodus steinmani*	*Heteroptychodus kokutensis*	*Isanodus*	*Dicheiropollisetruscus*	*Cicatricosisporites* sp.	*Corollina* sp.	*Concavissimisporites punctatus*	*Koreanaia (Eokoreanaia)*	*Yumnanoconcha*	*Nakamuranaia*	*Sinonaia*	*Pseudohyris (Matsumotoina) somanai*
Phu Phan Thong	X	X	X	X	-	X	X	X	X	X	X	X	X	X	X	-
Huai Lao Yang	X	-	-	-	-	X	-	-	-	-	-	X	X	X	X	-
Phu Noi	-	-	-	-	X	-	-	-	-	-	-	-	-	-		X

5.4.1 Age of some fauna and flora in the Sao Khua Formation

5.4.1.1 Pollen

Racey and Goodall (2009) discovered the pollens *Dicheiropollis etruscus*, *Cicatricosisporites* sp., *Corollina* sp. and *Concavissimisporites punctatus* in Phu Phan Thong locality. *Dicheiropollis etruscus* was found in a Berriasian to Early Barremian interval in West Africa, North and South America, Southern Europe, China and Yemen. *Cicatricosisporites* sp. was found in the Barremian and Aptian of England, North America, Africa and Asia (Kemp, 1970). *Corollina* sp. and *Concavissimisporites* were found throughout the Barremian, Aptian and Albian deposits of England, North America, East Germany, Africa and Asia (Doring, 1964, Brenner, 1963, Kemp, 1970 and Racey and Goodall, 2009). From the evidence of *Dicheiropollis etruscus*, Phu Phan Thong locality was not younger than Early Barremian age.

Table 5.2 Geological range of pollens that have been found from Phu Phan Thong locality

STAGE may	Range of *Dicheiropollis etruscus*	Range of *Cicatricosisporites* sp.	Range of *Corollina* sp.	Range of *Concavissimisporites punctatus*
Maastricchian 66 71				
Campanian 84				
Santonian 86				
Coniacian 90				
Cenomanian 99				
Albian 112				
Aptian 125				
Barremian 130				
Hauterivian 136				
Valanginian 140				
Berriasian 145				

5.4.1.2 Bivalves

Four bivalves taxa , i.e., *Koreanaia (Eokoreanaia)* sp., *Yunnanoconcha* sp., *Nakamurania* sp. and *Sinonaia* sp. were found in Phu Phan Thong and Huai Lao Yang. *Pseudohyria (Matsumotoina) somanai* was only discovered from the lower part of Phu Noi.

Koreanaia (Eokoreanaia) includes two species, i.e., *Koreanaia* (*Eokoreanaia*) *cheongi* (Yang, 1976*) and K (E.) fordi* (Baker *et al.*, 1997). *Koreanaia* (*Eokoreanaia*) has been reported from the Hauterivian, Myogog Formation of the Republic of Korea (Yang, 1976). *K (E.) fordi* were found in the Upper Hauterivian to Barremian of the Wessex Formation in southern England (Baker *et al.,* 1997). This might suggest that *Koreanaia* (*Eokoreanaia*) is restricted to Hauterivian-Barremian (Tumpeesuwan, 2010).

Yunnanoconcha includes two species, i.e., *Yunnanoconcha chuxiongensis* and *Y. khoratensis* (Kobayashi, 1963), which *Y. chuxiongensis* were discovered from the Hauterivian-Barremian Puchanghe Formation of Central Yunnan, Southern China (Ma, 1994; Sha, 2007). *Y. khoratensis* were found in the Aptian Khok Kruat Formation of Thailand (Kobayashi, 1984). Therefore, the stratigraphic range of this genus might be assigned to the Hauterivian-Aptian(Tumpeesuwan, 2010).

Nakamurania was found from the Hauterivian Okuodani Formation, Late Barremian Kitadani Formation, Hauiterivian Myogog Formation (Kozai *et al*., 2005) of Japan (Kozai *et al.,* 2005), the Hauterivian-Barremian Jingxing Formation of western Yunnan, southern China (sha, 2007) Aptian Qingshan Formation, Hauterivian-Barremian Hanyangpu Formation and in the Aptian-Cenomanian Bali Formation in Guangxi, southern China (Sha, 2007). Therefore, the range of this genus is assumed to be Hauterivian-Cenomanian in age (Tumpeesuwan, 2010).

Sinonaia includes two species, i.e., *Sinonaia tenuilonga* (Guo, 1981) and *S. chuxiongensis* (Gu and Ma, 1997). These two species were recorded from the Upper Member of the Jingxing Formation. A Hauterivian-Barremian age was suggested for this formation (Guo, 1984).

Pseudohyria (Matsumotoina) was found in the upper part of the Sao Khua Formation of Thailand. It has been also reported from Late Barremian- Early Aptian Yeonwhadong Formation, Korea (Yang, 1978, 1979; Matsukawa 1983,

Tumpeesuwan , 2010), Hauterivian-Baremian Monomiyama Formation in northeast Japan (Ogasawara, 1988); Barremian Kitadani Formation (Tamura, 1993; Isaji, 1993; Fujita, 1993; Kozai *et al.*, 2005) faunal association which composed of *Nippononaia ryosekiana* and other 5 of Late Barremian brackish water bivalves. This faunal association composed of the Kitadani, Sengoka and Sebayash fauna (Kozai *et al.*, 2005). Therefore, it might be proposed the taxon range of *Pseudohyria (Matsumotoina)* as Late Barremian.

Table 5.3 Stratigraphical range of bivalves that have been found from Phu Phan Thong, Huai Lao Yang, Phu Pratu Tee Ma and Phu Noi localities

STAGE May	Range of *Koreanaia (Eokoreanaia)* sp.	Range of *Yunnanoconcha* sp.	Range of *Nakamurania*	Range of *Sinonaia* sp.	Range of *Pseudohyria (Matsumotoina) somanai*
Maastricchian 66 71					
Campanian 84					
Santonian 86					
Coniacian 90					
Cenomanian 99					
Albian 112					
Aptian 125					
Barremian 130					
Hauterivian 136					
Valanginian 140					
Berriasian 145					

5.4.1.3 Hybodont sharks

Heteroptychodus includes three species, i.e., *Heteroptychodus steinmanni* which was found from the Early Cretaceous of Japan and Thailand (Cuny *et al.*, 2003; 2006; 2007; Cappetta *et al*., 2006). *H. chuvalovi*, which was discovered from the Aptian-Albian of Mongolia (Cuny *et al.*, 2008) and *Heteroptychodus kokutensis* that has been found from the Phu Kradung Formation (the Late Jurassic) (Cuny *et al.*, 2014)

and the lower part of Sao Khua Formation (Hauterivian-Early Barremian, based on pollen and bivalves evidences) (Racey, 2009; Tumpeesuwan, 2010) and Kut Island in Thailand (not older than Berriasian, Cuny *et al.*, 2010).

