OSTEOLOGY AND SCALE MICROSTRUCTURE OF LATE JURASSIC - EARLY CRETACEOUS GINGLYMODIANS FROM THAILAND: EVOLUTIONARY, TAXONOMICAL AND PALAEOGEOGRAPHICAL IMPLICATIONS

By
Uthumporn Deesri

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Examining Committee

.... Chairman

(Suravech Suteethorn, Ph. D.) (Faculty of Graduate Committee)

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.... Committee

(Varavudh Suteethorn, Ph. D.) (Internal expert)

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(Chantima Piyapong, Ph. D.) (External expert)

Mahasarakham University has granted approval to accept this dissertation as partial fulfillment of the requirements for the Degree of Doctor of Philosophy Program in Palaeontology.

La-orsri Sanoamuang .... P. Prathepha ....

(Prof. La-orsri Sanoamuang, Ph. D.) (Prof. Preecha Prathepha)

Dean of the Faculty of Science Acting Dean of the Faculty of Graduate Studies

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ชื่อเรื่อง กระดูกวิทยาและโครงสร้างขนาดเล็กของเกล็ดปลาในกลุ่มจิงกลิโมเดียน ช่วงอายุจูแรสสิกตอนปลายถึงครีเทเชียสตอนต้นของไทย เพื่ออธิบายวิวัฒนาการ อนุกรมวิธาน และบรรพภูมิศาสตร์โบราณ

ผู้วิจัย นางสาวอุทุมพร ดีศรี

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กรรมการควบคุม ผู้ช่วยศาสตราจารย์ ดร.คมสร เลาห์ประเสริฐ
Dr. Lionel Cavin

มหาวิทยาลัย มหาวิทยาลัยมหาสารคาม **ปีที่พิมพ์** 2556

บทคัดย่อ

การค้นพบปลา Actinopterygian ในช่วงหลังยุคไทรแอสสิกในประเทศไทยส่วนใหญ่พบเศษเกล็ด เศษกระดูกและฟัน โดยตัวอย่างที่ค้นพบนี้ได้มาจากตะกอนที่สะสมบนภาคพื้นทวีปบกหลายแหล่งขุดค้นใน 3 หมวดหิน ของกลุ่มหินโคราช บริเวณที่ราบสูงโคราช จากตัวอย่างทั้งที่เก็บรักษาในสภาพสมบูรณ์ และจากเศษเกล็ดที่ค้นพบ เป็นเหตุผลให้ทำการศึกษาโครงสร้างขนาดเล็กบนผิวชั้นกาโนอินของเกล็ดปลา เพื่อตรวจสอบว่า 1) มีความแตกต่างระหว่างเกล็ดในตำแหน่งต่าง ๆ บนตัวอย่างปลาแต่ละตัวหรือไม่, 2) มีความแตกต่างระหว่างเกล็ดบนตำแหน่งเดียวกัน ภายในตัวอย่างกลุ่มประชากรปลาหรือไม่ และ 3) เพื่อเปรียบเทียบโครงสร้างขนาดเล็กของเกล็ดปลาจากหมวดหินต่าง ๆ และเพื่อให้บรรลุในวัตถุประสงค์ของการศึกษา จึงจำเป็นต้องอธิบายและระบุชนิดของตัวอย่างทั้งที่อยู่ในสภาพสมบูรณ์ และตัวอย่างที่เป็นชิ้นกระดูกที่ค้นพบจากแหล่งต่าง ๆ ผลการศึกษากระดูกวิทยา พบปลาชนิดใหม่ในหมวดหินภูกระดึง 5 ชนิด ประกอบด้วย *Thaiichthys buddhabutrensis*, *Isanichthys palustris*, *I. lertboosi*, *T.* cf. *buddhabutrensis* และปลากลุ่ม ginglymodian ชนิดใหม่อีกหนึ่งชนิด ในขณะที่ในหมวดหินเสาขัวและหมวดหินโคกกรวด พบเฉพาะชิ้นกระดูกและเศษเกล็ดเท่านั้น ผลการศึกษาโครงสร้างขนาดเล็กของเกล็ด เบื้องต้นพบว่ารูปแบบโครงสร้างขนาดเล็กของเกล็ดจากแหล่งศึกษาใน 3 หมวดหิน มีความแตกต่างกัน คือ เกล็ดจากหมวดหินภูกระดึงซึ่งมีอายุแก่กว่า ปรากฏโครงสร้างขนาดเล็กที่มีลักษณะเป็นตุ่มนูนมนกระจายอยู่บนผิวเกล็ด โดยขนาดของตุ่มนูนที่ปรากฏบนผิวเกล็ดในแหล่งศึกษาของหมวดหินภูกระดึงมีขนาดเล็กกว่าตุ่มนูนที่ปรากฏบนผิวเกล็ดในแหล่งศึกษาของหมวดหินโคกกรวดซึ่งมีอายุอ่อนกว่า ยิ่งไปกว่านั้น ตัวอย่างจากแหล่งในหมวดหินเสาขัวปรากฏรูปแบบโครงสร้างขนาดเล็กของเกล็ดที่มีลักษณะเฉพาะซึ่งเป็นรูปแบบเฉพาะที่พบในปลา *Siamamia naga* ผลของสมมติฐานที่ได้จากการศึกษาโครงสร้าง

ขนาดเล็กของเกล็ดในครั้งนี้ ยังต้องทำการศึกษาและตรวจสอบกับตัวอย่างปลาที่มีสภาพการเก็บรักษาที่สมบูรณ์ต่อไปในอนาคต

คำสำคัญ: กลุ่มหินโคราช, กระดูกวิทยา, โครงสร้างขนาดเล็กของเกล็ด, หมวดหินภูกระดึง, จิงกลีโมเดียน

TITLE Osteology and Scale Microstructure of Late Jurassic-Early Cretaceous Ginglymodians from Thailand: Evolutionary, Taxonomical and Palaeogeographical Implications

CANDIDATE Miss Uthumporn Deesri

DEGREE Doctor of Philosophy Program in Palaeontology

ADVISORS Asst. Prof. Komsorn Lauprasert, Ph.D.
Lionel Cavin, Ph.D.

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ABSTRACT

Most post-Triassic actinopterygian fishes from Thailand are represented by isolated scales, bony fragments and teeth. This material was obtained from several outcrops located in three formations representing continental sedimentary sequences, the Khorat Group in the Khorat Plateau. Scales from these localities were the basis for studying the microstructure of their ganoin surface in order to test: 1) if there are differences between different parts of the body in a single fish, 2) if there are differences within a single population and 3) to compare microstructures of isolated scales from different formations. To accomplish these objectives, we need first to describe and identify the articulated remains as well as the fragmentary ossification discovered in various outcrops. The osteological study reveals at least five taxa in the Phu Kradung Formation comprising *Thaiichthys buddhabutrensis*, *Isanichthys palustris*, *I. lertboosi*, *T* cf. *buddhabutrensis*, and new taxon of ginglymodian, and fragmentary remains and isolated scales in the Sao Khua Formation and Khok Kruat Formation. The preliminary results of the microstructure are interesting because they show a different pattern among scales from the different formations; scales from the older Phu Kradung Formation present tubercles dispersed on the surfaces and are smaller in size than the tubercles from scales from the Khok Kruat Formation, which is younger in age. Moreover, scales from the Sao Khua Formation show a very typical pattern indicating that their probably belong to *Siamamia naga*. These first hypotheses on microstructure should be tested in the future with studies on other fishes known by articulated specimens.

Key words: Khorat Group, Osteology, Scale microstructure, Phu Kradung Formation, Ginglymodian

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CHAPTER 1

INTRODUCTION

1.1 Rational of Study

Concerning post-Triassic actinopterygian fishes from Thailand, most of them are represented by isolated scales, bony fragments and teeth. These materials were obtained from several outcrops occurring in several formations of continental sedimentary sequences, the Khorat Group in the Khorat Plateau. A few studies were based on mostly completed and articulated fishes which were collected from the important locality in Thailand named Phu Nam Jun. There were preserved numerous articulated fish specimens referred to *Lepidotes buddhabutrensis* (Cavin *et al.* 2003), together with a single complete elongate fish identified as a new genus and a new species, *Isanichthys palustris* (Cavin and Suteethorn, 2006) and a skull roof associated with jaws of lungfish, *Ferganoceratodus martini* (Cavin *et al.*, 2007). Although the morphology of *L. buddhabutrensis* in Phu Nam Jun locality is variable, statistical analyses showed that all specimens belong to a single population (Deesri *et al.* 2009). The result allows us to assess the variability of the microstructural ornamentation of the ganoin layer at the surface of the scales. According to Gayet and Meunier 1986; Meunier *et al.* 1987; Meunier and Gayet 1992, the microstructural ornamentation can be used for classification at specific level by measuring diameter of the tubercles and distance between the tubercles at the ganoin surface. The most interesting result of this study is possibly to get a new technique for identification semionotid fish in several outcrops distributed in various parts of Mesozoic formations in Thailand.

1.2 Objectives

This study consists of four main objectives including:

1. to study osteology of articulated and fragments of the semionotiforms.

2. to examine, whether there are microstructure differences between different parts of the body in single specimen of *L. buddhabutrensis*, and between different individuals within a single population,

3. to compare microstructure between *L. buddhabutrensis* and isolated scales from other areas, and

4. to observe the evolution of the microstructure and osteology of semionotid fish between the different formations, and their palaeogeographical distribution.

1.3 Scope of Research

The scope of the study is to describe the morphology and the tubercle on the external surface of ganoin of *L. buddhabutrensis* by scanning electron microscope observations for assessing the feature as a diagnostic specific character. It includes, the comparison of surface structure of isolated ganoid scales of this species from other localities of different post -Triassic formations (from the Late Jurassic of the Phu Kradung Formation to the Early Cretaceous Khok Kruat Formation in Kherat Plateau), in order to examine microstructural differences between different specimens and to assess the specific diversity.

1.4 Significance of the Research

Because of the large amount of available isolated bony fragments and scales which cannot be identified at a generic or a specific level on the basis of the superficial morphology, it is important to develop a method for identification on the basis of scanning electron microscope examination on microstructure of the scale surface. It has been proposed that the structural ornamentation of the scale of semionotid fish is diagnostic at the specific level (Gayet and Meunier 1986; Meunier *et al.*, 1987; Meunier and Gayet, 1992). This approach could be applicable to observe the evolution of the microstructure and this result could be correlation to the evolution of osteology of the semionotid fish among several localities in Thailand. Finally, this study could be important for addressing palaeogeographical affinities of the taxa.

CHAPTER 2

LITERATURE REVIEW

The objective of this research is to develop a new technique in order to identify semionotid fish in several localities belonging to Mesozoic formations in Thailand. To achieve the above mentioned objective, related literatures and documents (paper and unpublished reports) have been collected for preliminary study concerning:

2.1 General Geology of the Study Areas

Thailand consists of two continental blocks or microcontinents: the eastern part (The Khorat Plateau) belongs to the Indochina block, and the western part (including the southern penninsula) is called 'Shan-Thai' or 'Sibumasu' (Figure 1). In the Shan-Thai block, the stratigraphy of the non-marine sediments in southern peninsular Thailand has been reviewed by (Teerarungsigul *et al.*, 1999 and Meesook *et al.*, 2002). These clastic red beds are known as the Trang Group, which is now subdivided into the basal Khlong Min Formation, overlain by the Lam Thap, Sam Chom and Phun Phin formations in ascending order. The Mab Ching locality in the Khlong Min Formation was discovered by L. Raksaskulwong in 1993. Field work there in 1993, 1994 and 1996, yielded abundant vertebrate remains including hybodont sharks (Cuny *et al.*, 2009a), lungfishes (Martin *et al.* 1997), temnospondyls (Buffetaut *et al.*, 1994a), mesosuchian crocodiles and the turtle (Tong *et al.* 2002). This formation was dated to the Middle or Late Jurassic on the basis of charophytes and palynomorphs (Lei, 1993, Buffetaut *et al.* 1994b), the age was later confirmed by the occurrence of *Siamochelys peninsularis* (Tong *et al.*, 2002). In addition the occurrence of a euhelopodid sauropod in the Khlong Min Formation indicates a continental connection with the mainland Asia (Buffetaut *et al.*, 2006).

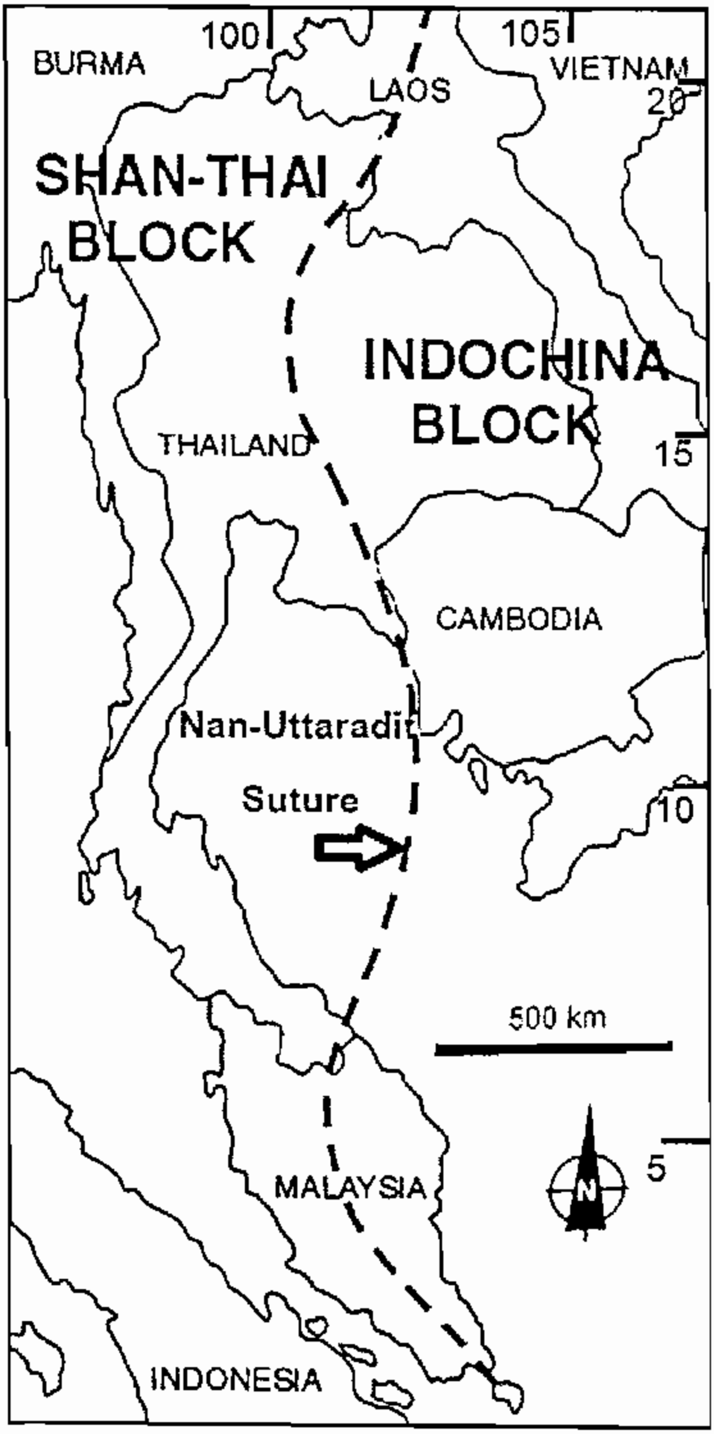

Figure 1 Thailand Map showing the Nan-Uttaradit suture indicated two continental blocks.

The Khorat Plateau in NE Thailand is composed of non-marine sediments deposited during the Mesozoic. A recent study restricted the Khorat Group to five formations: the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat Formations, in ascending order (Racey, 2009; Racey & Goodall 2009). Only three of the five formations have yielded vertebrate body fossils (Figure 2) which are Phu Kradung, Sao Khua and Khok Kruat formations, whereas in the Phra Wihan and Phu Phan formations only footprints were recorded. The Phu Kradung Formation comprises fluvial channel sandstone, siltstone and mudstone with intermittent calcrete. Overall, mudstone and siltstone dominate the formation, with calcrete locally common. The formation was deposited in a mainly lake-dominated floodplain cut by meandering and occasionally braided river channels. The formation is sandier in its upper part and shows a gradational conformable contact with the overlying Phra Wihan Formation. While the underlying Nam Phong Formation is considered unconformable in the subsurface along the SW margin of the Khorat Plateau, suggesting a possible minor hiatus based on a change in interval velocity at this boundary. The age of this formation on the basis of recent vertebrate discoveries is considered to be Late Jurassic (i.e. Tithonian; Buffetaut *et al.*, 2006; Racey & Goodall, 2009). However, the upper part of this formation is now considered as basal Cretaceous in age. The Phra Wihan Formation comprises fine- to coarse-grained sheet and channelled sandstone beds with rarer variegated siltstone and mudstone, with intermittent conglomerate beds, and was deposited in a fluvial environment dominated by high-energy, shallow braided rivers with subordinate lower energy meandering river systems and associated floodplains. The formation has a gradational and conformable contact with the underlying Phu Kradung and overlying Sao Khua Formations. It was previously assumed to be Middle Jurassic in age based solely on the fact that the vertebrates in the over- and underlying formations were thought to be Early and Late Jurassic in age, respectively. The Phra Wihan Formation is considered to be Berriasian–early Barremian in age based on the presence of palynomorphs: (Racey & Goodall 2009, Fig. 4-7.) *Dicheiropollis etruscus*, *Corollina* spp., *Cicatricosisporites augustus* and *C. dampieri*. *C. augustus* ranges no older than Early Cretaceous (Berriasian) whereas *D. etruscus* has its stratigraphic top in the early Barremian and its base in the Berriasian. The assemblage is very similar to that of the overlying Sao Khua Formation. The Sao Khua Formation comprises dominantly floodplain deposits including sandstone, siltstone and mudstone, together with common calcretes, and was deposited in a low-energy fluvial setting comprising meandering channels and extensive flood plains. The contact with the underlying Phra Wihan and overlying Phu Phan formations appears to be gradational and conformable at outcrop. There is no recorded spore or pollen indicative of sediments younger than Early Barremian were recorded. Based on the presence of *D. etruscus*, a Berriasian- early Barremian age is preferred for this formation. The Phu Phan Formation comprises dominantly medium- to coarse-grained sandstone beds (locally conglomeratic) and subordinate floodplain or lacustrine siltstone and mudstone. The overall depositional setting was in a high-energy, low-sinuosity braided river system. Racey *et al.* (1996) recorded a rare, long-ranging assemblage of *Corollina* spp., *Cyathidites minor*, ?*Todisporites* sp. plus indeterminate bisaccate pollen. This would indicate an age no younger than Cenomanian. In addition the contact with the underlying Sao Khua Formation is locally erosive and therefore may be unconformable, whereas the contact with the overlying Khok Kruat Formation is conformable. Based on the ages of the over- and underlying formations, the age of the formation is considered to fall within the interval 'mid' –Barremian to Aptian. The Khok Kruat Formation comprises sandstone, conglomerate, siltstone, shale and intermittent palaeosols deposited in a dominantly fluvial environment. This formation is considered as Aptian in age on the basis of palynomorphs (Sattayarak *et al.*, 1991), and vertebrates (Cappetta *et al.*, 1990; Buffetaut & Suteethorn, 1992).

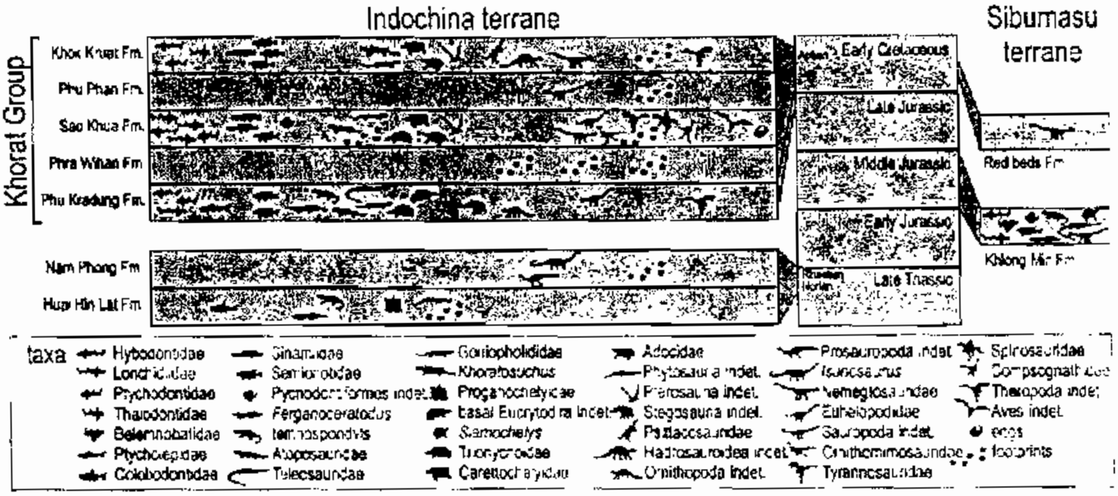

Figure 2 Distribution of main groups of vertebrates in the non-marine formations of Thailand. The Indochina Block comprises NE Thailand (Khorat Plateau). The Sibumasu (or Shan-Thai) Block includes western and southern peninsular Thailand. Figure courtesy of L. Cavin (Musée d'Histoire Naturelle, Geneva).

2.2 Bony Fishes Record in Thailand

Almost thirty years ago, the Thai-French expedition led by Dr. Varavudh Suteethorn (Department of Mineral Resources, Bangkok) and Dr. Eric Buffetaut (Centre National de la Recherche Scientifique, Paris) has focused on the Mesozoic non marine vertebrate fossils from Thailand, ranging in age from the Late Triassic to the late Early Cretaceous. Bony fishes have been discovered through the time, mostly represents by isolated rhomboid scales, and called semionotid-like fish scales (Buffetaut and Suteethorn, 1998). The first record of bony fish was described by Martin and Ingavat (1982), based on a single tooth plate of a lung fish from the Late Triassic (Huai Hin Lat Formation). The outcrop lies near Chulabhorn Dam (formerly Nam Phrom Dam), between Khon Kean and Phitsanuloke, where the presence of a phytosaur sample indicates a Norian age. This minute tooth plate bears 5 sharp ridges which radiate from the tip of the inner angle and was refer to a left upper tooth plate. On the account of morphology and biometrical results, this tooth plate was determinate as closely related to *Ceratodus szechuanensis* (Liu and Yeh, 1957) from China and this plate was referred to *Ceratodus* cf. *szechuanensis*. The occurrence of freshwater ceratodontids from China and Thailand provides evidence of terrestrial connections between China and SE Asia during the Late Triassic.

In 1997, Martin *et al.* described two tooth plates of lungfish from two different non marine formations. A complete one comes from the Southern peninsula of Thailand, in Mab Ching locality (Nakhorn Si Thammarat Province), which presents a section of alternate clays and limestone bed supposed to be middle Jurassic in age on the basis of charophytes (Buffetaut *et al.*, 1994b). The second one more poorly preserved, comes from North Eastern Thailand in Ban Khok Sanam, Phu Kradung Formation (Kalasin Province). This locality is regarded as Jurassic by the discovered of vertebrates assemblage. The Mab Ching specimen is a small right upper tooth plate because it bears 5 sharp ridges which radiate from the tip of the inner angle. The second is a left lower tooth plate that possesses 4 clear ridges. Comparison remains from Mab Ching is very similar in morphology to the small Triassic tooth plate described previously but it is different from the biometrical point of view. However, the standard deviation obtained from good samples of Triassic European tooth plates, indicates a large variability of this index among the Ptychoceratodontidae. The incomplete tooth plate from Ban Khok Sanam is not different from the lower tooth plate of *C. szechuanensis* (Liu and Yeh, 1957). At the specific level, it seems that the Chinese Triassic and Jurassic tooth plates referred to *C. szechuanensis* and the Triassic and Jurassic tooth plates from Thailand are similar, especially the specimens from Mab Ching. Since the discovery of tooth plates and isolated cranial roof bones of lung fish from the Callovian of Kirghizistan, Nessov and Kaznyshkin (1985) described a new taxon: *Ferganoceratodus jurassicicus*. Without the cranial element, the remains would have been referred to *Ceratodus* sp. Moreover, *C. szechuanensis* from China present the very deep first notch as in the callovian species suggesting regarding it as a synonym of this species. For these reasons the generic level has been change to *Ferganoceratodus* (Nessov and Kaznyshkin, 1985). *F. szechuanensis* is present in Thailand from the late Triassic till to the Middle Jurassic and recorded in China by the late Triassic to the Jurassic. A closely related species recorded in Mongolia, *F. sharategensis* (Late Jurassic), and in Kirghizistan, *F. jurassicicus* (Callovian), as well as *C. concinus* from the European late Triassic are also referred to the genus *Ferganoceratodus*. These geographical distributions suggest accretion of the Indochina block to South China as soon as the late Triassic and connection of South East Asian blocks with South China at least during Jurassic times. The dipnoans discovery in Mab Ching and Khok Sanam localities are indicate of a Jurassic age.

In 1999, Robert and Jumnongthai have described 11 species of teleosts fishes from Miocene age deposits in a lake- bed in the Phetchabun intermontane basin at Ban Nong Pla in Phetchabun Province, north-central Thailand. There are six cyprinoids, or carp, three siluroids, or catfishes, and two percoids. Five of the carps and one of the catfish are similar to living species. One carp represents an extinct new genus and species, *Proluciosoma pasakensis*, superficially similar to the living genus *Luciosoma*. Another carp is an extinct species of the living genus *Hypsibarbus*. One catfish represents an extinct new genus and species of the living family Pangasiidae, *Cetopangasius chaetobranchus*, specialized for feeding on plankton. The other two cannot be distinguished from the living bagrid catfish genera *Leiocassis* and *Hemibagrus*. The *Leiocassis* appears to be identical with the living species *L. siamensis*, while the *Hemibagrus* represents a previously underscribed extinct species, *H. major*. The two percoids, members of the family Chandidae or glassperches, are previously undescribed extinct species in the living genus *Parambassis*, *P. goliath* and *P. paleosiamensis*. *Parambassis goliath* attained nearly 27 cm of standard length and may have been larger than any living chandid species. The most frequently encountered species in the assemblage are *Parambassis paleosiamensis* and *Prolusiosoma pasakensis*, both with maximum standard lengths of about 10 cm. The pangasiid catfish *C. chaetobranchus*, attaining 50 cm, is relatively common, but *Leiocassis* is represented by a single 12 cm long specimen, and the *Hemibagrus* by a single incomplete specimen with an estimated standard length of nearly 1 m. The living carp genera are represented by only a few incomplete or fragmentary specimens of the subfamilies Barbinae (including *Mystacoleucus* sp) and Labeoninae (a single complete and one fragmentary specimen of *Bangana* sp.)

Lake Phetchabun probably was a self- contained or endorheic lake confined to the Phetchabun intermontane basin. Its endemic fishes presumably died out when the Miocene lacustrine ecosystem was replaced by the Pliocene and Recent fluvial ecosystem similar to today's Maenam Pa Sak.

piscivorous, 'semionotid'. It illustrates the great diversity and ecological adaptation of the semionotiforms during the Late Jurassic – Early Cretaceous.

One year later Cavin *et al.* (2007a) describe a new species of lungfish, *Ferganoceratodus martini* based on a single specimen discovered in Phu Nam Jun locality. The material comprises an almost complete skull roof with associated upper and lower jaws, as well as some postcranial remains. *F. martini* shows characters unexpected and/or unknown in other Mesozoic lungfishes, such as pieces of a 'hard snout'. The microstructure of the 'hard snout' provides support to the Bemis and Northcutt (1992) interpretation of the cosmine tissue of Palaeozoic lungfishes as homologous to the complex cutaneous vasculature of the living *Neoceratodus*. Because the homologies of the ossifications of the skull roof among lungfishes and among piscian sarcopterygians are unsatisfactorily understood, a topological nomenclature was used in the description of the specimen and in the discussion of post-Devonian dipnoan skull roof characters. The main feature is the ancient dichotomy between the *Neoceratodus* lineage and most of the other Mesozoic forms, including the Lepidosirenids. The palaeobiogeographical pattern shows a series of vicariant events between Laurasia and Gondwana in the Late Triassic – Early Jurassic, followed by a vicariant event between Africa and South America.

At the same year, Cavin *et al.* (2007b) described a new taxon of sinamiid halecomorph, *Siamamia naga* on the basis of three partly articulated skulls and a collection of isolated ossifications from Phu Phok locality, Sakhon Nakhorn Province, a continental Early Cretaceous (Sao Khua Formation) of north-eastern Thailand. Sinamiidae are hitherto known by two genera occurring in Early Cretaceous freshwater deposits in China and Japan. Although a complete revision of all species within the family is necessary, the Thai material consists of isolated skeletal remains preserved in 3D that show valuable features for anatomical description and it shows characters justifying a new genus, such as an epioccipital with a large internal cavity for the lateral cranial canal; paired small orbitosphenoid almost circular in shape; frontal deeply excavated above the orbit with a deep notch on the anterior margin; vomer bearing teeth on its whole anterior part; fourth (?) and fifth infraorbitals (postorbitals) extending posteriorly almost to the anterior margin of the preopercle; premaxilla with a triangular and proportionally small nasal process; premaxilla bears teeth irregular in size, with the posterior ones being larger than the anterior ones; maxilla with a postmaxillary notch present as a subtle concavity and with an elongated anterior articular process; coronoid process on the dentary posteriorly located; supratemporal sensory canal opens through numerous pores on the dorsal surface of the dermopterotic. It is the first sinamiid found outside eastern Asia (South and North Chinese blocks, plus small Central Asian terranes), thus validating the close paleogeographical affinities between mainland Asia and SE Asia in the Early Cretaceous.

So far, the fishes fossils were discovered during palaeontological field works conducted in the continental Mesozoic deposited of Thailand for more than 20 years. They have been mentioned in several publications, which mainly deal with descriptions for defining new taxa, except the study of Deesri *et al.* (2009) which is an analysis of the very rich articulated *Lepidotes buddhabutrensis* population deposited in Phu Nam Jun locality. Since 2002, fishes from the Phu Nam Jun locality have been collected during systematic excavation. The fish fossils show great variations in preservation states and body postures, which allow analysing taphonomic at features. Based on observations of the general feature of the fish by Cavin *et al.* (2004) it seemed that fishes show two different shapes. The presence of narrow and deep bodied fish in the assemblage suggests analysing the mode of variation of morphometric features in the fish population, the growth mode and the relationship between morphology and size. In contrast to preliminary field observations, statistical analyses show that all individuals belong to a single Gaussian population and that gross morphological shape variations are related only to size during fish growth. *L. buddhabutrensis* shows a positive allometric growth for the pectoral to dorsal, and pectoral to anal fin distances, and a negative allometric growth for the unpaired fins (dorsal and anal fins lengths). There are no relationships between the vertical location of the fishes within the fossiliferous deposit and the body shape of the specimens, nor between the state of preservation and the taphonomy, but there are significant differences in the state of preservation according to the position of the fishes in the fossiliferous deposit. The occurrence of a single Gaussian population and the absence of morphological and preservational variations through the depositional column are evidence that the fish assemblage is probably the result of a single mass mortality event. The apparent diversity in morphology is probably due to variations in the mode of preservation. The fish appear to have been oriented by a current at the time of deposition at the top of the fossiliferous deposit only.

2.3 Morphology and Histology of Scales

The morphology and histology of the scales mainly focus on the scales of extant fish, in order to understand the transformation of ganoid scales into elasmoid scales, such as the study of Meunier and Brito (2004) based on the basal teleost scales from fossil and living species. The scales of fish can be divided into two main types, ganoid and elasmoid scales.

Ganoid scales have a rhombic shape, they are thick, and display a peg-and-socket articulation. The general structure of the scales in all "ganoid" taxa is basically similar. They all show the lepidosteoid features, i.e. a bony basal plate with osteocyte spaces (osteocytic bone of Weiss and Watabe, 1979) overlain by a layer of ganoin of variable thickness, generally composed of several sheet, and lacking an intercalated dentin layer (Goodrich, 1907; Schultze, 1966, 1977, 1996; Orvig, 1977; Sire and Meunier, 1994; Brito *et al.*, 2000). The external surface of the ganoin layer shows characteristic tubercles in some groups such as in aspidorhynchids (Brito and Meunier, 2000) which are also found in some palaeoniscoid scales (Schultze, 1966; Esmin *et al.*, 1971; Gayet and Meunier, 1986; Richter and Smith, 1995).

The ganoin is pluri-stratified, and overlain by a mineralized, irregular layer; this external layer show thin, irregular lines of incremental growth and contacts the bony basal plate at the margin of the scale. In species with ganoid scales, the bony plate has Sharpey's fibers, which are interconnected with neighbouring scales and the dermis. The basal plate also shows a central area of woven bone (*sensu* Francillon-Vieillot *et al.*, 1990) with thin layers of lamellar bone above, and a thicker layer of lamellar bone below. The lamellae are between 0.5 and 2 μm in thickness, and they are alternatively bright or dark under polarized light. The woven bone shows isodiametric osteocytes, whereas the osteocytes of lamellar bone are flat and located between the bone strata. The basal plate is crossed by numerous canals of Williamson, 1.5-4 μm in diameter.

2.4 Scale Mineralization

Ganoid scales examined consist of two mineralized tissues: ganoin (which is hypermineralized) and bony basal plate. On the surface of the ganoin under observed by scanning electron microscopy is presence of numerous small, round relief called tubercles which Meunier and Gayet, 1992; Gayet and Meunier (1986, 2001); Gayet *et al.*, 2002; Brito *et al.*, 2000 and Schultze, 1996 have been used to studied for recognition of the taxa on the basis of the pattern (size and density) of tiny tubercles. The bony plate is entirely mineralized, in contrast to that of the elasmoid scales, which shows a different mode of mineralization, depending on the species (Meunier, 1984).

CHAPTER 3

MATERIALS AND METHODS

3.1 Materials

3.1.1 Reference materials: Three well preserved and articulated *L. buddhabutrensis*, were selected: K12-42, K12-97, K12-265 (Figure 3, 4). All specimens were collected from Phu Nam Jun, Tambon Lao Yai, Amphoe Kuchinarai, Kalasin Province.

Figure 3 The articulated of reference *L. buddhabutrensis* from Phu Nam Jun locality. A: K12-42, B: K12-97 and C: KS12-256.

3.1.2 Alternate reference materials: The alternated reference materials consist of one sub articulated fish (KS36-2) referable to *Isanichthys lertboosi*. It was collected from Phu Noi locality in Kham Muang District, Kalasin Province (Figure 4). And the other alternate materials are isolated scales of *Siamamia naga*, Phu Phok locality in Sakhon Nakorn Province.

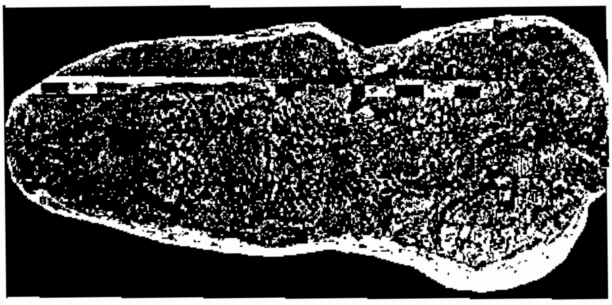

Figure 4 Alternate reference material; *I. lertboosi* from Phu Noi locality KS36-2.

Kuchinarai, Kalasin Province. The outcrop reveals a portion of the Khorat Group, namely the Phu Kradung Formation (Cavin *et al.*, 2004: 161-167). The Phu Kradung Formation is Late Jurassic or Basal Cretaceous in age (see chapter 2). The stratigraphic section studied in Phu Nam Jun is 4.5 meters thick. The slope of the fossiliferous beds dips about 12 degree towards the southeast. Beds consist of mudstones, siltstones and sandstones represented by 70-80% clay and 20-30% silt.

Figure 5 Location map of the localities. 1, Mab Ching; 2, Phu Nam Jun; 3, Phu Noi; 4, Khok Sanam; 5, Chong Chat; 6, Phu Phok; 7, Phu Phan Thong; 8, Ban Saphan Hin; 9, Lam Pao Dam; 10, Khok Pha Suam.

Figure 6 Mab Ching locality along the road in southern Thailand, exposes alternating grey and brown clay interbedded limestone beds.

Figure 7 Phu Nam Jun locality in 2004 during the beginning of the systematic excavation, sediments consist of mainly mudstone, siltstone and sandstone

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 grain size fine-medium. Roundness is rounded. The sorting is moderate. The fish remains are present throughout ca 1 meter thick of mudstone and sandstone layer.

The Phu Noi locality (Figure 8) is located at Phu Phan Mountain Range in Kalasin Province. The outcrop belongs to the Phu Kradung Formation of the Khorat Group of Northeastern Thailand. The stratigraphic section in Phu Noi locality is 7 meters thick. the slope of the fossiliferous layer where the isolated of fish scales were disperse 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. Fragments of plant remains (1-2 cm) and calcrete nodules have been found. 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. To clarify the origin of the scale microstructure from this locality can, the site can be separated into two areas: one scale sample were taken from a single fish found at the excavated site. another scale sample were taken on the surface around the hill by hand collection.

Figure 8 Landscape of Phu Noi area, a small hill located in Kham Muang District, Kalasin Province.

Khok Sanam locality consists of two close outcrops called Khok Sanam (K7) and Khok Sanam (K7D). Both localities (Figure 9) are located in the Phu Phan Mountain Range in Kham Muang district. Kalasin Province. Sediments and samples collection from both outcrops are similar, but only small outcrops 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 of the Khorat Group of Northeastern Thailand.

Figure 9 Two localities from Khok Sanam area in Kham Muang District, Kalasin.
A: Khok Sanam K7, B: Khok Sanam K7D.

The Phu Phok fish scales have been found on a slope of the Phu Phan Mountain Range in Sakhon Nakhorn Province. The outcrop 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 (Figure 10).

Spring way of Lam Pao Dam (Figure 11) is located in Kalasin Province. It consists of conglomeratic limestones with pebble grain of about 2 centimeters of diameter, purple to reddish brown, 10 centimeters thick. The overlying bed consists of reddish brown siltstone interbedded with sandstone with grain size fine-medium. Roundness is sub-rounded. The sorting is moderate, thick to massive bed. The locality is deposited in the Khok Kruat Formation of the Khorat Group.

The Khok Pha Suam locality is located at Sri Chiang Mai district, Ubon Rachathani Province. Only the surface of the layer can be observed in the outcrop. Sediments consist of grey and write clay interbedded with reddish brown and grey siltstone, overlying by a 30 centimeters thick layer of laterite (Figure 12). 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 10 Reddish brown siltstone from Phu Phok locality in Sakhon Nakhorn Province.

Figure 11 Spring way of Lam Pao Dam in Kalasin Province.

Ban Saphan Hin locality is a small outcrop (Figure 13), which located at a village in Khok Kruat subdistrict where it close to the city of Nakhorn Ratchasima Province. The outcrop is consisting of blocks of continental coarse sandstones and conglomerates interbeded with reddish siltstone or sand lens, about 3 – 4 meters thick. Because the rock is very hard, machine rock saw was used to remove the materials from the field. 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 12 Khok Pha Suam, Ubon Rachathani, exposes the grey and write clay interbedded with reddish brown and grey siltstone.

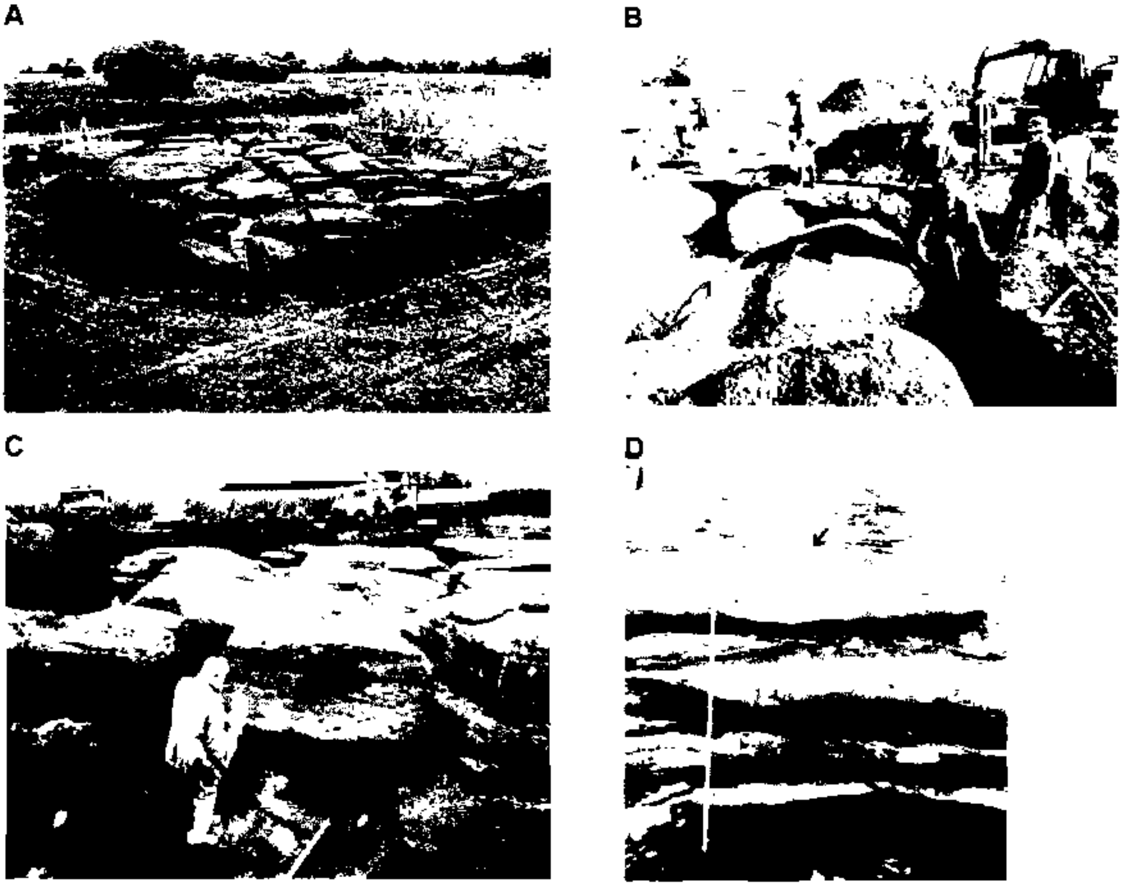

Figure 13 Ban Saphan Hin outcrop, Nakhorn Ratchasima, exposes the reddish coarse sandstones and conglomerates interbeded with sand lens (the black point).

3.3 Methods

3.3.1 Preparation and precise location of the sampled scales on the body

According to the high quality of fish preservation, the scales of *L. buddhabutrensis* have been selected in the squamation of three completed fishes in an attempt to obtain representative samples. The positions of the 9 sampled scales are defined by their row/line coordinates (Figure 14).

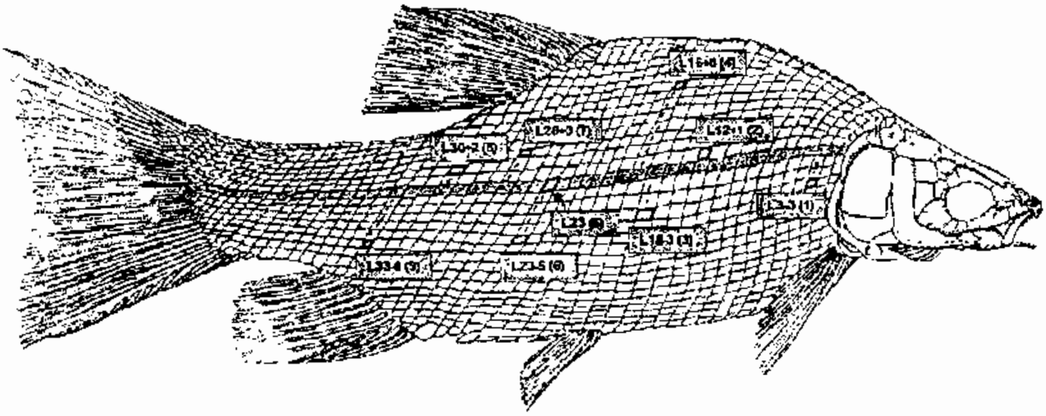

Figure 14 Outline drawing of a reference *L. buddhabutrensis* showing scale sampling points; numbers indicate row/line coordinate, with the sensory line as the reference line. Figure courtesy of L. Cavin (Musée d'Histoire Naturelle, Geneva).

3.3.2 Method of scanning electron microscope

For scanning electron microscopy, all scales were clean with ethanol and dried up. The scales were coated with a thin layer of gold and examined with a JEOL JSM-T20 scanning electron microscope conducted in Mahasarakham University.

3.3.3 Method of measurements

The morphometric characteristics of the tubercles are measured using the method of Gayet and Meunier (1986). All taken orthogonally and at the same magnification. Boundaries of distances on the scanned photographs are drawn on the photographs using a computer drawing program (COREL). Then measurements of diameters of and distances (space) between them are taken on the drawing to the contrary of Gayet *et al.* (2001), we measure inter-tubercle distances from the center of each tubercle, and not from their margin (Figure 15).

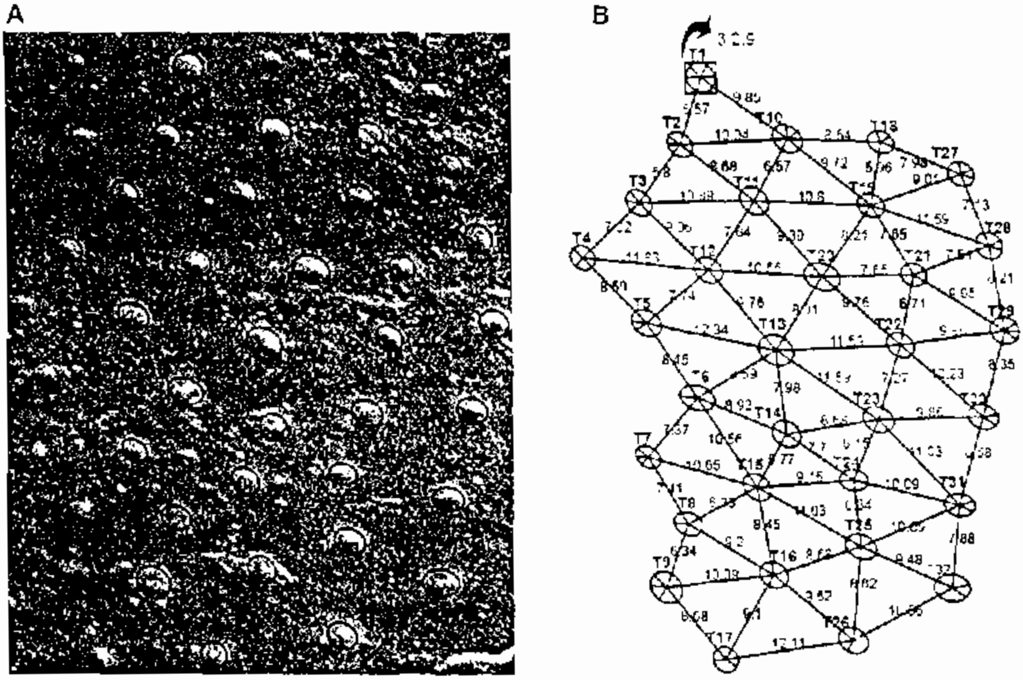

Figure 15 Plot of boundaries of the tubercles and distance on the scanned photograph (x1000). A: drawing of the tubercles on SEM photo. B: measurement of the tubercles (32 measurements) and of the distances between them (74 measurements). Figure from measurement of scale specimen KS 12-265 (26+3).

CHAPTER 4

SEMIONOTIFORMES FROM KHORAT GROUP, NORTH-EASTERN PART OF THAILAND

4.1 Introduction

This chapter deals with descriptions of the osteology and scale microstructure of the ginglymodian taxa from the Late Jurassic to Early Cretaceous outcrops of the Khorat Plateau ordering in age arrangement from the outcrops of the Phu Kradung Formation to those of the Khok Kruat Formation. The osteological study of the fish material is based mainly on material from the older Phu Kradung Formation, whereas very rare specimens were found in the younger Sao Khua and Khok Kraut formations. Depending on the material preservation, the descriptions focus on morphological description and descriptions of the braincase.