In Thailand, the oldest assemblage of *Heteroptychodus kokutensis* was found in the Phu Kradung Formation (Late Jurassic) (Cuny *et al.*, 2014). Moreover, *Heteroptychodus steinmanni* first appeared in the upper part of Sao Khua Formation (Late Barremain, based on *Pseudohyria (Matsumotoina) somanai*) (Tumpeesuwan *et al.*, 2010) and also known from the Aptian/Albian Khok Kruat Formation of Thailand and was found from the Early Cretaceous of Japan (Cuny *et al.*, 2003; 2008 and 2006; Tumpeesuwan, 2010; Yabe and Obata, 1930). Therefore, it should be assumed that the stratigraphic range of *Heteroptychodus* is the Late Jurassic to Early-Late Cretaceous (Aptian/Albian).

Table 5.4 Stratigraphical range of the genus *Heteroptychodus*.

STAGE		may	**Range of *Heteroptychodus chuvalovi***	**Range of *Heteroptychodus steinmanni***	**Range of *Heteroptychodus kokutensis***	**Range of *Heteroptychodus***
Late Cretaceous	Maastricchian	66 71				
	Campanian	84				
	Santonian	86				
	Coniacian	90				
	Cenomanian	99				
Early Cretaceous	Albian	112				
	Aptian	125				
	Barremian	130				
	Hauterivian	136				
	Valanginian	140				
	Berriasian	145				
Late Jurassic	Tithonian	152				
	Kimmeridgian	157				
	Oxfordian	163				

Isanodus includes two species, i.e., *Isanodus nongbualamphuensis* and *Isanodus paladeji* (Cuny *et al.,* 2006; Khamha *et al.,* 2015). The members of this genus were found in Thailand and Malaysia (Teng Yu He *et al.,* 2015). *I. nongbualamphuensis* was found only in Phu Phan Thong the lower part of the Sao Khua Formation (Hauterivian-Early Barremian, based on pollen and bivalves evidences) (Racey, 2009; Tumpeesuwan *et al.,* 2010). However, the species *Isanodus paladeji* was found in Phu Phan Thong and Kut Island that is located in the eastern part of the Gulf of Thailand. The finding of this genus in Kut Island would favour an age similar to that of the Sao Khua Formation, not older than Berriasian (Cuny *et al.,* 2010, Racey and Goodall, 2009). This study assumed that the stratigraphic range of *Isanodus* is the Berriasian-Early Barremian in age.

Table 5.5 Stratigraphical range of the genus *Isanodus*.

STAGE		Range of *Isanodus nongbualamphuensis*	Range of *Isanodus paladeji*	Range of *Isanodus*
Early Cretaceous	Albian 112			
	Aptian 125			
	Barremian 130			
	Hauterivian 136			
	Valanginian 140			
	Berriasian 145			

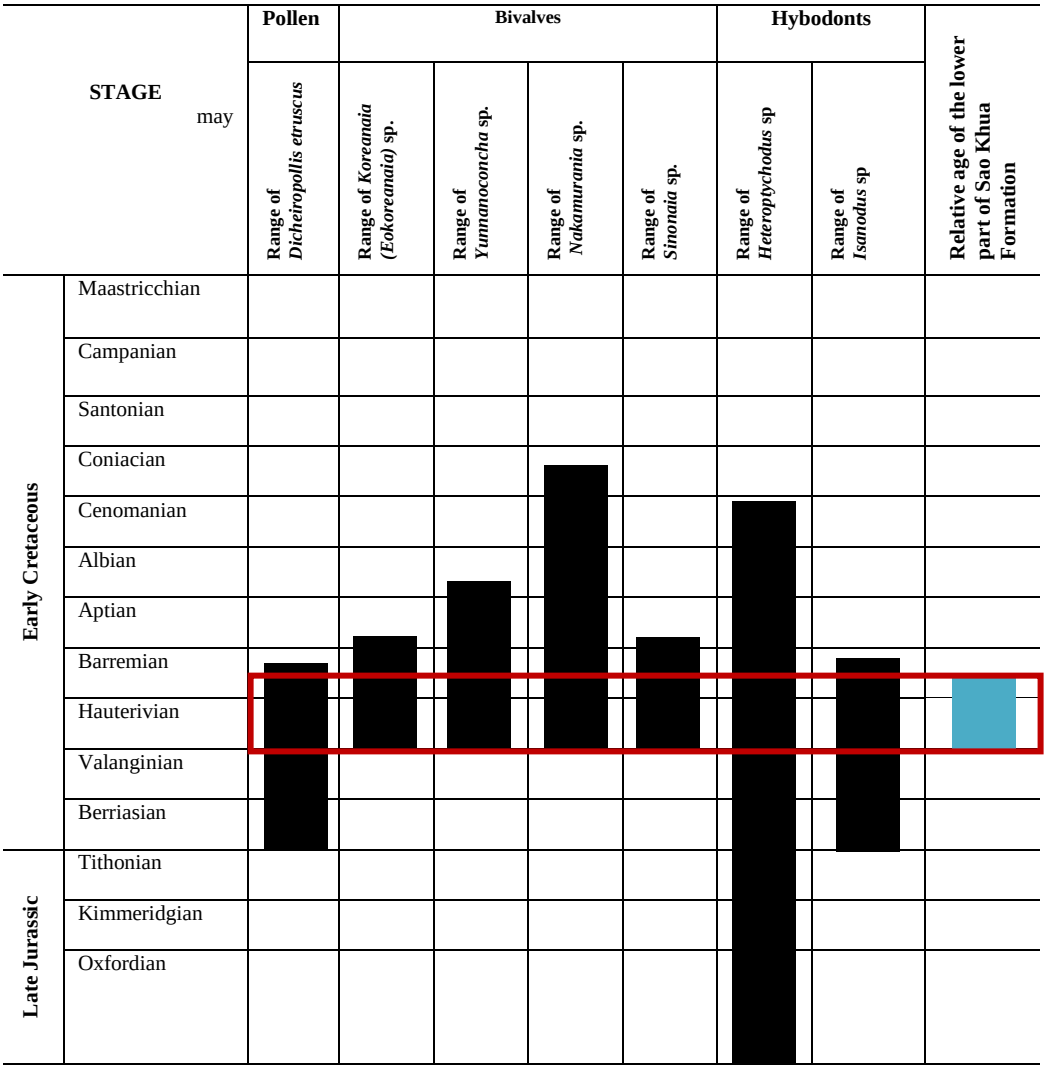
5.5 Relative age of the lower part of the Sao Khua Formation

Huai Lao Yang is not far from Phu Phan Thong and display a shell bed which is reminiscent of the molluscan assemblage of the lower layer of Phu Phan Thong, which shares a common fossil bivalve. They should be considered as belonging to the same range, suggesting a Hauterivian to Early Barremian age.

Comparison of the fossils from Phu Phan Thong locality with the other Sao Khua fossils consolidates the result from the above stratigraphic correlation. Phu Phan Thong locality is considered to be in the lower part of the Sao Khua

Formation based on the following fossils, i.e., a pollen (*Dicheiropollis etruscus*), bivalves (*Koreanaia (Eokoreanaia)* sp., *Yunnanoconcha* sp., *Sinonaia* sp.) and hybodont sharks (*Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis* and *I. paladeji*). These bivalve and shark fossils have an overlapping range in the Hauterivian. However, *Dicheiropollis etruscus* is considered a marker pollen species for the Berriasian- Early Barremian age (Racey and Goodall, 2009). In addition, *Pseudohyria (Matsumotoina) somanai* was found only in the upper part of Sao Khua (Table 5.3). This bivalve is restricted to the Late Barremian age (Tumpeesuwan, 2010). Therefore, biostratigraphic study could indicate that Phu Phan Thong is Hauterivian to Early Barremian in age (Table 5.6).

Table 5.6 Stratigraphic range of some fossils found in Phu Phan Thong locality and relative age of the later



CHAPTER 6

CONCLUSION

6.1 Diversity of the vertebrate microremains from Phu Phan Thong locality, the Sao Khua Formation

Phu Phan Thong locality, the Sao Khua Formation has yielded a numerous and diverse of microvertebrate remains. One thousand two hundred and seventy one specimens (1,271) in total were found from four hundred and fifty kilogram of sediment sieved. The fossil assemblages were discovered including;

Five hundred and sixty nine (569) isolated teeth of hybodont sharks were recognized (44.77%). Seven taxa have been identified including *Egertonodus* sp., *Hybodus* sp., *Parvodus* sp., *Isanodus paladeji*, *I. nongbualamphuensis*, *Lonchidion khoratensis* and *Heteroptychodus kokutensis*.

Two hundred and twenty one (521) isolated teeth and two hundred and fifty isolated scales of bony fishes have been found (40.99%), which are at least eight taxa including Ginglymodi indet., Cf. *Caturus*, (?)*Isanichthy* sp., *Siamamia* sp.,Cf. *Anomoeodus*, Cf. *Gyrodus*, *Ionocopus* sp. and Cf. *Thaiichthys*.

Fifty (50) isolated teeth of crocodiles were discovered (3.93%) that comprise of two morphotypes of Goniopholididae teeth.

Ninety eight (98) fragmentary shell plates of turtles were collected (7.71%) which difficult to identify at the generic level.

Thirty three (33) incomplete teeth of dinosaurs have been found (2.60%). The only one taxon of Dinosaur Cf. *Dromeosaur* can be identified.

The discovery of vertebrate microremains from Phu Phan Thong increased the palaeobiodiversity knowledge of hybodont sharks, bony fishes and dinosaurs from the Sao Khua Formation of Thailand. These included the appearance of a new hybodonts species, *Isanodus nongbualamphuensis* as well as two first record in Thailand of the bony fish which are Cf. *Gyrodus* and *Ionocopus* sp. together with the presence of new record from the Sao Khua Formation of the dinosaur, Cf. *Dromeosaur*. Although Turtles and crocodiles remains are very difficult to identify into the generic and specific

levels based on isolated teeth and fragment shell plates, these faunas could represent an important role and diverse component of the ecosystems of the Sao Khua Formation.

6.2 Palaeoecological and palaeobiogeographical implication

The total number of hybodonts species from the Early Cretaceous Sao Khua and Khok Kruat Formations are higher than the Late Jurassic Phu Kradung and the Middle Jurassic Khlong Min Formations, whereas total number of bony fish species from the Sao Khua and Khok Kruat Formations are lower than Phu Kradung and Khlongmin Formations. A numerous number of isolated teeth, dermal denticles and a few fragment spines of hybodont sharks in the Sao Khua and Khok Kruat Formations were found, whereas well-preserved fish specimens in the Phu Kradung Formation were classified as the highest taxa. According to the sedimentological interpretation by Meesook *et al.,* (2000), the most abundant sedimentary rock from fossiliferous sites of the Sao Khua and Khok Kruat Formations are sandstone and conglomeratic sandstone indicated a fluvial deposited. In the contrary , sediment in the Phu Kradung Formation are mostly mudstone-siltstone and fine sandstone indicated a floodplain or dried pond deposited. The difference in sedimentology and palaeoenvironment among the Phu Kradung, Sao Khua and Khok Kruat Formations might be explain the different modes of preservation of aquatic animals in each Formation. It is quite uncertainty to identify taxonomic status of bony fishes based on these microremains but most hybodont sharks were mainly identified their status on the basis of isolated teeth. And another reason why bony fishes were diverse during the Late Jurassic.

Additionally, the diversity of hybodonts increased during the Phu Kradung to Sao Khua Formations and decreased in the Khok Kruat Formation. Moreover, hybodonts from the Khok Kruat Formation are obviously different from the older two formations, especislly the disappearance of Family Lonchiidae, which appeared in Thailand since the Middle Jurassic Klong Min Formation to Early Cretaceous Sao Khua Formations. The diversity of bony fishes also showed the dramatic change between the deposition of the Phu Kradung, Sao Khua and Khok Kruat Formations. The Pycnodontiformes, Sarcopterygii and Caturidae are so far unknown in the Early Cretaceous Khok Kruat Formations. It may be cause by a palaeoclimate change.

Ecological niche of hybodont, Family Lonchiidae, and bony fishes (Pycnodontiformes, Sarcopterygii and Caturidae) seem to be replaced by specialized endemic hybodont sharks in the Aptian-Albian Khok Kruat Formation. The contrary pattern, the taxa number of turtle, crocodiles and dinosaurs were not differences within each Formation. Base on the previously palaeoclimate study, the Phu Kradung Formation was more humid than the Sao Khua and Khok Kruat Formations. The climate changes during the Late Jurassic to Early Cretaceous probably increased of dry areas and decreased of wet areas in the Khorat Plateau (Meesook, 2001). Consequently, habitat fragmentation and/ or loss could be another reason to explain why diversity of aquatic faunas during the Late Jurassic to Early Cretaceous in the Khorat Group was declined whereas semi-aquatics and terrestrials were not affected.

From a palaeobiogeographical point of view, the hybodont assemblage from the Sao Khua Formation appears to share both European (*Lonchidion khoratensis*, *Egertonodus* sp. and *Parvodus* sp.) and Asian (*Heteroptychodus kokutensis* and *Isanodus paladeji*) affinities. The palaeogeographical affinities of bony fishes are unable to assess because the exact affinities of the materials from Phu Phan Thong are unclear. The specimens of crocodiles (*Goniopholis*) and dinosaurs from Phu Phan Thong (Sao Khua Formation) are not to sufficient for identification at species levels. Therefore, the affinities of these specimens are imperfectly known. However, the crocodiles from the Sao Khua Formation which are "*Goniopholis*" *phuwiangensis*, *Siamosuchus phuphokensis* and *Theriosuchus grandinaris* show European affinities (Lauprasert *et al.*, 2001) whereas most of the turtles and dinosaurs belong to groups endemic to eastern Asia (Buffetaut and Suteethorn, 1998; Tong *et al.*, 2009).