Although there are many well preserved fish specimens from at least 4 outcrops in the Phu Kradung Formation, the microstructure examination is based primarily on referenced specimens from Phu Nam Jun, then comparisons are made with fish scales from the latter two formations in order to detect the evolutionary trend of the scales ornamentation pattern alongside the changes of osteological features.

The osteological descriptions of two of the best preserved taxa, *Thaiichthys buddhabutrensis* and *Isanichthys lertboosi*, together with phylogenetic analyses, are published in two peer-reviewed articles. Both papers are available in appendixes III and IV, and consequently their contents are not included in this chapter.

Collection abbreviations

KS (Kalasin): **TF** (Thai Fossil): Sirindhorn Museum, Sahat Sakhan, Kalasin Province; **PRC**: Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai, Maha Sarakham Province; **NRRU** (Nakhorn Ratchasima Ratchabhat University): Research Center of the Petrified Wood and Northeastern Mineral Resources, Suranari, Nakhorn Ratchasima Province.

Anatomical abbreviations- The nomenclature used in the description follow Grande (2010).

ar: ascending ramus of the parasphenoid; **Bo**: basioccipital; **Br**: branchiostegal ray; **Cha**: anterior ceratohyal; **Cl**: cleithrum; **Dpt**: dermopterotic; **Dsp**: dermosphenotic; **Es**: extrascapular; **Exo**: exoccipital; **Fr**: frontal; **fub**: basal fulcra; **fufr**: fringing fulcra, **fuun**: unpaired and froked basal fulcra; **Io**: infraorbital; **iocn**: infraorbital sensory canal; **Iop**: interopercle; **na**: neural arch; **Op**: opercle; **Pa**: parietal; **Pas**: parasphenoid; **Pcl**: postcleithrum; **plm**: middle pit line; **Pop**: preopercle; **Pro**: prootic; **ptf**: posttemporal fossa; **Ptt**: posttemporal; **Scl**: supracleithrum; **Sct**: scute; **So**: supraorbital; **Sob**: suborbital; **Sop**:subopercle; **Spo**: sphenotiv; **stf**: subtemporal fossa; **VII**: foramen for the facial nerve; **IX**: foramen for glossopharygeal nerve; **X**: foramen for the vagus nerve.

4.2 The Phu Kradung Formation

The Phu Kradung Formation is recognized in the lower part of the Khorat Group (Racey and Goodall, 2009). Its thickness varies from 1200 m in the basin centre to approximately 500 m on the basin flanks (Racey, 2009). It comprises fluvial channel sandstone, siltstone and mudstone with intermittent calcrete and was deposited in a mainly lake-dominated floodplain cut by meandering and occasionally braided river channels and is dated as either Late Jurassic based on fossil vertebrate evidence (Buffetaut and Suteethorn 2007; Tong *et al.* 2009) or Early Cretaceous on the basis of palynology (Racey and Goodall 2009), the detrital zircon thermochronology (Carter and Bristow 2003) and the similar appearance of shark teeth, *Heteroptychodus* sp. from Phu Kradung Formation localities with those from the Early Cretaceous Matsuo Group and the Ryoseki Formation in Japan, which is Hauterivian in age (Cuny, 2012).

4.2.1 The stratigraphic position

The Phu Kradung Formation can be divided into a lower and an upper parts, the latter is sandier and shows a gradational conformable contact with the overlying Phra Wihan Formation. It corresponds mostly to meandering rivers environment under a probable two season's semi-arid/ humid climate (Mouret, 1994; Racey *et al.*, 1996; Racey, 2009). The lower part corresponds to a lacustrine dominated alluvial floodplain. However, a lower and an upper member have not yet been officially established, although the uppermost part is sometime considered as a separate formation, the Waritchaphum Formation (Mouret, 1994; Philippe *et al.*, 2004). It consists of sandstone beds alternating with silty to sandy claystones, with pedogenetic horizons sometime reminiscent of the massive quartzitic sandstone body of the Phra Wihan Formation. For the majority, the Phu Kradung Formation has a comfortable contact with the overlying Phra Wihan Formation as mention above, but R. Liard (pers. comm.) observes a duality between low depositional energy, less mature, sandstones of the main Phu Kradung Formation and high flow velocity deposits, more mature, sandstones from the upper Phu Kradung and Phra Wihan Formations. This duality represents an event interpreted as a progressive changes or mix toward the basin source area. This transitional facies was used as an unformal stratigraphic marker. Interestingly, Liard has also found large silicified wood-stem at the base of this facies. Some authors assumed that the contact between both formations is a stratigraphic uncomformity (Mouret, 1994) or a possible sedimentary hiatus (Racey, 1996). They observed that the transitional facies sometimes shows an irregular surface, an evidence of erosion, and interpreted it as a disconformity in deposition. The presence of a stratigraphic break associated with transitional facies due to a regional shifting in the source rule area has been confirmed by Liard and Martin (2011). In addition, these authors have examined the stratigraphy of seven vertebrate-bearing localities (i.e.; Phu Nam Jun, Chong Chat, Phu Noi, Khok Sanam, Dan Luang, Dan Kerng and Kham Phok) in the Phu Kradung Formation and situated them in relation with the overlying Phra Wihan Formation (Figure 16). In term of stratigraphy, the Phu Nam Jun locality is located just below a Phra Wihan sandstones bed. There is less than 30 m of sediment between the base of the Phra Wihan sandstones and the site of Phu Nam Jun (observations follow the bed from the east border along the mountain nearby to the west side until Phu Nam Jun hill). The Chong Chat locality is located 10 m over to the last greenish-grey sandstone bed of the upper part of the Phu Kradung Formation and 10 to 20 m below the contact with the Phra Wihan Formation. The contact itself is not visible in that place due to rock falls and vegetation cover. The precise location of the Kham Phok site on a synthetic stratigraphy is difficult due to the complex topographic expressions of the area, rock falls and heavy weathering that prevent any clear positioning. It is clearly located inside the upper part of the Phu

Kradung Formation, not more than 50 m below the disconformity. Dan Luang and Dan Kerng sites are also difficult to precise stratigraphically. However, two vertebrate-bearing sites at least (Phu Noi and Khok Sanam) are located far below the identified transition and would be likely candidates for a Late Jurassic age (Liard and Martin, 2011).

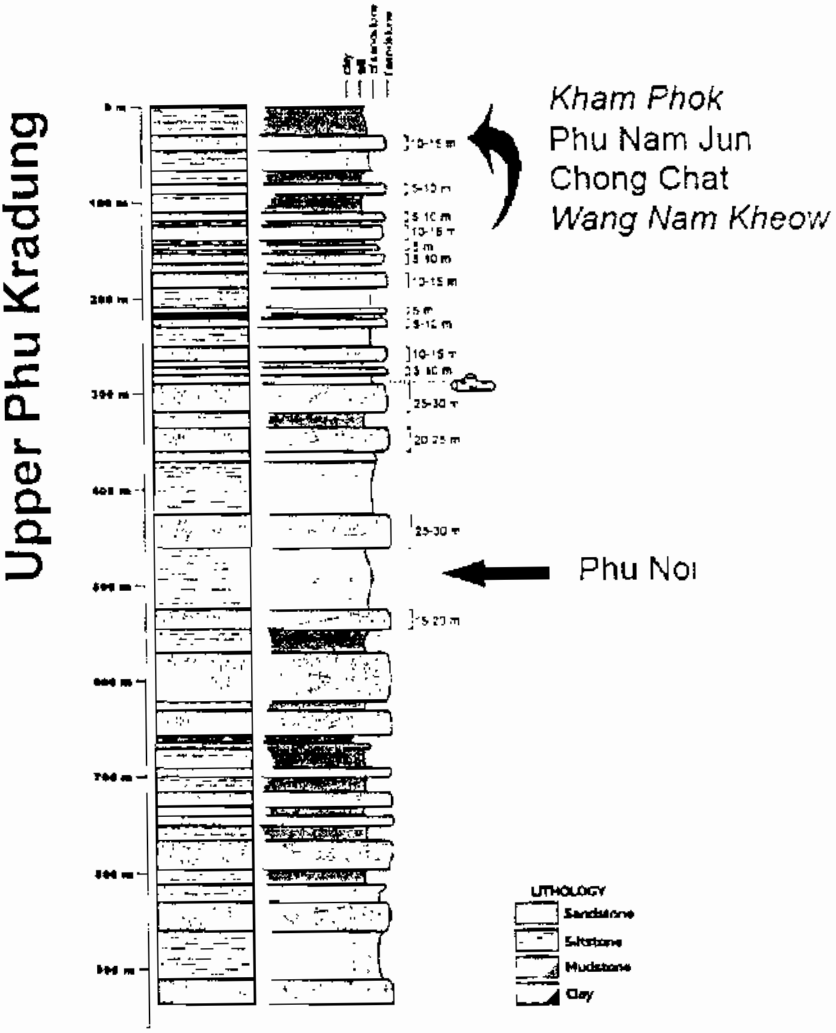

Figure 16 Log of the upper part of the Phu Kradung Formation. Figure courtesy of R. Liard (Cuny *et al.* in press).

4.2.2 The Localities

The fish remains described below were collected in five localities which are located in the lower and the upper parts of the Phu Kradung Formation.

The localities are ordering from the bottom to the top.

4.2.2.1 The Phu Noi Locality

4.2.2.1.1 Introduction

In September 2008, a new excavation called Phu Noi was opened in the Kalasin District, ca 75 kilometres to the NW of Phu Nam Jun. Although also located in the Phu Kradung Formation, this locality is situated in a lower (older) stratigraphical level than Phu Nam Jun. The locality of Phu Noi is located on the flank of a small hill at Ban Din Chi Kam Muang District, Kalasin Province (Figure 8). Stratigraphically, the Phu Noi locality is situated in the lower part of the Phu Kradung Formation, which is characterized by sandstone beds alternating with silty to sandy claystones. The deposits at Phu Noi consist of greenish gray sandy deposits interbedded with maroon siltstones, which are mica rich and contain laminated plant debris. The fish remains have been found in two main layers. The upper layer consists of an accumulation of dinosaur skeletons, which is ca 3 meters thick and dips ca 10 degrees towards the SE. The fossil assemblage consists of fragments of skeletons of sauropod dinosaurs, isolated theropod bones, fragments of skeletons of crocodile, turtle and shark remains, and includes two specimens of ginglymodian fishes. The lower layer is located ca 2 meters below the dinosaur assemblage, and has yielded two specimens of ginglymodians. However, there are no visible differences in term of sediment deposition between both layers. The studied specimens have cracks filled with sediment caused by roots from the soil, and were coated with a few centimeters of calcareous sandstone. We extracted the fossils from the field with the plaster jacket technique in order to keep their fins preserved, because they are very delicate and fragile structures. The preparation was performed using an air pen in the laboratory of the Sirindhorn Museum, Sahat Sakhan, Kalasin Province, where the specimens are housed. In the laboratory the upper part of the jackets were sawed in order to free the upper side of the specimens, which was visible in the field. The mechanical preparation does not aim at removing completely the matrix from the fossil, in particular in the fins' region. Details of the skulls were prepared under the binocular. The available sample comprises four specimens in total, all from Phu Noi locality of Kam Muang District, Kalasin Province: KS 36-2, a large sub complete specimen with complete skull visible from both sides; KS 36-3, fragments of the squamation of a smaller specimen with an almost complete skull except the snout region, lying above the caudal region of KS 36-2 (this part was destroyed during excavation) (Figure 17A); KS 34-281, portion of a skull showing in part the suspensorium; KS 34-380, skull roof with part of the braincase.

4.2.2.1.2 Systematic Palaeontology

Super Division HOLOSTEI sensu Grande, 2010
Division GINGLYMODI sensu Grande, 2010
Order LEPISOSTEIFORMES sensu López-Arbarello, 2012
Genus ISANICHTHYS Cavin & Suteethorn, 2006

Type species: Isanichthys palustris Cavin and Suteethorn, 2006

Isanichthys lertboosi Deesri *et al.*, in press
Figure 17

Description and Discussion --- see Deesri *et al.* in press and appendix III

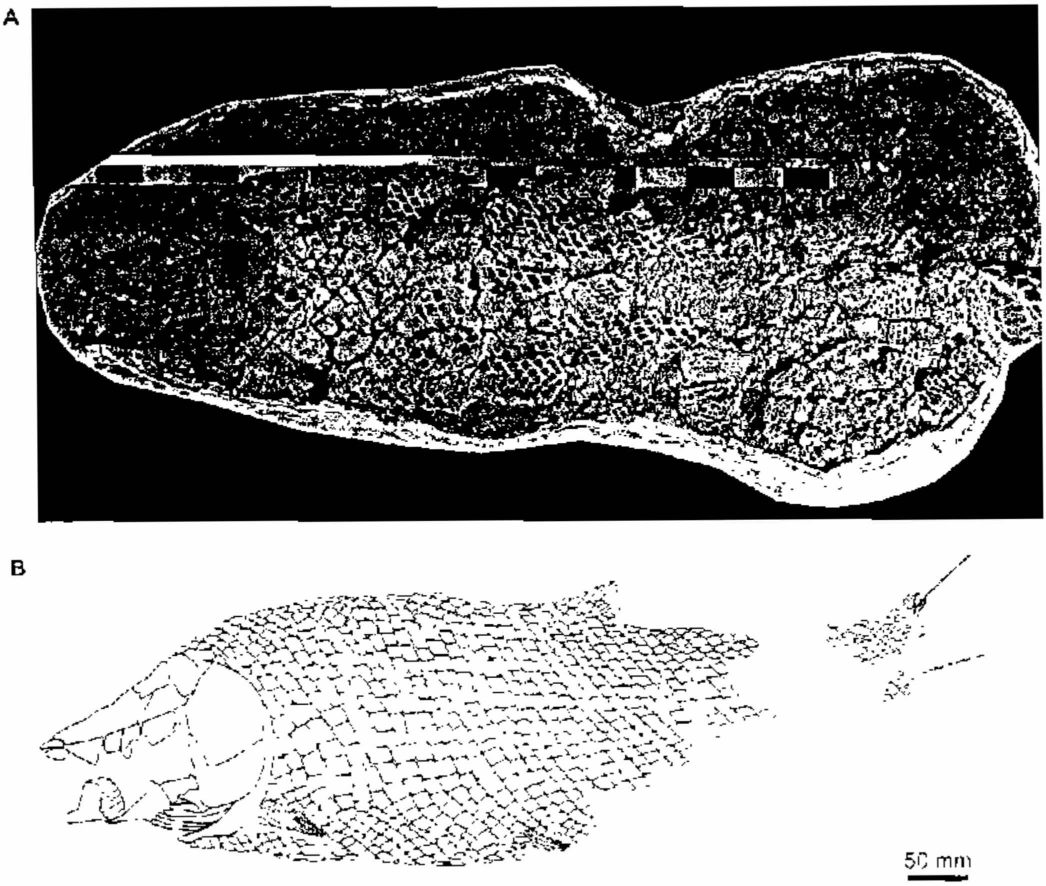

Figure 17 Holotype of *Isanichthys lertboosi* sp. nov. (KS36-2) in left lateral view.
A: Photograph. B: semi-interpretative line drawing.

4.2.2.1.3 Other Fish Remains

A piece consisting of dermal bones was collected from the surface of the Phu Noi locality, Kam Muang District, Kalasin Province. The specimen described below is now housed in PRC collection: PRC78.

Description of Specimen PRC78 (Figure 18)

The specimen shows only the lower part of the circumorbital ring of the right lateral side. It consists of 4 or 5 infraorbitals, 5 suborbitals at least located below and posteriorly to the orbit. The shapes of these infraorbitals are approximately rectangular, deeper than long with their ventral portion wider than their dorsal portion. The surface of the infraorbitals is slightly rough with strong knobs, and we cannot observe the sensory canal on the bone. The suborbitals are poorly preserved, with only the dorsal part visible. The shape of the ossifications is difficult to reconstruct because of preservation. There is one bone situated posterodorsally to the orbit, which is assumed to be the dermosphenotic, but we cannot precise its shape because it is badly preserved. The exactly number of infraorbitals is not available but we estimate it in between six and eight as they are generally in *I. lertboosi*. The shape, size and arrangement of the infraorbital and suborbitals, as well as the origin of the specimen, indicate that it could be referred with some confidence to *Isanichthys lertboosi*.

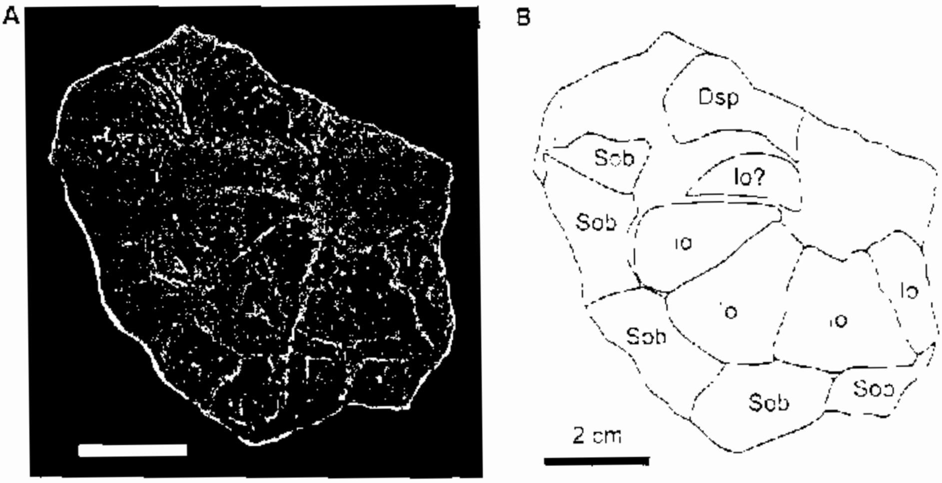

Figure 18 Photograph (A) and semi-interpretative line drawing (B) of fragment of the circumorbital bone of PRC78.

4.2.2.2 The Chong Chat Locality

4.2.2.2.1 Introduction

The locality named Chong Chat is situated in Non Sang District, Nong Bua Lamphu Province (Cuny *et al*., 2003, 2007; Cavin *et al*., 2007c, 2009; Lauprasert *et al*., 2011). The locality is located near the road connecting the Nong Bua Lam Phu Province to Udon-Thani Province, KM. 8, countryside road number NP- 4022. Stratigraphically, Chong Chat is located in the uppermost part of the Phu Kradung Formation, which is characterized by sandstone beds alternating with silty to sandy claystones. The deposits at Chong Chat consist of greenish gray sandy clay deposits interbedded with maroon siltstones, which contain plant debris. The fish remains have been found very close to the top of greenish gray sandy clays; the fish material consists mostly of isolated ganoid scales together with a single articulated incomplete specimen described herein. After preparation, the material is visible on both sides, the better preserved being the left side, in particular in the cheek region of the skull. Details of the skull, especially the lower jaw, were prepared under binocular microscope. TF 8026, Sirindhorn museum code; is a large sub-complete specimen with nearly complete dermal bones visible from both sides. The posterior part of the body, in particular the tail and the dorsal part, are not preserved.

4.2.2.2.2 Systematic Palaeontology

Super Division HOLOSTEI sensu Grande, 2010
Division GINGLYMODI sensu Grande, 2010
Order LEPISOSTEIFORMES sensu Grande, 2010
Genus THAIICHTHYS Cavin, Suteethorn, Deesri, 2013 and appendix IV

Diagnosis (emended): Ginglymodian fish with body deep, ca 2.6 times longer than high; preorbital region reduced; skull roof slightly concave in lateral view; frontal short, almost quadrangular in shape; more than one pair of extrascapulars; large dermosphenotic, few infraorbital (circa 9 or 10) and few suborbitals (generally 2); cheek region completely covered by bones, with an enlarged infraorbital, which contacts the preoperculum; numerous (circa 10), strong, slightly recurved teeth on the well-developed premaxilla; maxilla reduced with 4-6 small cylindrical teeth; no supramaxilla; mandible with an horizontal blade of bone at the symphysis that extends laterally; dentary bear ca 18 small teeth held horizontally with their acrodine apex upwards oriented; preoperculum with two limbs arranged at an approximately right angle, the horizontal branch is slightly shorter than the vertical one; 10 rays in the pectoral fin, 6 rays in the pelvic fin, 12 rays in the dorsal fin, 12 rays in the anal fin, 19 or more rays in the caudal fin; 46 scales along the lateral line.

Type species: Thaiichthys buddhabutrensis (Cavin, Suteethorn, Khansubha, Buffetaut, Tong, 2003)

Thaiichthys cf. *buddhabutrensis*

Figure 19-21

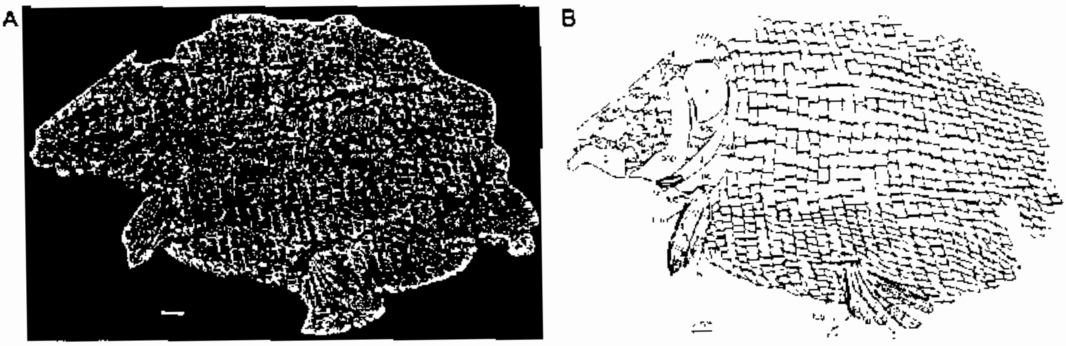

Figure 19 Photograph (A) and line drawing (B) of TF 8026, *Thaiichthys* cf. *buddhabutrensis*

Description

The posterior part of the skull is largely broken and better preserved on its left side. The general outline of the skull roof is curved in lateral view. The dimensions of the skull are as follows: the head is 155 mm in length (including the opercular series), and 110 mm in depth. The ossifications of the head have no ganoin cover and they are smooth on their surface except for the preserved part of the skull roof and some bones above the orbit presenting small tubercles (Figure 20C, D).

Skull roof (Figure 20). The frontal is best preserved on the right side; it is the longest element of the dermal skull roof and it is approximately rectangular, slightly narrowing anteriorly. The anterior frontal extremity possibly presents an indentation. The surface of the ossification is ornamented with tiny tubercles forming an irregular pattern mainly located on the posterior part of the bone. Several small grooves and ridges can be seen at mid length of the bone. Close to the lateral margin and at mid length of the bone, a dorsally convex ridge bounds dorsally a shallow groove, which was possibly overlapped by the dermosphenotic or supraorbital ossifications (Figure 20D). We estimate that the suture between both frontals is almost straight. The suture between the frontal and the parietal is slightly curved as visible on the left side. Both parietals are completely broken. The dermopterotic is damaged with only its anterior part preserved, and consequently it is difficult to estimate the shape of this ossification. Because the posterior part of the skull roof is completely destroyed, we cannot precise the exact limit between the dermopterotic and parietal. The lateral margin of the dermopterotic contacts with the dorsal border of the preoperculum and probably overlaps the anterodorsal corner of the opercle. The parietal and extrascapular are not preserved on this specimen. The nasal bone is not preserved in this specimen.

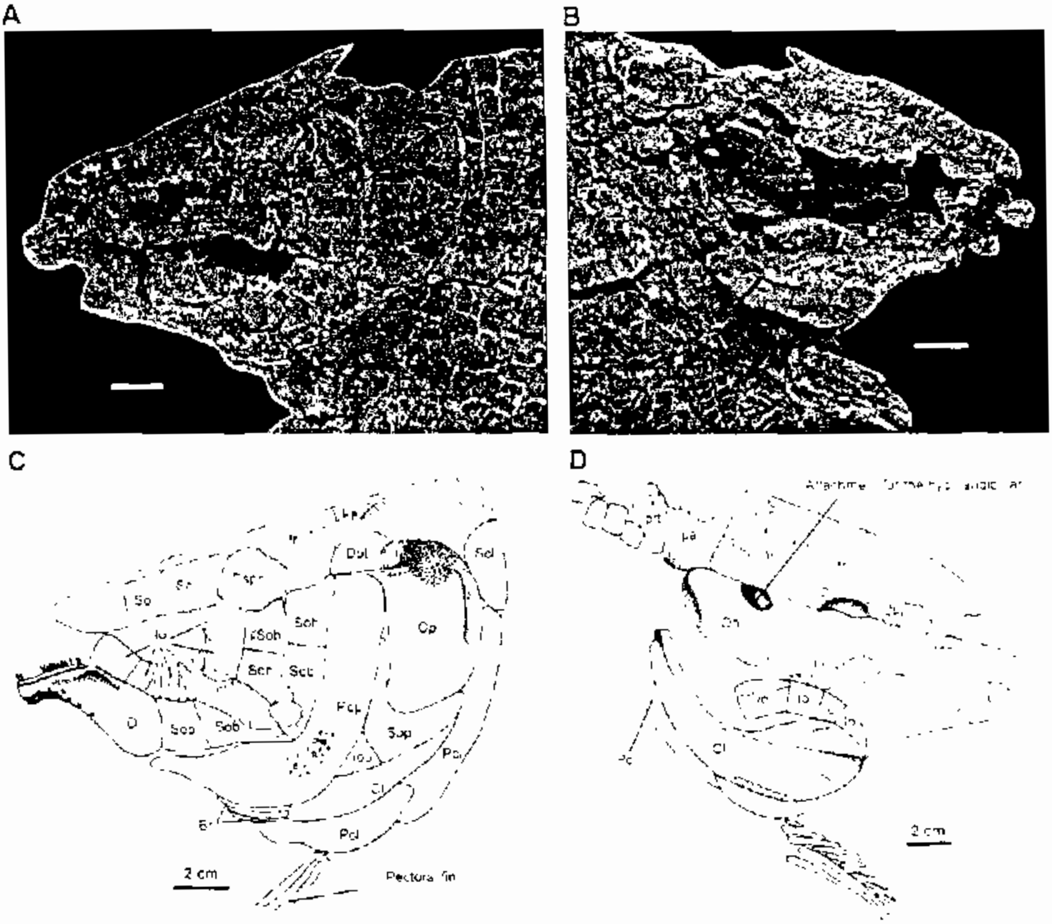

Figure 20 Photographs (**A**, **B**) and line drawings (**C**, **D**) of skull of TF 8026, *Thaiichthys* cf. *buddhabutrensis*

Circumorbital and suborbital series (Figure 20). The circumorbital is composed of a large dermosphenotic, two supraorbitals and at least six infraorbitals located posteriorly.

ventrally and anteriorly to the orbit. The first and second infraorbitals are located above the lower jaw; the four remaining infraorbitals are not preserved in situ, but we can reconstruct this series from the right side: it shows four articulate and square in shape bones, which were shifted and turned over, and lay underneath the cleithrum (Figure 20D). We assumed they were originally situated below and behind the orbit. On the left side, the dermosphenotic and two supraorbitals are shifted and they lay completely on the frontal. However, we can infer their original position from the shallow groove on the lateral edge on the other side of frontal. The shape of the dermosphenotic is slightly rounded with a waved margin visible on the dorsal margin of the bone. Its surface is ornamented with fine groove and ridges; although some part of the surface is destroyed, we assume that the ornamentation is located on the centre of the bone. The dermosphenotic was probably located on the posterodorsal part of the orbit as usual in neopterygians. Two supraorbitals are situated anterodorsally to the orbit. The anteriormost is small and rectangular in shape, the posterior one being rather elongated. They are ornamented with small tubercles on their surface. There are at least six suborbitals, four suborbitals are arranged in two longitudinal series of bones wedged between the posterior infraorbitals anteriorly, the dermopterotic dorsally and the preopercle posteriorly. They are squarish in shape, except the posteroventral one, which is deeper than long. Ventral to these four suborbitals is an empty space, in which two supplementary suborbitals at least should have been present as indicated fragments still preserved along the horizontal limb of the preopercle. A supplementary suborbital is preserved more anteriorly. In short, the suborbital series was probably mosaic-like, and covered completely the cheek.

Jaws (Figure 21). The left dentary only is preserved on this specimen, it is a robust ossification. An elongate crest is present along the anterior extremity, which is covered by a row of at least 13 conical teeth. Some teeth are broken, but we can count their number from the sockets still present. Each tooth is composed of a high cylindrical base, ca 3 mm in height, 1 mm in width and an acrodine cap which is characterized by a bulbous base and an inwardly curved and tapering apex (Figure 21C). The acrodine bulbous cap is short (1 mm high) compared to its base. The ventral margin of the mandible is strongly concave and its posterior edge is almost straight. Because of the preservation, the ossification is crushed and artificially increases its anteriorly depth. This condition indicates that the anterior extremity of the dentary developed laterally a horitontal bony blade. Because of the poor preservation, we cannot observe the suture between the dentary and the angular. Close to the ventral margin of the bone there is one row of ca 6 small foramens for the mandibular sensory canal (Figure 21B).

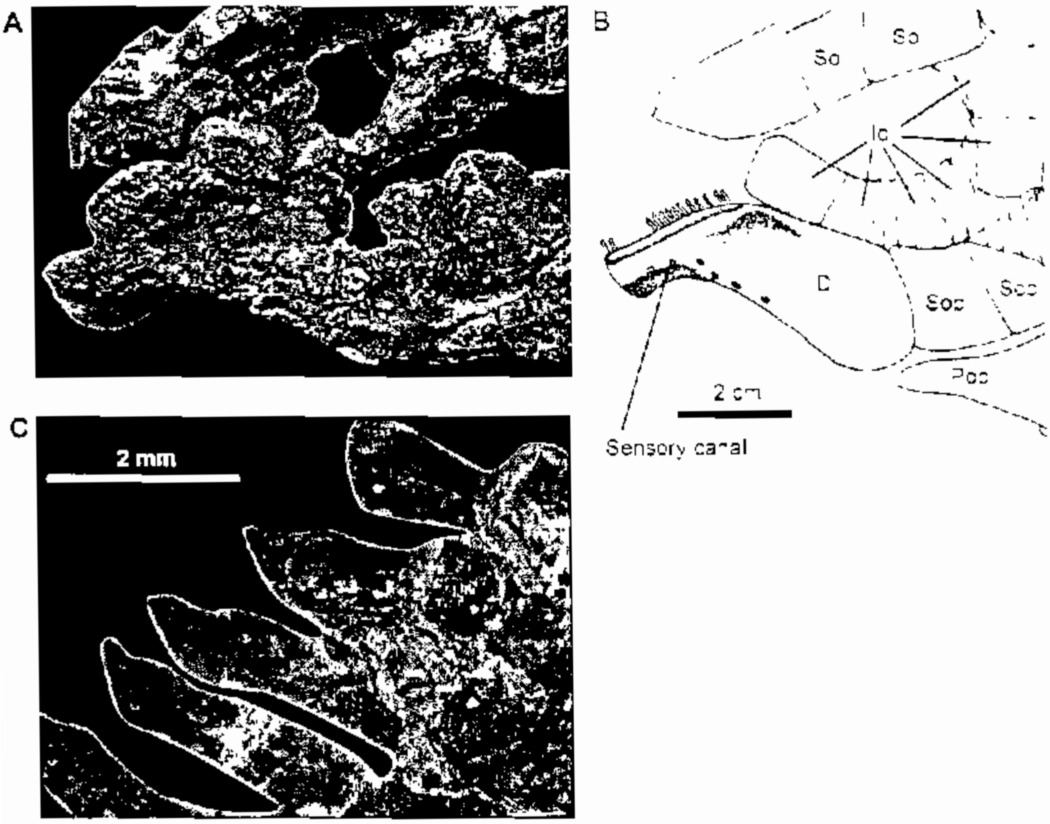

Figure 21 Photographs of dentary (A) and teeth (C) and semi-interpretive line drawing (B) of snout region of TF 8026, *Thaiichthys* cf. *buddhabutrensis*

Opercular series (Figure 20). The opercular series is complete, formed by the preoperculum, operculum, suboperculum and interoperculum. The preoperculum is present only on the left side (Figure 20C): its horizontal limb is shorter than the vertical one, and both limbs are arranged at almost right angle. The vertical branch has parallel margins without tapering dorsally and the ossification ends anteriorly as a blunt spine. The dorsal margin of the horizontal branch slightly widens in its posterior part before

4.2.2.3 The Phu Nam Jun Locality

4.2.2.3.1 Introduction

The locality of Phu Nam Jun in northeastern Thailand is an important Berriasian? continental fish locality worldwide. It is located in Tambon LaoYai, Kalasin Province and belongs to the Phu Kradung Formation (Cavin *et al*., 2004). It has yielded *'Lepidotes' buddhabutrensis* (Cavin *et al*., 2003) a semionotiform that was recently referred to a new genus of Ginglymodi, *Thaiichthys* (Cavin *et al*., 2013) and a single specimen of *Isanichthys palustris* (Cavin *et al*. 2006). The Phu Nam Jun outcrops lies in the upper part of the Phu Kradung Formation, a Late Jurassic-Berriasian geological unit, which constitutes the base of the Khorat Group as currently defined (Racey, 2009). Deposit at the Phu Nam Jun consists of greenish sand at the bottom of the excavated area and maroon-coloured mudstone at the top. The mudstone contains lens of sandstone composed of 70-80 percent clay and 20-30 percent silt, mica as well as concretions that enclose most of the specimens. The fish accumulation is approximately 1 m thick and dips approximately 12 degrees towards the SE. 288 specimens comprise different kinds of preservation, ranging from complete individuals with all the fins preserved to isolated 3D-preserved braincases.

4.2.2.3.2 Systematic Palaeontology

Super division HOLOSTEI sensu Grande, 2010
Division GINGLYMODI sensu Grande, 2010
Order LEPISOSTEIFORMES sensu Grande, 2010
Genus THAIICHTHYS Cavin, Suteethorn, Deesri, 2013

Type species: Thaiichthys buddhabutrensis (Cavin, Suteethorn, Khansubha, Buffetaut, Tong, 2003)
Figure 22

Description and Discussion--- see Cavin *et al*. 2013 and in appendix IV.

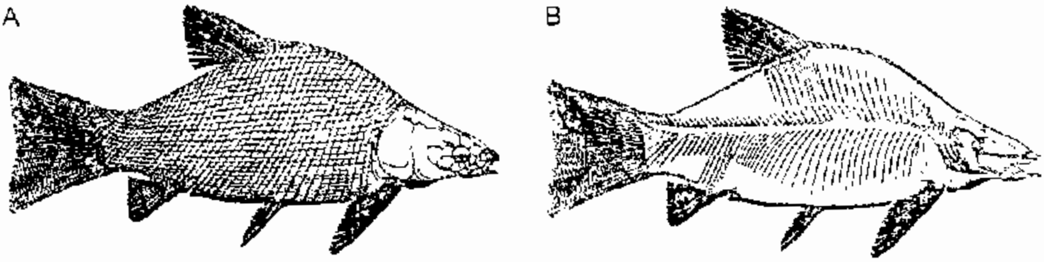

Figure 22 *Thaiichthys buddhabutrensis*, reconstruction (**A**) external view, (**B**) internal view with no scales and cheek and opercular ossifications.

Genus ISANICHTHYS Cavin & Suteethorn, 2006

Type species: Isanichthys palustris Cavin and Suteethorn, 2006
Figure 23

Description and Discussion--- see Cavin & Suteethorn, 2006. The species has been described and named based on a single specimen, TF 7764 (Thai fossil code and specimen housed in Sirindhorn collection).

Figure 23 *Isanichthys palustris*, (A) Photograph and (B) line drawing of type species (TF 7764) of *Isanichthys*. Scale bar 50 mm.

4.2.2.3.3 Other Fish Remains

Recently, isolated fragments of skulls preserved in the showcase of the Wat (temple) Buddhabutr have been stidied and provide new information on the anatomy of *I. palustris*, in particular of the braincase, which are not available on the holotype. Both specimens are now housed in PRC collection (PRC76, PRC77).

Description of Specimen PRC76; KS12-281

Specimen PRC76 is a nearly complete skull roof with anterior half part of the frontals missing, and with an estimated head length of ca. 12 cm (Figure 24). The bones of the left side are better preserved: it consists of the posttemporal, two left extrascapulars, complete dermopterotic and parietal, and with probably half length of the frontal. Moreover, a dermosphenotic and a piece of suborbital are preserved. On the right side, only half of frontal and parietal bones are preserved. The skull is slightly dorso-ventrally compressed, and the bones bear rough tubercles concentrated on the centres of ossification and radiating along ridges towards their margins. Braincase ossifications comprises the median orbitosphenoid, basisphenoid, basioccipital, and the paired pterosphenoids, prootics, exoccipitals and the autosphenotic, which is visible only on the left side while the epioccipital is visible on the right side.

Skull roof. The frontal bears coarse tubercles concentrated on the centre and several ridges radiating towards the margins, particularly on the median and posterior margins. We can observe the supraorbital sensory canal on the left frontal, which is the better preserved: it shows a series of large pores (7 pores visible) opening close to the lateral edge of the bone (Figure 24B). The frontal is slightly narrower anteriorly than posteriorly on its preserved portion. The median suture of the frontal is straight and aligned with the suture between both parietals, whereas the posterior margin of the frontal sutures with the parietal along an interdigitated suture and with the dermopterotic along a deep indentation. The parietal is rectangular in shape, about 1.6 times longer than wide. The parietal bear the same ornamentation with the frontal but roughly strong tubercles. The sutures of the parietal with other bones are straight except the anterior one, with the frontal, which forms a interdigitated line. There is a groove situated on the posterior third of the length which passes through the dermopterotic along an oblique line. It indicates the middle pit line. The dermopterotic is slightly larger than the parietal: it is rectangular in shape with the anterior margin narrower. The posterior suture with the lateral extrascapular is straight and there is a short oblique posterolateral margin with the opercle. There are two extrascapulars visible on the left side; the lateral one is much larger than the medial one. It is trapezoidal in shape and the smaller medial one is probably rectangular in shape. According to the arrangement on the left side, we assume that there were two pairs of extrascapulars showing the same pattern of ornamentation as on the parietals and frontals. The opening for the supratemporal sensory canal is not visible because of the strong ornamentation on the external surface of the skull roof bones. The posttemporal is visible as a triangular shaped bone with the ornamentation similar to the extrascapulars. We can also observe the ventral side of the posttemporal which overhangs the occipital region. The ventral process of the posttemporal is well-developed and protrudes as a slightly bent process, whose anterior extremity contacts the braincase ventrally (Figure 24D). We cannot determine yet if the contact is with an independent ossified intercalar, as present in *T.*

buddhabutrensis, or with the exoccipital as in *Macrosemimimus lennieri* and possibly in *Isanichthys*.

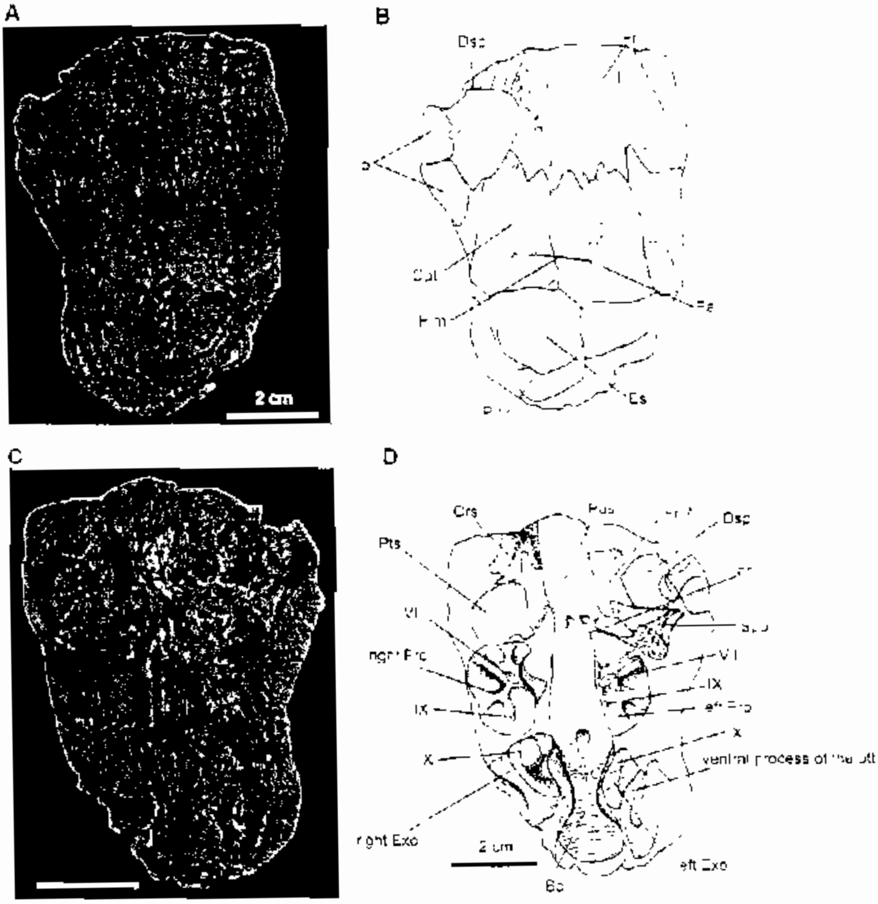

Figure 24 Specimen PRC76. (**A, C**) Photographs and (**B, D**) semi-interpretative line drawings of skull roof and braincase.

Endocranial braincase region (Figure 24C, D). The specimen PRC76 shows a fairly well-ossified and well- preserved braincase, which is slightly distorted laterally. The basioccipital is destroyed on its ventral face but its general shape can be reconstructed. The lateral side of the ossification shows a concavity in its mid-length. Because the ventral surface was destroyed, we cannot observe the foramen for the occipital artery. The suture between the basioccipital and the exoccipital ossifications is almost straight. The anterior ventral border of the basioccipital contacts the parasphenoid. According to the distortion of the braincase, especially of the left side, neither exoccipital nor prootic ossifications are in original position. The better preserved exoccipital is on the right side and shows a similar arrangement to *Thaiichthys*: it comprises a laterally-oriented face, extending above the basioccipital, and a horizontally oriented dorsal face. Both faces are separated by a rounded ridge which spreads out laterally. A small process is located on the dorsomedial edge of the bone. There are several small foramina that open in the mid-length of the rounded ridge, placed slightly on the posterodorsal surface of the ossification, for the dorsal and ventral roots of spinal nerves or the occipital nerve. The anteroventral surface of the exoccipital shows a large foramen for the vagus canal (X). On the right side, the foramen is not completely bone-enclosed and forms a notch in the anterior margin of the ossification. The exoccipital ossification meets its counterpart above the foramen magnum where the posterodorsal side of the exoccipital articulates with the first neural arch. We cannot determine with confidence if an intercalar is present or not. The epioccipital is visible on the right side and forms a deep cavity. There is no supraoccipital. The prootic is well-developed and contacts the exoccipital posteriorly. The posterior margin of the prootic is regularly curved, except the right one, which shows a slight concavity on its posteroventral margin. Prominent crests radiate from to centre of the bone and decrease in depth towards the centre of the ossification, where opens a large pore for the hyomandibular branch of the facial nerve (VII). Posterior to that large opening runs a shallow crest that delimitates a groove leading posteriorly to the small foramen for the glossopharyngeal nerve (IX). A notch, of unknown function, is dug in the anterodorsal edge of the prootic margin. The dorsal end of a ridge running from the facial opening to the posterior margin of the notch probably contacts the slightly shifted autosphenotic as indicate a surface of attachment. The anterior portion, which forms a groove between two ridges, is wedged between the posterior main body of the parasphenoid and the ascending ramus of the parasphenoid. The irregular in shape autosphenotic is visible only on the left side: it comprises a strong ridge anteriorly inclined and an anteromedial wing-like portion. The orbital part of the braincase of this specimen is formed by median basisphenoid and orbitosphenoid, which are visible on the right side; they are located at the level of the posterior limit of the frontal. The basisphenoid is the smallest bone of the preserved series and it is situated anteromedially to the ascending ramus of the parasphenoid. The bone is formed by a vertical lateral blade and a median, poorly preserved blade. The pterosphenoid has an irregular shape with it dorsolateral margin forming a rounding rim, whereas its medial margin is straight and the posterior margin has a notch, possibly for accommodating the middle cerebral vein by comparison with *M. lennieri* (‘*Lepidotes tombsii*’, Patterson, 1975). The posteromedial edge of the bone is sutured to the basisphenoid and the anterior edge sutured to the orbitosphenoid. The lateral surface of the bone is slightly concave. Only the posterior portion of the orbitosphenoid is preserved, it shows a deep notch nearly in its mid-depth. The lateral surface of the bone presents alternating slight grooves and ridges. The posterodorsal half sutures with the pterosphenoid whereas the ventral margin contacts the parasphenoid. The shape and proportion of the parasphenoid is difficult to reconstruct because of its missing anterior portion. The lateral margins of the bone form slightly parallel edges except at the level of the ascending rami, which present a constriction. The left ascending ramus of the parasphenoid only is preserved; it is posteriorly directed and contacts the anterior edge of the left prootic. Almost in the mid-length of the portion of the parsphenoid and posterior to the ascending rami is an excavation for the recess housing origin of subcephalic muscles. The surface of the parasphenoid ossification is smooth and with no trace of teeth.

Description of Specimen PRC77, KS12-282

Of the skull roof, only the parietals are preserved (Figure 25). They bear strong tubercles concentrated on the centres of ossification and several ridges radiating and extending into the margins of the ossifications. However, the bones are poorly preserved, especially on the lateral edge; we assume that the bones had a rectangular shape. The suture of the parietal with the frontal anteriorly forms a fine interdigitate suture, while the median suture between parietals is nearly straight. The suture between both frontals is not aligned with the suture between both parietals.

Endocranial braincase and parasphenoid. A part of the braincase is preserved, and slightly crushed especially on the right side. The basioccipital is damaged on the ventral face but its general shape can be reconstructed. The lateral side of the ossification shows a concavity in its mid-length. Because the ventral surface is destroyed, we cannot observe the foramen for the occipital artery. The suture between the basioccipital and the exoccipital ossifications is smooth. The anterior border of the basioccipital is situated at the same level as the anterior margin of the exoccipital. The exoccipital is a curved ossification. The exoccipital comprises a ventral laterally-oriented face, located dorsally to the basioccipital, and a concave posteriorly oriented dorsal face. Both faces are separated by a rounded ridge which spreads out laterally. Its anteroventral surface shows a large foramen for the vagus canal (X). The epioccipital ossifications are probably present but are very poorly preserved. There is no evidence of an intercalar and we suspect that this ossification was absent as in some ginglymodians, in particular *Isanichthys lertboosi*. The prootic is better preserved on the left side but it is damaged on its anterior and ventral parts, and its surface has slightly shifted under the exoccipital ossification posteriorly. The prootic bears a large foramen for the hyomandibular branch of the facial nerve (VII) nearly in the centre of the lateral face of the bone. The foramen for the glossopharyngeal nerve (IX) is small and opens posteriorly. The parasphenoid is completely broken, with just a fragment resting ventral to the limit between the prootic and basioccipital; it has a very smooth ventral surface.

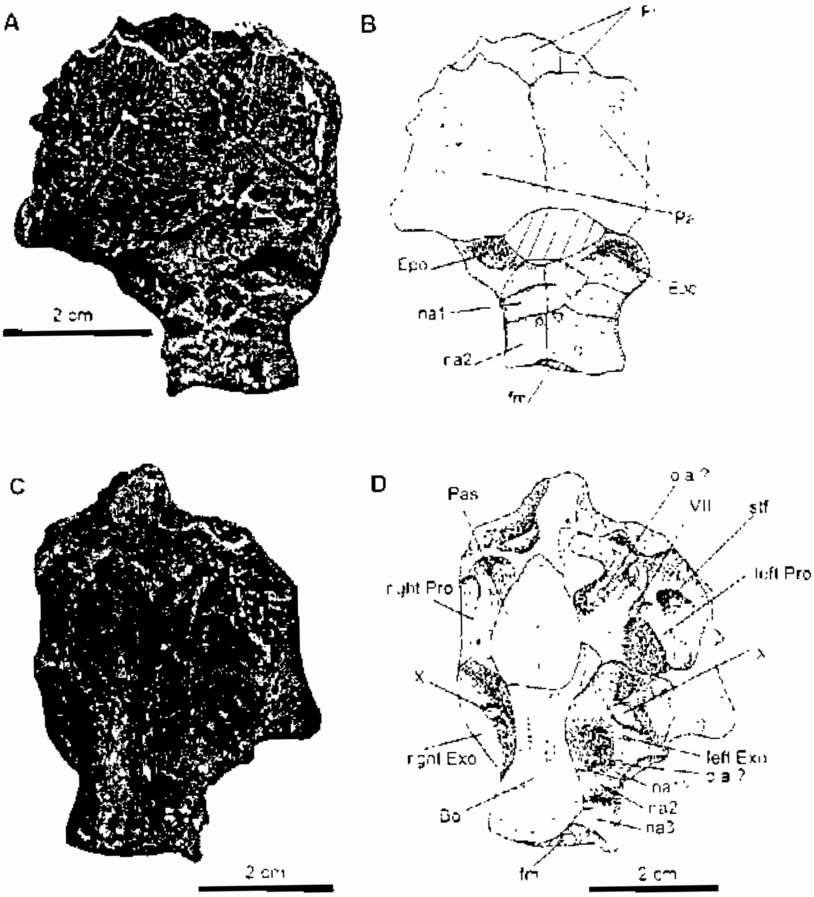

Figure 25 Specimen PRC77, (**A, C**) Photographs and (**B, D**) semi-interpretative line drawings of skull roof and braincase.

4.2.2.3.4 Comparison and Discussion

PRC76 is difficult to assign to one of the ginglymodian species present in the Phu Nam Jun locality. However, the shape of the parietal, the arrangement of the prootic, the gap of ossification between prootic and occipital bones, the exit of the Xth nerve through a notch indicate that this specimen likely belongs to *Thaiichthys*.

PRC77 belongs to the genus *Isanichthys* because it shares with the type specimen the strongly ornamented skull roof bones with tubercles and a reticulated pattern, the arrangement of the prootic, the absence of gap of the ossification between prootic and occipital bones, the exit of the Xth nerve through a foramen and the possible absence of the intercalar.

4.2.2.3.5 Microornamentation

The microornamentation study of fish scales from Phu Nam Jun locality focuses on three specimens, which are regarded as reference material: KS12-42, KS12-97 and KS12-265. Photographs of the ganoin surface of the scales were taken with a scanning electron microscopy; sixteen scales from 8 positions on different part of the body of KS12-97 and KS12-265 reveal tubercles (Figure 26-27), but not on KS12-42 because all samples of this specimen were coated by hardener and the SEM can not access to the ganoin layer. Tubercles on the ganoin scales of specimen KS12-97 have their width range between 3.6 to 4.27 μm except for the position L(26+3), which is relatively small, nearly 3 μm, and with their length range between 3.5 to 4.2 μm. The same condition is true for position L(26-3), with a shorter length, 2.6 μm, and the position L(33-6) is not much different with a length of nearly 3 μm. The average dimensions of the tubercles of specimen KS12-97 are width and length of 3.75 and 3.52 μm respectively, indicating that the tubercles are roughly rounded in shape. The average intertubercle distance is 7.84 μm. The scale in position L(26+3) shows apparently the shortest intertubercle distance, as well as the smallest tubercles size. Contrary to the tubercles on the ganoin scales of specimen KS12-265, the width ranges from 3.0 to 4.3 μm and the length ranges from 2.5 to 3.5 μm. The average dimensions of the tubercles of specimen KS12-265 are width and length of 3.5 and 3.0 μm respectively, indicating that the tubercles are generally oval in shape. The average intertubercle distance is 8.1 μm. The position L(23) shows apparently the shortest intertubercle distance, as well as the smallest tubercles size. Compared between KS12-97 and KS12-265, the tubercle size of KS12-97 is larger than KS12-265 but the distances between the measurement is reverse. In conclusion, when we compare microstructure between different parts of the body (parameters) in a single specimen, the parameters slightly differ. In addition there are differences between different individual fish even if they belong to a single population as for samples from KS12-97 and KS12-265. The measurements and distances between the measurements in KS12-97 and KS12-265 are summarized in table 1 and table 2. These hypotheses will be statistically tested.

Photographs of plots of tubercles on a micrograph of the scale KS 12-97 and KS12-265 and tables of raw data of measurements of the tubercles and of the distances between them are present in appendix I and appendix II.

Table 1 Measurement of the tubercles and of the distances between them of KS12-97

Parameter	Measurements	Number of distances	Average width	Average length	Average distances
(1)L3-3	T46	110	3.61	3.94	7.99
(2)L12+1	T34	78	3.72	4.18	9.02
(3)L15-3	T31	70	3.77	3.8	7.61
(4)L16+8	T33	75	3.62	3.77	7.86
(6) L23-5	T33	77	4.16	3.54	8.54
(7)L26+3	T34	82	2.9	2.58	6.51
(8)L30+2	T33	75	4.27	3.48	7.47
(9)L33-6	T34	83	3.98	2.93	7.72
			3.75	3.52	7.84

Table 2 Measurement of the tubercles and of the distances between them of KS12-265

Parameter	Measurements	Number of distances	Average width	Average length	Average distances
(2)L12+1	T33	77	4.31	3.53	8.11
(3)L15-3	T31	71	3.24	3.34	9.97
(4)L16+8	T33	77	4	3.4	7.85
(5)L23	T32	74	3	2.47	6.94
(6) L23-5	T30	68	3.23	3.1	7.59
(7)L26-3	T32	74	3	2.71	8.8
(8)L30+2	T31	72	3.25	2.8	7.97
(9)L33-6	T32	70	4.04	2.7	7.63
			3.51	3.00	8.1

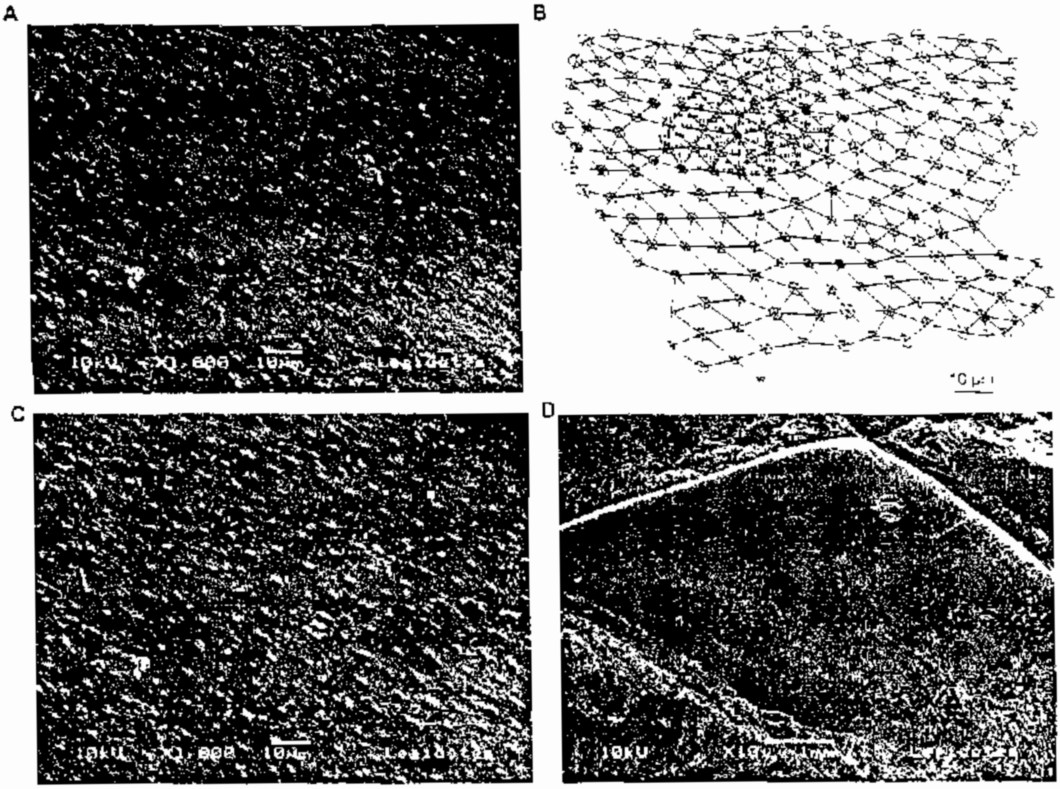

Figure 26 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L26−3, B: measurement of the tubercles (34 measurements) and of the distances between them (82 measurements). C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

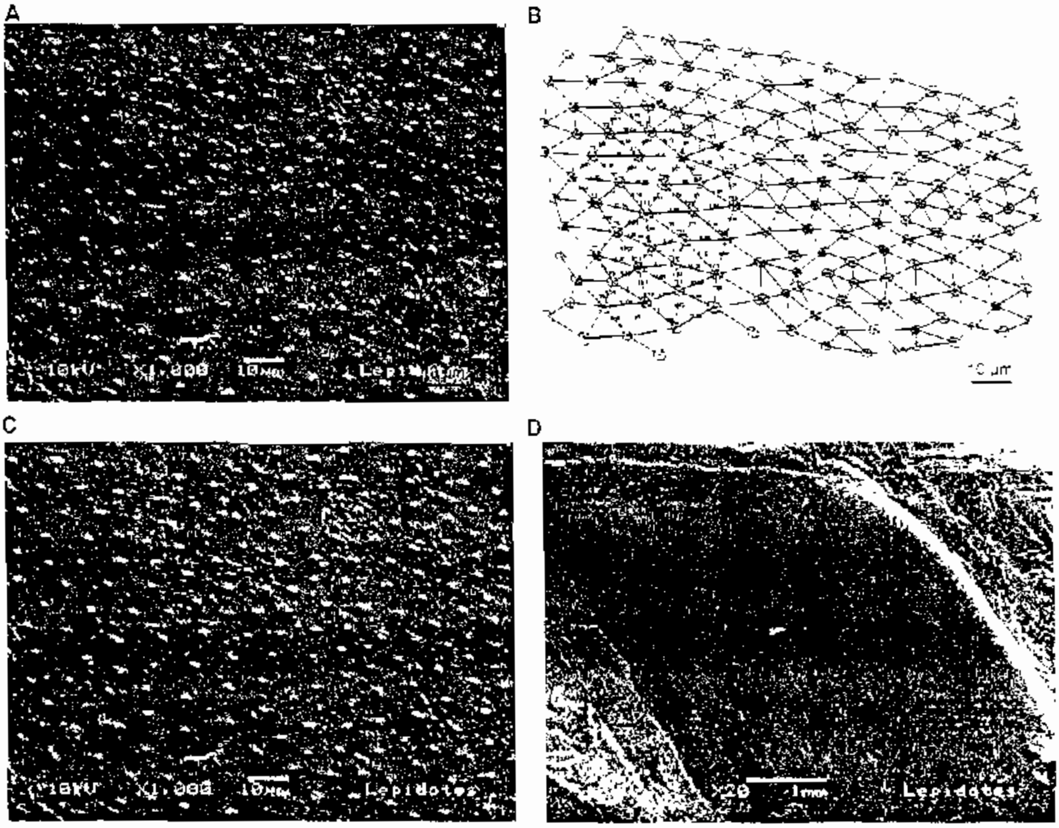

Figure 27 Specimen KS12-265. A: Plot of tubercles on a micrograph of the scale L26+3. B: measurement of the tubercles (32 measurements) and of the distances between them (74 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

4.2.2.4 The Ban Nong Rua Locality

4.2.2.4.1 Introduction

The first Mesozoic fossil locality discovered in the Nakhorn Ratchasima Province was the theropod dinosaur footprint site at Khao Yai National Park, which is located in the Phra Wihan Formation (Lockley *et al.*, 2002, 2006; Le Loeuff *et al.*, 2009). A little bit later, a cooperation between the Petrified Wood Museum and a Japanese Team have excavated another site with numerous dinosaur bones and bone fragments together with isolated teeth of the freshwater shark *Thaiodus*. The site, located near the village of Ban Khok Kruat, was referred to the youngest Aptian Khok Kruat Formation (Cappetta *et al.*, 1990). Before this excavation started in Ban Khok

Kruat site, the Petrified Wood Museum had collected in the Phu Kradung Formation two slabs of sandstones, which preserve the imprint of an articulated fish and its counterpart. Unfortunately, the slabs of rock were not located in-situ. They were located at an offering site for the spirit of Chao Phor Khun Satan nearby the Khun John water fall (Figure 28) used by the respectful people from Ban Nong Rua and people from adjacent villages. This discovery is the first one of a fish from the Phu Kradung Formation situated so far southward from the Phu Phan Mountain Range.

The study is based on a single individual (NRRU 6011-01) housed in the Petrified Wood Museum, Nakhorn Ratchasima Province, Thailand. The specimen is preserved as negative imprint with impressions of the articulated fish visible from both sides (Figure 29). A silicone peel provided a good-quality copy of the positive fossil: the cast is well observable on both sides, except some part of the skull especially the roof bones and the chin area, which are unobservable (Figure 31A, B).

Figure 28 Photographs of the 2 slabs of sandstone with the imprint of articulated fish (black arrow point) situated in front of the spirit Chao Phor Khun Satan's house of Ban Nong Rua village.

Geological settings

The locality of Ban Nong Rua is located in the Khao Phu Luang national forest of Wang Nam Kheow District, Nakhorn Ratchasima Province where the presence of the Phu Kradung outcrop but the exact stratigraphical position of the slabs is unidentified, as it was not found in-situ, we assume from the thick sandy matrix containing the imprint that it comes from the upper part of Phu Kradung Formation.

Material and method

The single specimen is preserved as a negative imprint and presents the impression of an articulated squamation with all fins and the skull preserved. The left and right lateral sides are preserved on two slabs of sandstone (Figure 29). Details of the skull, especially the cheek bones, are better preserved on the right side. NRRU 6011-01A and B represent the silicone copies of the part and counterpart, and illustrate the lateral sides of the specimen with nearly all the dermal bones and all the fins. Silicone copies were prepared at the Petrified Wood Museum (Figure 30), Amphoe Muang, Nakhorn Ratchasima Province, where the slabs of specimens are housed. Details of the skulls need to be lighted with a nearly horizontal beam in order to reveal the fine limits of dermal bones. The nomenclature used in the description follows Grande (2010).

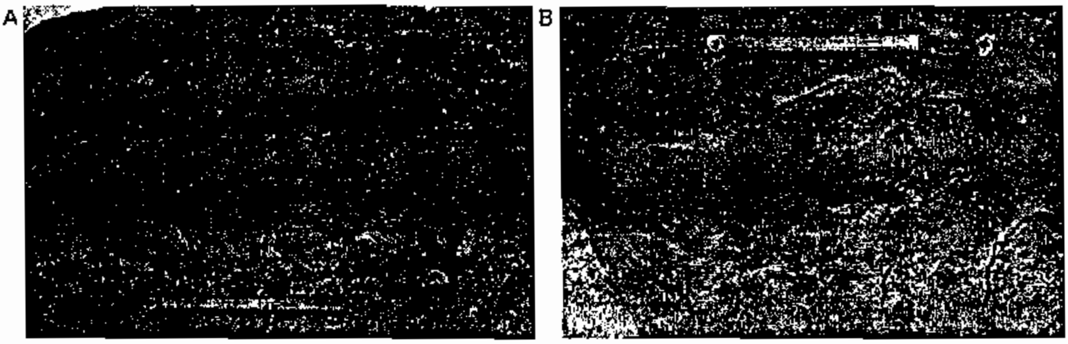

Figure 29 Photographs of the left and right lateral sides of the negative imprint in the matrix with the articulated impression of the fish from Ban Nong Rua locality.

Figure 30 Photograph of the preparation of silicone copies at the collection of Petrified Wood Museum. (**A**), photograph of a silicone peel (**B**).

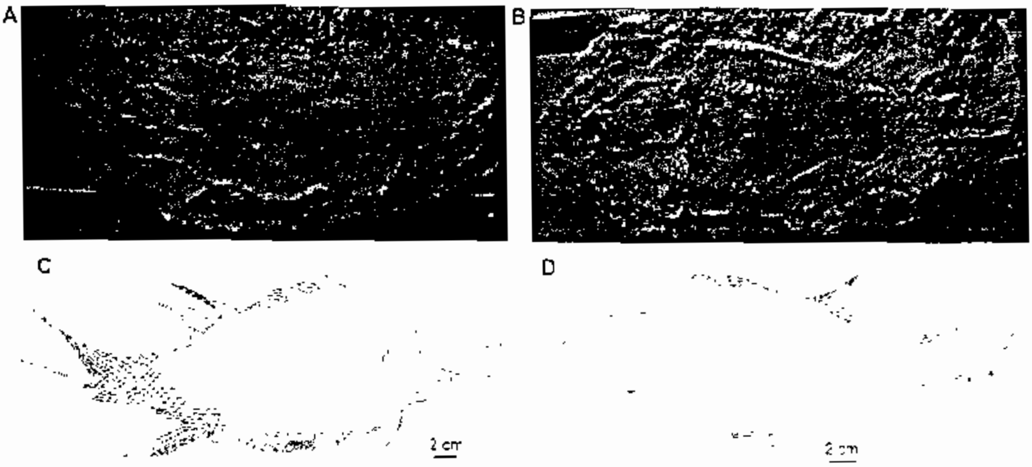

Figure 31 Photographs and simplified line drawings of the silicone cast of NRRU 6011- 01 on both sides. A, C: NRRU 6011-01B (part); B, C: NRRU 6011-01A (counterpart).

4.2.2.4.2 Systematic Palaeontology

Super Division HOLOSTEI sensu Grande, 2010
Division GINGLYMODI sensu Grande, 2010
Order and Family *incertae sedis*
Figures 31-37

Description

General features and proportions.– The general outline of the fish shows a gently curved ventral border and a dorsal border with a distinctly abrupt hump in the nape (Figure 31B, D). The standard length (SL: the length from the tip of snout to the base of the caudal fin) of the studied specimen is ca 300 mm and the maximum body depth, measured mid-way between the insertion of the pectoral and pelvic fins is 11.5 mm. The head is 950 mm long including the opercular series, and 65 mm in depth. The orbit is relatively large with a longitudinal diameter of 20 mm. The ossifications of the head have no ornamentation except the first and the second anterior infraorbitals bearing some tiny tubercles restricted at the ventral border of the bone, and appearance of a ridge is visible on the surface of the posterior most infraorbital and runs through the dermosphenotic, indicating the path of the sensory canal. Both unpaired fins are located close to caudal peduncle (predorsal ca 200 mm, preanal ca 225 mm). The insertion of the dorsal fin is right in front of the level of the anal fin. The dorsal ridge scales are large and bear an elongate posterior spine (Figure 35). The caudal peduncle is relatively narrow comparing to the body depth, approximately 3 times shallower (caudal peduncle ca 40 mm).

Skull roof (Figure 32). The frontal, parietal, extrascapular and dermopterotic are not observable. However, the trace on the counterpart of the skull shows the general outline of the frontal, parietal and the extrascapulars, which is slightly concave anteriorly.
The path of the supraorbital sensory canal is visible as a groove on the anterior portion of the frontal. The length of the frontal is approximately 45 mm long. The surface of the bone from the imprint shows no trace of the ornamentation. Although, the total shape of

the frontal is not visible, we can confirm that the frontal is quite long, probably 4 times longer than wide. The parietal measures ca 20 mm in length. Its surface is smooth. The shape of the dermopterotic is not visible. Details of the extrascapular are difficult to see on the specimen; our reconstruction of this bone is tentative. The nasal bone is not visible in this specimen.

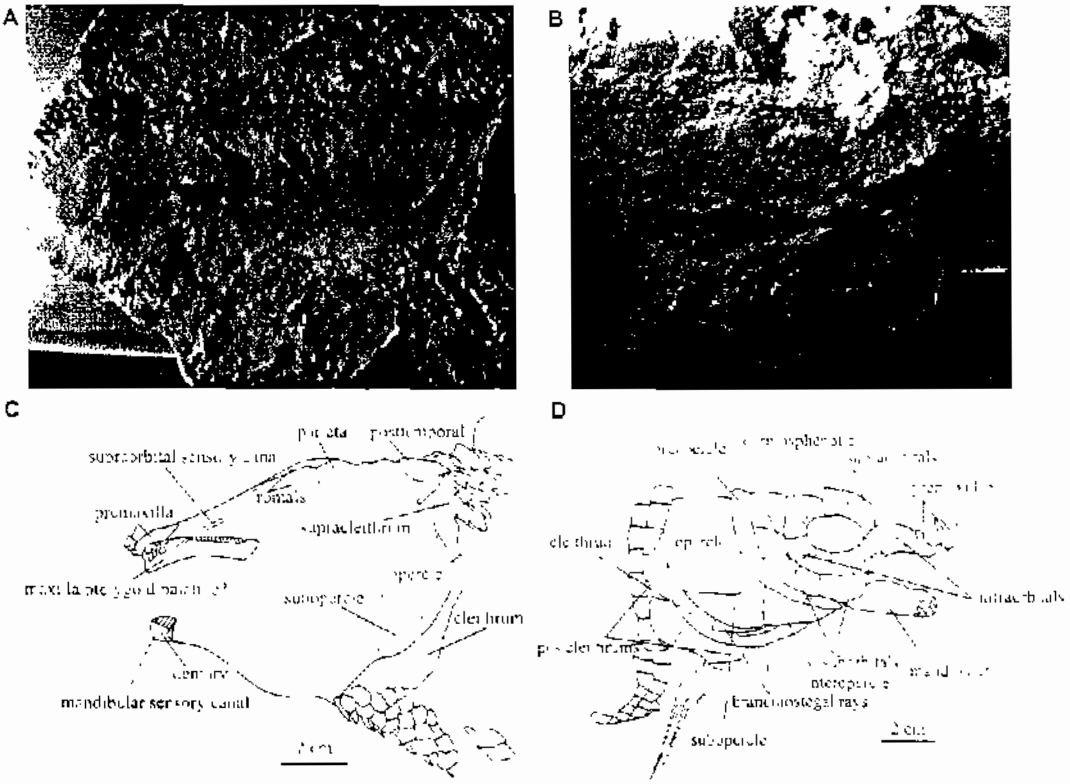

Figure 32 Skull of NRRU 6011-01 in left and right lateral views. A, B: Photographs; C, D: semi-interpretative line drawings.

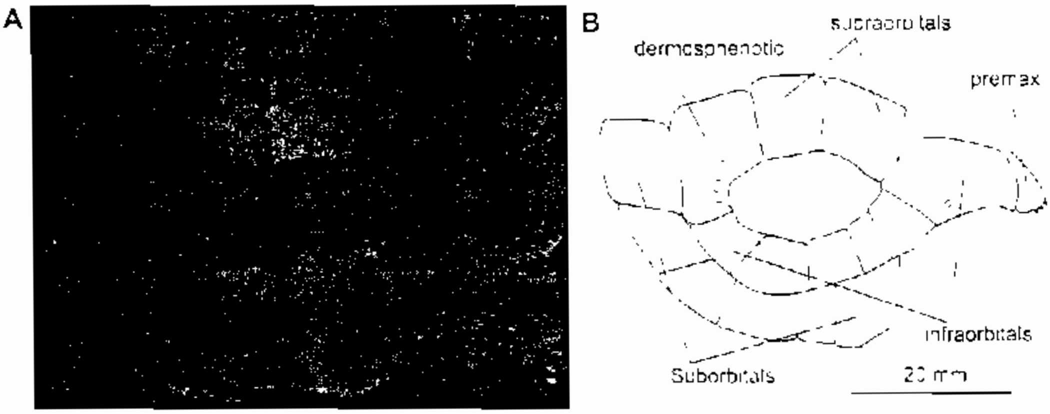

Figure 33 A: Photograph, B: semi-interpretative line drawing of the upper jaw of NRRU 6011-01B.

Circumorbital and suborbital series (Figure 33). The circumorbital series is composed of a large dermosphenotic, two supraorbitals and at least six infraorbitals located ventrally and anteriorly to the orbit. The first, anterior most infraorbital is the largest and does not contact the orbit, except a tiny contact of its posterodorsal corner. We consider that this infraorbital is homologuous to the anterior infraorbital(s) with no contact with the orbit, which is a character shared by most ginglymodians. It is longitudinally elongate, roughly rectangular in shape, and about 1.7 times longer than deep. Its dorsal and ventral margins are gently curved while the anterior and posterior margins are oblique. The surface of this bone is smooth but close to its ventral margin is a narrow curved groove. Under that curved groove are several rugae regularly spaced running to the ventral edge of the bone. The second infraorbital is approximately rectangular and is deeper than long with its ventral margin longer than the dorsal margin. Regularly-spaced rugae occur in continuation with the first infraorbital, but we cannot observe the canal. The third infraorbital is the smallest circumorbital bone; it has a rectangular shape. It is articulated with the neighbor infraorbital laterally and the anteriormost suborbital ventrally. The three remaining infraorbitals are approximately square in shape, with their dorsal and ventral margins apparently curved. Their surfaces are smooth but the dorsalmost one present a ridge running at its dorsal margin that reaches the dermosphenotic. The shape of the dermosphenotic is rather trapezoidal with its anterior margin concave, following the shape of the orbit. Close to the anterior margin, at the half depth of the bone are present at least three nodes-like arranged in the continuation of a ridge of the posteriormost infraorbital. These nodes on the dermosphenotic and the ridge on the infraorbital indicate the presence of the path of infraorbital sensory canal and the connection with otic sensory canal. The dermosphenotic is located on the posterodorsal part of the orbit. It articulates with the posterior supraorbital anteriorly, the dermopterotic dorsally, the dorsalmost suborbital posteriorly and the posteriormost infraorbital ventrally. Two supraorbitals are situated anterodorsally to the orbit. The anteriormost is larger, square in shape and contacts the anteriormost infraorbital, the posterior one being rather rectangular and deeper than long. It seems that they have tiny tubercles restricted only on their ventral edges, which are most clearly visible on the anterior one. There are six suborbitals arranged in a single row wedged between the third infraorbital and the dermosphenotic anteriorly, the dermopterotic dorsally and the preopercle posteriorly. The surface of these bones lacks ornamentation. Their shapes are rectangular but they show variations: the anteriormost suborbital is subrectangular with its ventral margin forming a curvy line while the other margins are straight. The second suborbital is approximately rectangular, deeper than long, with its anterior margin longer than the posterior margin. The third suborbital is elongated, rectangular, with a gently concave dorsal border and convex ventral border. It is ca 1.7 times longer than wide. Among the six suborbitals, the fourth and the fifth are quite similar in shape. They are sub rectangular, with the dorsal border shorter than the ventral border and the ventral margins gently convex. The most dorsal suborbital is ca square in shape and it is the largest one in the series.

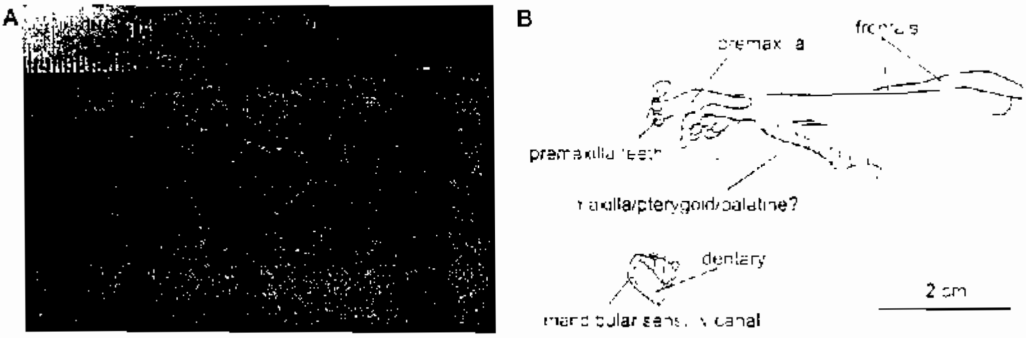

Figure 34 A: Photograph, B: semi-interpretative line drawing of the upper jaw of NRRU 6011-01A.

Jaws (Figure 32, 34). The dentary is partially preserved on both sides of this specimen; only the anterior portion of the bone with a pack of teeth is visible in lateral view. The visible part shows apparently parallel curved margins. It seems to present two rows of small foramens for the mandibular sensory canal close to the dorsal margin of the visible part. However, it is uncertain as they appear exactly in the broken area. According to the preservation, we cannot estimate the exact number of these foramens in addition to the exact shape of the bone. The teeth on the dentary ossification are probably arranged in four lines, which run along the horizontal axis of the bone from the posterior to the anterior margins. The arrangement of the teeth in these 4 lines shows variation of the size; teeth on the posterior most line are large and decrease in size gradually. The largest tooth is ca 3 mm in height. Each tooth is composed of a cylindrical base, 1 mm high, and of a small bulbous tiny acrodine apex ca 2 mm high. A bone on the upper jaw with seven teeth visible on the counterpart of the silicone peel is present. This bone may possibly be referred to the maxilla; it is thin and elongates. The dentigerous portion is restricted on its anterior margin. However, this ossification could also be interpreted as a compound structure including part of the pterygoid ossification and the palatine. There are several teeth preserved on the premaxilla but their exact number is unknown. The teeth are similar in shape, but slightly smaller, than the teeth borne by the dentary and maxilla. The premaxillary ossification is relatively small with its anterior rim rounded. Posteriorly, the narrow and elongate nasal process of the premaxilla seems to extend under the frontal (Figure 34). Based on the location of the lower and upper jaws, it seems that this fish had a wide gape.

Opercular series. The opercular series is complete, formed by the preopercle, opercle, subopercle and interopercle (Figure 32D). The preopercle is a distinctly narrow and curved bone. The bone seems to have parallel lateral margins, except at the postero corner which show a gently convex contour, making slightly broader the mid depth of bone. There is no tapering dorsally and the ossification ends anteriorly as a blunt spine. A series of seven large pores located in the centre of the bone represent the preopercular sensory canal. The operculum is relatively square in shape, about 1.2 times deeper than wide (32 x 25 mm). The anterior border is straight, while the posterior border is rather convex. The dorsal margin is not clearly visible but we can assume it has straight line.

The external surface is smooth. Ventrally, the opercle fits with the dorsal margin of the subopercle. The subopercle is relatively shallow, with its maximum depth about 0.4 of the depth of the opercle. The anterior ascending process of subopercle is relatively low; its height is about one third of the opercle depth. Posterior to the ascending process, the subopercle narrows posterodorsally, so that the dorsal border of the bone is concave while the ventral border is convex. The posterior border of the subopercle follows the slight convexity of the posterior border of the opercle. Anteriorly, the subopercle articulates with the interopercle through a vertical suture. The interopercle is visible as a large triangular bone; its maximum depth and length are equal to the subopercle. Its anteriorly extends up to the level of the anterior end of the preopercle. The interopercle articulates posteriorly with the subopercle and is laterally overlapped by the ventral portion of the preopercle.

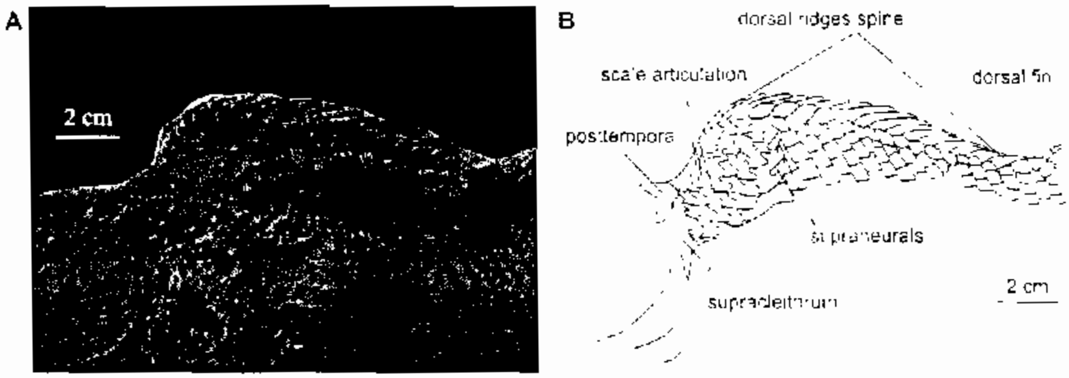

Figure 35 A: Photograph, B: semi-interpretative line drawing of the squamation of NRRU 6011-01A.

Hyoid arch and branchiostegal rays. We cannot distinguish the ceratohyals. Similarly, the number of branchiostegal rays is difficult to establish, but at least two can be observed laying under the subopercle (Figure 32D).

Pectoral girdle. The posttemporal and the supracleithrum are visible only from the internal side of the couterpart (Figure 32C). The posttemporal appears as a deep crescent-shaped bone excavated anteriorly. The supracleithrum shows a vertical groove situated close to the anterior margin of bone. This groove possible corresponds to the path of supratemporal sensory canal. It is difficult to recognize the shape of the bone as we cannot see its posterior margin. The cleithrum and the postcleithrum are visible on the right side. However, the cleithrum ossification was covered by the matrix, but we can estimate its shape as a large crescent-shaped ossification. There are four postcleithra, all with a smooth surface. The anterior most is the smallest of the series (Figure 32D).

Cephalic sensory canal. The supraorbital sensory canal is visible as a groove on the internal side of frontal of the silicone copy of left side. Because we have seen only the anterior trace of this groove, we don't know if this canal runs through the parietal or the dermopterotic. Only the path of the infraorbital sensory canal and of the preopercular sensory canal are visible on the better preserved side of the skull bones, i.e. on the right side of silicone copy, as well as some evidence of the mandibular sensory canal which is partially preserved on the left side. There is no evidence of a sensory canal running within the supraorbital bones. The preopercular sensory canal is present as a series of large pores located in the centre of the ossification (Figure 32D). The mandibular sensory canal can be observed as at least three pores arranged in one line close to the dorsal edge of the bone (Figure 34B).

Pectoral fins (Figure 32D).– the pectoral fin is slightly twisted anteriorly; it consists of at least three basal fulcra, the anterior one possibly being unpaired and two posterior paired ones. Because sediment partially covers the pectoral fin, we are not sure if there are fringing fulcra or not. The visible five rays are very long, representing 52% of the head length (pectoral fin length = 50 mm, head length = 95 mm) and they appear to be un-segmented.

Pelvic fins.–The pelvic fin is mostly destroyed; we know only its location at the level of the 9th and 10th transverse scale rows, halfway between the pectoral and anal fins. The pelvic fin is originating at the level of the 4th vertical scale rows up from the ventral midline scales (Figure 31A, C).

Unpaired fins (Figure 36).–The dorsal and anal fins are almost complete. The dorsal fin inserts a little in front of the anal fins; it is composed of 4 basal fulcra, approximately 5 fringing fulcra and 9 rays (Figure 36A, B). The proximal un-segmented portion is long: it is nearly half the fin length of the anterior ray and gradually decreases posteriorly. The branching pattern of the dorsal fin rays is asymmetric, the anterior first is unbranched and the second ray branches at least once then the following rays show four branches and fine segmentation. The length of the dorsal fin is nearly half the head length. Although we cannot see the very tips of the rays, we assume that the distal margin of the fin was straight.

The anal fin originates right behind the level of the 20th transverse scale rows. It is slightly smaller than the dorsal fin, comprising 3 basal fulcra, at least 3 stout fringing fulcra, and approximately 11 anal fin rays (Figure 36C). The proximal un-segmented portion represents one third of the whole length of the rays and decreases progressively posteriorly. There are two large pre-anal scutes, which are about two times larger than the adjacent scales.

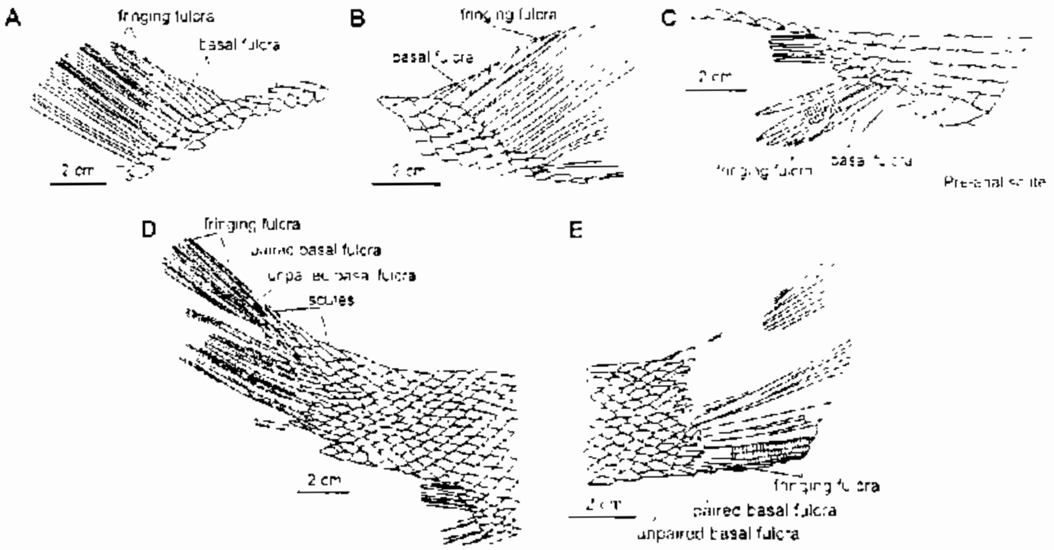

Figure 36 Unpaired fins of NRRU 6011-01. A, B: dorsal fin in left and right lateral views. C: anal fin. D, E: caudal fin in left and right lateral views.

The caudal fin is also relatively complete (Figure 36D, E). There are 18 rays; 8 in the ventral lobe and 10 in the dorsal lobe, separated by a deep fork. The dorsal lobe is preceded by 4 scutes covering the body lobe of the tail, following by 2 thin and elongate basal fulcra (the anterior one is unpaired), and possibly 6 paired of very thin fringing fulcra lying on the dorsal marginal ray. The caudal fin rays are intensively branched, with the exception of the two marginal rays. The proximal unsegmented portion is short. Ventrally, the caudal fin is preceded by one short unpaired basal fulcrum and 3 paired basal fulcra, and at least 4 thin and small fringing fulcra on the ventral marginal ray.

Squamation (Figure 37).– the body is covered with rhomboid scales, which have smooth surfaces and smooth border. The anterior margin of each abdominal scale presents a "double-peg" articulation, with the anterior dorsal process more protruding than the anterior ventral process (visible on the postcranium region of the counterpart). In addition there is a small process protruding from the dorsal border of the scale, which fits in a conical socket excavated in the ventral median border of the scale lying above. This arrangement indicates the presence of a vertical peg and socket articulation (visible nearly in the center of the trunk of the right side). There are 36 transverse scale rows carrying the lateral line. There are 23 vertical rows of scales dorsoventrally and 14 inverted row scales forming the body lobe of the tail. As usual in ginglymodians, the shape of the scales varies in different part of the body, from rectangular, somewhat deeper than long in the anterior and central region of the flank, to rhomboidal in the caudal peduncle. The dorsal ridged scales are conspicuous, very large and bear a stout posterior spine inclined posteriorly; they are approximately 18 dorsal ridged scales. Ventrally, the median lateral mid line also bears a short posterior spine directed backward. The lateral line scales are characterized by a small pore on their surface. There are two stout bones exposed just behind the cranium (Figure 35). These two bones are referred to supraneural ossifications. No vertebrate centrum ossifications can be observable.

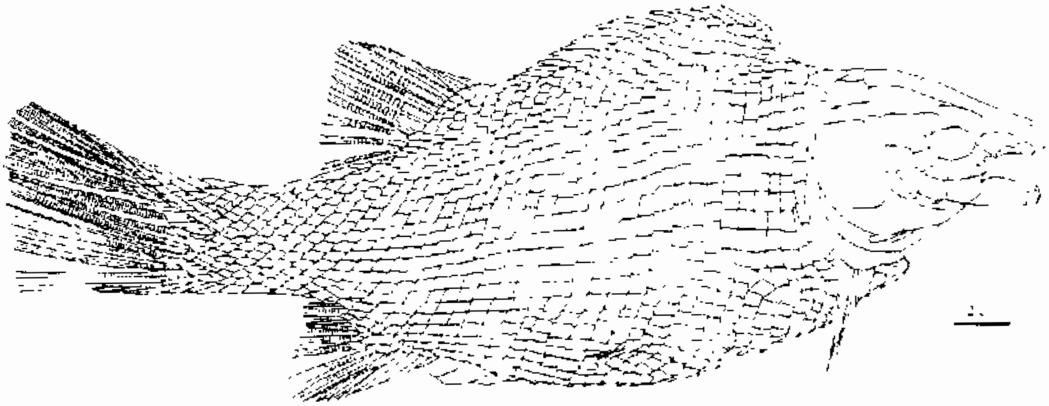

Figure 37 Reconstruction of new taxon of ginglymodian fish based on specimen NRRU 6011-01, preserved as a negative imprint of both side of impression from Ban Nong Rua, Wang Nam Kheow District, Nakhon Ratchasima Province.

4.2.2.4.3 Comparison and Discussion

The specimen from Wang Nam Kheow shows the following characters, which may be regarded as diagnostic of a new taxon. However, we wait for the achievement of a phylogenetic analysis showing its relationships with other ginglymodians before coining a new name. Medium-sized semionotiform fish of up to ca 30 cm in standard length (SL) with the following combination of morphological features: skull roof slightly concave at the level of frontal in lateral view; nape upraised abruptly and steeply; skull bones smooth, lacking ornamentation; long frontal, ratio of frontal by parietal length ca 2.5; ratio of skull length to orbit length ca 5; closed orbital ring; few infraorbitals (6) with an elongated anteriormost infraorbital with a tiny contact with the orbit; two squarish supraorbitals, the posterior one contacts the dermopterotic; large dermosphenotic; 6 suborbitals arranged in one row; cheek region completely covered by bones; gently curved preopercule; large interopercule; semi-tritorial dentition; 36 rows of ganoid scales along the lateral line and approximately 23 scales in the transverse row at the deepest level of the body; well-developed median dorsal row of scales with posterior spine; 2 large preanal scales; unpaired fins located posteriorly, close to caudal peduncle; narrow caudal peduncle; ca 7 pairs of numerous long and slender fringing fulcra on the dorsal lobe of caudal fin.

So far three species of ginglymodian have been described and named in Thailand from the Phu Kradung Formation based on well-preserved material, : *Thaiichthys buddhabuternsis*, *Isanichthys palustris*. *I. lertboosi*. Among the Thai ginglymodian fishes, the specimen from Wang Nam Kheow shares similar characteristic with *Isanichthys*. such as the slightly curved preopercule; closed orbital ring; cheek region completely covered by bones; large interopercule; semi-tritoral dention (*I. lertboosi*); 6 suborbitals arranged in one row (*I. lertboosi*); unpaired fins placed slightly close to caudal peduncle. But there are also some differences with *Isanichthys*, such as few infraorbitals (6), with the anteriormost infraorbital still reaching the orbit; two supraorbitals, but the anterior supraorbital does not contact two infraorbitals in the Wang Nam Kheow specimen; skull roof bones lack ornamentation in the Wang Nam Kheow specimen; ratio of skull length to orbit length ca 5 in the Wang Nam Kheow specimen while more than 6 in *Isanichthys*; no visible dermal component of the sphenotic on the cheek. The Wang Nam Kheow specimen differs from *Thaiichthys* by the long frontal, ratio of frontal by parietal length ca 2.5; much more suborbitals (6) wedges between the infraorbital and the preopercule while generally 2 suborbitals are present in *Thaiichthys*; gently curved preoperculum, whilst *Thaiichthys* presents two limbs arranged at an approximately right angle; a semi-tritoral dentition while the teeth are much more specialised in *Thaiichthys*.

Consequently, this specimen may be regarded as a new taxon, which shows a combination of characters unique for ginglymodian in Thailand, and in general: a medium size up to 30 cm SL with 36 rows of ganoid scales along the lateral line whereas the specimens of *Thaiichthys* are ca 50 cm SL with 46 ganoid scales along the lateral line and *Isanichthys* is ca 90 cm SL with 50 row of ganoid scales along the flank; nape upraised abruptly while *Thaiichthys* is gently convex dorsally and slightly straight ventrally whereas the contour is elongate and slender in *Isanichthys*; well-developed median dorsal row of scales with posterior spine whereas *Thaiichthys* shows median dorsal scales but they bear a relatively short posterior spine and sometimes show a slightly concave surface; narrow caudal peduncle whereas *Isanichthys*, which is elongate and slender, has a caudal peduncle apparently broad.

The presence of conspicuous dorsal ridges scales was proposed as a synapomorphy shared by *Lepidotes* and *Semionotus* by Olsen & McCune 1991 but the phylogeny analysis by Arbarello (2012) shows that, except for *Neosemionotus*, the relationships of which are not resolved, conspicuous dorsal ridge scales occur only in Semionotiforms but ridge scales with high posterior spines are uniquely derived in *Semionotus*. Nevertheless, the specimen from Wang Nam Kheow shows characters that differ from the type species, *Semionotus bergeri* Agassiz, 1833, such as the number of posterior infraorbitals: few in the Wang Nam Kheow specimen and more in the type species; the infraorbital at the posteroventral corner of the orbit notably larger than adjacent ones in the type species, while the Wang Nam Kheow has infraorbitals slightly similar in size except the elongated anteriormost one; the type species of *Semionotus* has a dorsal fin base about two times longer than the anal fin base while the Wang Nam Kheow both are relatively similar in length; presence of 4 irregularly arranged suborbital bones and two preopercular bones in the type whereas the Wang Nam Kheow has one row of 6 suborbital with a gently curve preoperculum.

In sum, the Wang Nam Kheow specimen presents sufficient differences to be regarded as a new taxon of ginglymodian.

4.2.2.5 Other Localities from the Phu Kradung Formation

Recently, a nearly complete fish was collected from the Kham Phok locality. It is preserved in a greenish siltstone from the Phu Kradung outcrop just a few centimetres under the surface, but the specimen itself was enclosed in highly compact calcareous fine sandstone. The calcareous sandstone that enclosed the specimen was first prepared with acid, and then the specimen was mechanical prepared under the binocular because it is small and fragile. The specimen was chemically and mechanically prepared in the Palaeontological Research Centre (PRC) and housed in the PRC collection with the collection number PRC83. After preparation (especially the skull part), the specimen was visible from both sides. This is the first discovery of a small in size semionotid fish from the Phu Kradung Formation.

4.2.2.5.1 *Description of Specimen PRC83; KP101-5*

Specimen PRC83 is a nearly complete fish with only unpaired fins missing, and with an estimated total length of less than 20 cm. It shows scattered scales in the centre of its squamation, but the dorsal and ventral portions are well

The ossifications of the head have no ornamentation, except small pits corresponding to the path of the sensory canals visible on infraorbitals, dermosphenotic and the preopercle. This fish has a relatively small head compared with the deep squamation: it has an approximately steep incline dorsal outline from the anterior tip to the row of the dorsal median scales. The ventral margin of the squamation is slightly straight except the region between the head and the abdominal region, which shows a concave outline. However, this situation may be caused by the preservation, as shows the location of the pectoral fin situated backwards. The insertion of the dorsal fin is approximately opposite to the pelvic fin. The dorsal median scales show a unique character: a longitudinal ridge at the centre of the scale with a posterior end seemingly bearing a short spine. There are two large pre-anal scales situated in front of the insertion of anal fin. The scales at the level of postcranium are in average squarish in shape, with those from the ventral and posterior parts of the body extremely elongated.