6.3 The relative age of the of the Sao Khua Formation

Form the Stratigraphic correlation, Phu Phan Thong might belong to the lower part of the Sao Khua Formation. The biostratigraphic studied could indicate that the lower part of the Sao Khua Formation is Hauterivian to Early Barremian in age based on the founding of a pollen (*Dicheiropollis etruscus*); bivalves (*Koreanaia (Eokoreanaia)* sp., *Yunnanoconcha* sp., *Sinonaia* sp, *Pseudohyria (Matsumotoina)*

somanai; and hybodont sharks (*Heteroptychodus kokutensis*, *Isanodus nongbualamphuensis* and *I. paladeji*).

6.4 Recommendations and Suggestions

1. The data presented here are strongly affected by the incompleteness of specimens during fossilization process . The specimens from Phu Phan Thong was identified by the isolated teeth, scales or fragment vertebrae. Taxonomic status of bony fishes based on few characters of teeth are quite uncertainty to identify whereas most hybodont sharks were mainly used isolated teeth, scales and cephalic spines to identified their status. .

2. Teeth of *Isanodus* were recently found in Kut Island and Malaysia. The teeth characters, at first sight, suggested that the materials from Kut Island represented a species different from the teeth recovered at Phu Phan Thong. Further studies, identification and comparison, more materials might lead to a new revision of this genus.

3. The microstructure ornamentation of the ganoin scales should be study on the material from the Sao Khua and Khlong Min Formations . It is necessary for identify taxonomic status and it might be help to explain their affinity.

4. At the present, a lot of sediments from many sites have been already screen washed. All of them are keep in the collection of Sirinthorn Museum (Kalasin Province) and Palaeontological Research and Education Centre, (Mahasarakham University). These sediments need to study under the stereomicroscope. Further detailed studies are now needed for a deeper understanding of palaeobiodiversity during the Mesozoic of Thailand.

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APPENDIXES

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Revision of Isanodus paladeji *(Elasmobranchii, Hybodontiformes) from the Lower Cretaceous of Thailand*

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Revision of *Isanodus paladeji* (Elasmobranchii, Hybodontiformes) from the Lower Cretaceous of Thailand.

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Introduction

In February 2006, more than a ton of sediments were collected from the Phu Phan Thong locality (Nong Bua Lam Phu Province, Sao Khua Formation, Barremian). Many taxa, including hybodont sharks, actinopterygians, turtles, crocodiles and dinosaurs, were identified among the thousands of microremains retrieved. Six taxa of hybodont sharks were identified based on isolated teeth by Cuny et al. (2006), including *Isanodus paladeji,* a species showing an important heterodonty. Its heterodonty pattern was reconstructed based on a comparison with *Lissodus nodosus* (Duffin, 1985). At the present, all material from the Phu Phan Thong locality were completely sieved and one ton were searched by concentrate under stereomicroscope. More teeth belonging to *Isanodus* have been retrieved. Some material possess shared characters and should be replaced to some of the type series of *Isanodus paladeji* wherwas some show different characters. We therefore present here a revision of the genus *Isanodus* to re-assess its taxonomic status.

Material and method

The specimens described in this work have been recovered from the banks of road 210 between Udon Thani and Nong Bua Lam Phu, Nong Bua Lam Phu Province. To protect the fossiliferous site, its exact location cannot be provided here, according to Department of Mineral Resources' policy. For scientific purposes, its global positioning system coordinates can, however, be obtained on request from the senior author. The sediment was screen washed in water using 0.5 mm and 1.7 mm mesh sized sieves. The

concentrate was then dried in the sunlight and the fossils were picked from the concentrate under a stereomicroscope. The material is housed in the collections of the Sirindhorn Museum, Kalasin Province (TF numbers) and in the collections of the Palaeontological Research and Education Centre of Mahasarakham University, Mahasarakham Province (PRC numbers).

Geological setting

The outcrop is located in Nong Bua Lam Phu Province (northeastern part of Thailand) near Phu Phan Thong hill. It belongs to the Sao Kua Formation (Khorat Group, Northeastern Thailand). This formation has been deposited in low-energy, meandering fluvial channels and extensive floodplains under semi-arid conditions (Meesook, 2000, 2011). The formation contains various cycles of reddish brown mudstone, siltstone and fine to medium grained sandstones. The sandstones tend to be light grey in colour. In some sandstone beds, there are lenses of fine-clast conglomerate with calcareous cement and mica content. The evidences from fossil assemblages and stratigraphic correlation point to an Early Cretaceous age (Sattayarak et al., 1991). A new species of bivalve *Pseudohyria* (*Matsumotoina*) *somanai* was recently described from the Sao Khua Formation. The subgenus *Matsumotoina* is only found from the Late Barremian of Japan and Korea. It therefore suggests a Late Barremian age for the Thai Formation (Tumpeesuwan et al., 2010).