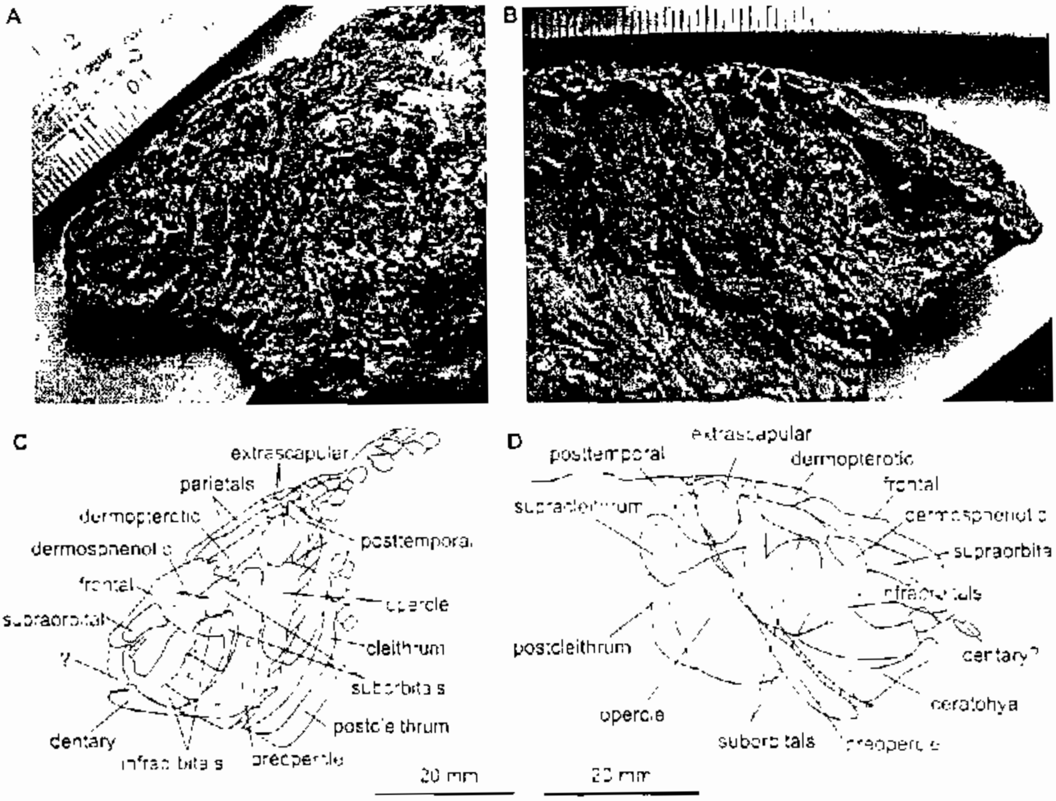

Figure 39 Photographs (A, B) and semi-interpretative line drawings (C, D) of the left and right skull bones of specimen PRC83.

Skull roof (Figure 39). The frontal is relatively elongated and rectangular, and is slightly broader anteriorly than posteriorly on its preserved portion. Its anterior end bears a constriction at the center and a zig zag posterior suture. At the level of the constriction of the anterior part of the frontal is visible a slender tube with an open hole indicating the path of the supraorbital sensory canal. The median suture of the frontal is straight. The length of the frontal is approximately 20 mm long, which is a little more than two times its width. The surface of the bone has no trace of ornamentation. The parietal and the dermopterotic are tightly connected together with a straight suture. The parietal is rather elongated with a smooth surface. The parietal is rectangular in shape, about 2.5 times longer than its wide (measure from the shifted right one). The dermopterotic is relatively small compared to the parietal; it is a small rectangular ossification with several pits for the sensory canal excavated at its lateral edge. Two paired of extrascapulars are present, with the medial one much smaller than the lateral one. Because they are crashed and broken, the extrascapulars are rather fragmentary and their shapes are difficult to estimate: the lateral one shows a large rounded shape with its margin suturing to the posttemporal posteriorly, to the median extrascapular dorsally and to the dermopterotic anteriorly. Their surface is smooth. The lateral extrascapular bears small pits for the path of occipital sensory canal that extends through the posttemporal bone, and the medial extrascapulars bears pits for the supratemporal commissure.

Circumorbital and suborbital series (Figure 39). The circumorbital series is composed of a supraorbital, a large dermosphenotic, and at least four infraorbitals located ventrally and posteriorly to the orbit but the circumorbital is seemingly not completely close. One anterior infraorbital has no contact with the orbit. The first, anterior most infraorbital is the subrectangular in shape with its ventral margin gently curved. The surface of this bone is smooth, with two pits for the infraorbital sensory canal excavated on the anteroventral corner and on the centre of bone. The second infraorbital is approximately rectangular and is longer than deep with its dorsal margin showing a concavity while the other margins are straight. The surface of the ossification is smooth and it bears two pits of the infraorbital sensory canal: one on the centre of the bone and a much smaller second one on the posterodorsal corner. The third and the fouth infraorbitals on the left side are preserved above the ventral suborbital; they are approximately rectangular with their margin apparently concave, following the shape of the orbit. The fourth infraorbital is the smallest circumorbital bone; it is articulated with the adjacent infraorbital ventrally and with the dorsal suborbital posteriorly. The shape of the dermosphenotic is roughly rectangular, with its anterior margin concave, following the shape of the orbit. At its posteroventrally corner is apparently a deep notch for the opening of sensory canal. Although the left ossification has shifted a little bit and is laying above the frontal, we can assume that it was located at the posterodorsal corner of the orbit as visible on the other side. Its articulate probably with the supraorbital anteriorly, the suborbital posteriorly and the posteriormost infraorbital ventrally. Only one supraorbital is preserved on this specimen; it is located dorsal to the orbit, and is laying on the ventral half depth of the frontal on the left side. The supraorbital is relatively elongated and rectangular, but its posterior portion is slightly broader than the anterior one on the preserved portion. There are two suborbitals located in front of the vertical arm of the preopercle. Their shapes are rectangular but the dorsal one is smaller than the ventral and is slightly longer than wide, while the ventral one is much larger and it is deeper than long. The dorsal suborbital articulates dorsally with the frontal.

Jaws. The snout region is very fragmentary preserved, but the dentary is apparently present. The visible part shows a narrow and elongate posterior portion while the anterior portion shows a blade-like horizontal part. Unfortunately, we cannot observe any teeth on the bone.

Opercular series. The opercular series is better preserved on the left side, with only the preopercle and the opercle visible (Figure 39C). The preopercle is a distinctly L-shaped bone (its height is 23 mm, 10 mm long) but not on the right side which is slightly curve. The vertical arm is narrow parallel with lateral margins, except the posterior margin at the half depth of the bone which shows a little constriction, making slightly narrower the mid-depth of bone. The ventral arm is quite short with its dorsal margin gently concave and the posterior margin gently convexe, making a slightly broader angle between the vertical and horizontal arms. There is no tapering dorsally and the ossification ends anteriorly as a blunt spine. A series of pores located in the centre of the bone represent the preopercular sensory canal. The opercle is relatively rectangular in shape, about 1.5 times deeper than wide (9 x 14 mm). The anterior border is straight, while the posterior border is rather convex. The dorsal and ventral margins are not clearly observable as it is very fragmentary but can assume that they are tapering. The external surface is smooth.

Hyoid arch and branchiostegal rays. Because of preservation, the branchiostegal rays are not visible. The ceratohyal is visible on the right side; it is hourglass-shaped, with its dorsal and ventral margins gently concave. Its anterior portion is smaller than its posterior portion. According to its shape we regard it as the anterior ceratohyal (Figure 39D).

Pectoral girdle. The posttemporal is visible on both sides (Figure 39). The posttemporal is a relatively large bone; its shape is approximately triangular with its anterior margin showing a deep concave curve following the shape of lateral extrascapular. The supracleithrum is visible on the right side; its shape is subrectangular. It sutures with the posttemporal dorsally, and its surface bears at least three small pits for the sensory canal of the lateral line. The cleithrum is seemingly present on the left side, while the postcleithrum is visible on the right side but both of them are very fragmentary. However, the cleithrum ossification is present as a large crescent-shaped ossification whereas the postcleithrum is visible as a subrectangular with its posterior gently curved margins. It is very difficult to estimate the number of postcleithrum as they are very fragmentary.

Cephalic sensory canal. The supraorbital sensory canal is visible as just one hole opening at the tube-like region of the anterior constriction of the frontal, then is present as a series of small pits on the dermopterotic. The path of the infraorbital sensory canal is visible as a series of small pits running close the dorsal margin of the infraorbitals, and then going through the dermosphenotic. The preopercular sensory canal is visible on the center of the preopercle, then at the connexion with the dermopterotic. The supratemporal sensory canal runs through the median and lateral extrascapular, then extends as the lateral line to the posttemporal and through scales, where it is present as small pit on the scales. There is no evidence of a sensory canal running within the supraorbital bones.

Pectoral fins (Figure 38B).– It is difficult to reconstruct the pectoral fin as it is fragmentary, but we know at least that it presents segmented rays. However, we cannot estimate how many they were because of the preservation.

Pelvic fins.–The pelvic fin is located approximately at half-length between the pectoral and anal fins (Figure 40). According to the visible part, it seemingly presents unsegmented and very elongated portion of rays. The total number of the pelvic fin ray is difficult to reconstruct.

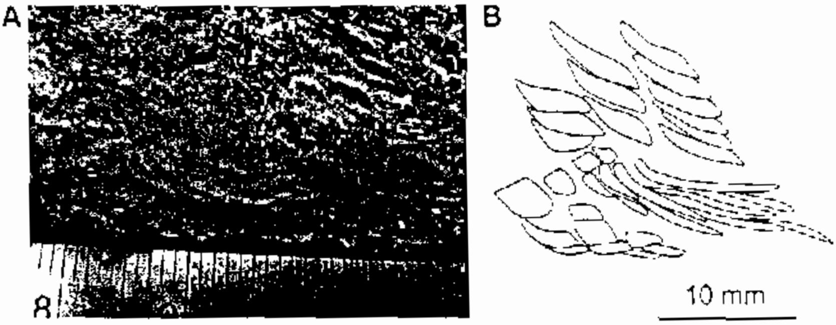

Figure 40 Photograph (A) and line drawing (B) of the pelvic fin of specimen PRC83.

Unpaired fins.–The dorsal and anal fins are not preserved but we know where they are located. The dorsal fin was situated just opposite to the pelvic fin, but the complete shape and total composition is difficult to estimate as it is broken. We assume the origin of the anal fin from the presence of pre-anal scales, but its exact shape and the number of rays is very difficult to recognize.

Squamation (Figure 38).– the body is covered with very thin and smooth ganoid scales, which present the typical scale articulation. The anterior margin of each scale probably presents only the anterior ventral process. However the vertical articulation is seemingly present only at the dorsal half portion of the body, but not in the ventral portion, as show very elongated scales with only an anterior spine corresponding to the anterior ventral process. The lateral line scales present a hole on its surface but the exact number of lateral line scales is impossible to count. It is the same condition with the median dorsal scales row but we know, however, that they show a very unique character, i.e. a structure like a roof at the centre of scale with a posterior spine. Ventrally, the ventral mid line scales also present a different pattern as they show a notch like at the centre of posterior edge. There are definitely two larger scales compared with the adjacent ones, which are regard as the pre-anal scales.

4.2.2.5.3 Comparison and Discussion

The specimen from Kham Phok shows the following set of characters, which may be possibly regarded as diagnostic of a new taxon. Small-sized semionotiform fish of up to ca 15 cm in standard length (SL) with the following combination of morphological features: skull roof marks a very deep angle in lateral view: skull bones smooth, lacking ornamentation; frontal broad anteriorly; small orbit, ratio of skull length to orbit length ca 7; open orbital ring; few infraorbitals with enlarged ventroposterior infraorbital contacting the preopercle; one elongate supraorbital; large dermosphenotic; 2 suborbitals; preopercule with two limbs arranged at an approximately right angle, the horizontal branch is much shorter than the vertical one; two paired of extrascapulars; large posttemporal; median dorsal row of scales with short posterior spine; dorsal fins located opposite to the pelvic fin, two large preanal scales. The specimen can be compared with three species of Thai ginglymodians from the Phu Kradung Formation based on well-preserved material: *Thaiichthys buddhabuternsis*, *Isanichthys palustris*, *I. lertboosi*. Among the Thai ginglymodian fishes, the specimen from Kham Phok shares similar characteristics with *Thaiichthys*, such as preopercle with two limbs arranged at an approximately right angle; two paired of extrascapulars with an enlarged lateral one; large dermosphenotic; two suborbitals; cheek region completely covered by bones, with an enlarged infraorbital, which contacts the preopercle; dorsal fin located slightly opposite to the pelvic; slightly conspicuous dorsal median ridge scales; two large preanal scales. But there are also some differences with *Thaiichthys*, such as the small size of the fish up to ca 15 cm in standard length whereas the specimens of *Thaiichthys* are ca 50 cm in SL; the circumorbital ring is not completely closed: only one supraorbital in the Kham Phok specimen whereas two supraorbitals in *Thaiichthys*; frontal broader anteriorly in the Kham Phok specimen while roughly rectangular in *Thaiichthys*. The Kham Phok specimen differs from *Isanichthys* by its much smaller size, ca 15 cm in standard length whereas ca 90 cm SL in *Isanichthys*; the long frontal which broadens anteriorly while it slightly tapers anterior in *Isanichthys*; 2 suborbitals making some infraorbitals contact with preopercle whilst non of infraorbitals contact with preopercle in *Isanichthys*; preopercle with two limbs arranged at an approximately right angle whereas it is gently curved in *Isanichthys*.

4.2.3 Conclusion

The osteology of the articulated ginglymodian fishes from the Phu Kradung Formation reveals a high diversity. There is at least five taxa and probably a juvenile of *T. buddhabutensis* from the Kham Phok locality. However, in most localities they are rare in term of number of specimens and their preservation is not as well as in the Phu Nam Jun locality. Although not as abundant and well preserved as in the Phu Nam Jun locality, the distribution and diversity of the ginglymodians from the Phu Kradung Formation are important, and indicate that the palaeoenvironment and the palaeoecology of the Phu Kradung localities represent widely open or wet land ecosystems, while the Phu Nam Jun locality is probably restricted and corresponds to a drying area from which all tetrapods ran out when the water evaporated. On the other hand, among the fish remains, most of them consist of disarticulated fragments and isolated scales. The microstructure of the surface of fish scales is not achieved yet, and does not allow assessing the fish diversity, on the basis of this feature.

4.3 The Sao Khua Formation

During almost 30 years of Thai-French expedition, the Sao Khua Formation (Early Cretaceous) has yielded a rich assemblage of continental vertebrate faunas in the northeastern part of Thailand, especially a rich and diverse dinosaur assemblage (Buffetaut and Suteethorn, 1999) comprising sauropods, theropods, pterosaur and bird

(Buffetaut *et al.*, 2003, 2005) crocodiles (Buffetaut and Ingavat, 1983; Lauprasert *et al.*, 2007) turtles (Tong *et al.*, 2004, 2006) and the highest diversity of freshwater sharks from the Khorat Group (Cuny *et al.*, 2003, 2006, 2009b) but only rare bony fish remains have been found. So far the only ray-finned fish known is a sinamiid halecomorph (Cavin *et al.*, 2007b).

4.3.1 The Stratigraphic Position

The Sao Khua Formation comprises dominantly floodplain deposits including sandstone, siltstone and mudstone, together with common calcretes, and was deposited in a low-energy fluvial setting comprising meandering channels and extensive flood plains. The contact with the underlying Phra Wihan and the overlying Phu Phan Formation appears to be gradational and conformable at outcrop (Racey and Goodall, 2009). The Sao Khua Formation is now considered as Late Barremian in age on the basis of freshwater bivalve species, *Pseudohyria (Matsumotoina) somanai*, the subgenus being limited to the Late Barremian Formation of Japan and Korea (Tumpeesuwan *et al.*, 2010). These results correspond to the recent palynological analyses of samples from Phu Phan Thong and Hui Sai localities, which have yielded an assemblage dominated by *Dicheiropollis etruscus* (an important age diagnostic taxon) indicating an age no younger than Barremian-Aptian (Racey and Goodall, 2009).

4.3.2 The Localities

No articulated "semionotiforms" have been discovered in the Sao Khua Formation, but isolated scales are not rare, and may be rather common in some localities. We focus here on the microornamentation of some of these scales. The fish scales used to examine microornamentaion with SEM photographs were collected in two localities.

4.3.2.1 The Phu Phok Locality

4.3.2.1.1 Introduction

The Phu Phok outcrop is situated on the top of the hill of

Phu Phan Mountain range in the Sakhon Nakhon Province. The fossils assemblage consists generally of isolated pieces of bone small in size spread over of an area of approximately 500 m^2 of the typical reddish sandstones of the Sao Khua Formation. It consists of remains of sinamiid fish, a single button like crushing tooth referable to a probably semionotid fish, small isolated bony plates from two types of tutles, crocodile skull (including a goniopholidid), theropod teeth, one pterosaur tooth and several minute lizard eggs (Fernández, 2010).

4.3.2.1.2 Systematic Palaeontology

Subclass ACTINOPTERYGII sensu Rosen *et al.*, 1981
Superdivision HOLOSTEI sensu Grande, 2005
Division HALAECOMORPHI sensu Patterson, 1973
Order AMIIFORMES sensu Grande and Bermis, 1998
Family SINAMIIDAE Berg, 1940
Genus *Siamamia* Cavin *et al.*, 2007

Type species.-*Siamamia naga* Cavin *et al.*, 2007
Figure 41

Description and Discussion --- see Cavin *et al.*, 2007b. The species has been described and named based on two semi-articulated skulls, TF 8001, 8003 (Thai fossil code and specimens housed in Sirindhorn collection), plus isolated ossifications.

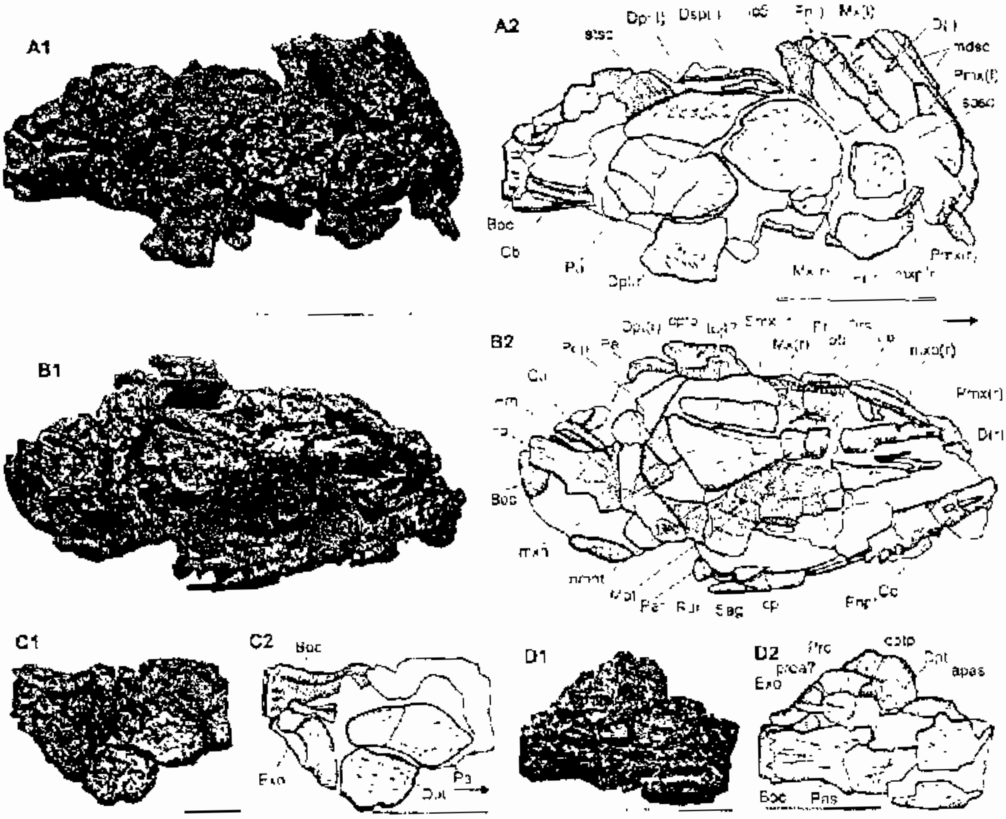

Figure 41 *Siamamia naga*: A, B: holotype, TF 8001: semi-articulated skull. Photographs (1) and interpretative drawing (2) in dorsal (**A**) and right lateral (**B**) views. Scales bar equal 30 mm. C, D: TF 8003: semi-articulated skull: Photographs (1) and interpretative drawing (2) in dorsal (**C**) and ventral (**D**) views. Scales bars equal 20 mm. The arrow indicates anterior direction.

Morphology of the isolated scale

The isolated scales of *S. naga* from this locality are rarely found during surface collecting, but they are proportionally abundant when screening and washing techniques are used. The morphology of these scales is reminiscent of the scales *S. zdanskyi* (Stensiö, 1935). The general shape and out-line of the scales are vaiable corresponding to their postion of the fish body (Figure 42). They are small in size and covered with a thin layer of ganoin, which is generally smooth except some very faint irregular ridge.

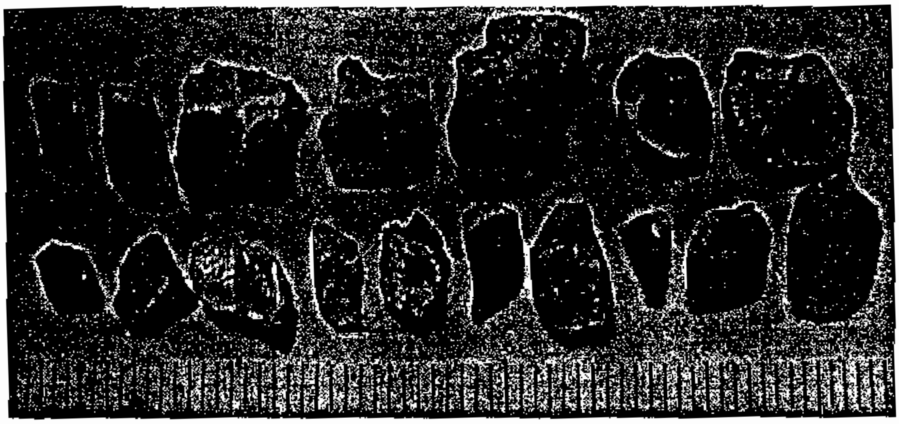

Figure 42 Photograph of the scales in external view from Phu Phok locality.

4.3.2.1.3 Microornamentation of Scales

The microornamentation study of the *S. naga* fish scales of the Phu Phok locality is based on 8 scales of different shape and out-lines, which were located on different parts of the body. Photographs of the ganoin surface of the scales have been taken under scanning electron microscope. The microornamentation shows a very typical pattern with the presence of concentrated tubercles (disperse) plus one or two lines of regular in size holes arranged along the lateral sides of the scales only,and absent from the centre of the scale (Figures 43-48). Tubercles are also present where faint ridges are observed by eyes (Figure 49). In addition, scales of the lateral line with a pore opening, also show concentrations of tubercles (Figure 45D, E). To conclude, the tubercles and ornamentation pattern of the scales of *S. naga* from Sao Khua Formation display a typically pattern, very different from the patterns generally observed in ginglymodians.

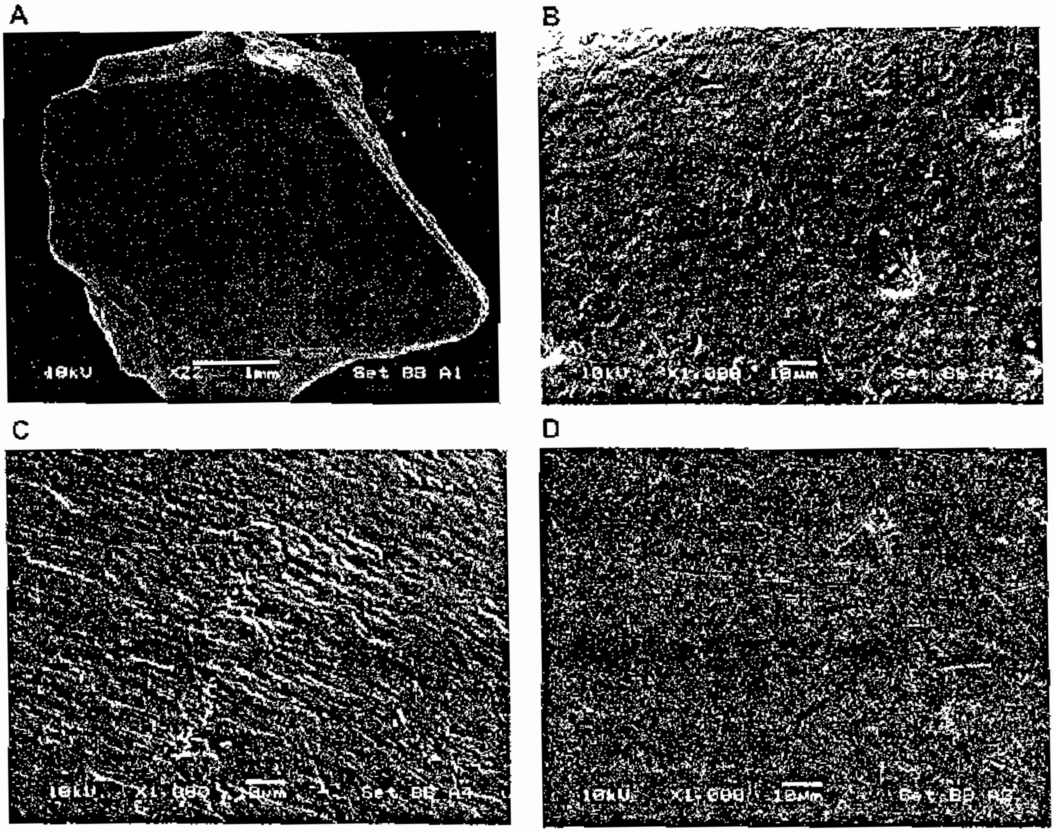

Figure 43 Photographs of the scales from Phu Phok; PP-A. A: external surface of the scale, B: tubercle presence on the lateral edge of the scale in SEM view, C-D: SEM view of the surface of the scale around its centre.

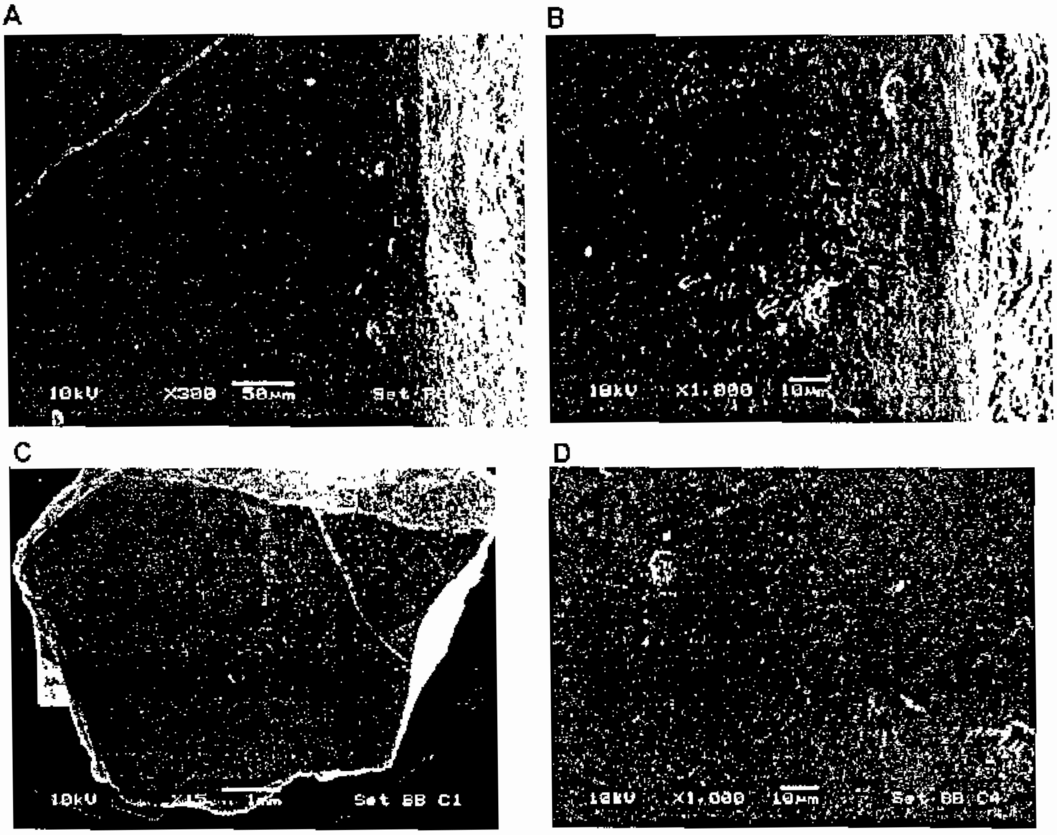

Figure 44 Photographs of the scales from Phu Phok: PP-C. A-B: tubercle and line of holes present on the lateral edge of the scale in SEM view, C: external surface of the scale, D: SEM view of the central surface of the scale.

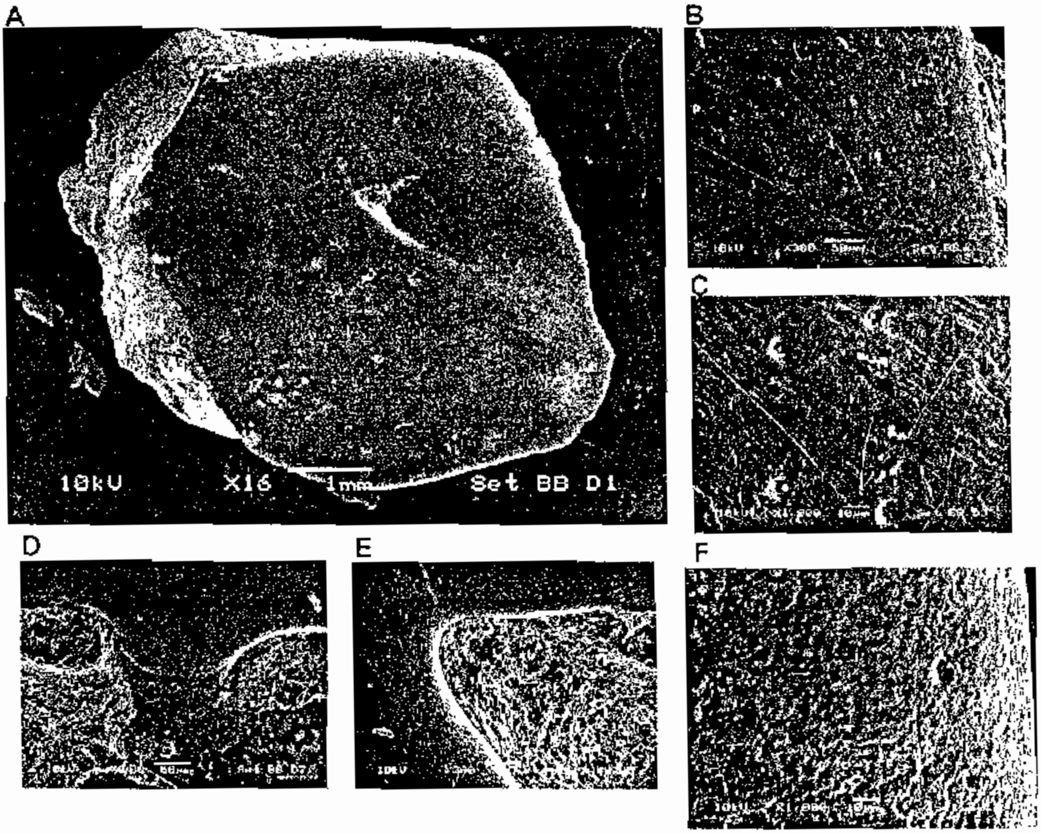

Figure 45 Photographs of the scales from Phu Phok; PP-D. A: external surface of the scale, B,C,F: tubercle and line of holes present on the lateral edge of the scale in SEM view, D-E: SEM view of the surface scale around the opening for lateral sensory canal.

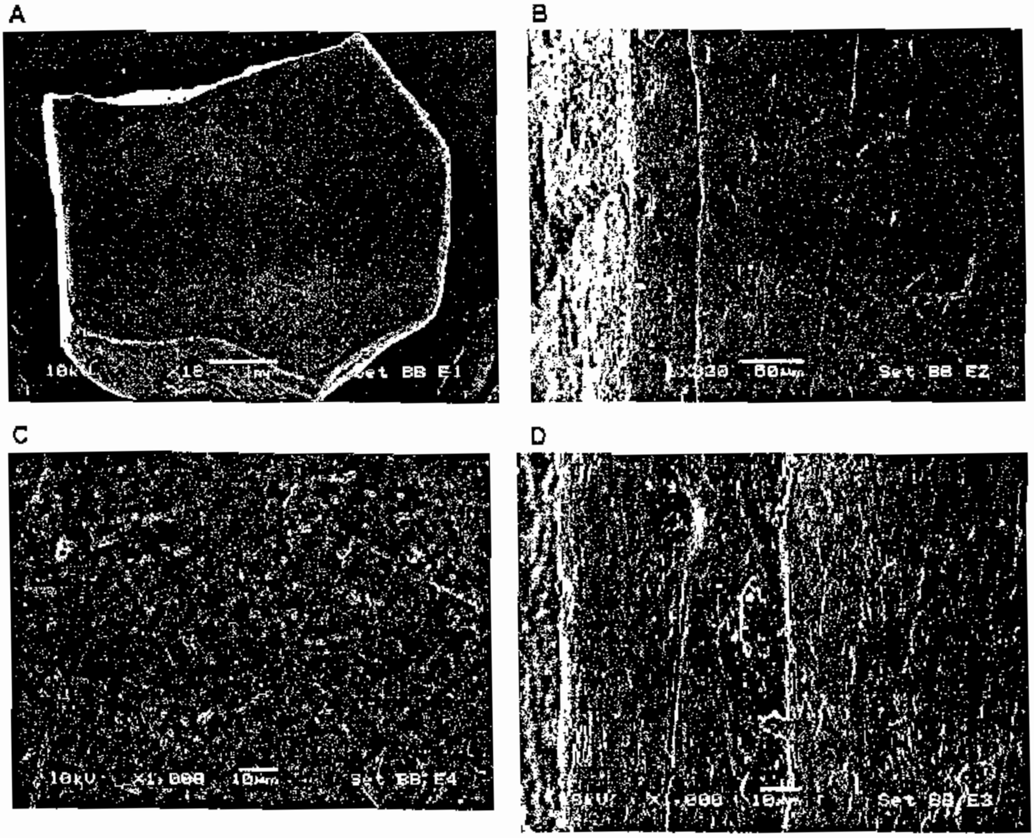

Figure 46 Photographs of Phu Phok scale; PP-E. A: external surface of the scale, B,D: tubercle and line of holes present on the lateral edge of the scale in SEM view, C: SEM view of the surface of the scale approximately at its centre.

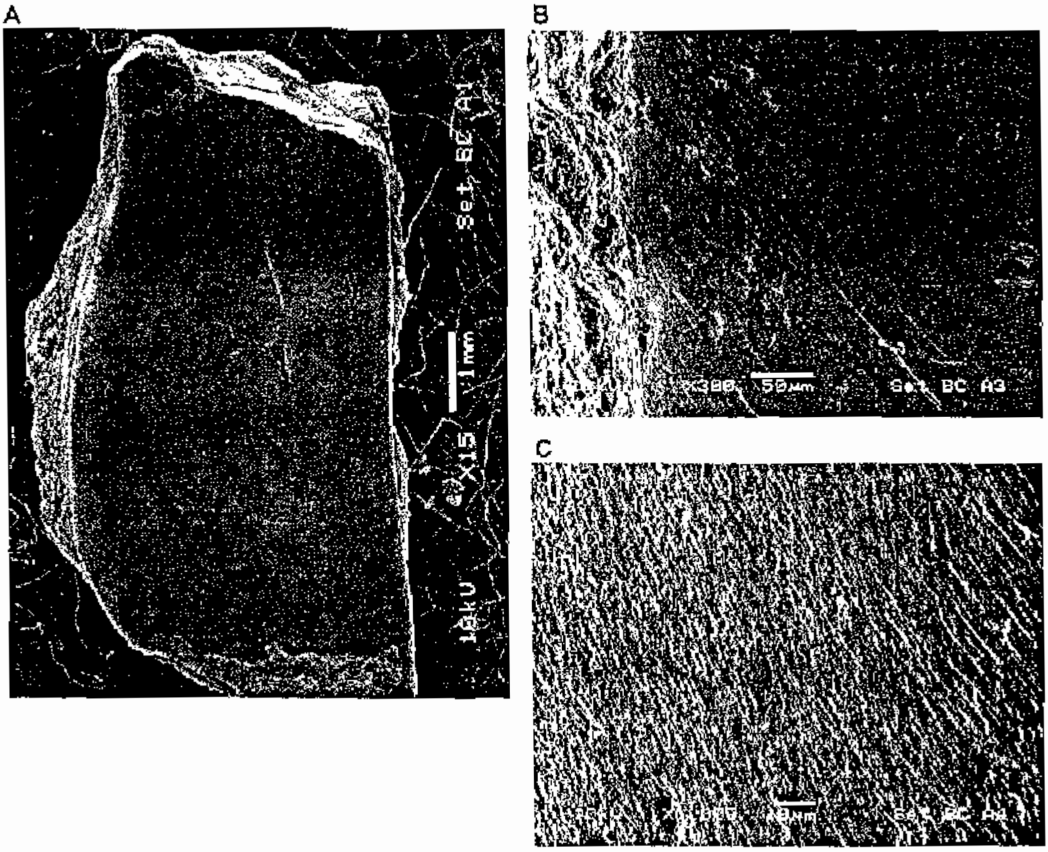

Figure 47 Photographs of Phu Phok scale; PP-F. A: external surface of the scale, B-C: tubercle and line of holes present on the lateral edge of the scale in SEM view.

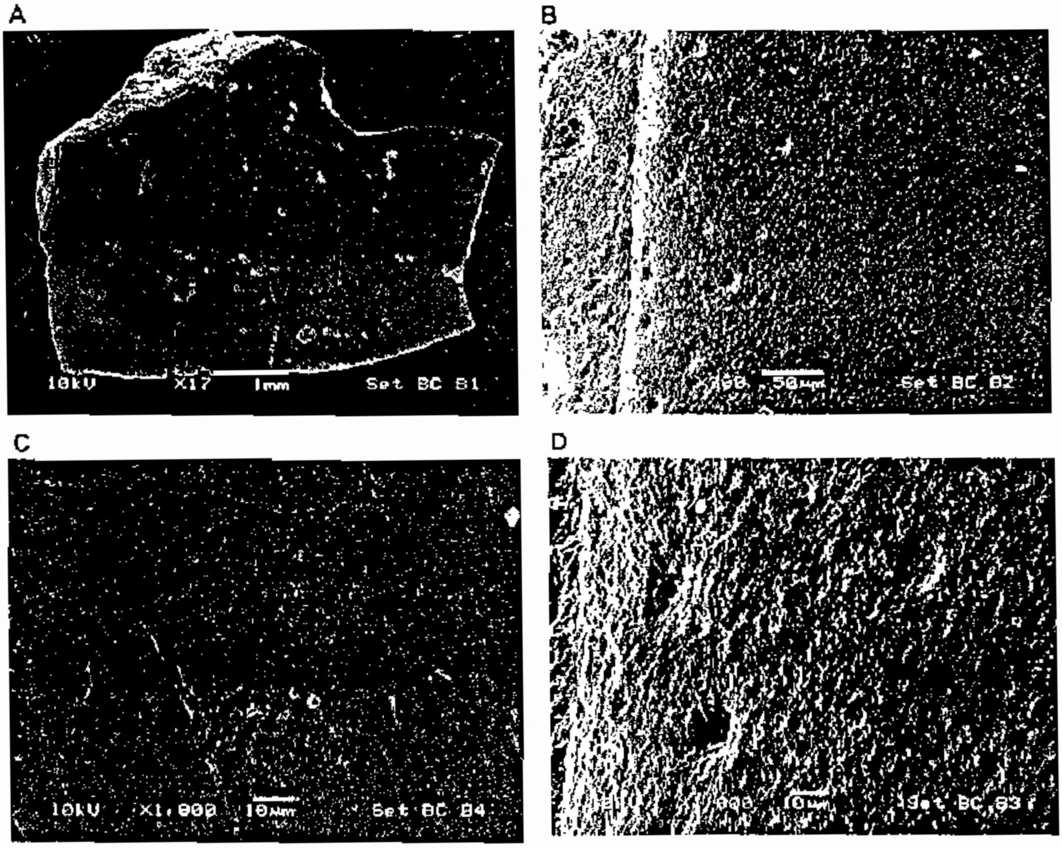

Figure 48 Photographs of Phu Phok scale: PP-G. A: external surface of the scale. B,D: tubercle and line of holes present on the lateral edge of the scale in SEM view. C: SEM view of the surface of the scale approximately at its centre.

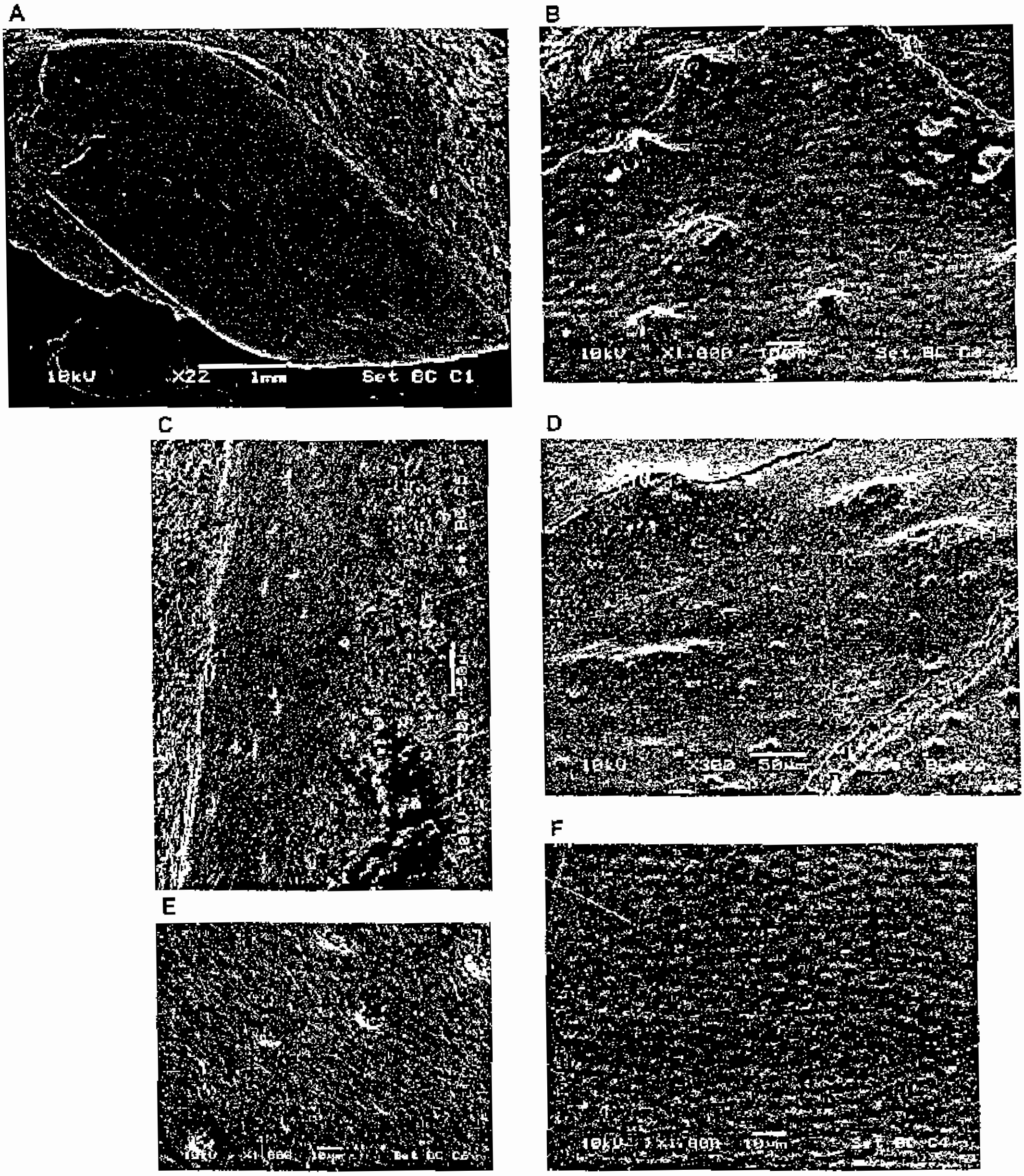

Figure 49 Photographs of Phu Phok scale; PP-H. A: external surface of the scale, B,D: tubercles and large prominence with acute point present on the posterior part of the scale in SEM view, C,E,F: tubercles and line of holes present on the lateral edge of the scale in SEM view.

4.3.2.2 The Phu Phan Thong Locality

4.3.2.2.1 Introduction

The Phu Phan Thong locality is well known by the presence of a large number of hybodont shark teeth of *Heteroptycodus steinmani* and *Lonchidian khoratensis* (Cuny *et al.*, 2003, 2006). The locality is located along the roadside between Nong Bua Lam Phu and Udon Thani, near the village of Phu Phan Thong.

4.3.2.2.2 Systematic Palaeontology

Super Division HOLOSTEI sensu Grande, 2010
Division GINGLYMODI sensu Grande, 2010
Order and Family *incertae sedis*

Morphology of the isolated scales

All isolated scales from this locality were found by the screening and washing technique. The general morphology of these scales is small lozenges, longer than deep and covered with a thin layer of ganoin, which is generally smooth.

4.3.2.2.3 Microornamentation of Scales

The microornamentation study of the fish scales of the Phu Phan Thong locality is based on a few scales. Photographs of the ganoin surface of the scales taken under scanning electron microscopy show many tubercles on their surface with large in size holes along the lateral sides only, and absent from the centre of the scale (Figure 50). To conclude, the tubercles and holes of the scales from Phu Phan Thong locality show a similar pattern with the one on the surface of the scales of *S. naga* from Phu Phok locality. In addition, they are located in the same formation; this probably indicates that the scales from Phu Phan Thong belong to *Siamamia*. At least two species of *Siamamia* are likely present in the Sao Khua Formation (Cavin *et al.*, 2009).

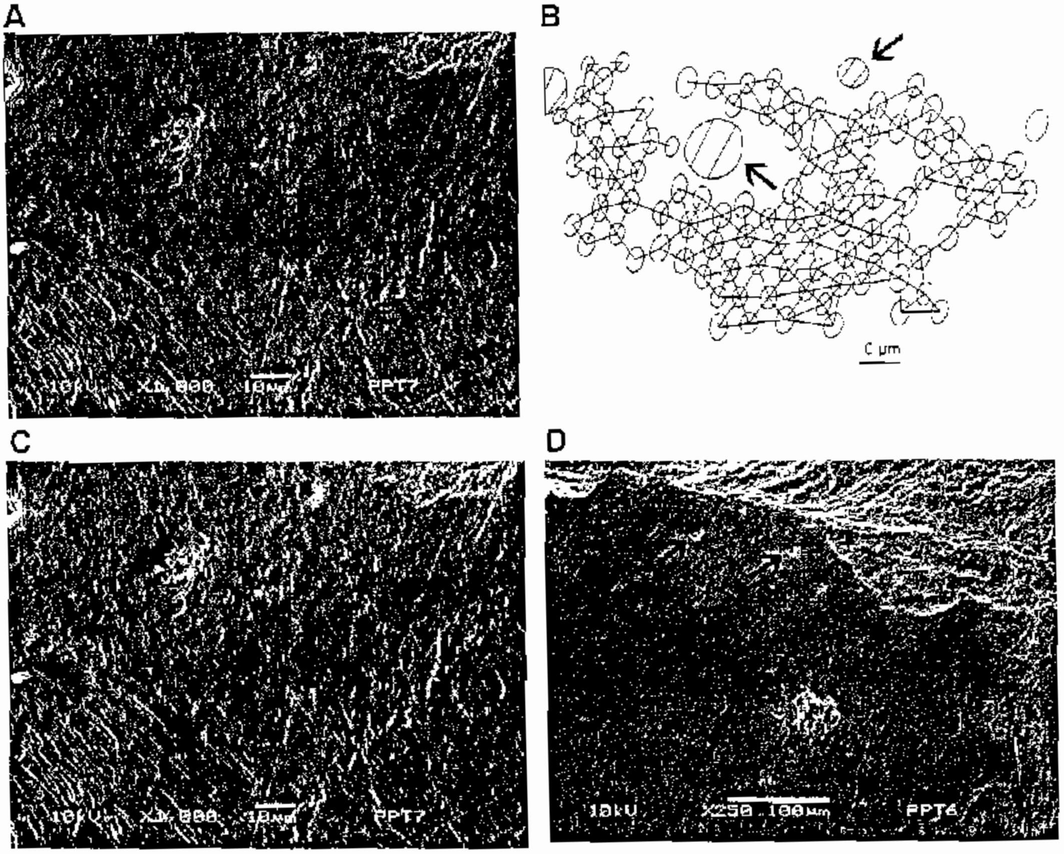

Figure 50 SEM views of the ganoin surface (A, C, D). B: Plot of the tubercles on a micrograph of the scale from Phu Phan Thong locality. Arrows point to the specially large holes on the ganoin surface.

4.3.3 Comparison and Discussion

The materials from Sao Khua localities come mainly from the Phu Phok locality, with *Siamamia naga*, and some scales from Phu Phan Thong locality together with rare of button-like crushing teeth refereable to "semionotiforms" in the Phu Wiang and Phu Phan Thong localities (Cavin *et al*., 2009). The observed scales are from different parts of the body according to the variable overall shape of the scale. The result of the microornamentation pattern from both localities is similar with the presence of concentrations of tubercles and with the occurrence of lines of several holes along the lateral edge of the scale. However, we did not measure so far the average diameter of these tubercles and the distances between them. Although, this observation does not rest on statistical comparisons, the qualitative decriptions of the microornamentation of scales from both sites indicates that they are probably belongs to the same taxa.

4.4 The Khok Kruat Formation

In the past 29 years of palaeontological work on the Khorat Plateau of Thailand, within the Khorat Group, the Khok Kruat Formation (late Early Cretaceous; Aptian-Albian on the basis of vertebrates and palynomorphs) has yielded a large number of continental vertebrate faunas, especially a rich and diverse dinosaur assemblage comprising ornithischian dinosaur *Psittacosaurus* (Buffetaut and Suteethorn, 1992) three new iguanodontian dinosaurs (Buffetaut and Suteethorn, 2011; Shibata *et al.*, 2011a, 2011b) sauropod with peg-shaped teeth which probably belong to nemegtosaurids (Buffetaut and Suteethorn, 2004), theropods (Buffetaut *et al.*, 2005) theropod and ornithopod trackways (Le Loeuff *et al.*, 2003; 2005; 2009) crocodiles (Lauprasert *et al.*, 2009) turtles (Tong *et al.*, 2005) and the highest diversity of freshwater sharks (Cappetta *et al.*, 1990, 2006; Cuny *et al.* 2008) but rarely bony fish remains have been found. So far 5 vertebral centra, fragments of a basioccipital and jaws, a piece of a left dermopterotic and scales from the locality of Khok Pha Suam have been recorded and they are assigned to a sinamiid fish. Moreover, at least 2 ginglymodian fishes occurred in this locality based on the presence of peg and socket articulation at the anterior margin of two morphotypes of the scales.One taxon of ginglymodian occurs in the locality of Lam Pao Dam by the presence of a large button shaped crushing tooth associated with thick ganoid scales, which present many parallel rows of small pits on their surface (Cavin *et al.*, 2009).

4.4.1 The Stratigraphic Position

The Khok Kruat Formation is assigned to the top of the Khorat Group as it is separated from the basal anhydrite of the overlying unconformtably Maha Sarakham Formation, but rests conformably on the underlained Phu Phan Fomation. In general, the formation consists mainly of reddish brown silstones, fine- to medium grained sandstones, mudstones and conglomerates are also present (Meesook, 2000). The sediment deposit indicates a predominant fluvial depositional environment

(Racey *et al.*, 1996). The age of the Khok Kruat Formation is well constrained as Aptian-Albian by the occurence of the freshwater hybodont shark *Thaiodus ruchae* which is also discovered in the Takena Formation of the Lhasa block of Tibet, which is dated as Aptian-Albian on the basis of foraminifera (Cappetta *et al.*, 1990). It is considered as Aptian based on palynology (Racey *et al.*, 1994, 1996; Racey & Goodall, 2009).

4.4.2 The Localities

The fish remains described below are mainly isolated scales and bones fragments collected from three outcrops, i-e. Ban Saphanhin, Nakhorn Ratchasima Province; Khok Pha Suam, Ubon Ratchathani Province and Lam Pao Dam, Kalasin Province. These outcrops are located in the Khok Kruat Formation.

4.4.2.1 The Ban Saphan Hin Locality

4.4.2.1.1 Introduction

The excavation from Ban Saphan Hin, a village close to city of Nakhon Ratchasima, occurs in a small outcrop of the Khok Kruat Formation. It is one of richest assemblage from the Khok Kruat Formation in term of diversity of vertebrate comprising dinosaurs, turtles, crocodiles, hybodont sharks and fishes (Shibata *et al.*, 2011a, 2011b; Buffetaut and Suteethorn, 2011; Lauprasert *et al.*, 2009; Tong *et al.*, 2005; Cappetta *et al.*, 1990). The material of these assemblages is mainly fragmentary and not articulated remains, which are embedded in the reddish conglomeratic sandstone of the Ban Saphan Hin locality. Because the rock is very hard, machine rock saw was used to remove the materials from the field. The preparation was performed using an air pen in the laboratory of the Research Center of the Petrified Wood and Northeastern Mineral Resources, Tambon Suranari, Nakhorn Ratchasima Province, where the specimens are housed. The rock is very hard and necessitates, the use of hard tools to take out specimens. A lot of materials are damaged, but the preservation is good as shows the material under this study.

4.4.2.1.2 Systematic Description

Class: OSTEICHTHYES
Super Division: HOLOSTEI
Division: GINGLYMODI
Order *indeterminate*
Figures 51-68

Material: part (NRRU-A 2435.1-2,) and counterpart (NRRU-A 2435.4,) of the posterior portion of a fish, Figure 51. The split of the rock did not preserve equivalent portion of the body in the part and counterpart. The part (Figure 51A, B) consists of the articulated fragment of a squamation associated with a tail. The counterpart (Figure 51C, D) shows a dorsal part of caudal peduncle and a nearly complete dorsal fin. According to the part and counterpart, the material can be reconstructed and shows the dorsal fin, the caudal peduncle and the caudal fin of a single individual (Figure 51E).

Description of Specimen NRRU-A 2435

The scales of the preserved portion of the body are in articulation (Figure 51). Some are complete with their ganoin cover and others are scratched or are missing (Figure 51A). There are 16 scales along a transverse row originating at the posterior end of the dorsal fin. The scales in the mid-depth of the body are rather rhomboidal in shape and small in size near the origins of the fins, whereas the scales at the dorsal and ventral midline of the peduncle are triangular in lateral view with their posterior end tapering. Some authors define these scales as scutes (López-Arbarello and Codorniú 2007; Arratia, 2009). The peduncle is 2 times longer than deep. The caudal fin is deep in general outline and its posterior margin is slightly concave. There are 31 lepidotrichia, eighteen are placed under the level of the lateral line and forms the ventral lobe of the fin. The caudal fin rays branch at least four times except the two ventral ones, which are not branched. The proximal unsegmented portion is very short, this portion being less than 20% of the total length of the fin ray. The basal segments are much longer in the central rays than in the marginal rays. The ventral lobe of the caudal fin is characterized by the posterior most scales, which are modified and extend in length. The pattern of fulcra is distinctive in both dorsal and ventral lobes. The dorsal lobe consists of a pack of seventh small and long basal fulcra, which are followed by 10 fringing fulcra, which are thin and paired. On the ventral lobe, only 3 basal fulcra and 9 fringing fulcra are visible. The dorsal fin, mostly visible on the counterpart (Figure 51C, D), is high, ca 10 cm long, and its dorsal margin outline is almost straight. It is composed of 3 unpaired basal fulcra, 4 fringing fulcra and 17 rays. The height of the rays decreases progressively posteriorly. The basal segments represent approximately one-third of the length of the lepidotrichia, which are finely segmented in their distal part and symmetrically branched twice.

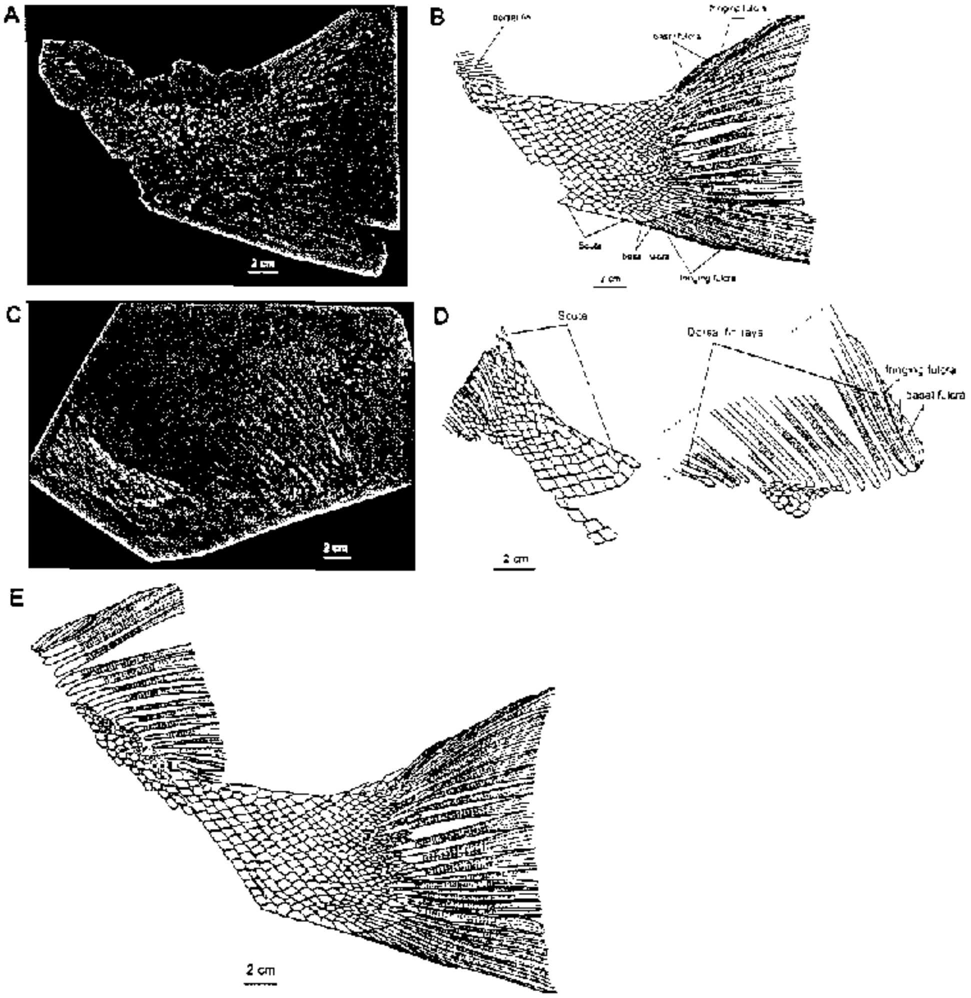

Figure 51 Photographs and line drawings of fragments of the tail and dorsal fin of NRRU-A 2435.

Material: a piece of dermal bone, identified as an opercle (NRRU-A 2437, Figure 52).

Description of Specimen NRRU-A 2437

The opercle (Figure 52) is quite large and deeper than long (8 x 6.5 cm.). Although all margins are broken, we can estimate the outline from the trace of the imprint. The dorsal, posterior and ventral margins are slightly curved, while the anterior margin is straight. The external surface of the ossification is fully ornamented by ganoin rugae (Figure 52A), which alternate with many grooves, which radiate from its ganoid-free center. The anterior margin of the opercle has a smooth surface (lack of the ganoin covered) corresponding to the overlapped area of the preopercle.

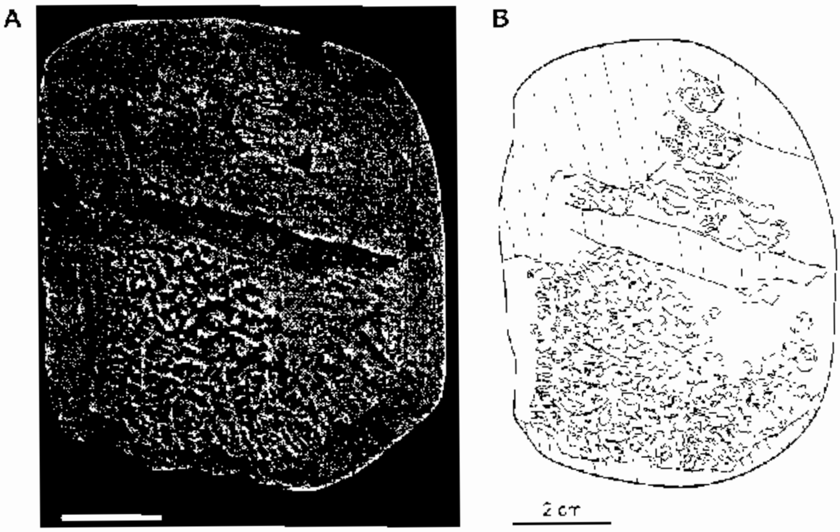

Figure 52 Photograph (A) and line drawing (B) of the opercle bone, NRRU-A 2437.

Material: part (NRRU-A 110.1/2,) and counterpart (NRRU- A 110.2/2,) of the dermal bone of a fish, Figure 53. The part (Figure 53A) consists of two articulated dermal bones identified as the frontal and the parietal, with the anterior part of the frontal missing. The limit of the anterior part of the frontal is visible on the counterpart (Figure 53B) and it shows a smooth internal face with the imprint of the ornamentation of the external face on the connecting area. The complete shape of the ossifications can be reconstructed with part and counterpart using Adobe Illustrator CS3 (Figure 53C).

Description of Specimen NRRU-A 110

The shape of the frontal is slightly rectangular with its anterior extremity tapering at one-third of the ossification's length. Its length is 2.5 times longer than its maximum width and 1.8 times longer than the parietal length. The length of the frontal is 8.3 cm long and 3.3 cm at the maximum width with 2 cm at the narrowest portion. The posterior margin of the frontal forms a slightly crenulated suture with the parietal and a deep notch at its medial depth. The median margin of the ossification is gently curvedly while the lateral margin is slightly concave at it mid-length before it widens at the level of the maximum width of the bone. The parietal is roughly rectangular with the lateral margin shorter than the median margin. There is no limit between the lateral and posterior margins, which presents a serrated edge. The length of the parietal is about 2 times longer than wide. The surface of both ossifications bears a very strong ornamentation consisting of several ridges radiating from the center of the bones and covered by ganoine. Due to the state of preservation, only some traces of the sensory canal are visible along the ridges of the ornamentation.

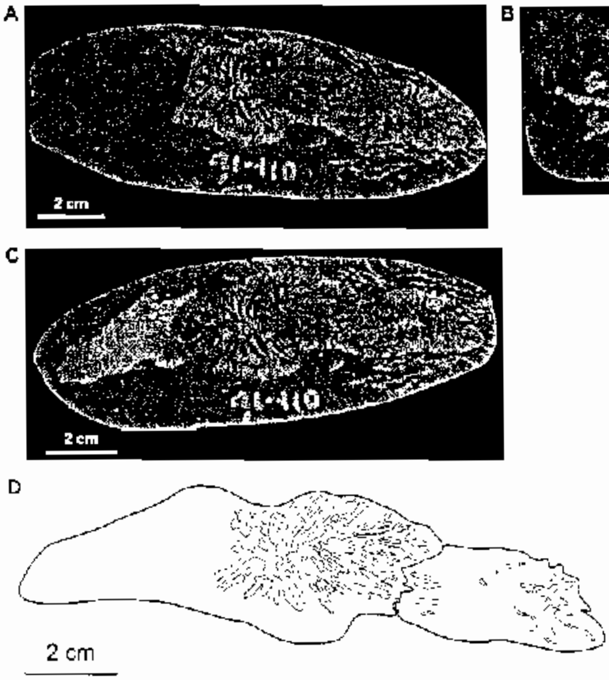

Figure 53 Photographs (A-C) and line drawing (D) of the articulated frontal and parietal ossifications of NRRU-A 110.

Material: a dermal bone, identified as a dermopterotic (NRRU-A 611, Figure 54).

Description of Specimen NRRU-A 611

The dermopterotic (Figure54) is trapezoidal in shape with its dorsal margin longer than its ventral margin. The anterior margin and posterior margins are approximately straight, while the lateral and medial margins are gently curved. Although the surface of the bone is damaged, we can observe some ornamentation on its surface, which mostly radiates from its center. Unfortunately we cannot observe the sensory canal on this bone.

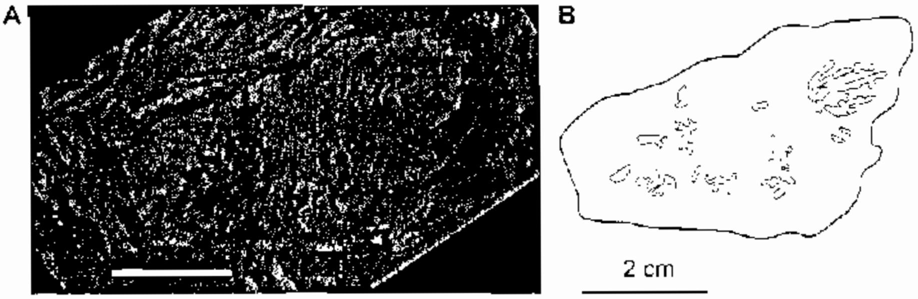

Figure 54 Photograph (A) and line drawing (B) of the dermopterotic bone, NRRU-A 611.

Material: a dermal bone, identified as a left subopercle (NRRU-V-3005, Figure 55).

Description of Specimen NRRU-V-3005

The subopercle (Figure 55) is visible as a deep, roughly triangular ossification with a well-developed process visible from the internal face, which is smooth. The height of the anterodorsal process equals almost half the subopercle depth. Although the posteroventral corner is broken, we can assume that it had a curved edge, which makes the ventral border completely convex while the dorsal border is straight.

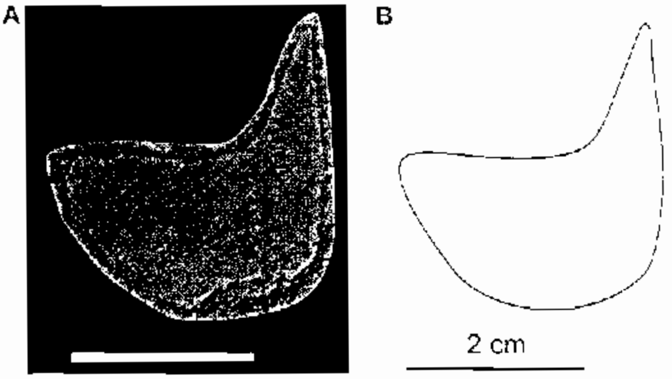

Figure 55 Photograph (A) and line drawing (B) of the internal view of the left subopercle, NRRU-V 3005.

Material: a dermal bone, identified as a preopercle (NRRU-CY-6002, Figure 56).

Description of Specimen NRRU-CY-6002

The bone is completely broken but we can see the limit of its shape and identify it as a left preopercle (Figure 56). The preopercle is composed of a narrow vertical limb with parallel margins. The dorsal extremity is straight without tapering and the horizontal limb, which has a tapering anterior end, forms a right angle with the vertical arm. The vertical limb is longer than the horizontal one. The ventral margin of the ventral arm is almost straight while its dorsal margin is slightly curved. Because of the bad preservation, we neither observed the surface of the ossification nor the path of the preopercular sensory canal.

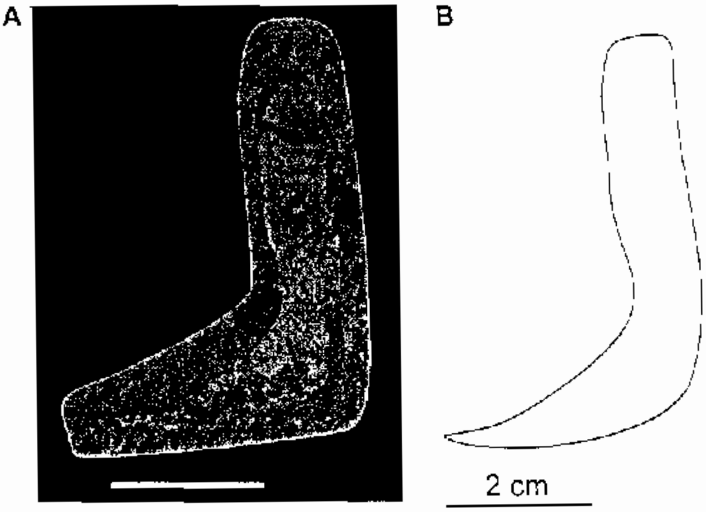

Figure 56 Photograph (A) and line drawing (B) of the right preopercle, NRRU-CY 6002.

Material: part and counterpart of a dermal bone of the pectoral girdle identified as a left cleithrum (NRRU- CT-1002, Figure 57). The bone is mainly preserved on the part (Figure 57A) while on the counterpart the vertical arm only is visible (Figure 57B).

Description of Specimen NRRU-CT-1002

The shape of the bone is roughly triangular with a high vertical limb and an extremely short but deep horizontal limb (Figure 57). The anterior margin is gently concave with a small prick present at its mid-depth. The posterodorsal margin presents a straight line on its dorsal half-depth, and then the ventral part shows a median crenulated edge. The lateral surface of the bone is apparently smooth without ganoin covered. According to the broken part at the anterior portion of the ventral limb and the vertical limb, a canal is apparently present. At the mid depth of the bone, which is the narrowest portion, a large pore is present (Figure 57A). The shape of the bone is reminiscent of a cleithrum but the possible presence of a canal is unusual in this kind of ossification. Its function and structure is unknown.

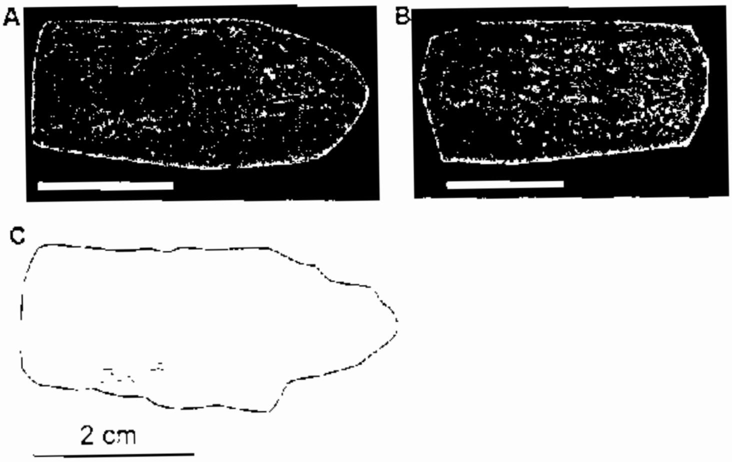

Figure 58 Photographs (**A-B**) and line drawing (**C**) of part and counterpart of the supraorbital, NRRU-BM 4003.

Material: A piece of the dermal bone identified as an extrascapular (NRRU-A 1040, Figure 59).

Description of Specimen NRRU-A 1040

The bone is nearly complete, except a little area destroyed after glued (Figure 59). The ossification is sub rectangular with the anteroventral corner narrowing anteriorly. The posterior margin is not straight; the lateral and dorsal margins have approximately parallel margins. The external surface of the bone presents several ridges of ganoin. The pattern of the ridges shows a regular pattern with an anteroposterior parallel arrangement of the ridges along the dorsal half and oblique arrangement of the ridges in the ventral half.

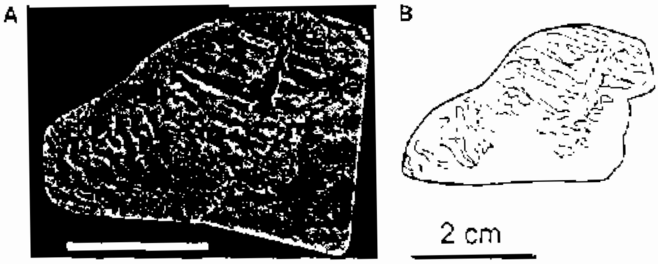

Figure 59 Photograph (A) and line drawing (B) of the extrascapular, NRRU-A 1040.

Material: A piece of a dermal bone identified as a right frontal (NRRU- ZY-3011, Figure 60).

Description of Specimen NRRU-ZY-3011

The bone is an extremely narrow and elongate element (Figure 60), about 4 times longer than the maximum width, with the anterior portion narrower than the posterior portion. The lateral and median margins are parallel, while the anterior margin is oblique. Although, the surface of the bone is totally scratched, some faint patches of ganoin are preserved at the posterior corner of the bone. Along the lateral margin, several pits indicate the path of the sensory canal.

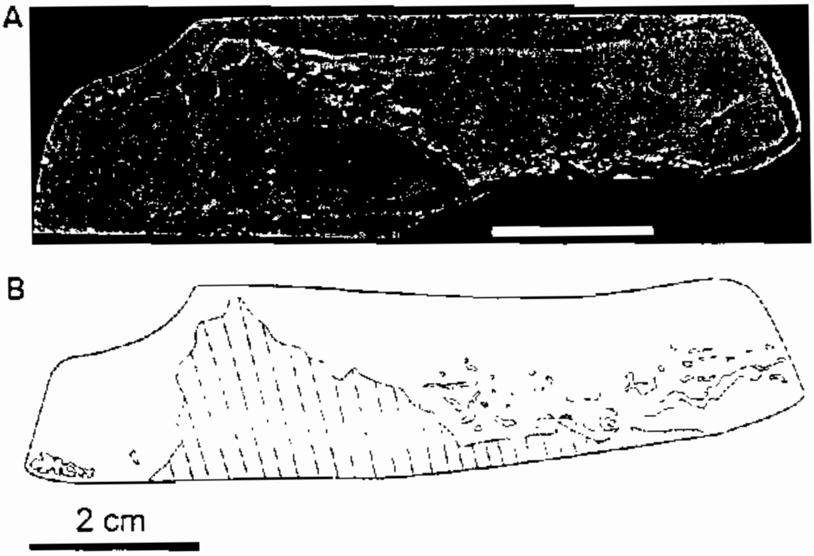

Figure 60 Photograph (A) and line drawing (B) of the right frontal, NRRU-ZY 3011.

Material: A piece of a dermal bone identified as a right frontal (NRRU- A-612, Figure 61).

Description of Specimen NRRU-A 612

The bone has a roughly rectangular shape with its anterior extremity tapering (Figure 61); its length is about 2.4 times longer than the width posteriorly. The anterior extremity of the bone presents an indentation; the posterior margin, which sutured with the parietal posteriorly, shows a deep notch at its mid width. The posterolateral margin shows a crenulated edge and the posteromedial forms a smooth curve. The anterior half of the lateral margin is rather straight whereas the posterior half presents a concavity then a convexity at the anterolateral corner. The medial margin of the bone is slightly curved. The external surface of the bone bears a huge ridge from the lateroposterior corner, at one-fourth of the width, which runs to the constriction of the anterior indentation. There is some ornamentation consisting of ridges of ganoin present in the posterior part; the rest is totally scratched but we can observe the trace of the path of the sensory.

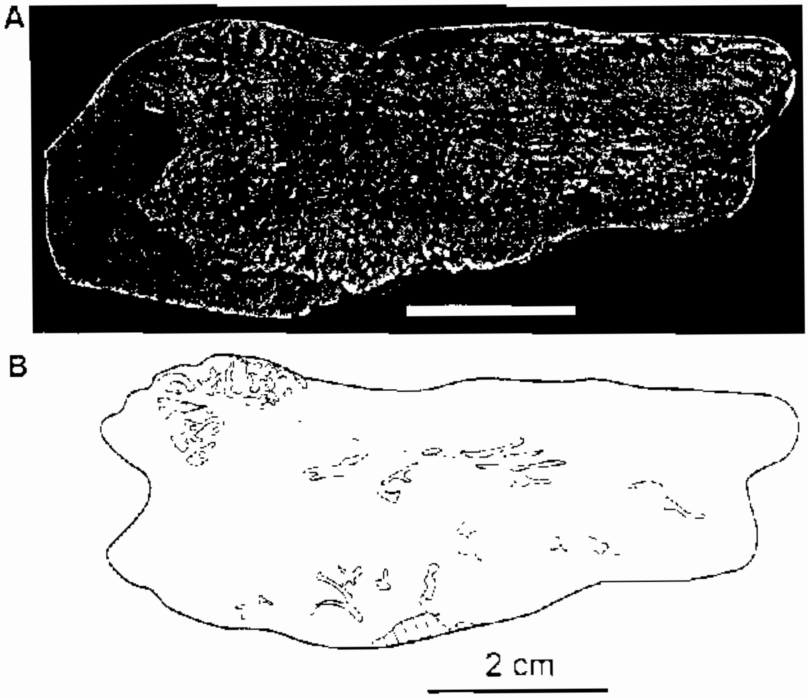

Figure 61 Photograph (A) and line drawing (B) of the right frontal, NRRU-A 612.

Material: part and counterpart of a dermal bone of the pectoral girdle identified as a left cleithrum. The bone is mainly preserved on the counterpart (NRRU- AL 15008, Figure 62B), which shows the internal face of the bone, while the missing area of the counterpart is presented on the part (NRRU-AL 15008, Figure 62A).

Description of Specimen NRRU-AL 15008

The cleithrum is slightly crescent shaped, with its anterior margin gently concave while its posterior margin is strongly convex (Figure 62). The vertical arm is much longer than the ventral arm with its dorsal end, which is slightly narrower than the ventral end. The bone is quite high; its height equals 8.5 cm. Its lateral surface is smooth and shows a huge convex ridge running along the posterodorsal portion, as assumed from the deep groove visible on its counterpart. This groove is possibly similar to the sensory canal of the large cleithrum. The anterior portion of the ventral part shows a shallow groove, which was possibly overlapped by the opercular series.

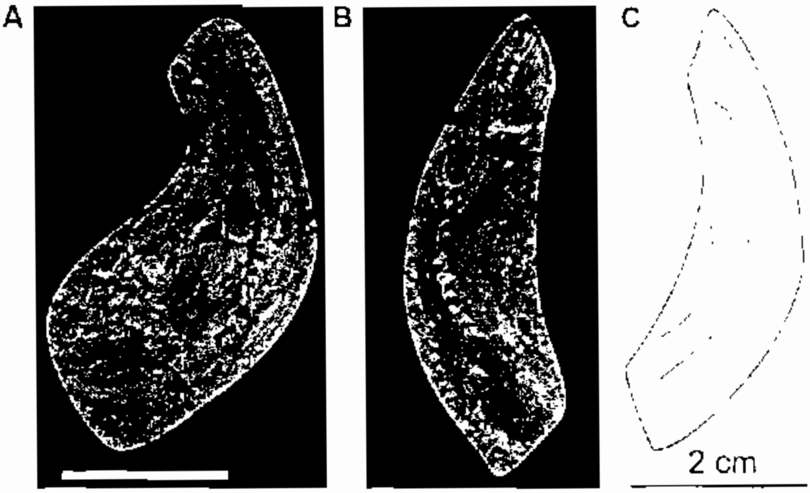

Figure 62 Photographs (A-B) and line drawing (C) of part and counterpart of the left cleithrum, NRRU-AL 15008.

Material: part (NRRU-BZ 11001, Figure 63B) and counterpart (NRRU- BZ 11001, Figure 63A) of a dermal bone from the pectoral girdle identified as a right cleithrum. The part presents only the imprint of the bone, which is visible as a convex surface, whilst the counterpart shows a deep groove of the smooth internal face of the bone.

Description of Specimen NRRU-BZ 11001

The bone is crescent shaped (Figure 63), with the vertical arm slightly longer than the horizontal arm (3.8 x 3.0 cm.). Its vertical and horizontal ends are almost straight. The anterior and posterior margins of the ossification are curved with parallel margins, but apparently tapering at the dorsal end. The external surface of the bone shows a gently convex ridge particularly at the center of the bone, as assumed from the deep groove visible on its counterpart. Close to the posterior edge of the vertical arm is present a narrow groove including at least two notches observed above this groove (Figure 63B).

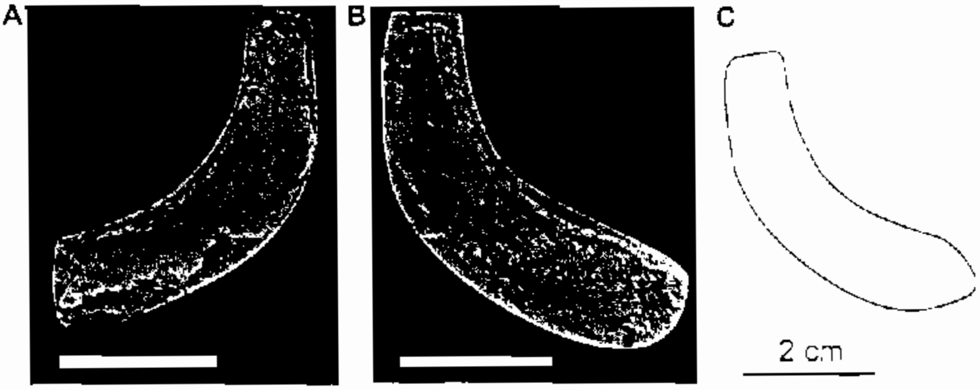

Figure 63 Photographs (**A-B**) and line drawing (C) of part and counterpart of the right cleithrum, NRRU-BZ 11001.

Material: a dermal bone, identified as a dermopterotic (NRRU-A-333, Figure 64).

Description of Specimen NRRU-A 333

The bone is broken especially on its lateral and medial edges as well as on its external surface (Figure 64). However, we assume that the bone has a trapezoidal shape with its anterior margin slightly curved. Although the surface of the bone is damaged we can observe some ornamentation on its surface, which mostly radiates from its center. Besides the shape of the bone itself, the occurrence of the sensory canal located near its lateral margin, where the bone is broken, confirms that this bone is the dermopterotic.

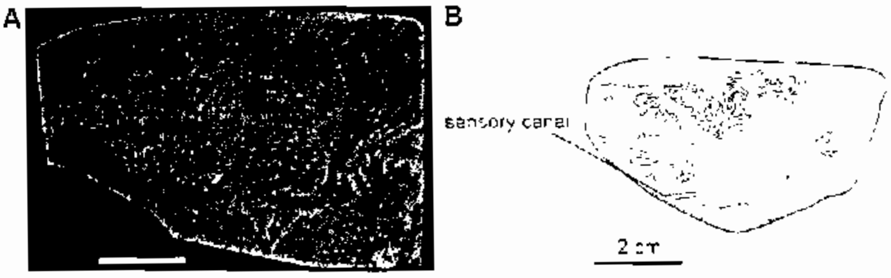

Figure 64 Photograph (A) and line drawing (B) of the dermopterotic, NRRU-A 333.

Material: a piece of dermal bone, identified as a supraorbital (NRRU-AJ 1005, Figure 65).

Description of Specimen NRRU-AJ 1005

The bone has a sub rectangular shape with its posteroventral part broken (figure 65). The ossification shows a shallow concavity visible as a large rhombus shape situated on the ventral half of the anterior portion of the bone. This structure is referred to the area that overlapped the infraorbital. Based on the visible part, on which a ganoin cover is present, the supraorbital tapers anteriorly and widens abruptly in its posterior portion. There is no trace of sensory canal.

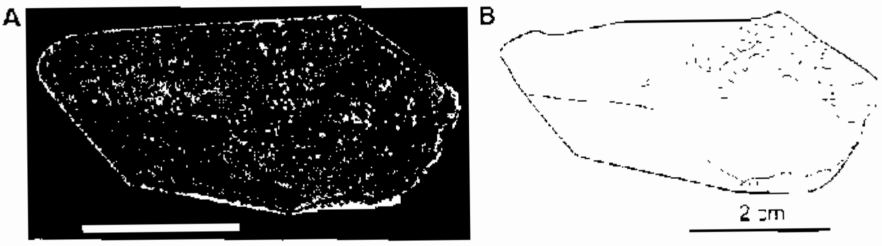

Figure 65 Photograph (A) and line drawing (B) of the supraorbital, NRRU-AJ 1005.

Material: a piece of a dermal bone, identified as a right nasal (NRRU-ZA 9005, Figure 66).

Description of Specimen NRRU-ZA 9005

The shape of the bone is rather triangular with its anterior part tapering (Figure 66). The ossification presents a smooth internal surface with a large hole located nearly

The fossil assemblage is mainly fragmentary and very fragile because of the highly wheathered erosion present in a badland type landscape, deposited of reddish brown siltstone. Most items are isolated teeth of crocodile, theropod, sauropod dinosaurs (Buffetaut *et al.*, 2002, 2005) and various types of shark teeth corresponding to various species of freshwater shark (Cappetta *et al.*, 1990; 2006; Cuny *et al.*, 2003; 2005; 2007; 2008) as well as a large number of isolated scales collected on the surface (Cavin *et al.*, 2009). The Khok Pha Suam locality is situated in a wild area, near the town of Sri Muang Mai District, Ubon Ratchathani Province.

4.4.2.2.2 Systematic Description

Class: OSTEICHTHYES
Super Division: HOLOSTEI
Division: GINGLYMODI
Order *indeterminate*

Morphology of the isolated scale

The isolated fish scales from this locality are easily classified into two morphotypes (Figure 69); morphotype I with a smooth surface and morphotype II, with ridges or several parallel lines of numerous holes on their surfaces. The general shape and outline of the scales are variable because they belong to different part of the fish body, i.e. rectangular shaped, more rhomboid and narrow, or triangular in shape, the latter correlate to the median dorsal or ventral midline, or to the scutes on the tail (Figure 69A). The anterior extremity of the scales shows the peg and socket arrangment for the articulation as common in other ginglymodians.

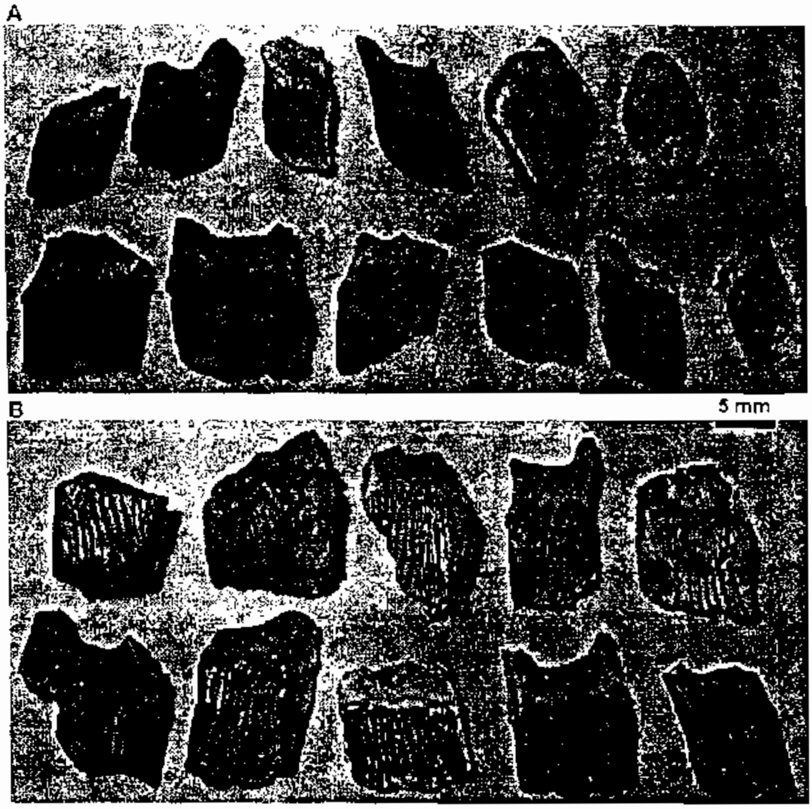

Figure 69 Photographs of the scales from Khok Pha Suam locality. A: morphotype I with smooth surface. B: morphotype II with parallel ridges on their surfaces.

4.4.2.3 The Lam Pao Dam Locality

4.4.2.3.1 Introduction

The outcrop is situated at the spring way of Lam Pao Dam in Sahat sakhan district, Kalasin Province. So far isolated teeth of freshwater shark, fish remains and pieces of bones have been found in a conglomerate of clastic sandstones layer containing calcareous pebbles. The fragments of bones are colourful due to their mineral composition.

4.4.2.3.2 Systematic Descripion

Class: OSTEICHTHYES
Super Division: HOLOSTEI

Division: GINGLYMODI

Order *indeterminate*

Morphology of the isolated scale

So far the fish remains discovered in this locality are isolated button crushing teeth (Figure 70A) and very large ganoid scales with its surface showing several pit arranged in parallel lines along its length (Figure 70). The general out-line of the scales are rectangular and quite thick.

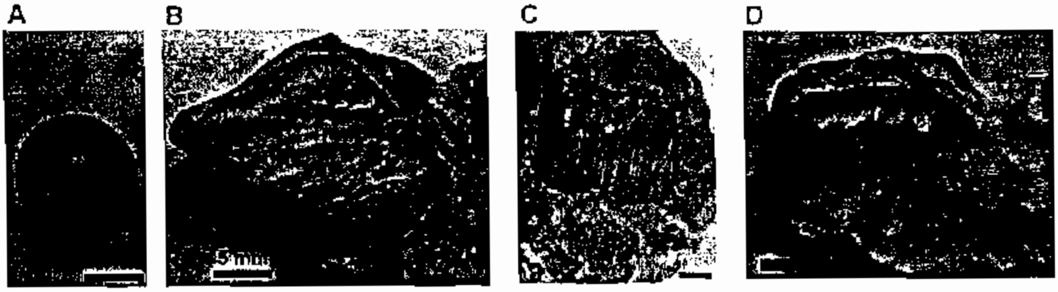

Figure 70 Photographs of the tooth and scales from Lam Pao Dam locality. A: a button crushing tooth. B-D: scales examination with ornamentation on their surfaces.

4.4.2.3 Microornamentation of The Khok Kruat Formation

The microornamentation study of the fish scales of the Khok Kruat Formation is based on specimens from three localities; Ban Saphan Hin, Khok Pha Suam and Lam Pao Dam localities. Three scales from each outcrop were used to examine the microstructure; they are referred as Ban Saphan Hin1, Ban Saphan Hin2 and Ban Saphan Hin3; Khok Pha Suam1, Khok Pha Suam2 and Khok Pha Suam3; Lam Pao Dam1, Lam Pao Dam2 and Lam Pao Dam3. Photographs of the ganoin surface of the scales have been taken under scanning electron microscope; only scales from two outcrops, Ban Saphan Hin and Khok Pha Suam, present tubercles on their surface (Figure 71-77). The scales from these two localities show two gross morphotypes; one with a smooth surface and the other with several parallel lines of numerous holes or ridges on its anterior surface. Nevertheless the tubercles on the surface of the scales from Khok Pha Suam locality are extremely weatherworn (Figure 74-77). Tubercles of the ganoin scales of specimens from Ban Saphan Hin have their width and length ranging between 4 to 7 µm and 3.7 to 6.8 µm respectively. The average width and length of the tubercles are 5.6 and 5.68 µm respectively, indicating that the tubercles are roughly large and rounded in shape. The average intertubercle distances is 8.42 µm. Compared to the other localities situated in the Khok Kruat Formation, the Khok Pha Suam scales present a relatively smaller size of the tubercle on their ganoin surfaces. This is correlated to the intertubercle distances, which is more reduced. The range of their width is 4.3-5.6 µm and of their lengths is 4.5-5.7 µm long. The average width and length of the tubercles are 4.9 and 5.1 µm respectively, indicating that the tubercles are slightly rounded in shape. The average intertubercle distance is 7.24 µm. To conclude, the tubercles of the scales from both localities from the Khok Kruat Formation are quite large and rounded. The tubercle size and intertubercle distances in KS12-97 and KS12-265 are summarized in table 3 and table 4.

Table 3 Measurement of the tubercles and of the intertubercle distances of the three scales from Ban Saphan Hin locality.

Parameter	Measurements	Number of distances	Average width	Average length	Average distances
Ban Saphan Hin1	T34	79	4.06	3.77	7.2
Ban Saphan Hin2	T30	68	5.81	6.44	9.05
Ban Saphan Hin3	T32	75	6.95	6.83	9.03
			5.60	5.68	8.42

Table 4 Measurement of the tubercles and of the intertubercle distances of the three scales from Khok Pha Suam locality.

Parameter	Measurements	Number of distances	Average width	Average length	Average distances
Khok Pha Suam1	T31	65	4.35	4.56	6.91
Khok Pha Suam2	T31	72	5.63	5.71	7.52
Khok Pha Suam3	T25	47	4.73	5.04	7.3
			4.90	5.10	7.24

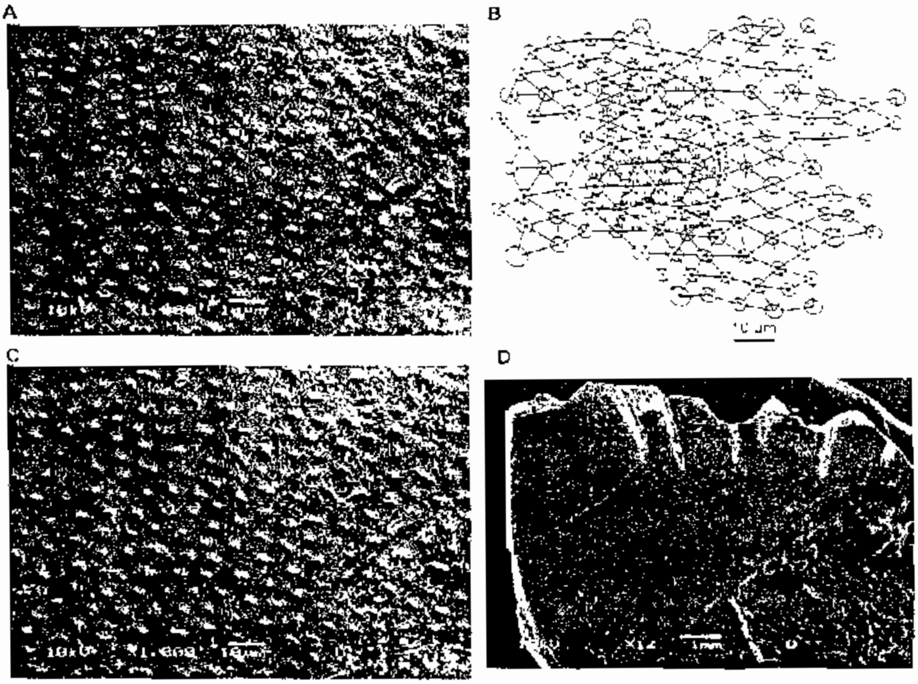

Figure 71 Specimen Ban Saphan Hin1. A: Plot of tubercles on micrograph. B: measurement of the tubercles (34 measurements) and of the intertubercle distances (79 measurements). C: SEM view of the ganoin surface of the scale. D: external view of the scales.