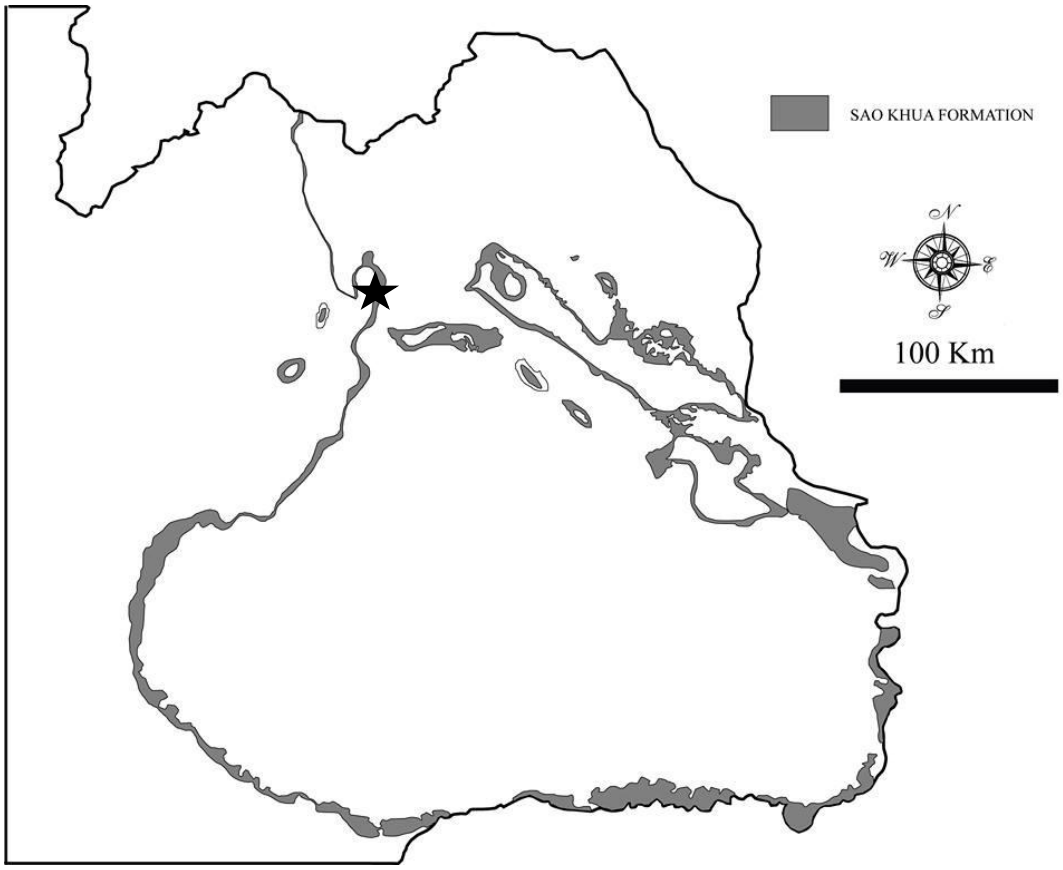

Fig 1. Sketch map of part of northeastern Thailand showing the position of the Phu Phan Thong locality (star point).

Systematic palaeontology

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Order Hybodontiformes Maisey 1987

Family *incertae sedis*

Genus *Isanodus* Cuny et al., 2006

Type species: *Isanodus Paladeji* Cuny et al., 2006 : Phu Phan Thong, Sao Khua Formation (Late Barremian).

Emended diagnosis : not gradient mononathic heterodonty showing four types of teeth: anterior, anterolateral, posterolateral, and posterior; main cusp pyramidal with a triangular base, labial peg present, ornamentation consisting of a longitudinal crest with up to one mesio-distal V-shaped labial ridge, up to four labial nodes on mesial and distal part of anterolateral and posterolateral teeth, anterior and posterior teeth lack labial nodes, longitudinal crest is reduced in posterolateral teeth.

Isanodus paladeji

Material: 109 incomplete teeth, 22 teeth with a root preserved

Holotype: TF 7674

Paratype: TF7671

Referred material: PRC 241 (anterior tooth), PRC 242 (anterolaeteral tooth), PRC 243 (posterolateral tooth) and PRC 244 (posterior tooth)

Type locality: Phu Phan Thong, Nong Bua Lamphu province, northeastern Thailand

Type stratum: Lower Sao Khua Formation, Khorat Group, Early Cretaceous (Barremian)

Emended dianosis: moderate heterodonty, anterolateral and posterolatera teeth small, narrow and elongated, labial nodes not well developed, labio-lingually oriented ridges not well developed, presumed posterolateral tooth and posterior teeth asymmetric

Description

The teeth of this species show moderate heterodonty and four type of teeth can be identified: anterior, anterolateral, posterolateral and posterior. The well preserved presumed anterior tooth (PRC 241) possesses a root and measures about 2.5 mm mesio-distally, 1.5 mm labio-distally and is 2 mm high including the root. The crown shows a pyramidal shape with a triangular base and a well-developed main cusp as high as the

root. The longitudinal crest is well developed. There are two V-shaped ridges parallel to each other on the lingual side. The labial peg is well developed at the base of the crown. The crown overhangs the root and is separated from the latter by a groove. The labial face of the root is concave. The root is straight under the crown.

The presumed anterolateral tooth (PRC-242) is narrow and elongated, lacking of its edge in both lateral side. It measures 3 mm mesio-distally, 0.5 mm labio-lingually and is 1 mm high including the root. The crown is curved mesially, elongated and shows a well developed longitudinal crest without lateral cusplets. On the lingual side, it presents two V-shaped ridges showing short perpendicular ridges on their lingual side. The labial peg is not well developed, but there are small, additional labial nodes at the base of the crown, up to three mesially and four distally. On the labial face, there is a short ridge starting from the apex but not reaching the base of the crown. The crown overhangs the root, which shows randomly distributed small foramina on its surface. The lingual side is straight under the crown.

The largest presumed posterolateral tooth (PRC 243) shows an asymmetric crown, with a labial side more developed than the lingual one. It measures 3 mm mesio-distally, 0.6 mm labio-lingually and 2 mm in height, including the root. The crown is elongate with a high central cusp and the longitudinal crest is not well-developed. The lingual face is smooth. The labial peg is not well-developed. On the labial face, the tooth is ornamented by four small, short ridges originating from the apex but not reaching the base of the crown. The crown overhangs the root, the latter showing randomly distributed small foramina on its surface. The root is as high as the crown and is slightly projected lingually.

The largest presumed posterior tooth (PRC 244) measures 2 mm mesio-distally, 1 mm labio-lingually and 1.5 mm in height, including the root. The tooth shows a well developed longitudinal crest and is similar to the anterior one but with an asymmetric crown. There are up to two V-shaped ridges parallel to each other on the lingual side and one on the labial side. The root is as high as the crown and slightly projected lingually.

Discussion

The genus *Isanodus paladeji* was erected by Cuny et al. (2006) based on four types of isolated teeth, i.e., anterior, anteroateral, posterolateral and posterior ones. According to these authors, *Isanodus* possesses a heterodont, clutching-grinding dentition with teeth possessing a labial peg, all characters that can be found in *Lissodus nodosus*, an European shark from the Triassic. However, new material, including presumed anterolateral and posterolateral teeth were recovered from Phu Phan Thong. These teeth show a shape and ornamentation equivalent to what can be seen on the presumed anterior (TF7671) and posterior teeth (TF7674) of *Isanodus paladeji*. In addition, new material of the presumed anterior and posterior teeth were also discovered and can be compared with the presumed anterolateral (TF7672) and posterolateral teeth (TF7673) of *Isanodus paladeji*. This new material suggests a re-definition of the species *I. paladeji.*

The new series of *Isanodus paladeji* teeth possess high main crowns in all types of teeth, whereas the original series show low main crowns in the presumed anterolateral and posterolateral teeth. The presumed anterior, anterolateral and posterior teeth of the new series share the following combination of characters: well-developed longitudinal crest and similarity in the pattern of V-shaped ridges on the lingual side (up to four ridges and possess a weak labio-lingully oriented ridges run to each V-shape ridge. whereas these characters disappear in the presumed posteralateral teeth. The presumed anterolateral (PRC 242) and posterolateral (PRC 243) teeth of the new series of *Isanodus paladeji* teeth possess a narrow and elongated crown mesio-distally, whereas their labial peg and labial nodes are not well developed. On the contrary, the former presumed anterolateral (TF 7672) and posterolateral teeth (TF 7673) show wider crown.The root of both presumed anterior and anterolateral teeth is straight under the crown, whereas the one of both presumed posterolateral and posterior teeth is slightly projected lingually.