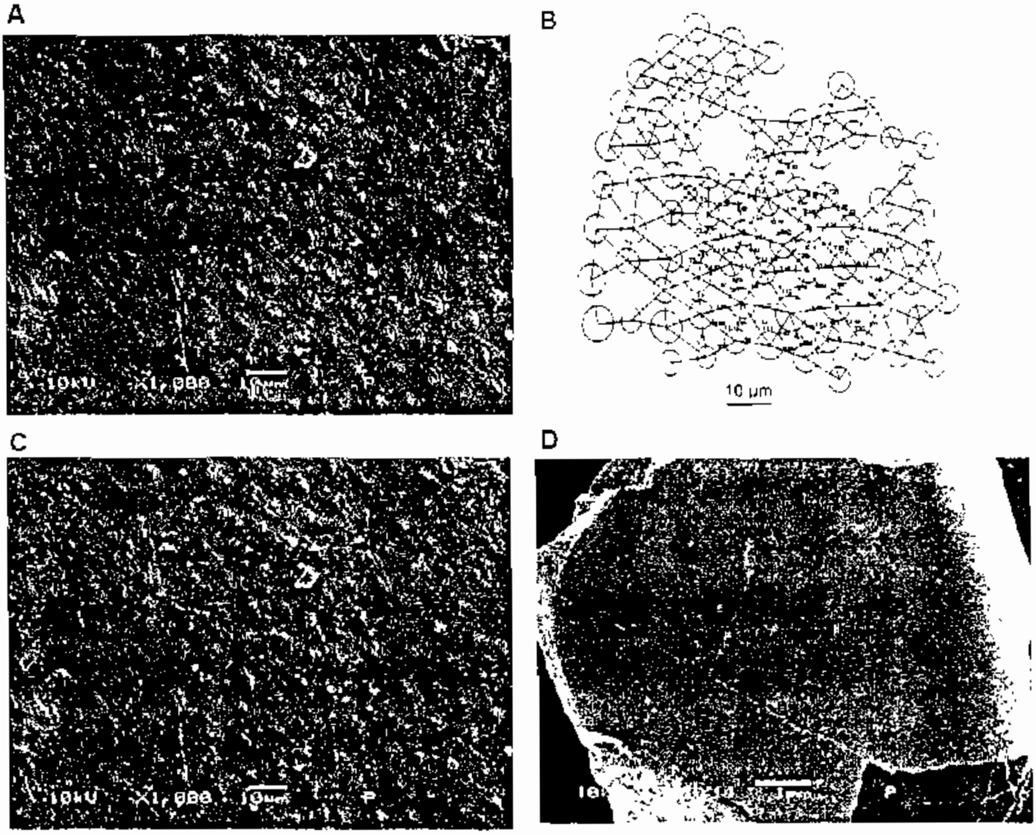

Figure 72 Specimen Ban Saphan Hin2. A: Plot of tubercles on micrograph. B: measurement of the tubercles (30 measurements) and of the intertubercle distances (68 measurements). C: SEM view of the ganoin surface of the scale. D: external view of the scales.

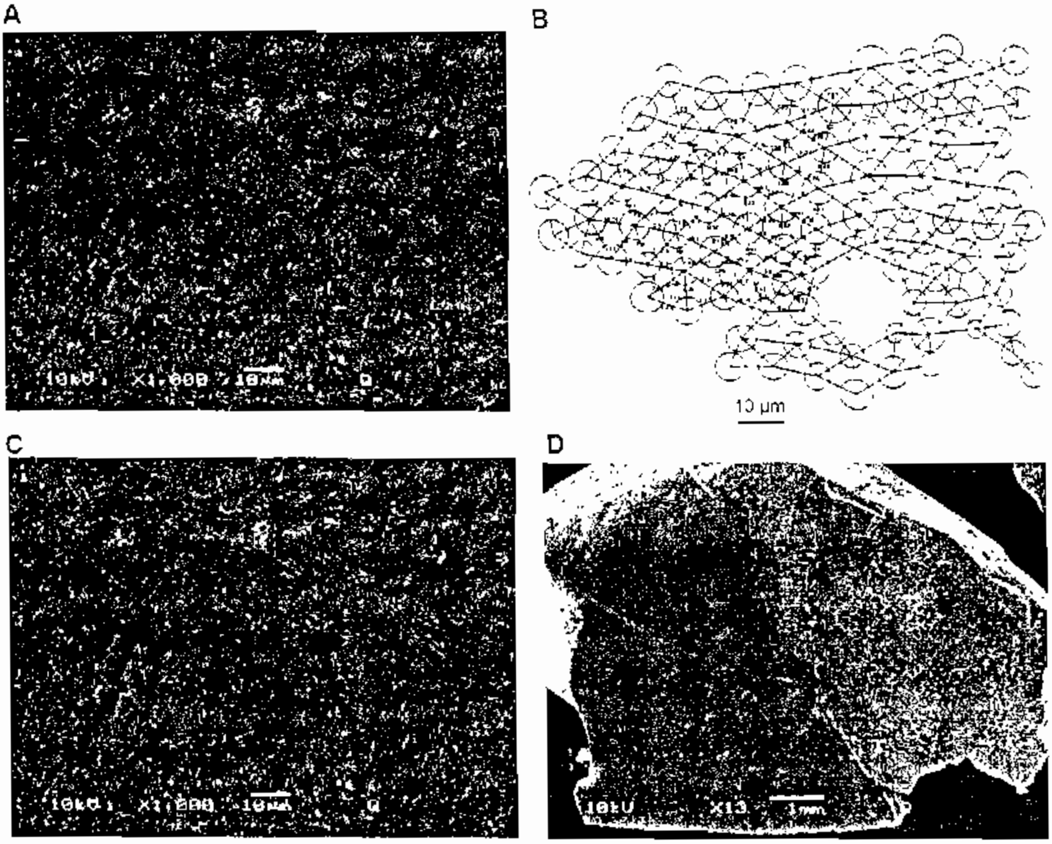

Figure 73 Specimen Ban Saphan Hin3. A: Plot of tubercles on micrograph, B: measurement of the tubercles (32 measurements) and of the intertubercle distances (75 measurements). C: SEM view of the ganoin surface of the scale, D: external view of the scales.

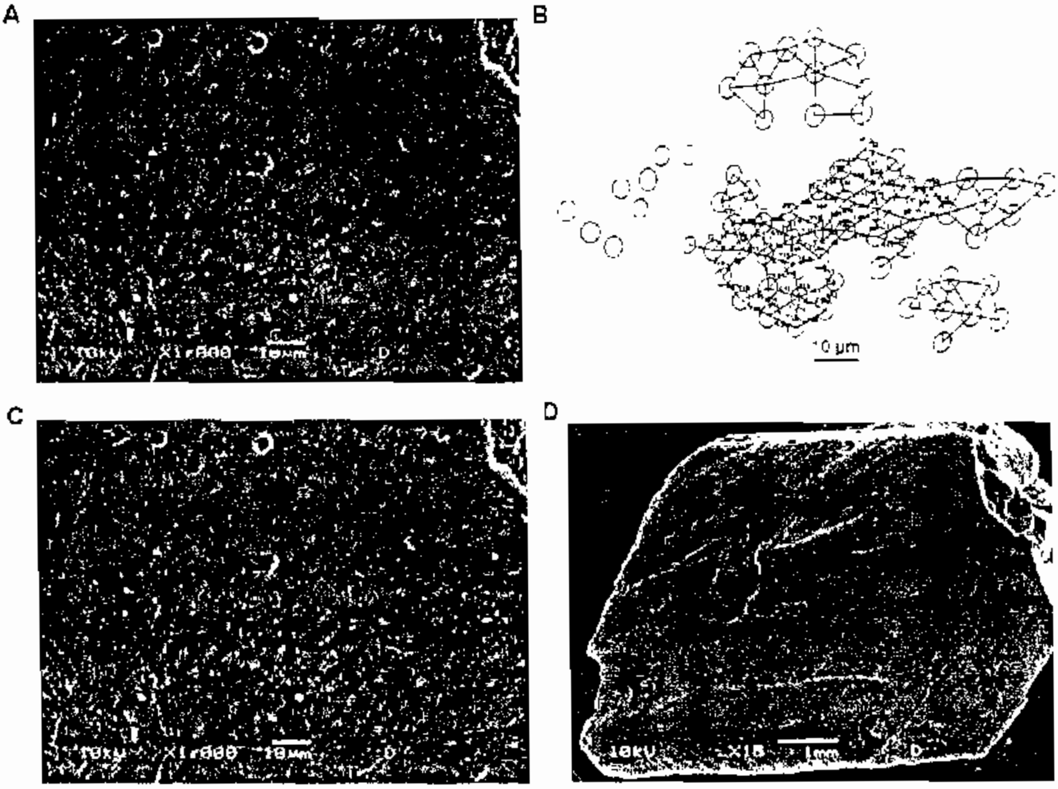

Figure 74 Specimen Khok Pha Suam I. A: Plot of tubercles on micrograph. B: measurement of the tubercles (31 measurements) and of the intertubercle distances (65 measurements), C: SEM view of the ganoin surface of the scale, D: external view of the scales.

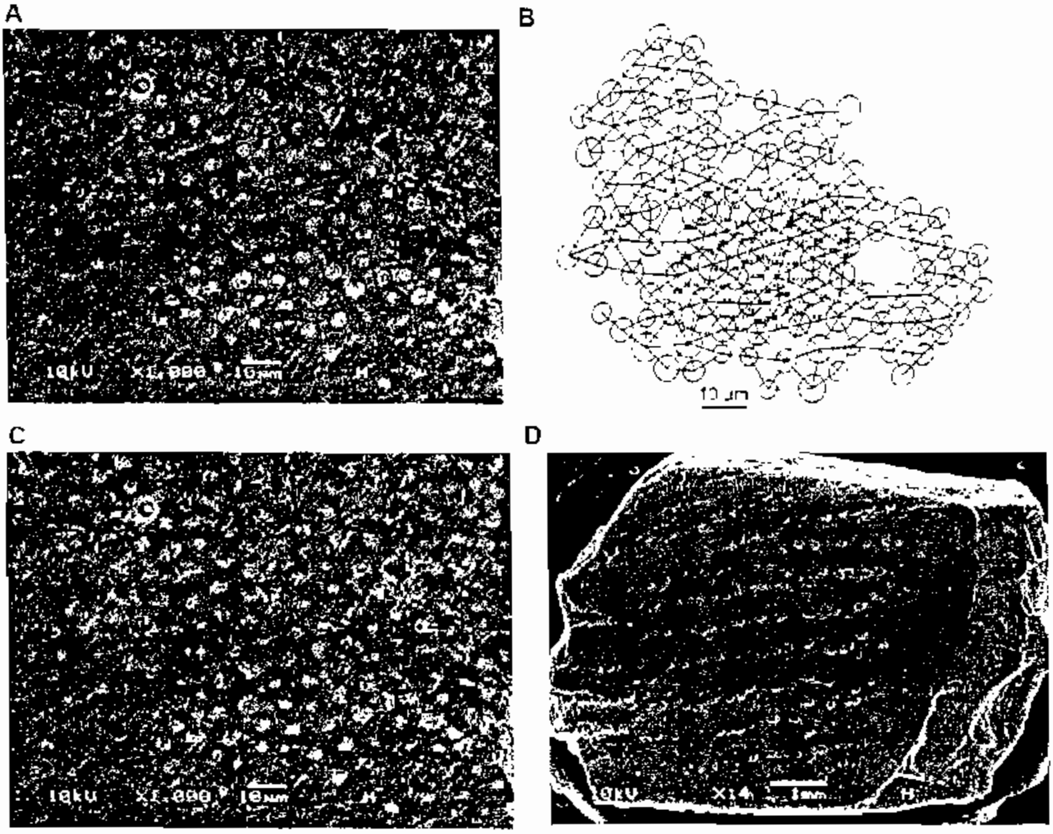

Figure 75 Specimen Khok Pha Suam2. A: Plot of tubercles on micrograph, B: measurement of the tubercles (31 measurements) and of the intertubercle distances (72 measurements). C: SEM view of the ganoin surface of the scale, D: external view of the scales.

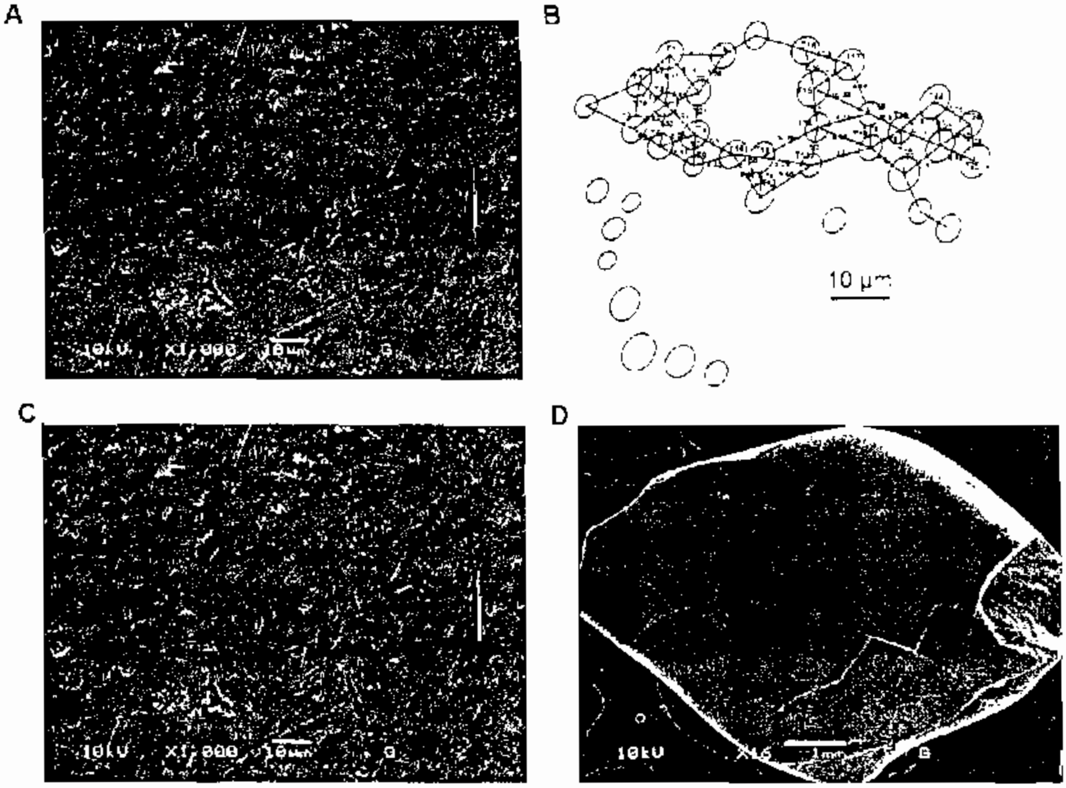

Figure 76 Specimen Khok Pha Suam3. A: Plot of tubercles on micrograph. B: measurement of the tubercles (25 measurements) and of the intertubercle distances (47 measurements), C: SEM view of the ganoin surface of the scale, D: external view of the scales.

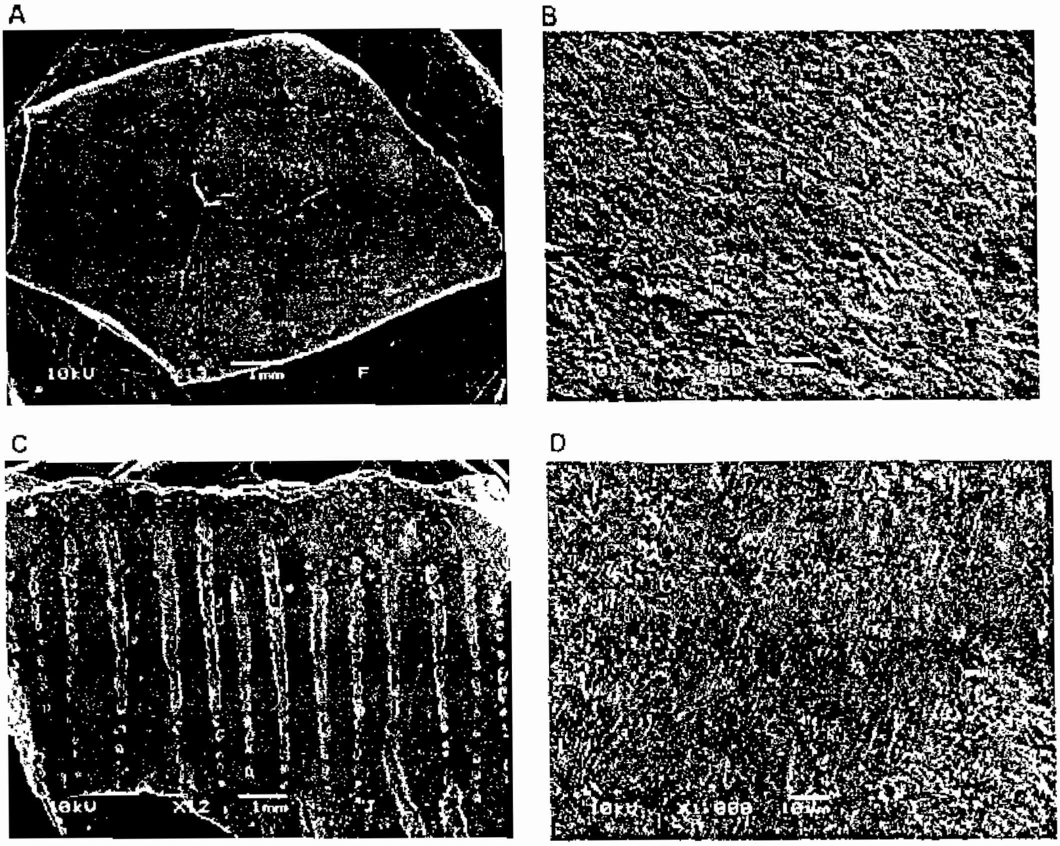

Figure 77 Scales observed from Khok Pha Suam F and J. A: External surface and B: SEM view of scale of specimen Khok Pha Suam F; C: External surface and D: SEM view of the ganoin surface of the scale of Khok Pha Suam J.

4.4.3 Comparison and Discussion

The materials from localities of the Khok Kruat Formations are mainly fragmentary and mostly isolated pieces of bones are preserved, which allow examining the microornamentation of the scale surfaces. The scales from only two localities present a microstructure, and scales from both sites show a similar pattern of the external scales referable to two morphotypes. Concerning the Khok Pha Suam locality, the scales are highly wheatering as revealed SEM photographs, with much crashes on their surface and with less tubercle present. The tubercle structure on scales from both localities show a rounded and slightly large size, with the average width and length 5/5.7 μm respectively. The sample from Ban Saphan Hin show larger tubercle size (5/5.6 μm in their width and length) whereas the sample from Khok Pha Suam show

4.9/5.1 µm in average tubercle size. The intertubercle distances appear to be correlatated with the size of the tubercles. The Khok Pha Suam scales have smaller tubercles size and shorter intertubercle distance. Finally, the Lam Pao Dam scales do not present tubercles, probably because of the smaller sample size with only poorly preserved scales.

4.4.4 Conclusion

The osteology of the partially articulated specimens and of several isolated dermal bones from the Ban Saphanhin locality (Nakhorn Ratchasima Province) of Khok Kruat Formation reveals a typical kind of ornamentation on the dermal bones. Compared with fishes from the older Phu Kradung Formation, the caudal fin and the dermal bones are very different, especially the dermal bones. None of fishes from Phu Kradung localities show ganoin patches with delicated ornamentation on their dermal bones, although *Isanichicthys* had also a strong ornamentation, but in this taxon it lacks ganoin on the dermal bones to the contrary of samples from the Ban Saphan Hin locality in the Khok Kruat Formation. It means that based on the osteology; there is at least one taxon of ginglymodian fish Khok Kruat Formation that differs from those in the older formations. The microstructure of the surface scales from the Ban Saphan Hin and Khok Pha Suam localities of the Khok Kruat Formation show a similar pattern of the microornament, even through they are different morphological features inducing that they belongs to the same species.

CHAPTER 5

CONCLUSIONS

5.1 Diversity of Bony Fishes in the Khorat Group (Morphology, Ornamentation of Scales)

In 2009, Cavin *et al.* described the bony fishes record from the Middle Late Jurassic Khlong Min Formation in the Peninsula of Thailand to the Early Cretaceous Khok Kruat Formation of the Khorat Plateau (Cavin *et al.*, 2009 and appendix V). At that time, the diversity comprised at least 6 'semionotids' and 3 sinamiids from three formations (Phu Kradung, Sao Khua and Khok Kruat Formations) of Khorat Group. In the present study, the number of taxa has significantly increased by comparison with this former study; in particular it shows a higher diversity of ginglymodian fishes in the older Phu Kradung Formation as shown in the table below. In an opposite way, Cavin *et al.* have identified three taxa of 'semionotids' in the youngest Khok Kraut Formation on the basis of the morphotypes of the scales and on the evidence of button crushing teeth, but the present study based on the microstructure of the scales reveals that these scales belong to the same species. We question the occurrence of a distinct taxon with button crushing teeth and thick ganoid scales from the locality of Lam Pao Dam as we have no evidence of a different microstructure pattern on the scales. Similarly with the crushing teeth and ganoid scales from several localities of the Sao Khua Formation, we prefer to retain the occurrence of a single taxon of ginglymodi in this Formation because the microstructure of the scales examined in this work from two localities (Phu Phok and Phu Phan Thong outcrops) belongs to a typical form of sinamiid, *Siamamia naga*.

Table 5 Diversity of ginglymodian fishes in three formations of Khorat Group.

	Cavin *et al.* 2009	This work
Khok Kruat Fm	- Thick & large ganoid scales with button shaped teeth - ganoid scales with parallel grooves - smooth ganoid scales	- Thick & large ganoid scales with button shaped teeth - two set of scales within one taxon - a taxon with strong ornamentation of ganoin on the dermal bones
Sao Khua Fm	- ganoid scales with button shaped teeth	- ganoid scales with button shaped teeth
Phu Kradung Fm	- *'Lepidotes' buddhabutrensis* - *Isanichthys palustris*	- *Thaiichthys buddhabutrensis* - *Isanichthys palustris* - *Thaiichthys* cf. *buddhabutrensis* - *Isanichthys lertboosi* - new ginglymodian fish with hump back and tritorial dention

5.2 Palaeoecology

5.2.1 Variation within the Phu Kradung Formation

The locality of Phu Nam Jun shows a moderate diversity of fishes with two ginglymodians, *Thaiichthys buddhabutrensis* and *Isanichthys palustris*, one dipnoan, *Ferganoceratodus martini*, and one tooth of a hybodont shark (Cuny *et al.*, in press), but no evidence of tetrapod has been found so far. Petrified wood fragments have not been found in situ in the outcrop, but they are abundant around the outcrop. Eventhough the Phu Nam Jun locality shows a relatively high diversity of fishes, its total diversity is quite low in term of the global fossil assemblages compared to the other localities in Phu Kradung Formation. The vertebrate fossils that have been collected in other localities consist of both complete and incomplete remains such as the Kham Phok locality, which has yielded a large turtle as well as a theropod tibia (Buffetaut and Suteethorn, 2007; Tong *et al.*, 2009), crocodile and shark remains (Cuny *et al.*, in press) as well as small ginglymodian (described in chapter 4); the Chong Chat locality has yielded a part of a cf. *Theriosuchus* dentary (Lauprasert *et al.*, 2011) and an articulated ginglymodian fish (described in chapter 4), as well as turtle shell, sharks and dinosaurs remains; and the richest and most diverse Phu Noi locality contains at least 2 taxa of turtle (H. Tong, pers.comm.), new taxon of crocodile (J. Martin, pers. comm.), *Isanichthys lertboosi* (Deesri *et al.* in press), theropod (Chanthasit, 2011), sauropod dinosaurs, pterosaur (E. Buffetaut, pers. comm.), new taxon of shark (Cuny *et al.*, in press) as well as the trunk of plant.

5.2.2 Variation between the Formations

The vertebrate fossil assemblages of the localities from the Sao Khua and Khok Kruat formations are quite diverse but less fishes have been found in these localities than in the Phu Kradung Formation. So far, fishes are preserved as fragments and isolated scales and teeth in these localities, while in Phu Kradung localities a high number of well preserved specimens have been found (Table 5). According to the sedimentology, the sediment in Sao Khua and Khok Kruat localities are mostly deposited in a fluvial system, whereas in the Phu Kradung localities, sediment are mostly siltstone, mudstone and fine sandstones indicative a floodplain – lacustrine deposition. The difference in the sedimentology, and consequently in the palaeoenvironments between the Phu Kradung and the younger two formations may explained, at least in part, the different modes of preservation of the fish material.

5.3 Palaeobiogeography

From a palaeobiogeographic point of view, the phylogenetic analysis (Deesri *et al.*, in press) of the genus *Isanichthys*, including *Isanichthys palustris*, from the Phu Nam Jun locality, Kalasin Province; *Isanichthys lertboosi*, fish from Phu Noi locality, Kalasin Province; *Isanichthys latifrons* (previously referred to '*Lepidotes*' *latifrons*) from the Middle Jurassic marine assemblage from Europe and *Isanichthys luchowensis* (previously referred to '*Lepidotes*' *luchowensis*) from the Upper Shaximiao Formation in Sichuan, a series of continent Early to Middle Jurassic deposits, provides some interesting results. The study reveal that *I. lertboosi* is the sister group of the pair *I. palustris* and *I. latifrons*. Although few characters have been coded for *I. luchowensis* it appears to belong to the genus *Isanichthys*. From the relationships result, we point out affinities between species from Eastern Asia with one from Europe, which were connected via areas situated along the northern margin of the Tethys during most of the Mesozoic. The assemblage of sharks also shows a similar pattern in the Middle Jurassic of both China and Europe (Cuny *et al.*, in press) as well as the cf. *Theriosuchus* from the Phu Kradung Formation, which also indicates European affinity (Lauprasert *et al.*, 2011).

The phylogenetic position of *Thanichthys buddhabutrensis*, from the Late Jurassic Phu Kradung Formation (Cavin *et al.*, 2013) has been resolved as the sister group of *Araripelepidotes*, a fish from the Early Cretaceous of Brazil and *Pliodetes*, a fish from the Lower Cretaceous of Gadoufaoua, Niger Republic. The palaeobiogeographical pattern probably resulted from vicariant events, firstly between the *Thanichthys* lineage in Laurasia and the *Araripelepidotes-Pliodetes* lineage in Gondwana some when in the Jurassic, and secondly during the opening of the South Atlantic that split western Gondwana into South America and Africa during the Early Cretaceous separating *Araripelepidotes* and *Pliodetes*.

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APPENDIXES

APPENDIX I

Tables of the measurements of the tubercles diameter and the distances between them.

Table 6 Measurements of Scale specimen KS12-97(3-3) from Phu Nam Jun with 46 measurements and 110 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	6	2.790698	7	3.255814	8.4	6.6	8.23					7.743333
T2	6.5	3.023256	7	3.255814	8.23	7.16	6	8.83				7.555
T3	6.6	3.069767	7	3.255814	8.83	5.86	6.6	6.97				7.065
T4	6.3	2.930233	6.7	3.116279	6.97	7.7	7.2					7.29
T5	9.2	4.27907	10.9	5.069767	13.95	10.46	8.12	8.12	8.65	8.41		9.618333
T6	5.8	2.697674	7	3.255814	7.06	6.97	8.65	6.6	7.16	8.1		7.423333
T7	5.7	2.651163	6.8	3.162791	6.14	5.21	8.1	6	5.86	6.6		6.318333
T8	7.6	3.534884	8	3.72093	6.97	6	7.81	6.14	6.6	7.7		6.87
T9	8.4	3.906977	9	4.186047	7.21	7.44	8.6	6.97	7.2			7.484
T10	8.1	3.767442	7.2	3.348837	8.46	7.21						7.835
T11	6.7	3.116279	7.8	3.627907	8.56	7.06	5.21	7.81	7.67	6.79		7.183333
T12	6.8	3.162791	8.2	3.813953	8.3	7.67	6	8.6	7.53	7.53		7.605
T13	8.5	3.953488	8.5	3.953488	7.25	8.18	7.53	7.44	8.46			7.772
T14	6.4	2.976744	7.2	3.348837	9.3	8.12	6.97	8.56	7.67	11.26		8.646667
T15	6.2	2.883721	7.2	3.348837	7.67	6.79	8.3	8.19	8	10.23		8.196667
T16	7.5	3.488372	8.1	3.767442	8	8.19	7.53	8.18	6.51	6.7		7.518333
T17	7.6	3.534884	8	3.72093	7.9	8	6.51	7.25				7.415
T18	7.5	3.488372	9.5	4.418605	13.86	12.79	8.56	7.44				10.6625
T19	8	3.72093	9.4	4.372093	7.44	8.14	7.53	13.95				9.265
T20	8	3.72093	10.2	4.744186	7.67	8.37	7.53	10.46	9.3	8.6		8.655
T21	8.5	3.953488	9	4.186047	8.93	9.3	8.12	9.3	12.1	8		9.291667
T22	7.5	3.488372	8.5	3.953488	9.1	12.1	11.26	10.23	6.51	7.21	6.98	9.055714
T23	7.2	3.348837	7.8	3.627907	6.51	8	8	6.5	6.12			7.026
T24	8.2	3.813953	8.6	4	8.37	6.5	6.7	8	6.98	7.44		7.331667
T25	8.5	3.953488	8.5	3.953488	7.91	8.93	6.98	7.9				7.93
T26	8.5	3.953488	9.6	4.465116	8.14	8.56	8.14	8.37	6.6	7.9		7.951667
T27	7	3.255814	8.5	3.953488	6.4	6.6	7.67	7.21	6.98			6.972
T28	8	3.72093	8.3	3.860465	6.98	7.4	8.6	8.93	8.14	8.14		8.031667
T29	8	3.72093	8.5	3.953488	8.1	8.14	8	9.1	8.37	8.23		8.323333
T30	7.8	3.627907	8.5	3.953488	7.4	7.21	8.37	6.98	7.21	7.44		7.435

Table 6 (continued)

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T31	6.4	2.976744	7	3.255814	7.21	7.21	6.12	8.37	7.9	7.21		7.336667
T32	8.2	3.813953	8.4	3.906977	7.9	7.9	7.44	8.93	6.74	7.91		7.803333
T33	8.2	3.813953	8.4	3.906977	8.1	8.93	6.74	7.91				7.92
T34	8	3.72093	8.5	3.953488	8.37	6.98	7.44	7.21	7.9	6.74		7.44
T35	8.9	4.139535	9.5	4.418605	8.84	9.07	6.74	7.91	8.93	7.64		8.188333
T36	9.4	4.372093	10	4.651163	9.3	9.3	7.67	8.1				8.5925
T37	9.5	4.418605	9.9	4.604651	13.86	8.84						11.35
T38	8.5	3.953488	8.5	3.953488	8.84	12.79	8.14	7.44				9.3025
T39	8.2	3.813953	9	4.186047	7.44	7.9	6.4	7.9				7.41
T40	8.5	3.953488	9.5	4.418605	7.9	6.98	6.98	7.35				7.3025
T41	7.9	3.674419	8.5	3.953488	7.35	8.14	8.1	7.21				7.7
T42	8.6	4	9.5	4.418605	7.21	8.23	7.21	6.51				7.29
T43	7.2	3.348837	7.6	3.534884	6.51	7.21	6.98	6.98				6.92
T44	9.4	4.372093	10	4.651163	6.98	8.37	9.07	8.37				8.1975
T45	8	3.72093	8	3.72093	8.37	8.84	9.3	8.6				8.7775
T46	10	4.651163	11	5.116279	8.6	9.3						8.95
		3.614762		3.941355								7.998943

Table 7 Measurements of Scale specimen KS12-97 (12+1) from Phu Nam Jun with 34 measurements and 78 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	8.2	3.904762	9.3	4.428571	9.19	8.01						8.6
T2	8.1	3.857143	9	4.285714	9.19	9.38	9.76	12.14				10.1175
T3	8.6	4.095238	9.3	4.428571	12.14	7.38	10.19	11.04	9.43			10.036
T4	6.5	3.095238	8	3.809524	9.43	7.95	9.14					8.84
T5	8.4	4	8.8	4.190476	9.14	9.71	10	9.52				9.5925
T6	7.6	3.619048	9	4.285714	8.01	9.38	7.67	10.14	9.28			8.896
T7	7.3	3.47619	8	3.809524	7.67	9.76	7.38	9.19	8.62			8.524
T8	8.1	3.857143	9	4.285714	8.33	9.19	10.19	9.28	8.57	8.67		9.038333
T9	8.1	3.857143	8.6	4.095238	9.28	11.04	7.95	9.71	8.95	9.28		9.368333
T10	8.4	4	9	4.285714	9.14	8.95	10	7.52	10.19	8.67		9.078333
T11	7	3.333333	7.5	3.571429	9.52	7.52	9.38	7.47				8.4725
T12	9	4.285714	10.2	4.857143	9.28	9.38	8.76	8.28				8.925
T13	8.5	4.047619	9.5	4.52381	9.38	10.14	8.62	8.33	8.1	8.1		8.778333
T14	6.6	3.142857	7.5	3.571429	8.28	7.62	10.24	9.43				8.8925
T15	9	4.285714	9.5	4.52381	7.62	8.76	8.1	9.04	10.19	9.86		8.928333
T16	7	3.333333	8.2	3.904762	9.04	8.1	8.67	8.81	8.42	8.33		8.561667
T17	7.8	3.714286	8.5	4.047619	8.81	8.57	9.28	9.14	8.95	7.43		8.696667
T18	7.5	3.571429	8	3.809524	9.43	8.33	9.28					9.013333
T19	7.5	3.571429	8	3.809524	8.33	10.24	9.86	9.28	10	8.57		9.38
T20	7.5	3.571429	8.1	3.857143	9.28	10.19	8.33	8.57	8.1	10.24		9.118333
T21	6.5	3.095238	7.4	3.52381	8.57	8.42	7.43	9.14	7.38	8.33		8.211667
T22	8.5	4.047619	9.5	4.52381	9.14	8.95	8.67	8.57	8.95	7.14		8.57
T23	8.5	4.047619	9	4.285714	8.57	10.19	9.38	9.62	11.19	10.38	9.33	9.808571
T24	7	3.333333	8.2	3.904762	7.47	9.62	10.57					9.22
T25	7.5	3.571429	9.5	4.52381	9.28	8.57	9.76					9.203333
T26	8.5	4.047619	9.5	4.52381	9.76	10	10.24	9.28				9.82
T27	7.7	3.666667	8.5	4.047619	9.28	8.1	8.33	8.57				8.57
T28	7.3	3.47619	8.3	3.952381	8.57	7.38	7.14	7.52				7.6525
T29	8.1	3.857143	9	4.285714	7.52	8.95	9.33	7.62				8.355
T30	7.5	3.571429	9	4.285714	7.62	10.38	9.24	8.57				8.9525

Table 7 (continued)

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(μm)	mm	(μm)								
T31	8.4	4	10	4.761905	10.57	11.19	9.24	9.04	11.04	9.76		10.14
T32	8.4	4	9.5	4.52381	8.57	9.04	7.38					8.33
T33	7.8	3.714286	9.5	4.52381	7.38	11.04	9.76					9.393333
T34	7.6	3.619048	9	4.285714	9.76	9.76						9.76
		3.72549		4.186275								9.02484

Table 8 Measurements of Scale specimen KS12-97 (15-3) from Phu Nam Jun with 31 measurements and 70 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	9	4.186047	8.2	3.813953	9.3	6.23	10.69					8.74
T2	7	3.255814	7	3.255814	10.69	7.67	8.65	6.37	6.74			8.024
T3	6.6	3.069767	6.8	3.162791	6.74	7.81	5.86					6.803333
T4	8	3.72093	8.8	4.093023	5.86	9.58	8.28	7.58	7.76			7.812
T5	7.8	3.627907	7.5	3.488372	7.76	9.3	6.04	8.37				7.8675
T6	8.3	3.860465	8.6	4	8.37	8	6.6	8.28				7.8125
T7	8.6	4	9	4.186047	8.28	7.07	8.28	5.9				7.3825
T8	6.3	2.930233	7.1	3.302326	5.9	10.09	5.58	7.3				7.2175
T9	7.1	3.302326	6.6	3.069767	7.3	7.72	8.09					7.703333
T10	8.1	3.767442	9.1	4.232558	9.3	7.72	10.88					9.3
T11	7	3.255814	8	3.72093	6.23	7.67	6.42	12.18	7.72			8.044
T12	8.1	3.767442	8	3.72093	6.42	8.65	8.55	6.88	8.97	8.14		7.935
T13	9.5	4.418605	9.9	4.604651	6.37	7.81	6.04	9.53	10.56	7.62	8.55	8.068571
T14	8.8	4.093023	8.4	3.906977	6.04	8.28	6.97	7.35	8.6			7.448
T15	8.5	3.953488	9.2	4.27907	6.97	7.58	9.3	9.07	6.37	9.02	9.67	8.282857
T16	8.5	3.953488	8.3	3.860465	9.07	6.04	8	6.04	7.12	8.18		7.406667
T17	8	3.72093	7.8	3.627907	6.04	6.6	7.07	6.18	8.14			6.806
T18	9.9	4.604651	9.4	4.372093	8.46	6.18	8.28	10.09	6.88	7.16	9.58	8.09
T19	8.5	3.953488	8.2	3.813953	6.88	5.58	7.72	5.14	7.58			6.64
T20	8.5	3.953488	8.5	3.953488	8.14	5.44	8.09					7.223333
T21	7.5	3.488372	8	3.72093	10.88	12.18	8.14	4.51				8.9275
T22	7.6	3.534884	7.8	3.627907	4.51	8.97	7.12					6.866667
T23	7.5	3.488372	8.3	3.860465	7.12	6.88	7.62	4.88				6.625
T24	9.3	4.325581	9.1	4.232558	4.88	10.56	8.6	5.58				7.405
T25	8.1	3.767442	8.5	3.953488	5.58	7.35	9.67	6.04				7.16
T26	8.6	4	8.3	3.860465	6.04	9.02	7.07	6.88				7.2525
T27	8	3.72093	7.8	3.627907	7.07	6.37	8.18	5.58	6.97			6.834
T28	8.5	3.953488	8.7	4.046512	5.58	7.11	8.14	8.46	6.51	8.6		7.4
T29	8.5	3.953488	7.6	3.534884	6.88	6.97	8.6	7.3				7.4375
T30	8.6	4	8.1	3.767442	7.3	6.51	9.58	7.9				7.8225
T31	7.5	3.488372	6.7	3.116279	7.9	7.16	7.58	8.14				7.695
		3.777944		3.80015								7.61396

Table 9 Measurements of Scale specimen KS12-97 (16–8) from Phu Nam Jun with 33 measurements and 75 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	7.5	3.488372	8	3.72093	6.51	7.67	6.14					6.773333
T2	10.2	4.744186	10	4.651163	6.97	9.3	8.83	6.51				7.9025
T3	7.5	3.488372	8.5	3.953488	6.97	7.76	8					7.576667
T4	8.4	3.906977	8.8	4.093023	8	8.28	10	8.14	8.83			8.65
T5	9	4.186047	8.8	4.093023	8.83	7.81	9.58	8.83				8.7625
T6	7	3.255814	7.4	3.44186	8.83	7.44	7.67	9.02				8.24
T7	7.1	3.302326	7.5	3.488372	9.02	6.18	8.83	6.51				7.635
T8	6	2.790698	6.2	2.883721	7.11	8.56	7.62	6.51				7.45
T9	8.5	3.953488	8.5	3.953488	8.6	7.11						7.855
T10	7.4	3.44186	7.5	3.488372	6.14	5.86	8.14	6.97				6.7775
T11	8	3.72093	9	4.186047	5.86	7.67	8.83	6.04	6.65	8.14		7.198333
T12	7	3.255814	7.4	3.44186	6.04	9.3	7.76	8.28	9.02	8.83		8.205
T13	7	3.255814	7.6	3.534884	7.58	9.02	10	7.11	10.23	8.97		8.818333
T14	8.6	4	8.4	3.906977	7.11	8.18	7.81	7.9	9.53			8.106
T15	8.2	3.813953	8.2	3.813953	7.9	9.58	7.44	7.67	8.51	8.42	9.02	8.362857
T16	7	3.255814	7.5	3.488372	7.67	7.67	6.18	8.04	7.44			7.4
T17	8.4	3.906977	9	4.186047	10.23	9.53	9.02	5.21	10	10		8.998333
T18	7	3.255814	6.5	3.023256	10.23	5.21	8.42	5.02	6.74			7.124
T19	7.4	3.44186	8.5	3.953488	5.02	8.51	7.44	9.02	7.9	7.9		7.631667
T20	7.5	3.488372	8.2	3.813953	9.02	8.04	8.83	7.62	9.21	7.11	8.46	8.327143
T21	8.5	3.953488	8.5	3.953488	9.3	7.35	9.21	8.56	8.6			8.604
T22	7.5	3.488372	7.5	3.488372	6.97	6.6	8.23	4.79				6.6475
T23	7.1	3.302326	7.8	3.627907	6.6	8.14	8.14	6.74	8.83	6.74		7.531667
T24	7.4	3.44186	8	3.72093	6.74	6.65	8.83	7.58	9.3	8.14		7.873333
T25	7.4	3.44186	7.3	3.395349	4.79	7.07						5.93
T26	8	3.72093	8.8	4.093023	7.07	8.23	6.74	7.44				7.37
T27	9.2	4.27907	9.5	4.418605	7.41	8.83	8.14	8.14				8.1375
T28	7.8	3.627907	8	3.72093	8.14	9.3	8.93	10	9.3			9.134
T29	8	3.72093	8.2	3.813953	9.3	10	10.32	7.07				9.1725
T30	8.4	3.906977	8.5	3.953488	7.07	6.74	7.9	8.83				7.635
T31	7.5	3.488372	7.6	3.534884	8.83	7.9	8.46	6.97				8.04
T32	7.4	3.44186	7.8	3.627907	6.97	7.11	7.35	7.53				7.24
T33	8	3.72093	8.5	3.953488	7.53	9.3						8.415
		3.62086		3.770261								7.864384

Table 10 Measurements of Scale specimen KS12-97(23-5) from Phu Nam Jun with 33 measurements and 77 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	A8	Average
	mm	(µm)	mm	(µm)									
T1	8.5	3.953488	6.7	3.116279	10.23	9.86	6.79						8.96
T2	8	3.72093	7	3.255814	6.79	9.21	8.28	11.62					8.975
T3	8	3.72093	7.5	3.488372	11.62	7.64	8.37	8.23					8.965
T4	8.6	4	7.6	3.534884	8.23	7.44	7.62	6.88					7.5425
T5	8.5	3.953488	6	2.790698	10.23	7.67	8.46						8.786667
T6	7.4	3.44186	6.3	2.930233	7.67	9.86	9.21	6.6	11.49	8.46			8.881667
T7	10.3	4.790698	7.8	3.627907	6.6	8.28	7.64	7.11	13.25				8.576
T8	9.5	4.418605	7.3	3.395349	11.07	7.11	8.37	7.44	8.6	9.86			8.741667
T9	7.6	3.534884	7.2	3.348837	7.9	8.6	7.62	8	5.35	9.37			7.756667
T10	9.9	4.604651	7.6	3.534884	6.88	8	8.74	6.51	6.51				7.328
T11	8.5	3.953488	8	3.72093	6.51	6.23	7.9	6.6					6.81
T12	10.5	4.883721	7.6	3.534884	6.5	8.74	6.04						7.126667
T13	11.6	5.395349	9.5	4.418605	6.04	9.79	10.09						8.64
T14	8.5	3.953488	6.5	3.023256	4.18	6.51	6.23	6.6	8.04				6.312
T15	10	4.651163	9.4	4.372093	6.6	7.9	8.74	9.79	8.37	8.83	9.53		8.537143
T16	10.6	4.930233	9.4	4.372093	10.09	8.37	8.51						8.99
T17	9.5	4.418605	8.6	4	4.83	5.35	8.74	4.18	7.16	9.02			6.546667
T18	9	4.186047	7.5	3.488372	8.55	7.16	8.04	9.53	6.88	8.28			8.073333
T19	8	3.72093	8.2	3.813953	9.76	6.88	8.83	8.51					8.495
T20	7.9	3.674419	5.5	2.55814	8.46	8.16	8.14	7.34					8.1
T21	13.2	6.139535	9	4.186047	9.67	8.14	11.49	13.25	11.07	10.79	10.93	14.04	11.1725
T22	7.5	3.488372	6.8	3.162791	10.79	9.86	7.9	8.14	8.09	9.85			9.106667
T23	8.4	3.906977	8.2	3.813953	6.37	8.14	9.07	4.83	7.34	8.5			7.291667
T24	8.7	4.046512	8.4	3.906977	7.53	7.34	9.02	8.55	7.31	9.3			8.18
T25	8.5	3.953488	7.4	3.44186	8.83	9.62	7.31	8.28	9.76				8.76
T26	8	3.72093	6.5	3.023256	7.34	9.67	10.79						9.266667
T27	11.2	5.209302	7.5	3.488372	10.79	14.04	7.58	11.44					10.9625
T28	8	3.72093	7.6	3.534884	7.58	10.93	9.86	7.67	9.76				9.16
T29	8	3.72093	6.8	3.162791	7.67	8.09	6.37	6.97	10.23				7.866
T30	8	3.72093	8	3.72093	11.44	9.76	10.23	10.6					10.5075
T31	7.6	3.534884	7.4	3.44186	19.6	6.97	8.6	7.53	7.9				10.12
T32	8.6	4	7.8	3.627907	7.9	9.3	9.62	8.37					8.7975
T33	9.5	4.418605	9	4.186047	8.37	8.83							8.6
		4.166314		3.546139									8.546696

Table 11 Measurements of Scale specimen KS12-97(26–3) from Phu Nam Jun with 34 measurements and 82 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	6.2	2.883721	5.8	2.697674	10.69	9.39	7.11	5.67				8.215
T2	6.5	3.023256	5.8	2.697674	5.67	8	6.69	5.49				6.4625
T3	6.7	3.116279	5.6	2.604651	5.49	7.3	7.3	5.49				6.395
T4	6.3	2.930233	5.5	2.55814	5.49	7.81	6.04	6.04				6.345
T5	6.8	3.162791	6	2.790698	6.04	8.83	8.04	5.67				7.145
T6	5.5	2.55814	5	2.325581	5.67	6.04	5.9					5.87
T7	7.5	3.488372	6.8	3.162791	5.35	9.39	5.95	6.28	8.23	5.21		6.735
T8	6	2.790698	5.5	2.55814	5.95	7.11	8	5.21	6.51	7.9		6.78
T9	6.5	3.023256	5.5	2.55814	5.21	6.69	7.3	5.02	5.81	7.11		6.215
T10	7.5	3.488372	6.3	2.930233	5.02	7.3	7.81	5.02	7.3	5.76		6.368333
T11	6.5	3.023256	6	2.790698	5.02	6.04	8.83	5.02	6.51	7.81		6.538333
T12	6.5	3.023256	5.7	2.651163	5.02	8.04	6.04	6.04	7.34	5.95		6.405
T13	5.8	2.697674	5	2.325581	7.44	6.04	5.9					6.46
T14	6.5	3.023256	6	2.790698	4.88	6.51	7.44	4.65	6.32	7.16		6.16
T15	5	2.325581	4.5	2.093023	4.65	5.81	5.76	4.73	6.74			5.538
T16	5.4	2.511628	5	2.325581	4.74	7.3	7.81	5.67	6.74	8.6	6.88	6.82
T17	6.5	3.023256	5.6	2.604651	5.67	6.51	5.95	5.02	7.58	7.25		6.33
T18	6.3	2.930233	4.8	2.232558	6.83	5.02	7.34	7.44				6.6575
T19	6	2.790698	5.5	2.55814	5.67	6.28	7.9	4.88	6.32	8.56		6.601667
T20	5.5	2.55814	4.5	2.093023	5.81	6.32	7.16	4.79	6.51	6.42		6.168333
T21	7	3.255814	6	2.790698	4.79	6.32	6.74	6.88	5.25	7.44		6.236667
T22	5.9	2.744186	5.4	2.511628	5.81	5.25	8.6	4.74	6.28	8.69		6.545
T23	6	2.790698	5.6	2.604651	4.74	6.74	7.25	4.56	6.14			5.886
T24	5.7	2.651163	5.5	2.55814	6.65	4.56	7.58	6.83				6.405
T25	6.2	2.883721	5.4	2.511628	7.16	6.18	6.14	6.65				6.5325
T26	6	2.790698	5.6	2.604651	10.69	5.35	6.04					7.36
T27	6	2.790698	5.5	2.55814	6.04	5.21	4.92					5.39
T28	5.4	2.511628	4.6	2.139535	4.92	8.23	5.67	6.51				6.3325
T29	5	2.325581	4.6	2.139535	6.51	8.56	5.81	5.11	7.62			6.722
T30	5.7	2.651163	5.3	2.465116	5.11	6.42	4.18	7.9	5.58			5.838
T31	6.5	3.023256	6.2	2.883721	4.18	6.51	7.14	5.81	6.88	8.69		6.585
T32	7.2	3.348837	6.8	3.162791	7.35	6.88	8.69	7.16				7.52
T33	5.5	2.55814	4.5	2.093023	7.62	5.58	6.04					6.413333
T34	8.5	3.953488	7.5	3.488372	6.04	7.9	8.69	7.35				7.495
		2.901505		2.584131								6.514725