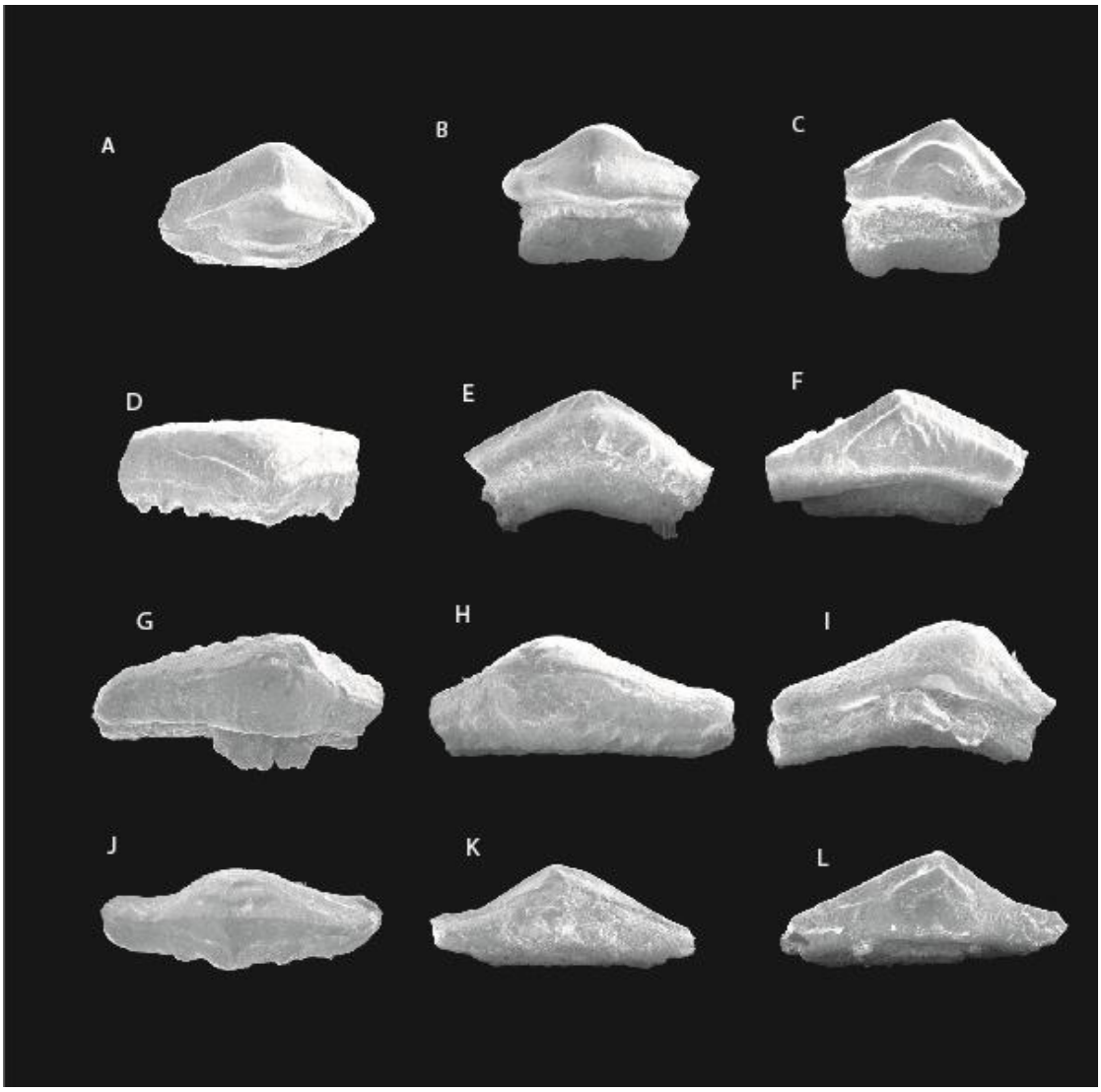

Fig 2. A-K: *Isanodus paladeji*. A—C: anterior tooth (PRC241) in A: apical, B: labial and C: lingual views. D-F: anterolateral tooth (PRC242) in D: apical, E: labial and F: lingual views. G-I: posterolateral tooth (PRC243) in G: apical, H: labial and I: lingual views. J-L: posterolateral tooth tooth (PRC 244) in J: apical, K: labial and L: lingual views. Scale bare 1mm

Isanodus nongbualamphuensis nov.sp.

Derivation of name: from Nong Bua Lam Phu province, where the type material was found.

Material: 115 incomplete teeth and including 12 teeth with a root preserved

Holotype: PRC 248 (posterior tooth)

Paratypes: PRC245 (anterior tooth), PRC246 (anterolateral tooth), PRC247 (posterolateral tooth) including TF 7672 (anterolateral tooth) and TF7673 (posterolateral tooth) which had been identified as paratype of *I. paladeji*

Type locality: Phu Phan Thong, Nong Bua Lam Phu province, northeastern Thailand

Type stratum: Sao Khua Formation, Khorat Group, Early Cretaceous (Barremian)
Diagnosis: weakly heterodont, asymmetric crown, well developed labial nodes in anterolateral tooth, well developed labio-lingually ridges in anterior, anterolateral and posterior teeth, well developed V-shaped ridges on lingual side, short strong labio-lingually oriented ridge in presumed anterior, anterolateral and posterolateral originating from the mesio-distal ridges,

Description

The teeth of *I. nongbualamphuensis* nov.sp. show four types of teeth: anterior, anterolateral, anteroposterior and posterior. The well preserved presumed anterior tooth (PRC245) lacks the root and measures 2 mm mesio-distally, 2 mm labio-lingually and is 1 mm high. The tooth shows a bulky crown and a well developed main cusp, pyramidal in shape with a triangular base. The longitudinal crest is well developed. On the lingual side, there are four, well-developed V-shaped ridges and each ridges is ornamented by short ridges originating from the top of each V-shaped ridge. On the labial side, there are several short ridges, which is not as well developed as the lingual ones.

On the mesial and distal part of the labial ridge, there are three granulae close to the base of the crown.

The largest presumed anterolateral tooth (PRC 246) measures 2 mm mesio-distally, 1.5 mm labio-lingually and is 2 mm high, but the root is not preserved. The tooth shows a bulky main cusp, pyramidal in shape with a triangular base. The longitudinal crest is well developed. The lingual side shows three well developed V-shaped ridges and each ridge is ornamented by short ridges originating from the top of each V-shaped ridge and reaching the following one. The labial side shows one V-shaped ridge, which is smaller than the ones on the lingual side. There are five well-developed labial nodes at the base of the crown.

The largest presumed posterolateral tooth (PRC 247) mesures 2 mm mesio-distally, 1.5 mm labio-lingually and is 1.5 mm high including the root. This tooth is very similar to the anterolateral one but the pattern of ornamentation is not as well developed. However, it shows a well developed labial node at the base of the crown. The crown overhangs the root.

The largest presumed posterior tooth (PRC 248) measures 3 mm mesio-distally, 1.5 mm labio-ligually and the crown is 1 mm in height, whereas the root is 0.5 mm high. The morphology of this tooth is very similar to the anterior one, but it is more elongated and it shows a more asymmetric crown. There is a well developed longitudinal crest. There are four V-shaped, parallel ridges on the lingual side and each ridge is ornamented by short ridges. The labial peg is not well-developed. Some of the teeth show some granulaes on the labial part of the crown. The crown overhangs the root and a long groove separates them on the labial side.

Discussion

The material described above does not belong to *Lissodus* because it shows a pyramidal cusp with a triangular base, ornamented with mesio-distal V-shaped ridges on the lingual side and it lacks lateral cusplets (Patterson, 1966; Duffin, 1985, 2001; Rees and Underwood, 2002). However, these characters are found in the genus *Isanodus* (see detail in Cuny et al., 2006). Comparison with *Isanodus paladeji*, shows, however, several differences. The new material shows a low main cusp. The ornamentation between the V-shaped lingual ridges, made of labio-lingually oriented ridges, is more developed than on the teeth of *I. paladeji.* The labial peg in all type of *I. nongbualamphuensis* teeth is reduced in size, whereas only its presumed anterolateral and posterolateral teeth present well developed labial nodes. On the contrary in the teeth of *I. paladeji*, the labial peg is always well-developed, whereas the labial nodes of the presumed anterolateral and posterolateral teeth are not well developed. The teeth previously considered as anterolateral and posterolateral teeth of *I. paladeji* show labio-lingual ridges together with a strong longitudinal crest, which are very similar to the presumed anterior and posterior teeth of *I. nongbualamphuensis*, although these characters are not well developed in the presumed posterolateral teeth. *I. nongbualamphuensis* nov. sp. should therefore encompasses the new presumed anterior

and posterior teeth described here and the previously presumed anterolateral (TF 7672) and posterolateral teeth (TF 7673) teeth of *I. paladeji*.

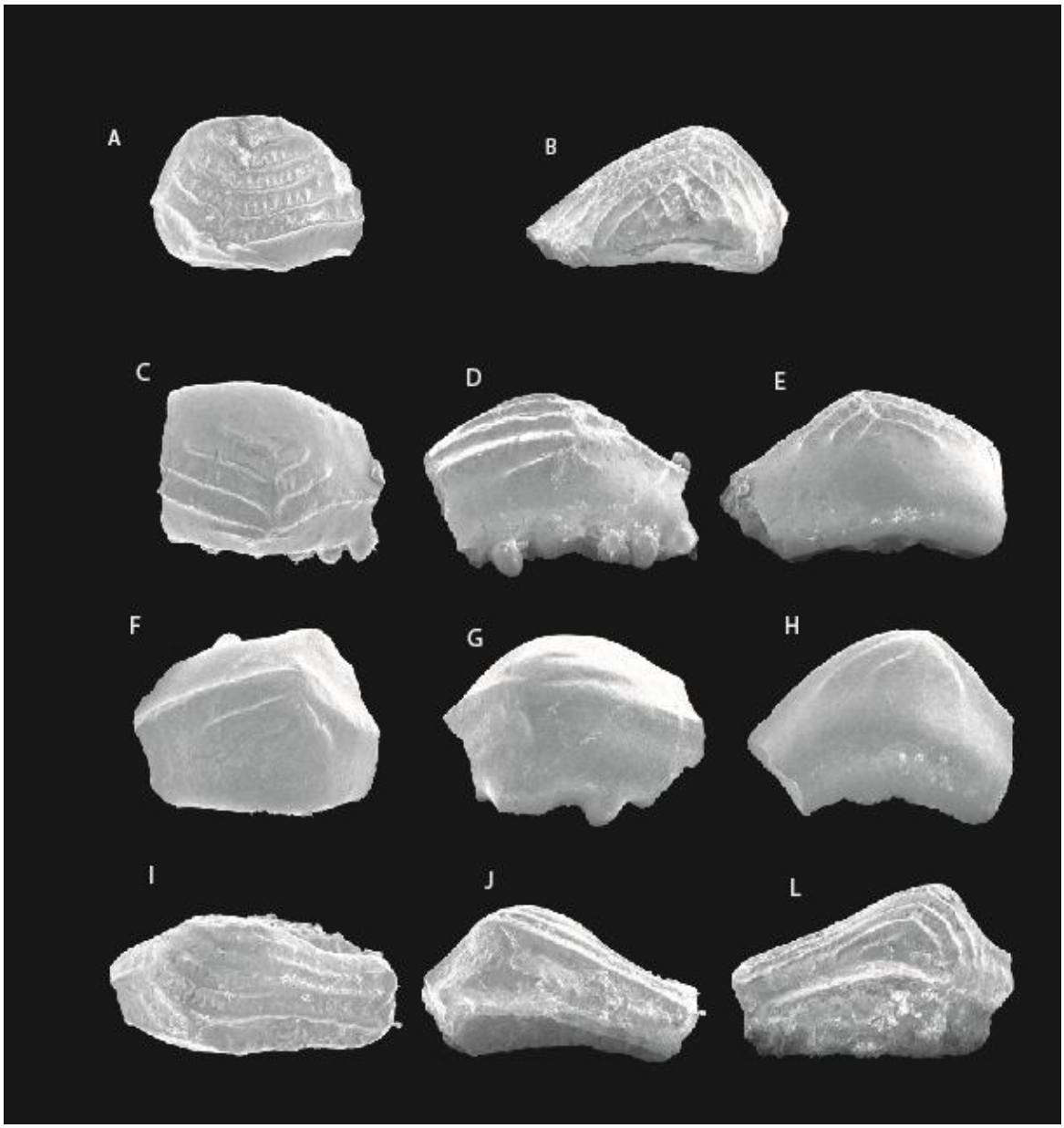

Fig 3. A-K: *Isanodus nongbualamphuensis* nov.sp. A—B: anterior tooth, paratype (PRC245) in A: apical, B: lingual views. C-E: anterolateral tooth, paratype (PRC246) in C: apical, D: labial and E: lingual views. F-H: posterolateral tooth, paratype (PRC247) in F: apical, G: labial and H: lingual views. I-K: posterior tooth, holotype (PRC248) in I: apical, J: labial and K: lingual views. Scale bar 1 mm.