Table 12 Measurements of Scale specimen KS12-97 (30+2) from Phu Nam Jun with 33 measurements and 75 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	9.5	4.318182	7.6	3.154545	5.63	5.9						5.765
T2	7.6	3.454545	6.5	2.954545	5.9	7.63	6.45	5.72				6.425
T3	8.3	3.772727	6	2.727273	5.72	7.95	6.27	7.27				6.8025
T4	9.8	4.454545	7	3.181818	7.27	8.77	8.45	5.36				7.4625
T5	8.5	3.863636	6	2.727273	5.36	8.27	8.77	6.09				7.1225
T6	9	4.090909	7	3.181818	6.09	9.77	6.13	7.27				7.315
T7	9	4.090909	8	3.636364	8.45	7.27	7.09	6.95				7.44
T8	11	5	9	4.090909	9.09	6.95						8.02
T9	7.8	3.545455	5.5	2.5	5.63	7.63	6.45	6.95				6.665
T10	7.5	3.409091	5.6	2.545455	6.45	6.45	7.95	6.59	5.9	7.95		6.881667
T11	6.4	2.909091	5	2.272727	6.59	6.27	8.77	6.22	7.27	8.4		7.253333
T12	8.5	3.863636	7.2	3.272727	6.22	8.45	8.27	6.45	8.09	8.18		7.61
T13	10.5	4.772727	8.6	3.909091	6.45	8.77	9.77	6.9	6.82	8.63	9.32	8.094286
T14	10	4.545455	8	3.636364	6.9	6.13	8.45	6.36	6.95			6.958
T15	8.5	3.863636	8	3.636364	8.95	9.63	6.36	7.09	9.09			8.224
T16	10.2	4.636364	7.8	3.545455	8.04	6.82	6.95	9.63	7.09	8.27		7.8
T17	13	5.909091	13	5.909091	9.32	7.63	9.45	7.09	8.95			8.488
T18	7	3.181818	5.5	2.5	6.95	7.95	6.04	10				7.735
T19	7.5	3.409091	6.5	2.954545	6.04	5.9	8.4	6.09	5.9	9.77		7.016667
T20	10.2	4.636364	7	3.181818	6.09	7.27	8.18	5.68	7.4	6.54		6.86
T21	12	5.454545	8.5	3.863636	6.59	5.68	8.09	9.32	6.09	8.5		7.378333
T22	9.5	4.318182	8.5	3.863636	9.82	6.09	8.63	8.04	6.27	8.63		7.913333
T23	10.5	4.772727	8.8	4	9	6.27	8.27	9.45	6.82	10	10.32	8.59
T24	9	4.090909	8	3.636364	6.82	7.63	7.04	8.41	9.09			7.798
T25	8.5	3.863636	8	3.636364	9.45	7.04	9.32					8.603333
T26	13	5.909091	14.3	6.5	7.27	8.14	9.45					8.286667
T27	8.5	3.863636	6.3	2.863636	10	9.77	7.09					8.953333
T28	12	5.454545	8	3.636364	7.09	5.9	6.54	5.77				6.325
T29	8.5	3.863636	6.4	2.909091	5.77	7.4	6.59	5.09				6.2125
T30	9.5	4.318182	6.5	2.954545	5.09	8.5	9.82	6.27				7.42
T31	7.8	3.545455	6.5	2.954545	6.27	8.63	9	7.77				7.9175
T32	11	5	9.5	4.318182	5.77	10.32	5.45					7.18
T33	10.5	4.772727	9	4.090909	5.45	10	9.09	7.27				7.9525
		4.27135		3.486226								7.468756

Table 13 Measurements of Scale specimen KS12-97(33-6) from Phu Nam Jun with 35 measurements and 83 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	8.3	3.860465	5.9	2.744186	6.74	8.14	9.11					7.996667
T2	9.7	4.511628	6.4	2.976744	7.21	8.74	8.6	10				8.6375
T3	7.6	3.534884	5.5	2.55814	5.9	9.44	9.16					8.166667
T4	10	4.651163	7.5	3.488372	5.9	10.04	8.69					8.21
T5	7.2	3.348837	5.5	2.55814	9.11	5.44	8.55	8.55				7.9125
T6	7.5	3.488372	5.5	2.55814	5.14	8.14	10	4.42	8.14	9.44		7.596667
T7	8.7	4.046512	5.4	2.511628	4.42	8.6	5.21	6.65	8.37			6.65
T8	8.2	3.813953	5.5	2.55814	5.21	8.74	9.16	5.44	10.88	7.67		7.85
T9	9.5	4.418605	6.5	3.023256	5.44	9.44	10.04	6.65	8.69	10.93		8.531667
T10	8	3.72093	5.5	2.55814	8.69	6.65	9.58					8.306667
T11	8.8	4.093023	7.5	3.488372	8.55	5.58	8.14	7.67				7.485
T12	7	3.255814	5.8	2.697674	5.58	8.55	9.44	5.11	7.67	8.14		7.415
T13	7	3.255814	5.5	2.55814	5.11	8.14	8.37	4.56	7.44			6.724
T14	7.3	3.395349	5	2.325581	6.65	7.67	5.67	8.83				7.205
T15	9	4.186047	7.5	3.488372	8.37	5.67	10.88	10.93	8	7.35	12.56	9.108571
T16	10.5	4.883721	8	3.72093	9.58	8.69	8	9.58	9.3			9.03
T17	8	3.72093	6	2.790698	7.67	6.28	5.35	8.37				6.9175
T18	8.5	3.953488	7.5	3.488372	6.28	8.14	8.14	6.23	8.37	9.3	5.21	7.381429
T19	7	3.255814	5.7	2.651163	6.23	7.67	8.6	5.9	9.07	8		7.578333
T20	6.7	3.116279	5.3	2.465116	5.9	7.44	8.83	8.37	8.65	9.62		8.135
T21	11	5.116279	6.7	3.116279	7.35	9.58	5.35	7.58	6.04			7.18
T22	9.8	4.55814	6.5	3.023256	9.3	5.35	8.14	6.37				7.29
T23	9.5	4.418605	6.5	3.023256	8.37	6.97	5.9					7.08
T24	8	3.72093	5.5	2.55814	6.97	5.35	5.21	6.04	6.97			6.108
T25	6.3	2.930233	4.8	2.232558	5.9	6.97	4.74					5.87
T26	9	4.186047	6.5	3.023256	4.74	6.04	9.3	5.67				6.4375
T27	10	4.651163	6.8	3.162791	5.67	8.37	8	6.32	8.6			7.392
T28	8	3.72093	6.5	3.023256	6.32	9.07	9.62	7.9	9.16	8.69		8.46
T29	9	4.186047	6	2.790698	7.9	8.65	12.56	6.04	7.11	10	12	9.18
T30	8	3.72093	6	2.790698	7.11	7.58	8.14	6.97	8.14	8.69		7.771667
T31	10	4.651163	7.8	3.627907	6.37	6.97	8.74					7.36
T32	10.4	4.837209	6.5	3.023256	6.79	8.69	8.6					8.026667
T33	9	4.186047	7.5	3.488372	8.14	12	9.16	6.79				9.0225
T34	8.2	3.813953	7	3.255814	6.65	8.69	10	8.14				8.37
T35	8.8	4.093023	6.8	3.162791	8.74	8.14	6.65					7.843333
		3.980066		2.928904								7.720852

Table 14 Measurements of Scale specimen KS12-265(12+1) from Phu Nam Jun with 33 measurements and 77 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	9.5	4.418605	8.5	3.953488	7.16	7.72	8.37					7.75
T2	8	3.72093	7	3.255814	7.11	6.74	8.09					7.313333
T3	8	3.72093	6.5	3.023256	5.95	9.95	7.76					7.886667
T4	7.5	3.488372	7	3.255814	5.95	11.16	8.69					8.6
T5	8.5	3.953488	8.5	3.953488	7.72	7.67	9.41	6.74				7.8925
T6	9.5	4.418605	8	3.72093	6.74	8.69	10.83	7.25				8.3775
T7	9	4.186047	8	3.72093	6.97	11.9	8.09	7.25				8.5525
T8	8.2	3.813953	7	3.255814	8.37	7.9	8.18	7.9				8.0875
T9	8.5	3.953488	7.5	3.488372	7.9	7.72	8.09	6.14	7.53	9.02		7.733333
T10	8.9	4.139535	8	3.72093	6.14	6.74	7.76	6.37	8.37			7.076
T11	9	4.186047	6.5	3.023256	6.37	9.95	11.16	6.51	9.3	10	9.02	8.901429
T12	8	3.72093	7	3.255814	6.51	8.69	7.67	6.74	9.39			7.8
T13	12	5.581395	8.5	3.953488	8.37	6.74	9.44	8.69	6.6	11.9		8.623333
T14	9.5	4.418605	6.5	3.023256	11.11	6.6	10.83	8.09	8.51	8.09		8.871667
T15	12.5	5.813953	8.5	3.953488	10	8.74	6.97					8.57
T16	7.5	3.488372	7.5	3.488372	7.9	9.02						8.46
T17	8.5	3.953488	7.5	3.488372	9.02	8.18	9.02	7.72	8.28			8.444
T18	8.5	3.953488	7	3.255814	7.72	7.53	8.37	9.02	7.72	6.93		7.881667
T19	9.8	4.55814	8.2	3.813953	7.44	7.72	10	7.25	7.9	8.83		8.19
T20	9.4	4.372093	10	4.651163	7.25	9.3	9.39	8.37	7.75	9.44		8.535
T21	12	5.581395	8	3.72093	7.58	7.76	11.9	11.11	6.14	8.04		8.755
T22	7.5	3.488372	5.5	2.55814	6.14	8.09	7.11	5.58	8.51			7.086
T23	11	5.116279	9	4.186047	7.11	8.51	11.9	8.74	7.11	9.86	8.14	8.767143
T24	10.5	4.883721	7.5	3.488372	10	9.16	7.11	10				9.0675
T25	8	3.72093	7.5	3.488372	8.28	6.93	7.44	7.39				7.51
T26	10.8	5.023256	9	4.186047	7.39	8.83	7.58					7.933333
T27	9.5	4.418605	8.5	3.953488	7.58	7.9	9.44	7.58				8.125
T28	8.5	3.953488	7	3.255814	8.04	8.51	5.34	7.44				7.3325
T29	8.2	3.813953	6	2.790698	5.34	5.58	8.14	5.88	7.9			6.768
T30	9	4.186047	7	3.255814	7.58	6.88	9.86	9.16	6.88	8.73		8.181667
T31	9.2	4.27907	6.8	3.162791	8.04	6.88	10					8.306667
T32	9	4.186047	6.5	3.023256	7.44	7.9	7.58	8.56				7.87
T33	12.5	5.813953	9	4.186047	8.56	8.74	8.04					8.446667
		4.312896		3.530655								8.13512

Table 15 Measurements of Scale specimen KS12-265(15-3) from Phu Nam Jun with 31 measurements and 71 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	6.5	3.095238	6	2.857143	8.33	11.09	10.23					9.883333
T2	5.5	2.619048	5.5	2.619048	8.33	9.9	8.95	8.47				8.9125
T3	7	3.333333	6.7	3.190476	8.47	12.57	11.9					10.98
T4	5.5	2.619048	6.5	3.095238	9.62	11.66	8.38	11.9				10.39
T5	6.2	2.952381	6.3	3	8.38	11.09	9.52					9.663333
T6	6.5	3.095238	6	2.857143	10.23	8.57	10.95	7.62				9.3425
T7	6.8	3.238095	6	2.857143	8.57	11.09	9.9	9.28	12.47	10		10.21833
T8	7	3.333333	6.6	3.142857	8.95	12.57	9.62	10.81	12.85	9.28		10.68
T9	6.5	3.095238	6.5	3.095238	10.81	11.66	11.09	8	10.38	10.71		10.44167
T10	6.6	3.142857	6.2	2.952381	9.52	8	10.33	9.66				9.3775
T11	7	3.333333	7.5	3.571429	7.14	11.43	9.11	7.62				8.8325
T12	7	3.333333	7	3.333333	9.14	10.95	10	10.85	11.66	11.09		10.615
T13	6.5	3.095238	7.4	3.52381	10.85	12.47	12.85	10.71	11.9	10.95	12.62	11.76429
T14	7	3.333333	6	2.857143	11.9	10.38	10.33	10.85	10.09	11.81	9.71	10.72429
T15	8.9	4.238095	9	4.285714	9.66	10.85	9.9	8.04				9.6125
T16	8.5	4.047619	8	3.809524	9.52	10.47	7.14					9.043333
T17	5.8	2.761905	5.5	2.619048	12.47	10.47	11.43	11.09	11.28	9.71	11.52	11.13857
T18	6.5	3.095238	6.5	3.095238	11.28	11.66	12.62	9.81	14.04	12.76	11.09	11.89429
T19	6	2.857143	6	2.857143	9.81	10.95	9.71	8.81	11.66			10.188
T20	7	3.333333	7.5	3.571429	9.42	8.81	11.81	8.33	9.76	10.38		9.751667
T21	6	2.857143	7	3.333333	8.33	10.09	9.9	6.19	8.47			8.596
T22	6.5	3.095238	7.8	3.714286	8.04	6.19	10.14	10.24				8.6525
T23	8	3.809524	8	3.809524	9.52	12.47	9.52					10.50333
T24	10	4.761905	9.5	4.52381	9.52	11.52	9.52					10.18667
T25	6.5	3.095238	7.3	3.47619	9.52	9.71	11.09	9				9.83
T26	7.5	3.571429	7.5	3.571429	9	12.76	9.76					10.50667
T27	5.5	2.619048	6.5	3.095238	9.76	14.04	11.66	9.42	11.66			11.308
T28	7.5	3.571429	6.8	3.238095	11.66	10.38	7.62	8.81				9.6175
T29	7	3.333333	8.5	4.047619	7.62	9.76	8.47	10.14	7.85	8.76		8.766667
T30	6.5	3.095238	8.5	4.047619	10.24	7.85	8.81					8.966667
T31	6	2.857143	7.5	3.571429	8.81	8.76	8.81					8.793333
		3.245776		3.34255								9.973578

Table 16 Measurements of Scale specimen KS12-265(16+8) from Phu Nam Jun with 33 measurements and 77 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	10	4.761905	6.2	2.952381	7.76	6.9	9.52					8.06
T2	8	3.809524	7.2	3.428571	7.76	8.81	10.24	8.14	9.04			8.798
T3	8	3.809524	7.5	3.571429	9.04	7.38	8.85	7.14				8.1025
T4	8	3.809524	7	3.333333	7.14	8.66	8.66	8.33				8.1975
T5	10	4.761905	8	3.809524	8.83	9.04						8.935
T6	7.3	3.47619	6.8	3.238095	8.09	10.95	8.09	7.28	9.52			8.786
T7	7.8	3.714286	6.5	3.095238	6.9	8.81	7.28	7.62	6.92			7.506
T8	8.5	4.047619	7	3.333333	10.24	6.52	6.92	6.33	8.47	7.62		7.683333
T9	7	3.333333	6.5	3.095238	8.14	7.37	6.38	7.71	6.52			7.224
T10	8.5	4.047619	6.5	3.095238	6.38	8.85	8.66	7.04	8.85	8.09		7.978333
T11	8.5	4.047619	7.5	3.571429	9.04	8.66	7.04	10.47	9.19	8.95		8.891667
T12	10	4.761905	8.5	4.047619	9.24	7.62	8.09					8.316667
T13	9	4.285714	6.5	3.095238	8.28	7.62	10.95	8.66	8.76	9.28	7.24	8.684286
T14	8	3.809524	8	3.809524	8.09	7.62	7.62	8.66	7.62	7		7.768333
T15	7	3.333333	6.5	3.095238	7	8.47	7.14	6.38	9.25	6.9		7.523333
T16	7.5	3.571429	7.5	3.571429	6.33	7.71	8.09	6.24	8.09	7.14		7.266667
T17	8.8	4.190476	6.5	3.095238	8.85	10.47	5.57	7.76	7.38	6.24		7.711667
T18	8.2	3.904762	6	2.857143	9.19	5.71	5.57	7.76	7.62			7.17
T19	11	5.238095	9.5	4.52381	8.95	5.71	8.47	8.71				7.96
T20	6.5	3.095238	7	3.333333	7.24	7.62	6.38	7.62	7.24			7.22
T21	7.8	3.714286	5.5	2.619048	6.9	8.09	7.38	7	7.76	8.47		7.6
T22	7	3.333333	5.5	2.619048	7	7.76	7.76	6.66	7.24	7.38		7.3
T23	8	3.809524	8.5	4.047619	6.66	7.62	8.47	6.52	8.09	8.09		7.575
T24	8.5	4.047619	8	3.809524	6.52	8.71	6.76	9.28	7.76			7.806
T25	8	3.809524	7.5	3.571429	9.24	8.28	7.23					8.25
T26	9	4.285714	7	3.333333	7.23	8.76	6.19					7.393333
T27	8	3.809524	6.5	3.095238	6.19	9.28	7.62	7.85				7.735
T28	8	3.809524	7.5	3.571429	7.85	7.24	9.52	8.47	7.04			8.024
T29	7.4	3.52381	7	3.333333	7.04	7.76	7.38	7.38				7.39
T30	8.5	4.047619	6.5	3.095238	7.38	7.24	8.09	6.47				7.295
T31	13.5	6.428571	9.5	4.52381	6.47	8.09	6.76	6.66				6.995
T32	8	3.809524	6	2.857143	6.66	9.28	8.33					8.09
T33	8.5	4.047619	8	3.809524	7.76	8.33						8.045
		4.008658		3.401154								7.857119

Table 17 Measurements of Scale specimen KS12-265(23) from Phu Nam Jun with 32 measurements and 74 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	5.5	2.55814	6	2.790698	8.37	5.35	6.65					6.79
T2	5.5	2.55814	5	2.325581	5.21	8.37						6.79
T3	8.6	4	5.5	2.55814	8.37	6.18	6.79	8.37				7.4275
T4	5.7	2.651163	5.2	2.418605	8.37	7.21	6.09					7.223333
T5	6	2.790698	5.4	2.511628	6.09	10.42	8	6.42				7.7325
T6	6.5	3.023256	5.2	2.418605	6.42	9.21	7.44					7.69
T7	7	3.255814	5.5	2.55814	6.18	7.21	10.42	6.74	7.21	9.07	7.84	7.81
T8	6.8	3.162791	5.5	2.55814	6.74	8	9.21	6.88	7.3	9.07		7.856667
T9	6.6	3.069767	5.4	2.511628	7.44	6.88	8.65	9.76	4.65			7.476
T10	6.5	3.023256	5	2.325581	4.65	10.04						7.345
T11	6	2.790698	5.5	2.55814	5.35	7.07	4.65	7.84	6.79			6.34
T12	5.5	2.55814	5	2.325581	6.65	7.07	7.9	6.51				7.0325
T13	6.5	3.023256	5.5	2.55814	7.9	4.65	9.07	6.04	6.04	9.9		7.266667
T14	6	2.790698	5	2.325581	8.83	7.21	9.07	6.18	5.76	6.04		7.181667
T15	7	3.255814	5.5	2.55814	6.18	7.3	8.65	6.04	5.58	8.04		6.965
T16	6.8	3.162791	5.5	2.55814	6.04	9.76	10.04	6.37	7.9	6.04		7.691667
T17	5.5	2.55814	5.4	2.511628	6.51	9.9	7.07	7.53				7.7525
T18	6.5	3.023256	5.5	2.55814	7.07	9.76	4.83	6.14	8.83	6.04		7.111667
T19	5.5	2.55814	5	2.325581	6.14	5.76	8.04	5.21	5.35	6.74		6.206667
T20	4.5	2.093023	4.7	2.186047	5.21	5.58	6.04	5.35	6.88			5.812
T21	7.6	3.534884	6	2.790698	6.37	7.21	6.88	5.11				6.3925
T22	7.5	3.488372	5.5	2.55814	7.53	9.76	8.04	5.86				7.7975
T23	5	2.325581	4.5	2.093023	8.01	6.42	4.74	6.74	4.83			6.154
T24	5.9	2.744186	4	1.860465	4.74	5.38	6.88	6.23	5.35	8.83		6.235
T25	6.5	3.023256	5	2.325581	6.23	5.35	7.9	7.21	5.02	8.14	8.6	6.921429
T26	7.5	3.488372	5.5	2.55814	5.86	6.42	8.83	5.58				6.6725
T27	8	3.72093	5	2.325581	5.58	5.35	8.6					6.51
T28	7	3.255814	6	2.790698	5.21	8.14	6.32	5.58				6.3125
T29	6.5	3.023256	5.3	2.465116	6.32	5.02	6.88	5.72	6.74			6.136
T30	7.5	3.488372	6	2.790698	5.11	5.72	8.83	7.21				6.7175
T31	7.7	3.581395	5.5	2.55814	5.58	6.74	8.83	5.44				6.6475
T32	7	3.255814	5.5	2.55814	7.21	5.44						6.325
		3.026163		2.472384								6.947399

Table 18 Measurements of Scale specimen KS12-265(23-5) from Phu Nam Jun with 30 measurements and 68 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	6.4	2.976744	6.5	3.023256	6.51	8.51	8.65	8.14				7.9525
T2	8.8	4.093023	7	3.255814	8.14	10.28	9.3	7.44				8.79
T3	8.5	3.953488	8	3.72093	7.44	7.81	7.58	6.6				7.3575
T4	6	2.790698	6	2.790698	6.6	4.41	7.21	6.56				6.195
T5	7	3.255814	7.5	3.488372	6.56	8.37	7.58	6.51				7.255
T6	6.3	2.930233	6.2	2.883721	6.51	8.6	9.3	8.6				8.2525
T7	8.5	3.953488	7.5	3.488372	8.6	9.76	11.02					9.793333
T8	6.5	3.023256	6.4	2.976744	6.88	7.21	6.51					6.866667
T9	8.4	3.906977	8	3.72093	8.51	6.74	7.53	6.51	7.21			7.3
T10	7.2	3.348837	6.5	3.023256	6.74	8.65	10.28	6.37	7.9	8.18		8.02
T11	5.7	2.651163	5	2.325581	6.37	9.3	7.81	5.81	7.35	8.65		7.548333
T12	7	3.255814	6.8	3.162791	5.81	7.58	4.41	6.74	6.6			6.228
T13	7	3.255814	7.5	3.488372	6.74	7.4	8.37	6.51	6.74	7.9	10.23	7.698571
T14	5.5	2.55814	5.8	2.697674	6.51	7.58	8.6	6.6	8.51	7.53		7.555
T15	8.5	3.953488	8.4	3.906977	6.6	8.83	8.65	9.21				8.3225
T16	7.8	3.627907	7.5	3.488372	11.02	8.83	9.62					9.823333
T17	7	3.255814	7	3.255814	6.85	6.51						6.68
T18	7.3	3.395349	6.7	3.116279	7.53	8.18	6.6					7.436667
T19	5.7	2.651163	5.3	2.465116	6.6	7.9	5.65	5.81	7.21			6.634
T20	6.5	3.023256	5.6	2.604651	5.81	7.35	6.6	10.23	6.97	7.07		7.338333
T21	7.8	3.627907	7.3	3.395349	6.97	7.9	5.67	8.37	8.37	7.67		7.491667
T22	6.5	3.023256	6.8	3.162791	5.67	6.74	7.53	6.18	7.21			6.666
T23	5.5	2.55814	5.8	2.697674	8.51	9.21	6.6	7.07	7.9	6.18		7.578333
T24	6.8	3.162791	6.5	3.023256	8.65	9.62	8.93	6.6				8.45
T25	7	3.255814	5.3	2.465116	7.21	7.07	7.67	6.65				7.15
T26	6.7	3.116279	5.5	2.55814	6.69	8.37	7.67	8.37				7.775
T27	6.4	2.976744	6	2.790698	7.67	8.37	7.21	7.9	6.51	7.67	9.21	7.791429
T28	7.8	3.627907	8	3.72093	8.93	7.07	6.51	6.93				7.36
T29	5	2.325581	5.8	2.697674	8.37	9.21	5.58					7.72
T30	7.5	3.488372	7.6	3.534884	6.93	7.67	5.58					6.726667
		3.234109		3.097674								7.592211

Table 19 Measurements of Scale specimen KS12-265(26+3) from Phu Nam Jun with 32 measurements and 74 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	6.5	3.051643	6.3	2.957746	6.57	9.85						8.21
T2	5.6	2.629108	5.5	2.58216	6.57	10.04	8.68	6.8				8.0225
T3	5.8	2.723005	6	2.816901	6.8	10.89	9.06	7.32				8.5175
T4	5.6	2.629108	5.5	2.58216	7.32	11.83	8.59					9.246667
T5	6.5	3.051643	6	2.816901	8.59	7.74	12.34	8.45				9.28
T6	7.5	3.521127	5.7	2.676056	8.45	8.59	8.92	10.56	7.37			8.778
T7	5.5	2.58216	5.3	2.488263	7.37	10.65	7.41					8.476667
T8	6.3	2.957746	5.4	2.535211	7.41	6.33	9.2	6.34				7.32
T9	7	3.286385	7	3.286385	6.34	10.09	8.68					8.37
T10	6.5	3.051643	6.2	2.910798	10.04	6.57	9.72	8.64	9.85			8.964
T11	6.3	2.957746	6	2.816901	6.57	8.68	10.89	7.84	9.39	10.8		9.028333
T12	6.3	2.957746	5.8	2.723005	7.84	9.06	11.83	7.74	9.76	10.56		9.465
T13	7.5	3.521127	6.8	3.192488	8.31	9.76	12.34	8.59	7.98	11.59	11.59	10.02286
T14	6.4	3.004695	6	2.816901	7.98	8.92	5.77	7.7	8.68			7.81
T15	6.2	2.910798	6	2.816901	5.77	10.56	10.65	6.33	8.45	11.03	9.15	8.848571
T16	6.3	2.957746	6	2.816901	8.45	9.2	10.09	9.1	9.62	8.68		9.19
T17	5.5	2.58216	5.5	2.58216	8.68	9.1	12.11					9.963333
T18	6	2.816901	5	2.347418	8.64	5.96	7.98					7.526667
T19	6.2	2.910798	5.4	2.535211	9.01	5.96	9.72	10.8	8.21	7.65		8.558333
T20	8	3.755869	6	2.816901	8.21	9.39	10.56	8.31	9.76	7.65		8.98
T21	5.6	2.629108	5	2.347418	7.51	7.65	7.65	6.71	9.95			7.894
T22	6	2.816901	5.5	2.58216	6.71	9.76	11.59	7.27	10.23	9.86		9.236667
T23	6.5	3.051643	6	2.816901	9.86	7.27	11.59	8.68	6.15	11.03		9.096667
T24	6	2.816901	5	2.347418	6.15	7.7	9.15	6.34	10.09			7.886
T25	6.8	3.192488	5.8	2.723005	10.09	6.34	11.03	8.68	8.82	9.48		9.073333
T26	6.5	3.051643	6	2.816901	12.11	9.62	8.82	10.56				10.2775
T27	6	2.816901	5.5	2.58216	7.98	9.01	7.13					8.04
T28	6	2.816901	6	2.816901	7.13	11.59	7.51	8.21				8.61
T29	6.2	2.910798	6	2.816901	8.21	9.95	9.86	8.35				9.0925
T30	6.5	3.051643	5.5	2.58216	8.35	10.23	9.86	8.68				9.28
T31	7	3.286385	5.4	2.535211	7.88	10.09	11.03	8.68				9.42
T32	8	3.755869	6	2.816901	10.56	9.48	7.88					9.306667
		3.001761		2.715669								8.835593

Table 20 Measurements of Scale specimen KS12-265(30+2) from Phu Nam Jun with 31 measurements and 72 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	Average
	mm	(µm)	mm	(µm)							
T1	7.2	3.428571	6	2.857143	9.43	6.28					7.855
T2	7	3.333333	6.8	3.238095	6.28	7.71	10.38	7.43			7.95
T3	6.5	3.095238	6.4	3.047619	7.43	7.76	9.28	7.43			7.975
T4	7.5	3.571429	6	2.857143	7.43	7.85	9.43	8.33			8.26
T5	5.6	2.666667	5.5	2.619048	9.43	7.71	6.66	10			8.45
T6	7	3.333333	6.8	3.238095	6.66	10.38	7.76	7.76	8.76	7.76	8.18
T7	7	3.333333	6	2.857143	7.76	9.28	7.85	6.76	9.28	7.62	8.091667
T8	7.4	3.52381	6.5	3.095238	6.76	9.43	6.19	8.24	10.24	7.43	8.048333
T9	8.5	4.047619	5.9	2.809524	5.33	6.19	8.09				6.536667
T10	7	3.333333	5.5	2.619048	8.09	8.24	7.38	10.24			8.4875
T11	7.5	3.571429	6	2.857143	10	7.76	8.09	11.43	10.57		9.57
T12	7	3.333333	5.5	2.619048	8.09	8.76	7.62	7.04	9.52	8.66	8.281667
T13	6	2.857143	5.5	2.619048	7.04	9.28	7.43	7.23	9.04	7.62	7.94
T14	7	3.333333	6	2.857143	7.23	10.24	7.38	7.76	8.57	6.57	7.958333
T15	5.9	2.809524	5	2.380952	10.24	7.76	7.14				8.38
T16	8	3.809524	6.2	2.952381	10.57	7.14	10	9.28			9.2475
T17	6.5	3.095238	5	2.380952	7.14	11.43	8.66	5.95	9.28	9.04	8.583333
T18	6.5	3.095238	5.5	2.619048	5.95	9.52	7.62	6.43	5.95	5.52	6.831667
T19	6.2	2.952381	5	2.380952	6.43	9.04	6.57	7.43	9.76	6.28	7.585
T20	6	2.857143	5.8	2.761905	7.43	8.57	7.14	9.04	6.76		7.788
T21	7.5	3.571429	5.5	2.619048	9.28	6.66	10	9.04			8.745
T22	6.5	3.095238	5.5	2.619048	6.66	10	9.4	6.14	10.71	8.95	8.643333
T23	6.4	3.047619	6	2.857143	9.28	5.52	5.58	9.52	9.28	6.14	7.553333
T24	6	2.857143	5.4	2.571429	5.95	6.28	6.66	6.9	5.85		6.328
T25	7.8	3.714286	7	3.333333	6.66	5.85	8.47	6.19	6.76	9.76	7.281667
T26	6.5	3.095238	6	2.857143	9.04	6.43					7.735
T27	8	3.809524	7.5	3.571429	6.43	10	8.95	7.62			8.25
T28	6.6	3.142857	5.6	2.666667	7.62	10.71	9.28	7.47			8.77
T29	6	2.857143	5	2.380952	7.47	9.52	6.9	5.85	7.42		7.432
T30	6.5	3.095238	5.5	2.619048	7.42	8.47	6.19				7.36
T31	6.7	3.190476	6.4	3.047619	9.04	6.19	6.19				7.14
		3.253456		2.860307							7.975419

Table 21 Measurements of Scale specimen KS12-265(33-6) from Phu Nam Jun with 32 measurements and 70 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	8.2	3.796296	5.5	2.546296	8.75	9.35	4.4					7.5
T2	8.5	3.935185	5.5	2.546296	4.4	11.11	7.13	6.25				7.2225
T3	9.7	4.490741	6	2.777778	6.25	10.37	7.87	5.23				7.43
T4	9.4	4.351852	6	2.777778	5.23	8.47	8.79	4.49				6.745
T5	8.5	3.935185	5.5	2.546296	4.49	7.68	9.26	4.86				6.5725
T6	8.5	3.935185	6	2.777778	4.86	10.51	7.27	6.71				7.3375
T7	8.2	3.796296	5.6	2.592593	6.71	10.65	6.25					7.87
T8	9.2	4.259259	5.5	2.546296	6.25	6.66	10.97	7.22	6.06			7.432
T9	9	4.166667	6.5	3.009259	9.26	6.85	6.06					7.39
T10	9	4.166667	6	2.777778	6.85	7.17	8.01	5.78				6.9525
T11	8.6	3.981481	5.8	2.685185	5.78	6.71						6.245
T12	7.3	3.37963	5.2	2.407407	8.75	7.17	7.64					7.853333
T13	8.4	3.888889	5.3	2.453704	9.35	11.11	7.31	7.17	9.49	7.73	7.17	8.475714
T14	9.5	4.398148	5.5	2.546296	7.13	10.37	5.23	7.13	9.81	7.31		7.83
T15	7.5	3.472222	4.9	2.268519	7.87	8.47	4.4	8.56	5.23			6.906
T16	8.3	3.842593	6	2.777778	8.79	7.68	5.65	9.81	9.02	4.4		7.558333
T17	9.8	4.537037	5.5	2.546296	9.26	10.51	8.01	8.15	11.02	9.26	5.65	8.837143
T18	9.5	4.398148	5.7	2.638889	7.27	10.65	6.66	7.87	11.2	8.01		8.61
T19	8.4	3.888889	6	2.777778	7.87	10.97	6.48	6.02	10.04	7.22		8.1
T20	7.5	3.472222	6	2.777778	7.22	9.26	7.17	6.25	9.02	6.48		7.566667
T21	8	3.703704	6	2.777778	6.71	8.01	6.25	7.54				7.1275
T22	9.5	4.398148	7.2	3.333333	7.64	7.73	5.78					7.05
T23	10.5	4.861111	7.3	3.37963	5.78	9.49	6.71					7.326667
T24	7.5	3.472222	5.5	2.546296	6.71	7.14	9.81	6.25				7.4775
T25	8	3.703704	5.5	2.546296	6.25	7.13	8.56	9.02	5.65			7.322
T26	8.5	3.935185	5.5	2.546296	5.65	9.81	9.26	5.65				7.5925
T27	8.5	3.935185	5	2.314815	5.65	11.02	7.13	7.4				7.8
T28	7.8	3.611111	5.5	2.546296	8.15	11.2	7.22	7.59	10.18	7.13		8.578333
T29	9	4.166667	6.5	3.009259	7.4	10.18	7.59					8.39
T30	10	4.62963	7.5	3.472222	7.59	10.04	8.05	7.13	7.59			8.08
T31	9	4.166667	6	2.777778	7.54	9.02	6.02	8.05	10.41			8.208
T32	10	4.62963	7	3.240741	7.13	10.41						8.77
		4.040799		2.727141								7.629897

Table 23 Measurements of Scale specimen Ban Saphan Hin2 from Khok Kruat Formation with 30 measurements and 68 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	12.3	5.72093	13.4	6.232558	8.28	9.21	6.51					8
T2	9.8	4.55814	10.5	4.883721	6.51	9.3	7.81	9.07				8.1725
T3	13.5	6.27907	15.5	7.209302	9.07	8.37	11.62	8.6				9.415
T4	13	6.046512	14.5	6.744186	8.6	9.76	9.85	10				9.555
T5	10	4.651163	12	5.581395	10	7.62						8.81
T6	12.6	5.860465	13	6.046512	8.28	8.74	7.3	9.62				8.485
T7	12.5	5.813953	14	6.511628	9.53	9.21	9.53	7.64	9.3	9.4	9.62	9.175714
T8	12	5.581395	13	6.046512	7.64	7.81	9.53	8.37	7.81			8.232
T9	13.5	6.27907	15.5	7.209302	8.6	11.25	11.62	8.93	9.76	11.62	9.53	10.18714
T10	12	5.581395	13	6.046512	7.62	9.86	8.93	7.9				8.5775
T11	11	5.116279	12	5.581395	6.28	9.3	8.74					8.106667
T12	12.6	5.860465	17.5	8.139535	11.39	7.11	10.79	10.79	9.53	7.3		9.485
T13	13.5	6.27907	13.5	6.27907	10.79	7.44	7.81	7.81	9.21			8.612
T14	12	5.581395	12	5.581395	9.86	11.16	8.6	7.81	9.53	7.81		9.128333
T15	15.8	7.348837	18	8.372093	10.79	10.46	10.93	8.83	9.62	11.25	11.16	10.43429
T16	14.2	6.604651	14.8	6.883721	7.9	11.62	8.69	8.69				9.225
T17	11.4	5.302326	12.5	5.813953	8.93	11.39	6.28					8.866667
T18	11.5	5.348837	12.5	5.813953	6.88	9.39	7.11	8.93				8.0775
T19	14.5	6.744186	15.4	7.162791	8.37	9.58	11.81	9.76	7.44	10.79	6.88	9.232857
T20	12.5	5.813953	13.8	6.418605	8.42	10.93	10.79	9.86	7.81	9.76		9.595
T21	11.8	5.488372	13	6.046512	9.07	8.37	6.88					8.106667
T22	11.5	5.348837	12.5	5.813953	9.07	9.58	9.3	11.3	9.53			9.756
T23	12.7	5.906977	14	6.511628	9.3	11.81	9.67	12.23	8.14	8.42		9.928333
T24	13.5	6.27907	14	6.511628	9.67	10.93	10.46	7.67	10.46	10		9.865
T25	13	6.046512	14	6.511628	6.74	9.62	7.67	8.14				8.0425
T26	13.2	6.139535	14.5	6.744186	8.69	10.93	6.74					8.786667
T27	11	5.116279	13	6.046512	9.53	8.14						8.835
T28	13	6.046512	15	6.976744	8.14	11.3	8.14	8.6				9.045
T29	12.5	5.813953	14.3	6.651163	8.6	12.23	10	10.14				10.2425
T30	12.8	5.953488	15	6.976744	8.14	10.46	10.14					9.58
		5.817054		6.444961								9.052028

Table 24 Measurements of Scale specimen Ban Saphan Hin3 from Khok Kruat Formation with 32 measurements and 75 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	Average
	mm	(µm)	mm	(um)							
T1	16	7.44186	15	6.976744	8.51	9.07	11.62				9.733333
T2	17	7.906977	15.5	7.209302	8.74	8.37	9.67	8.51			8.8225
T3	14.5	6.744186	15	6.976744	10	8.83	9.76	8.74			9.3325
T4	15.3	7.116279	14.5	6.744186	9.9	9.76	10				9.886667
T5	20.5	9.534884	17.5	8.139535	11.62	9.67	9.9	11.62	11.39		10.84
T6	15	6.976744	15	6.976744	9.07	9.67	10.23	9.39	9.67	9.67	9.616667
T7	15.4	7.162791	16	7.44186	8.37	9.76	9.4	8.14	9.07	10.23	9.161667
T8	14.5	6.744186	14	6.511628	8.83	9.76	8.6	8.83	9.3	9.4	9.12
T9	15	6.976744	15	6.976744	9.9	8.6	7.81				8.77
T10	17	7.906977	16.5	7.674419	9.9	9.67	9.76	10.23	9.53	9.3	9.731667
T11	14	6.511628	14.5	6.744186	9.39	9.07	8.6	9.58	9.58	9.76	9.33
T12	14	6.511628	14.5	6.744186	8.14	9.3	9.3	8.51	8.6	9.07	8.82
T13	12	5.581395	12	5.581395	7.81	8.83	9.3	8.37	6.74		8.21
T14	14.5	6.744186	15.3	7.116279	10.23	9.58	8.6	8.93	8.37	8.46	9.028333
T15	15	6.976744	15.5	7.209302	9.58	9.07	7.67	5.56	8.6	9.76	8.373333
T16	13.5	6.27907	13	6.046512	8.37	9.76	8.28	8.51	7.67	9.95	8.756667
T17	16	7.44186	14.5	6.744186	6.74	9.76	8.83				8.443333
T18	14.5	6.744186	12.8	5.953488	8.83	8.28	8.37				8.493333
T19	15	6.976744	15.5	7.209302	8.93	8.56	8.83				8.773333
T20	14	6.511628	12.8	5.953488	8.37	9.95	9.76	8.83	9.39		9.26
T21	13.5	6.27907	13.5	6.27907	9.39	9.53	7.44	8.37			8.6825
T22	17	7.906977	16.5	7.674419	11.39	8.6	9.53	10.79			10.0775
T23	15.5	7.209302	16	7.44186	8.6	11.62	9.3	9.49	9.21	9.3	9.586667
T24	15.5	7.209302	14.5	6.744186	9.29	9.53	8.46	8.83	8.83	9.21	9.025
T25	14	6.511628	14	6.511628	8.83	8.37	8.46	7.49	8.37	8.37	8.315
T26	11.5	5.348837	12	5.581395	7.49	7.76	7.44	7.07	7.44		7.44
T27	16	7.44186	16.5	7.674419	10.79	9.3					10.045
T28	14.5	6.744186	14.5	6.744186	9.3	9.53	9.3	8.83			9.24
T29	15.5	7.209302	15.5	7.209302	8.83	9.21	9.21	8.83			9.02
T30	15	6.976744	14.6	6.790698	8.83	8.83	8.37	8.6			8.6575
T31	13.5	6.27907	13.8	6.418605	8.6	8.37	7.44	8.74			8.2875
T32	14.5	6.744186	14.5	6.744186	8.37	7.07	8.74				8.06
		6.957849		6.835756							9.029375

Table 25 Measurements of Scale specimen Khok Pha Suam1 from Khok Kruat Formation with 31 measurements and 65 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	Average
	mm	(µm)	mm	(µm)							
T1	9.6	4.40367	9.6	4.40367	7.11	6.05		6.65			6.603333
T2	9.4	4.311927	10.3	4.724771	6.19	6.19	7.11				6.496667
T3	8.8	4.036697	10	4.587156	6.65	7.34	7.11	6.74	6.24		6.816
T4	9.3	4.266055	10	4.587156	7.15	6.19	6.05	7.34	5.13		6.372
T5	8.6	3.944954	8.8	4.036697	6.19	7.15	6.42				6.586667
T6	9	4.12844	9.5	4.357798	6.42	5.6	8.16	7.98			7.04
T7	8	3.669725	8.5	3.899083	5.6	6.74	7.11	5.96	7.57	7.11	6.681667
T8	8.5	3.899083	8.5	3.899083	7.11	5.13	7.11	6.19	7.11		6.53
T9	10	4.587156	10.2	4.678899	7.11	7.57	6.19	6.05	6.42		6.668
T10	9	4.12844	10	4.587156	6.42	6.42	7.02				6.62
T11	10.5	4.816514	11.5	5.275229	7.02	6.05	7.7	6.24			6.7525
T12	9	4.12844	9.6	4.40367	7.98	8.62	6.05	7.34			7.4975
T13	9.4	4.311927	9.8	4.495413	8.62	8.16	7.11	6.42	5.04	8.25	7.266667
T14	9.5	4.357798	10.3	4.724771	6.42	7.57	6.1	6.19	8.48		6.952
T15	8.5	3.899083	9.4	4.311927	7.24	7.57	6.19	5.96	6.1		6.612
T16	8.5	3.899083	9.5	4.357798	7.24	6.19	7.7	6.79	6.65	8.57	7.19
T17	8.5	3.899083	9.5	4.357798	6.24	6.79	7.43				6.82
T18	8.5	3.899083	9.2	4.220183	6.19	8.57	6.65				7.136667
T19	9	4.12844	9.5	4.357798	7.43	6.65	6.65				6.91
T20	10.5	4.816514	10	4.587156	7.34	6.56	7.66	6.97			7.1325
T21	9.6	4.40367	9.2	4.220183	6.56	6.05	8.25	6.65	7.43	7.11	7.008333
T22	10	4.587156	10	4.587156	6.65	5.04	8.48	6.79	8.48		7.088
T23	10	4.587156	11	5.045872	6.97	7.57					7.27
T24	9.5	4.357798	9.6	4.40367	7.57	7.66	7.11	5.73	6.65		6.944
T25	11.3	5.183486	11.3	5.183486	5.73	7.43	8.48	6.14	7.7	7.57	7.175
T26	10.3	4.724771	9.5	4.357798	6.79	6.14	8.35	6.69			6.9925
T27	11	5.045872	11	5.045872	6.65	7.57	7.57	5.96			6.9375
T28	11	5.045872	11.4	5.229358	7.57	7.7	8.35	6.05	7.89	8.48	7.673333
T29	10.5	4.816514	10.3	4.724771	6.69	6.05					6.37
T30	8.8	4.036697	9.6	4.40367	5.96	8.48	6.56				7
T31	10.2	4.678899	11.5	5.275229	7.89	6.56					7.225
		4.354839		4.559041							6.915091

Table 26 Measurements of Scale specimen Khok Pha Suam2 from Khok Kruat Formation with 31 measurements and 72 distances between them.

Measurements					A1	A2	A3	A4	A5	A6	A7	Average
	mm	(µm)	mm	(µm)								
T1	13.3	6.157407	12.5	5.787037	6.94	6.15						6.545
T2	13.8	6.388889	14.2	6.574074	7.54	6.73	8.61	6.94				7.455
T3	14	6.481481	14	6.481481	8.56	7.08	8.33	7.54				7.8775
T4	13	6.018519	13	6.018519	8.33	7.96	7.96	8.56				8.2025
T5	11	5.092593	11	5.092593	7.54	7.64	8.33					7.836667
T6	11.5	5.324074	12.5	5.787037	6.15	8.61	9.02	8.1	7.59			7.894
T7	11.2	5.185185	11.2	5.185185	9.02	6.73	8.33	7.87	6.71	7.64		7.716667
T8	15	6.944444	15.5	7.175926	7.87	7.08	7.96	8.24	6.02	8.7		7.645
T9	14	6.481481	14	6.481481	8.24	7.96	7.64	9.72	7.17	9.93	7.87	8.361429
T10	14	6.481481	14	6.481481	9.72	7.51	8.24					8.5
T11	11	5.092593	11.5	5.324074	7.59	7.17	6.57					7.11
T12	12	5.555556	12	5.555556	7.17	8.1	7.64	7.08	7.64	7.4		7.505
T13	13.8	6.388889	12.5	5.787037	7.08	6.71	8.7	6.62	7.87	9.07		7.675
T14	11	5.092593	11	5.092593	6.62	6.02	7.87	6.11	8.56			7.036
T15	11	5.092593	11.2	5.185185	6.11	9.93	7.77	6.62	6.48	8.24		7.525
T16	12.2	5.648148	12.8	5.925926	8.24	7.17	7.77	7.54				7.68
T17	11.6	5.37037	11.5	5.324074	6.57	7.4	6.11	6.94	8.24			7.052
T18	12.3	5.694444	13	6.018519	6.11	1.64	9.02	8.89	6.48	5.48		6.436667
T19	13	6.018519	13.2	6.111111	8.89	7.87	8.56	8.24	6.02	8.52	8.89	8.141429
T20	10.4	4.814815	10.5	4.861111	6.02	6.48	7.59	6.02	7.87			6.796
T21	11.5	5.324074	11.6	5.37037	7.54	6.62	7.59	8.89				7.66
T22	11.4	5.277778	12.4	5.740741	8.24	8.56	6.71					7.836667
T23	9.7	4.490741	10	4.62963	8.56	6.94	6.48	6.25	7.5	7.03		7.126667
T24	12	5.555556	12.5	5.787037	6.25	6.48	8.89	7.17	7.4	7.87		7.343333
T25	12.5	5.787037	13.2	6.111111	7.17	8.52	7.87	7.87	7.64	7.17		7.706667
T26	10.8	5	11.5	5.324074	8.89	6.02	7.87	9.02				7.95
T27	10.5	4.861111	10.5	4.861111	6.71	7.03	6.66					6.8
T28	12	5.555556	10	4.62963	6.66	7.5	7.87	6.02				7.0125
T29	12.5	5.787037	13.5	6.25	6.02	7.4	7.17	8.79	7.08			7.292
T30	13.4	6.203704	14	6.481481	8.79	7.64	9.02	7.4				8.2125
T31	11.5	5.324074	12.5	5.787037	7.4	7.08						7.24
		5.628734		5.716846								7.521651

Table 27 Measurements of Scale specimen Khok Pha Suam3 from Khok Kruat Formation with 25 measurements and 47 distances between them.