Isanodus sp. indet

Morphotype 1

Material: 10 incomplete teeth without the root preserved

Ten incomplete *Isanodus* morphotype 1 teeth were found. These teeth are different from those of *Isanodus paladeji and Isanodus nongbualamphuensis* nov. sp.. The largest tooth (PRC249) measures 2 mm mesio-distally, 1.2 mm labio-lingually and is 1.5mm high, which is lacking. The tooth shows a bulky main cusp, pyramidal in shape with a triangular base. The longitudinal crest is not well developed. The lingual side shows a V-shape ridge without any labio-lingual ridges. The labial side is smooth and show six well-developed labial nodes at the base of the crown. The thickness of the crown, the pyramidal main cusp with a triangular base and the presence of labial nodes indicate that they could represent posterolateral teeth of the genus *Isanodus*. However, the teeth of *Isanodus* sp. morphotype 1 are bulkier and thicker than those of the posterolateral teeth of the two other species and their exact taxonomic status is difficult to determine without finding more material.

Morphotype 2

Material: Only one tooth with root preserved

The tooth of *Isanodus* sp. morphotype 2 (PRC 250) mesures 2.5 mm mesio-distally, 0.5 mm labio-lingually and 1 mm high including root. The root as high as the crown. It is an upright strong central cusp with not well developed leteral cusplets. The longitudinal crest is well developed. The lingual side shows two V-shape ridge without any labio-lingual ridges. The labial side is smooth and its shows two labial nodes in addition to a well developed labial peg. This is some kind of *Isanodus* sp. However, its shows the lateral cusplets that different from those of the other *Isanodus* species. This character is more reminiscent of lateral teeth of *Lissodus minimus* but the teeth of latter species not possess the labial nodes on the base of the crown (Duffin, 2001). It is thus probable that tooth represent a new species but the material at hand is insufficient to correctly define it.

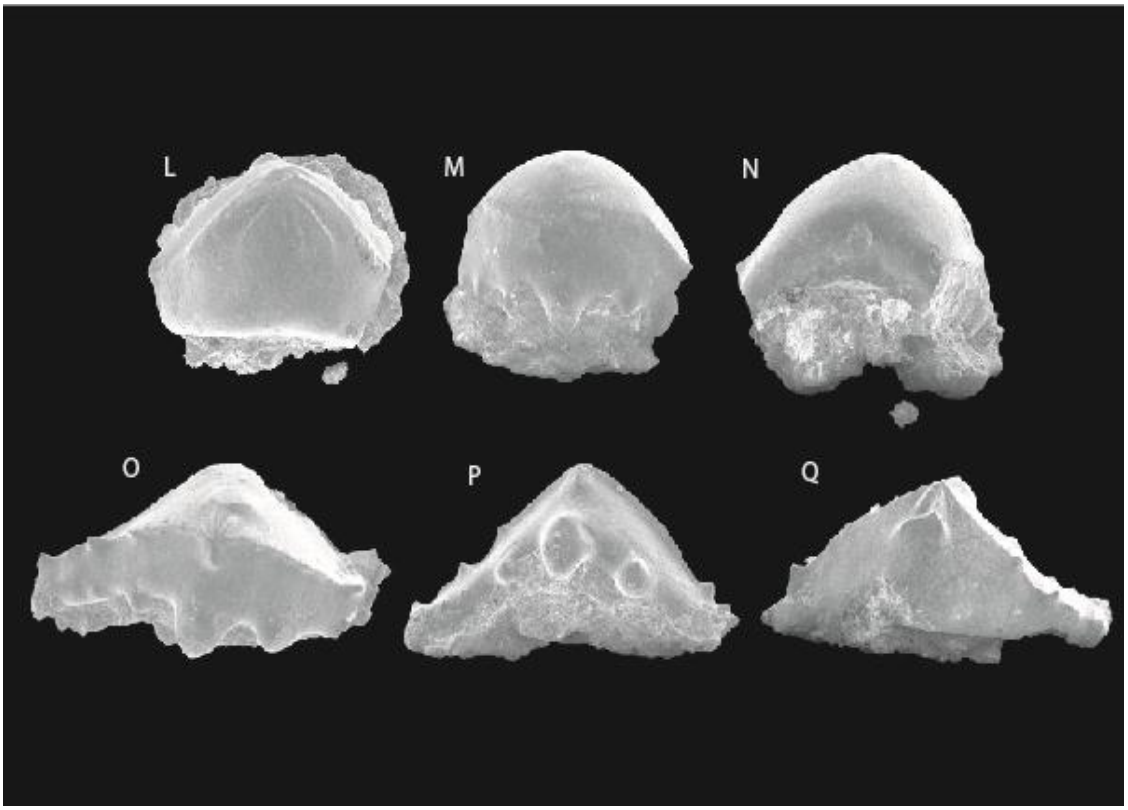

Fig 4. L-N: *Isanodus* sp. morphotype 1 (PRC 249) L—N: presumed posterolateral tooth in L: Apical, M: Labial and N: Lingual view. *Isanodus* sp. morphotype 2 (PRC 250) O-Q: presumed anterolateral tooth in O: Apical, P: Labial and Q: Lingual view.

Scale bar 1 mm.

Discussion and Conclusion

Isolated teeth of *Isanodus paladeji* have been found in many sites in the Sao Khua Formation: Phu Phan Thong (Nong Bua Lam Phu province), Nong Song (Mukdahan province), Phu Noi (Sakhon Nakhon province) and Kut Island (Cuny et al., 2006, 2007, 2010), but *I. nongbualamphuensis* nov. sp. is only present in Phu Phan Thong locality. *I. Nongbualamphuensis* shows a weaker monognathic heterodonty than *I. paladeji.* The two species share a pyramidal main cusp with a triangular base, the presence of a labial peg and V-shaped ridges on the lingual side of the crown, which suggests they belong to the same genus. In both species, the lingual V-shaped ridges are not as well developed on the posterolateral teeth than on the other ones. *I. paladeji* shows small and weakly developed labial node in its narrow presumed anterolateral and

posterolateral teeth, whereas the corresponding teeth of *I. nongbualamphuensis* nov. sp. present more developed labial nodes and a lower crown. The possession of larger nodes in *I. nongbualamphuensis* served probably to stabilize the large grinding teeth while processing hard-shelled preys. On the contrary, *I. paladeji* might have preyed on softer preys. The pattern of ornamentation in some teeth of *I. paladeji* and *I. nongbualamphuensis* is quite similar to the one observed in the genus *Heteroptychodus*, suggesting these two genera could be closely related.

Teeth of *Isanodus* were recently found on Kut Island (Cuny et al., 2010). The teeth recovered on the island are larger than the teeth found at Phu Phan Tong. Some teeth show a strong and asymmetric crown with a dense ornamentation and numerous labial nodes, which is different from what can be observed on the teeth of *I. paladeji* and *I. nongbualamphuensis* nov. sp.. These characters, at first sight, could suggest that the material from Kut Island could represent a different species from the teeth recovered at Phu Phan Tong (C. Laojumpon, pers. com.). If confirmed, this would indicate that this genus was abundant and diversified in the Lower Cretaceous of Thailand.

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