	Measurements				A1	A2	A3	A4	A5	A6	Average
	mm	(µm)	mm	(µm)							
T1	9.5	4.418605	11	5.116279	7.76	5.81	6.88				6.816667
T2	9.6	4.465116	10.3	4.790698	7.76	6.83	5.21				6.6
T3	11	5.116279	11	5.116279	6.88	8.37	8.14	9.07			8.115
T4	9.5	4.418605	9.5	4.418605	8.37	5.81	6.83	7.02	7.02	5.86	6.818333
T5	9.7	4.511528	9.9	4.604651	5.21	7.02	6.23	6.51			6.2425
T6	9.7	4.511628	10	4.651163	9.07	7.58					8.325
T7	9.5	4.418605	10	4.651163	7.58	8.14	5.86	7.21			7.1975
T8	11	5.116279	11	5.116279	7.21	7.02	6.23	5.21	6.97		6.528
T9	8	3.72093	8	3.72093	6.51	5.21	6.83				6.183333
T10	10.5	4.883721	10.6	4.930233	6.97	6.83	4.88	8.56			6.81
T11	10	4.651163	11.8	5.488372	4.88	6.74	8.28	10.69			7.6475
T12	11	5.116279	11.5	5.348837	6.74	9.95	8.56				8.416667
T13	8.4	3.906977	8.8	4.093023	9.95	8.28	6.37	10.51			8.7775
T14	9.6	4.465116	10.6	4.930233	6.37	10.69	6.51	8.18	9.53		8.256
T15	12.5	5.813953	13.8	6.418605	6.51	6.69	7.3	10.23			7.6825
T16	11	5.116279	10.6	4.930233	6.69	7.81					7.25
T17	11	5.116279	12.2	5.674419	7.81	7.3	8.74				7.95
T18	9	4.186047	9.5	4.418605	8.74	10.23	8.18	5.76	5.9		7.762
T19	9	4.186047	9.5	4.418605	10.51	9.53	5.76	5.76	7.21		7.754
T20	9.5	4.418605	10.5	4.883721	5.9	5.76	7.44	7.16	7.3		6.712
T21	11.8	5.488372	12.8	5.953488	7.21	7.44	7.67				7.44
T22	11.5	5.348837	13	6.046512	7.3	7.44	7.16				7.3
T23	11	5.116279	12.3	5.72093	7.67	7.16	7.44	6.42	6.51		7.04
T24	9.5	4.418605	10.2	4.744186	6.23	6.42	7.16				6.603333
T25	11.8	5.488372	12.5	5.813953	6.51	6.23					6.37
		4.736744		5.04							7.303913

APPENDIX II

Figures of the microornamentation of surface scales from Phu Nam Jun locality (KS 12-97 and KS 12-265) of Phu Kradung Formation, except figures of KS12-97 (L26+3) and KS12-265 (L26+3) which are appear in Chaper 4.

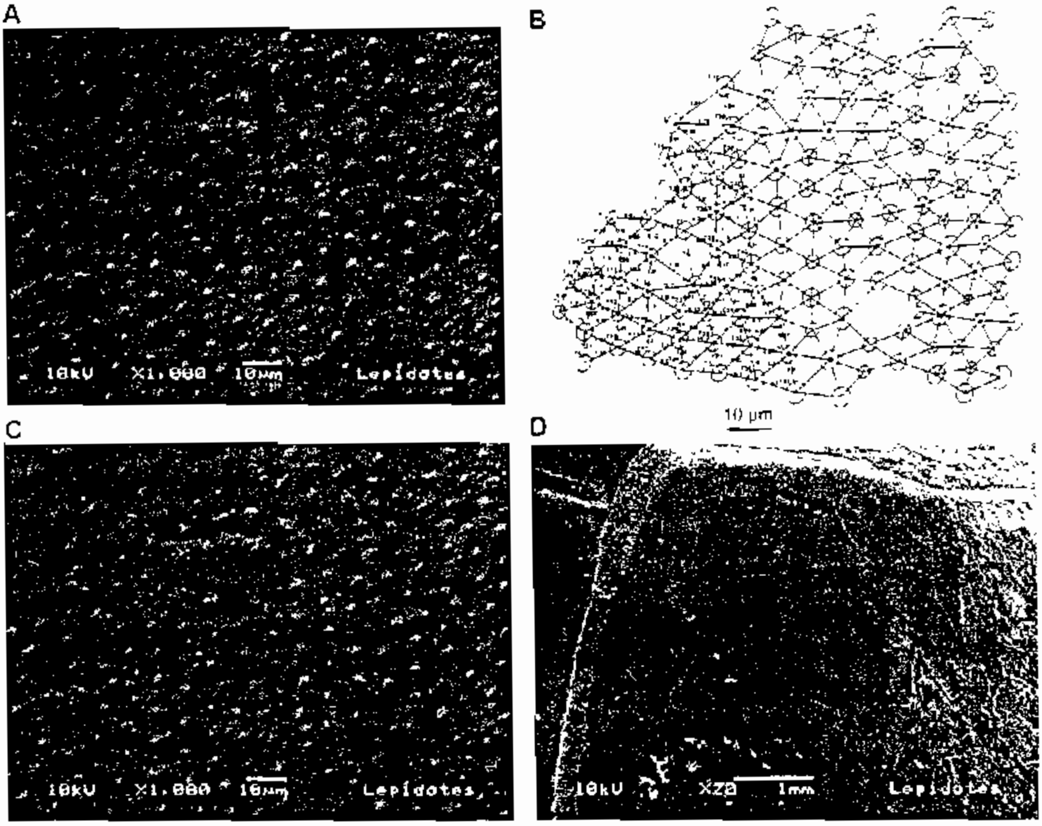

Figure 78 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L3-3. B: measurement of the tubercles (46 measurements) and of the distances between them (110 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

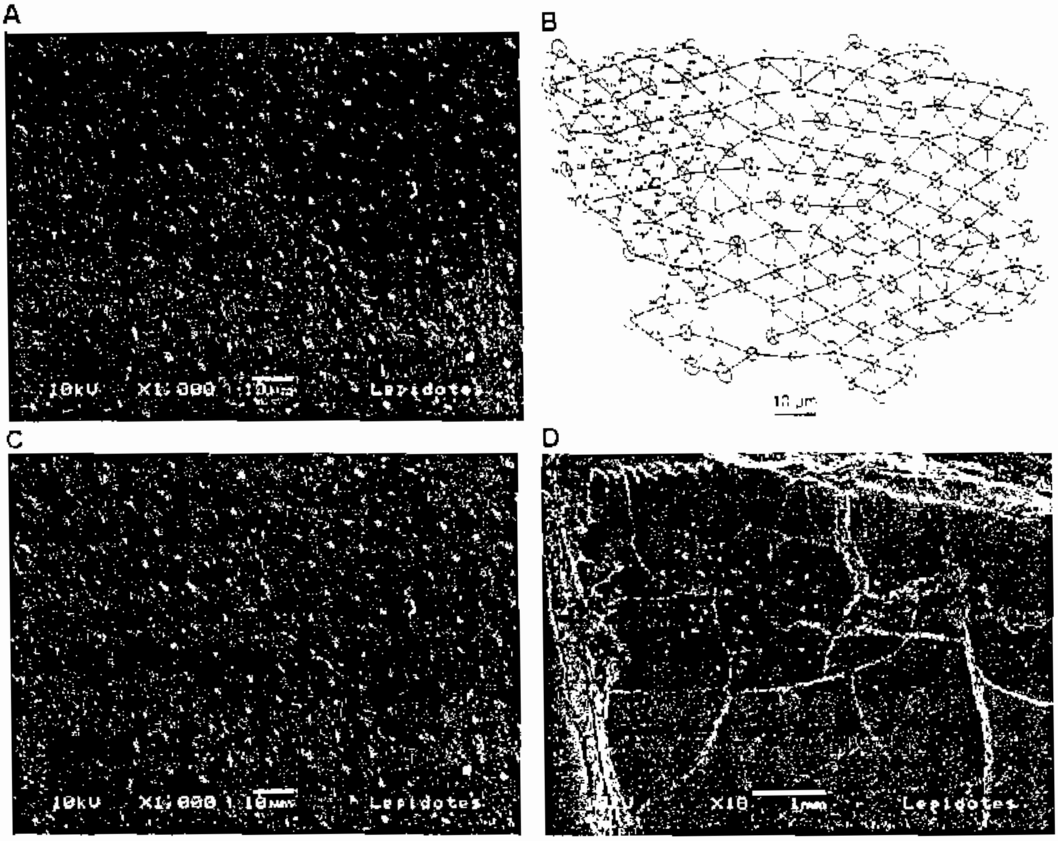

Figure 79 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L12-1. B: measurement of the tubercles (34 measurements) and of the distances between them (78 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

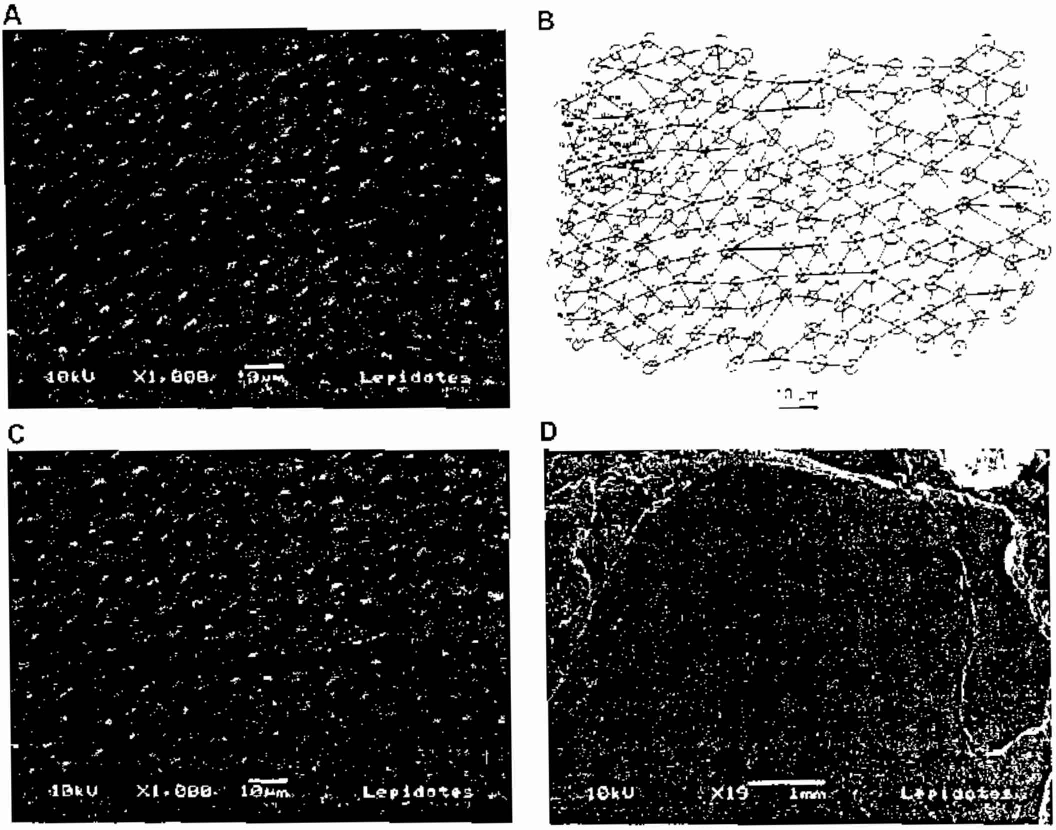

Figure 80 Specimen KS12-97. **A**: Plot of tubercles on a micrograph of the scale L15-3, **B:** measurement of the tubercles (31 measurements) and of the distances between them (70 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

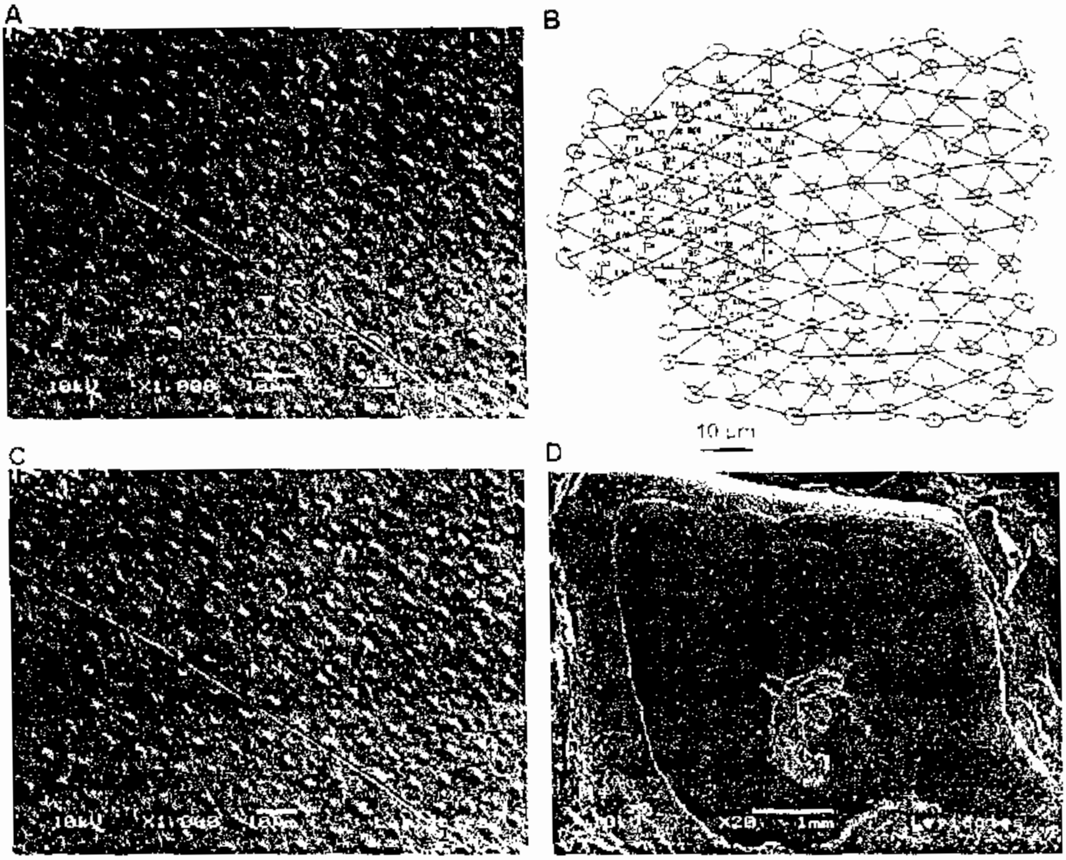

Figure 81 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L16-8. B: measurement of the tubercles (33 measurements) and of the distances between them (75 measurements). C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

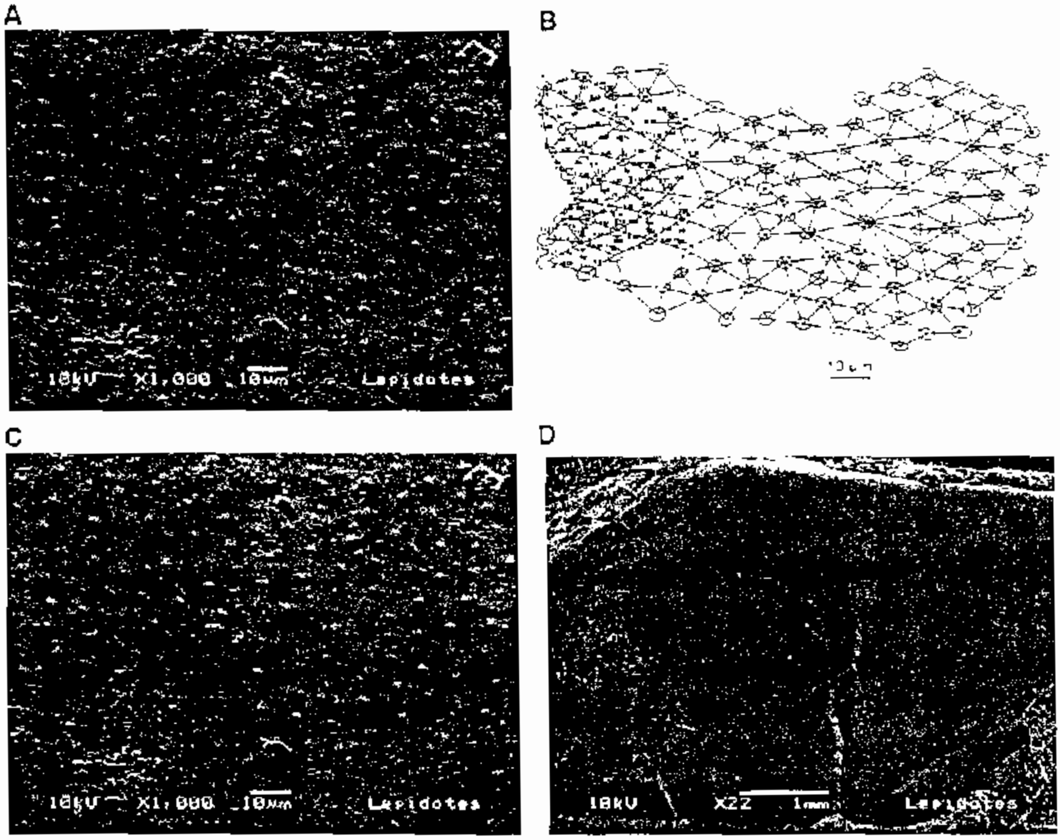

Figure 82 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L23-5. B: measurement of the tubercles (33 measurements) and of the distances between them (77 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

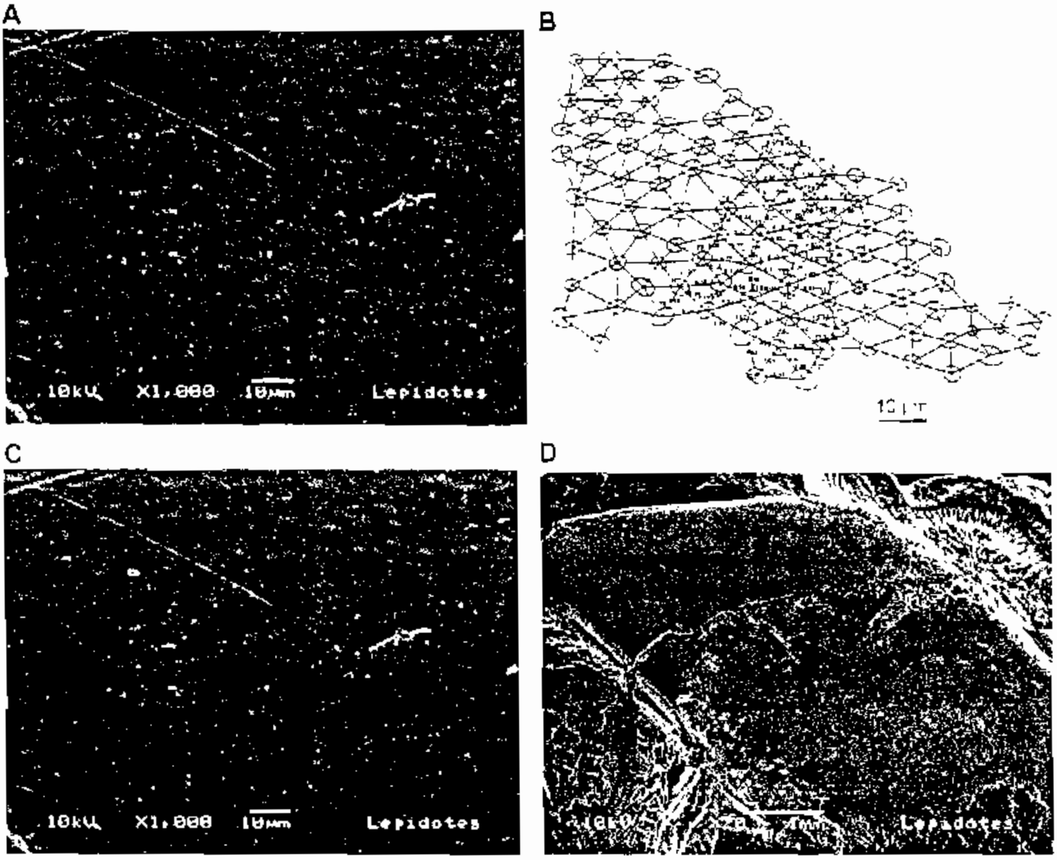

Figure 83 Specimen KS12-97. A: Plot of tubercles on a micrograph of the scale L30-2. B: measurement of the tubercles (33 measurements) and of the distances between them (75 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

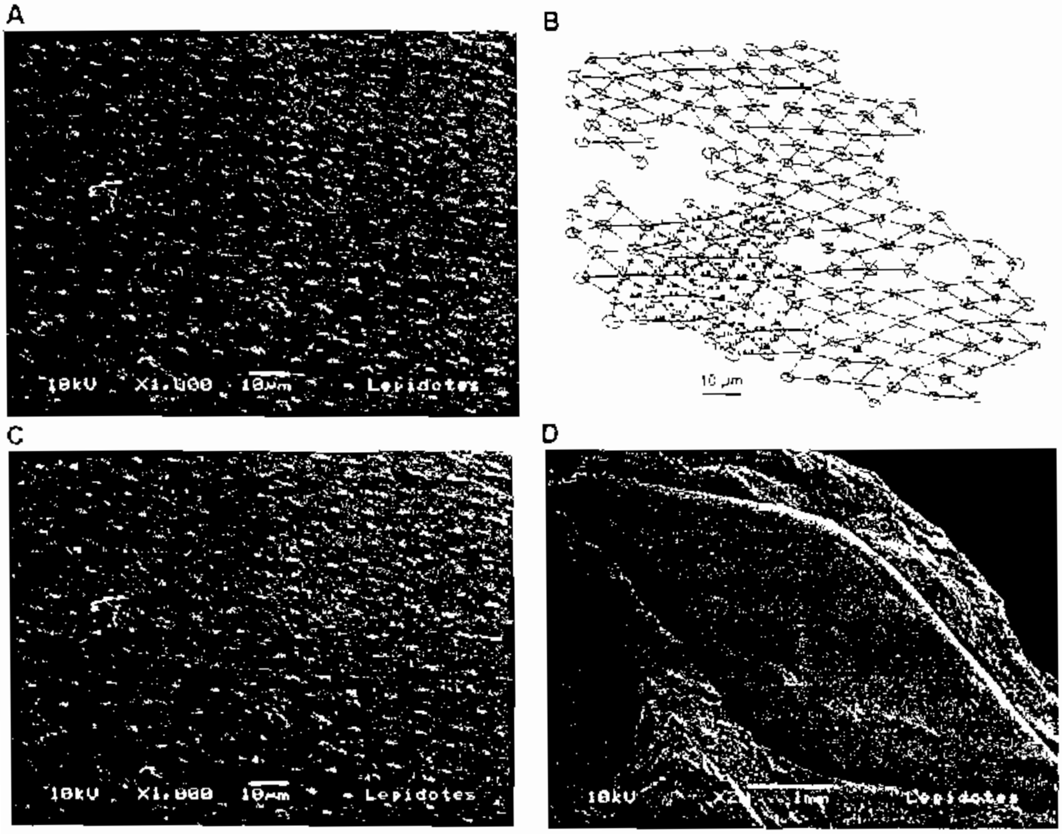

Figure 84 Specimen KS12-97. **A**: Plot of tubercles on a micrograph of the scale L33-6, **B**: measurement of the tubercles (35 measurements) and of the distances between them (83 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

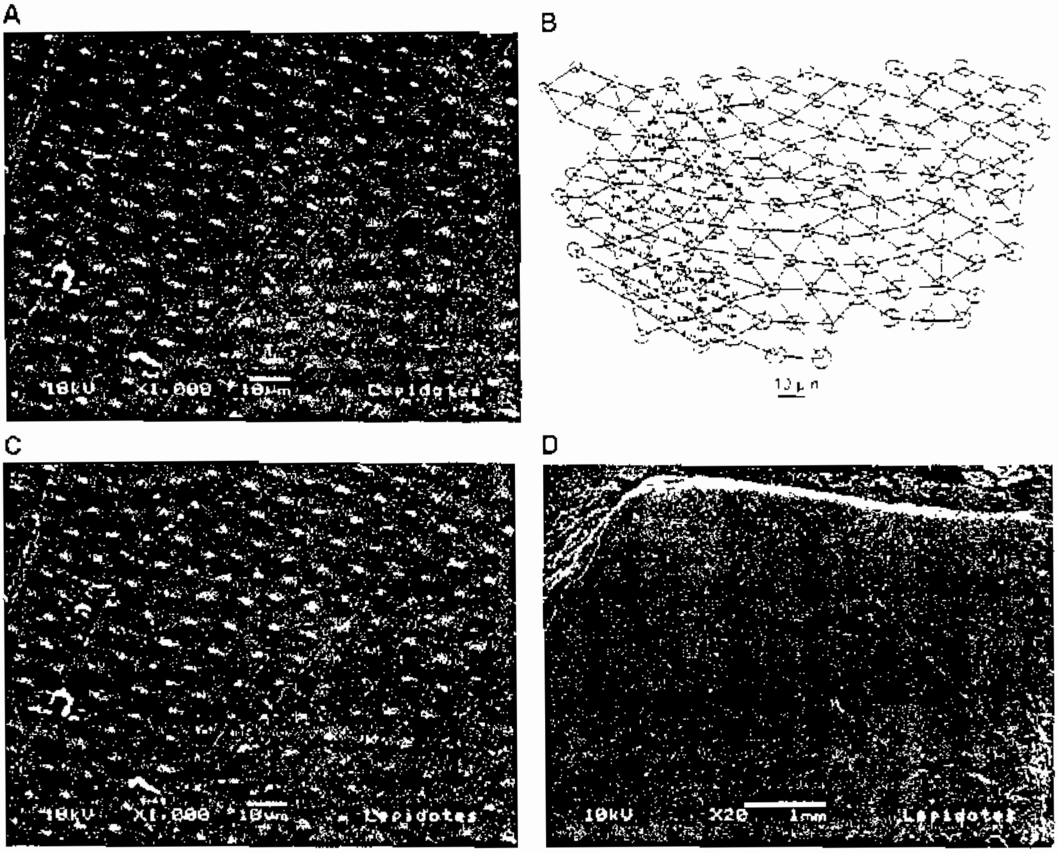

Figure 85 Specimen KS12-265. **A**: Plot of tubercles on a micrograph of the scale L12-1, **B**: measurement of the tubercles (33 measurements) and of the distances between them (77 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

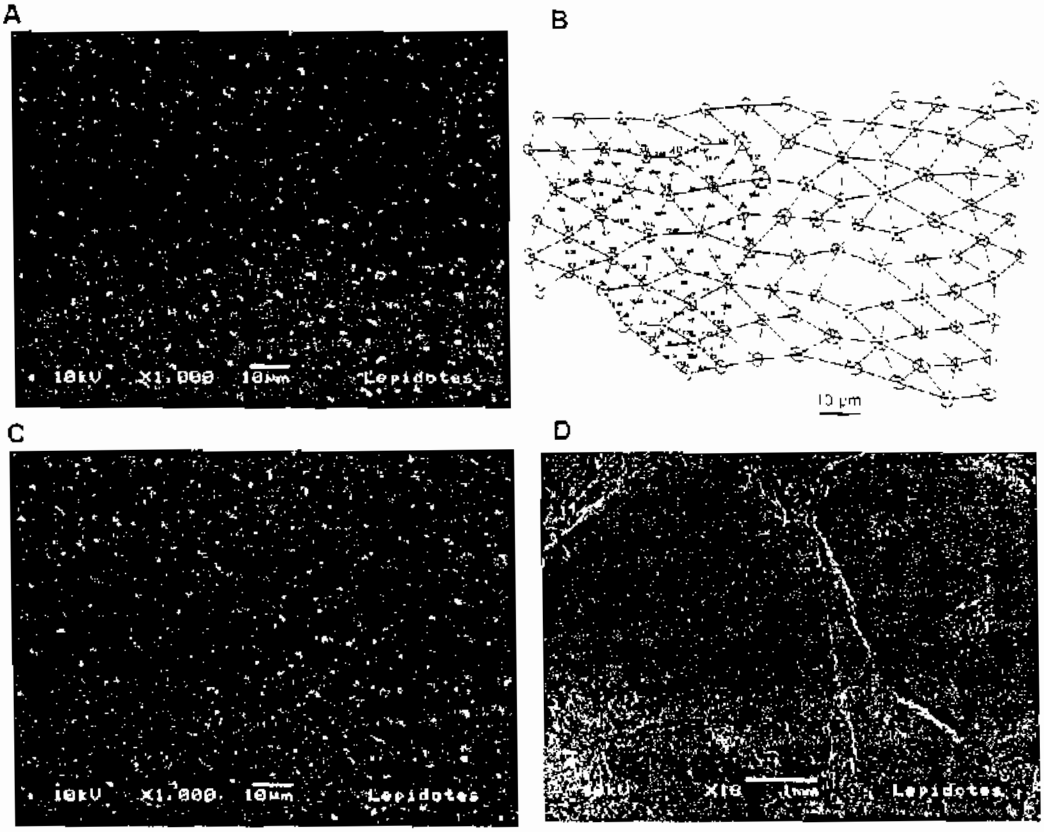

Figure 86 Specimen KS12-265. A: Plot of tubercles on a micrograph of the scale L15-3, B: measurement of the tubercles (31 measurements) and of the distances between them (71 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

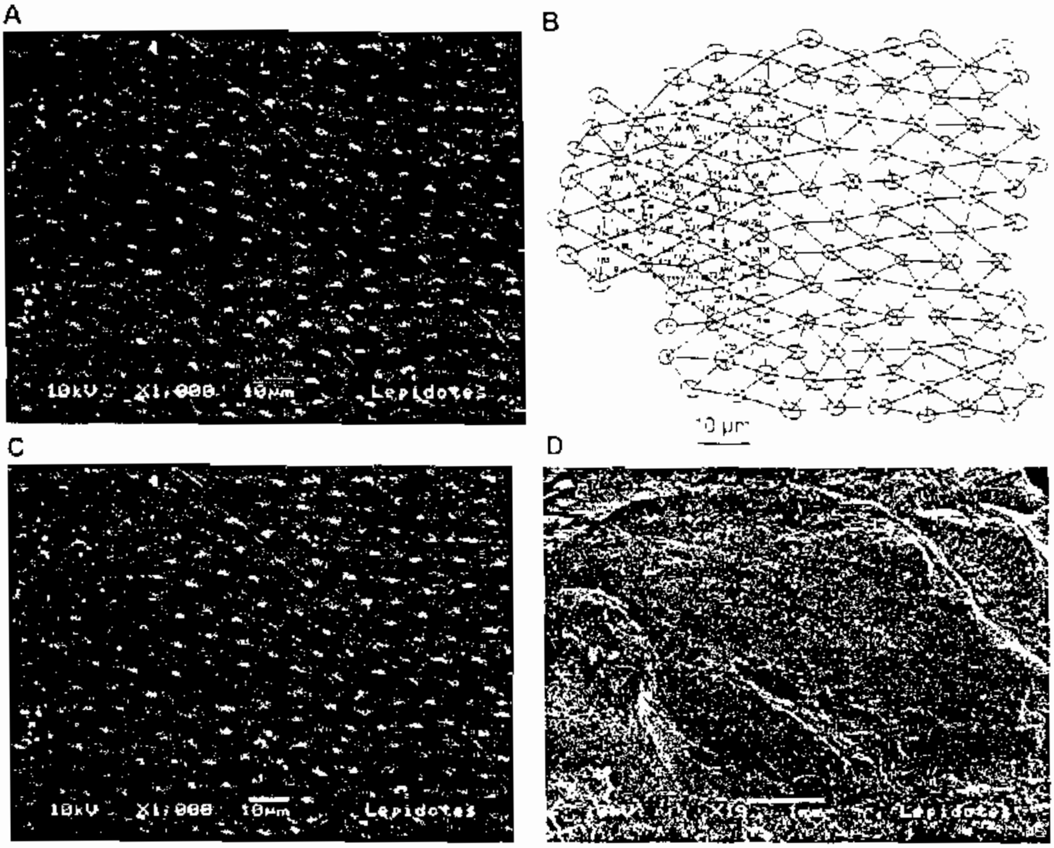

Figure 87 Specimen KS12-265. **A:** Plot of tubercles on a micrograph of the scale L16+8, **B:** measurement of the tubercles (33 measurements) and of the distances between them (77 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

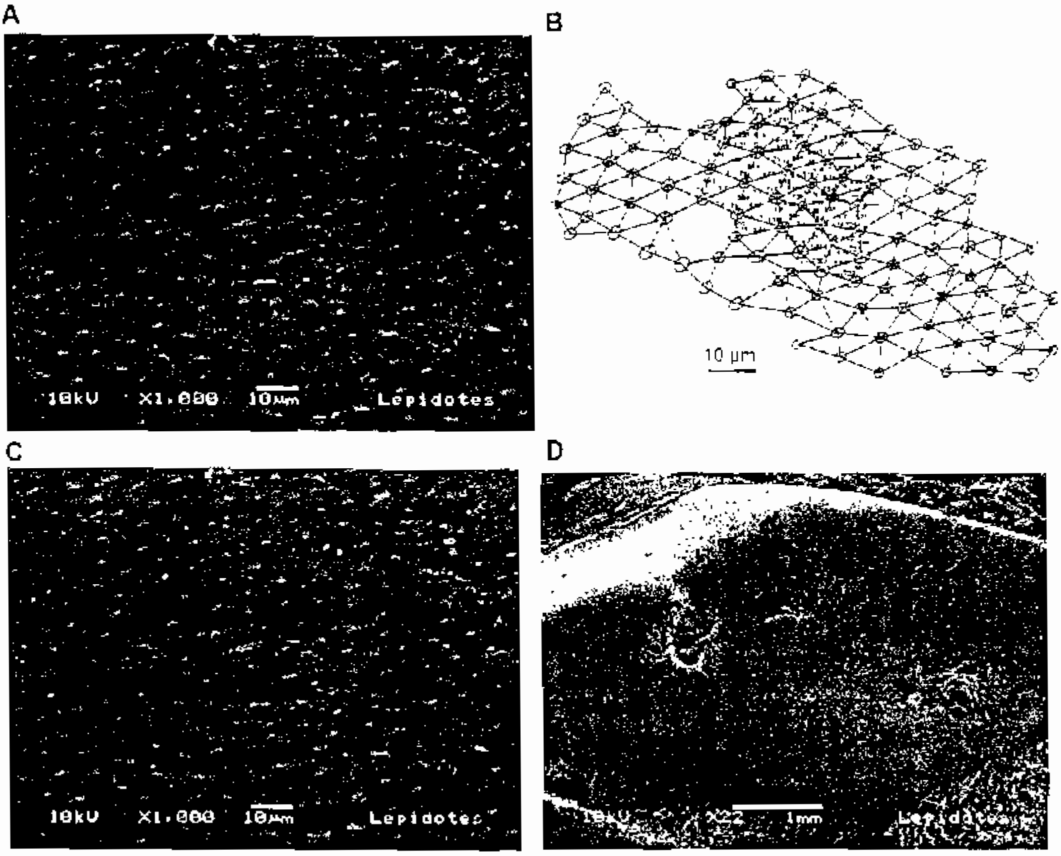

Figure 88 Specimen KS12-265. A: Plot of tubercles on a micrograph of the scale L23, B: measurement of the tubercles (32 measurements) and of the distances between them (74 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

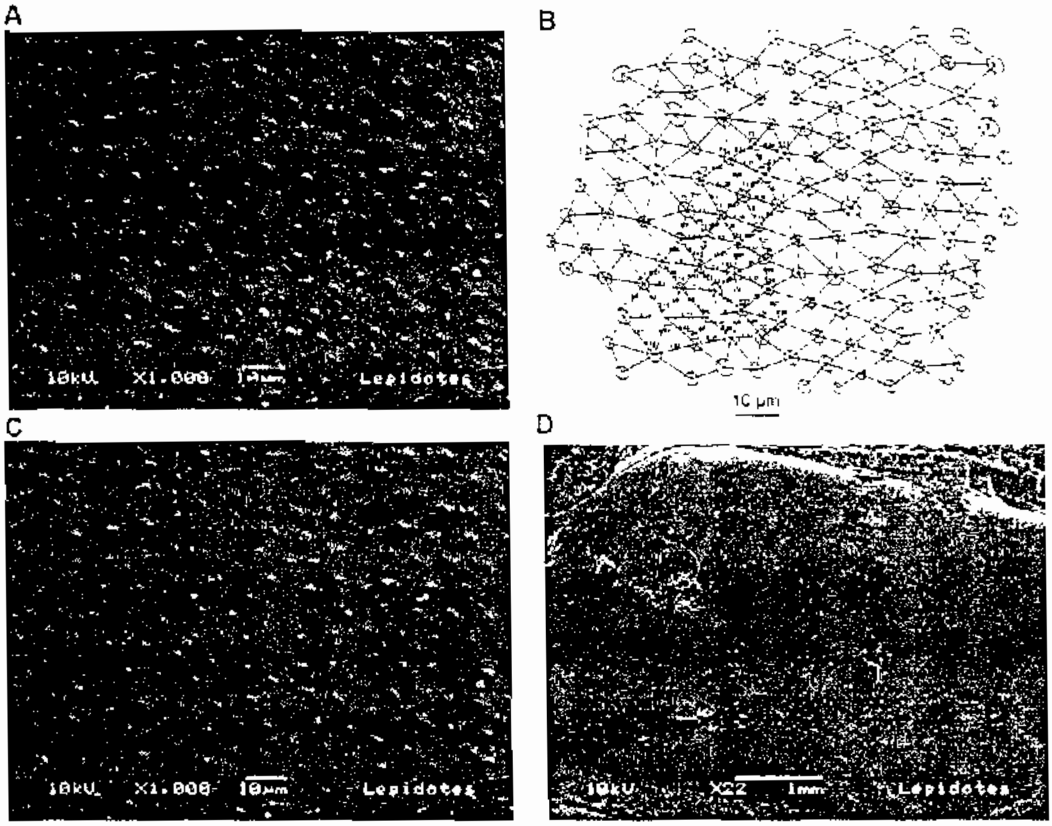

Figure 89 Specimen KS12-265. A: Plot of tubercles on a micrograph of the scale L23-5. B: measurement of the tubercles (30 measurements) and of the distances between them (68 measurements), C: SEM view of the ganoin surface of the scale, D: view of the external surface of scales.

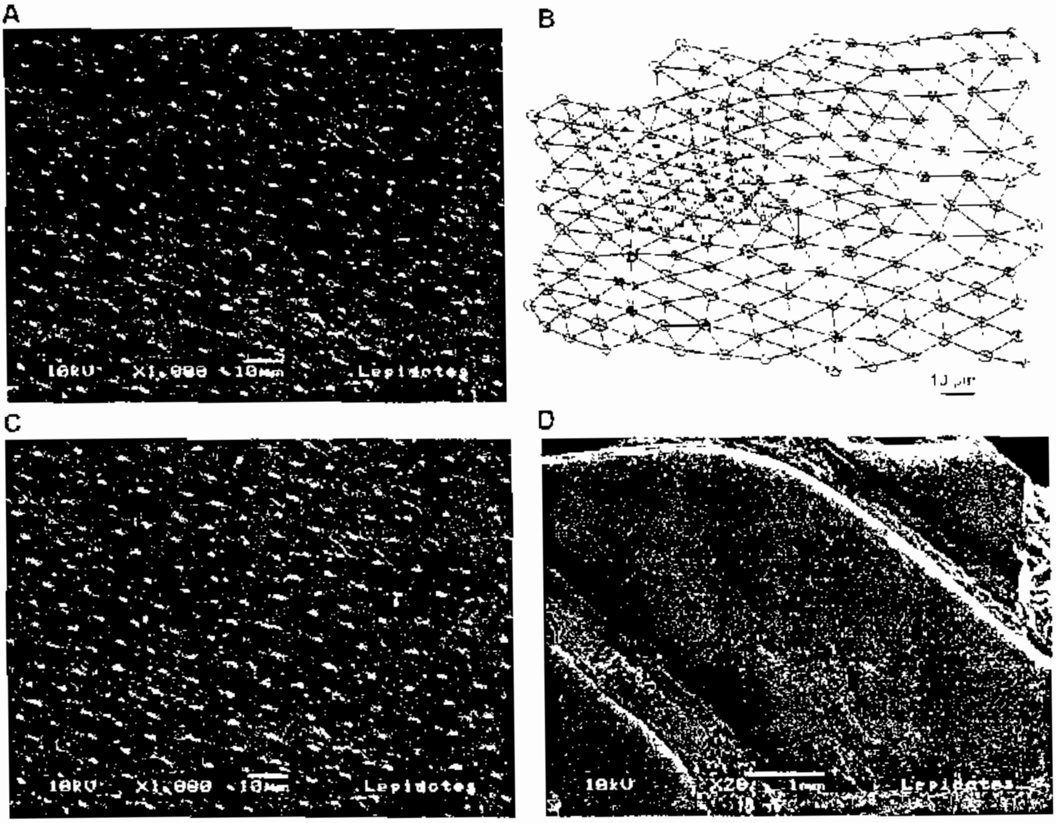

Figure 90 Specimen KS12-265. **A:** Plot of tubercles on a micrograph of the scale L30+2. **B:** measurement of the tubercles (31 measurements) and of the distances between them (72 measurements). C: SEM view of the ganoin surface of the scale. D: view of the external surface of scales.

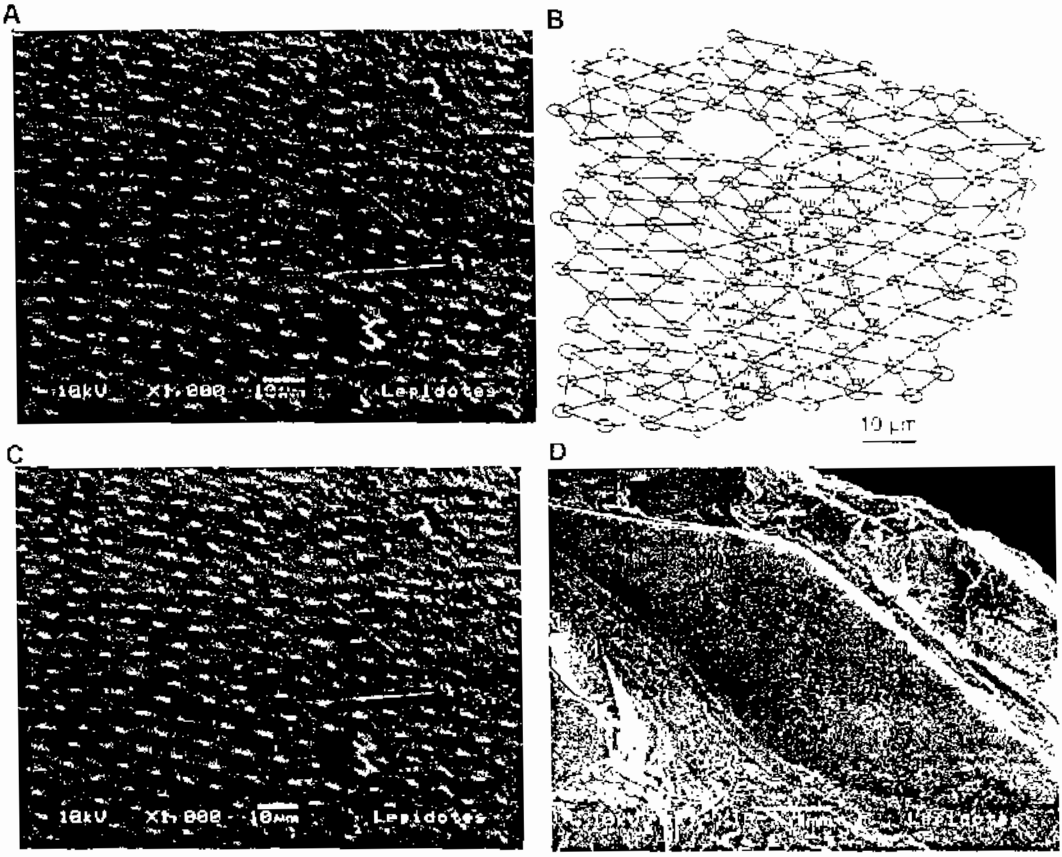

Figure 91 Specimen KS12-265. **A:** Plot of tubercles on a micrograph of the scale L33-6. **B:** measurement of the tubercles (32 measurements) and of the distances between them (70 measurements). C: SEM view of the ganoin surface of the scale. **D:** view of the external surface of scales.

APPENDIX III

This manuscript has been accepted for publication in Acta Palaeontologica Polonica Journal.

A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, northeastern Thailand

UTHUMPORN DEESRI, KOMSORN LAUPRASERT, VARAVUDH SUTEETHORN, KAMONLAK WONGKO, and LIONEL CAVIN

Deesri, U., Lauprasert, K., Suteethorn, V., Wongko, K., and Cavin, L. **In press.** A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, northeastern Thailand. *Acta Palaeontologica Polonica* 5X (X): xxx-xxx.
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Instytut Paleobiologii PAN
ul. Twarda 51/55
PL-00-818 Warszawa, Poland
e-mail: app@twarda.pan.pl, tel. (+48 22) [illegible], fax +48 22) 620 62 25

A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, northeastern Thailand

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Deesri, U., Lauprasert, K., Suteethorn, V., Wongko, K., and Cavin, L. 201X. A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, northeastern Thailand. *Acta Palaeontologica Polonica* 5X (X): xxx-xxx. http://dx.doi.org/10.4202/app.2012.0013

A new ginglymodian fish, *Isanichthys lertboosi*, is described from the Phu Kradung Formation, north-eastern Thailand, a freshwater deposit of probable Late Jurassic age. The species is represented by four specimens, from the Phu Noi locality, associated with a rich fauna of sharks, turtles, crocodiles, and theropod and sauropod dinosaurs. One specimen is an isolated braincase, which provides characters rarely observed in extinct ginglymodians. The species is referred to the genus *Isanichthys*, a taxon originally described on the basis of a single specimen from the Phu Nam Jun locality, a slightly younger site approximately 75 km from Phu Noi. *Isanichthys* is mainly distinguished by frontals slightly narrower anteriorly than posteriorly, two anterior intraorbitals not in contact with the orbit, reduced preorbital region, and a small orbit and a cheek region completely covered by bones. The new species is characterized, among other characters, by a dermal component of the sphenotic visible on the cheek, one pair of extrascapulars plus a small median one, the presence of few suborbitals (circa 4 or 6) arranged in one row, and a median dorsal row of scales with spine. Comparisons with other ginglymodian taxa and a cladistic analysis indicates that *Isanichthys* (*Lepidotes*) *latifrons* from the Late Jurassic of England, as well as probably *Isanichthys* (*Lepidotes*) *luchowensis* from the Early or Middle Jurassic of Sichuan, China, form a clade with both Thai species of *Isanichthys*. The new species provides evidence of the high diversity of ginglymodian fishes in the Phu Kradung Formation and suggests a new hypothesis of phylogenetic relationships among extinct ginglymodians.

Key words: Holostei, osteology, braincase, phylogeny, Late Jurassic, south-east Asia.

Uthumporn Deesri [uthumporn_deesri@yahoo.com], Department of Biology, Faculty of Science, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;
Komsorn Lauprasert [lauprasert@gmail], Department of Biology, Faculty of Science, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150 Thailand and Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;
Varavudh Suteethorn [suteethorn@hotmail.com], Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;
Kamonlak Wongko [luree40@yahoo.com], Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand;
Lionel Cavin [lionel.cavin@ville-ge.ch], Department of Geology and Palaeontology, Muséum d'Histoire naturelle, CP 6434, 1211 Genève 6, Switzerland.

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Introduction

Ginglymodi is a clade of ray-finned fishes comprising the Lepisosteiformes (gars and extinct relatives), and the extinct 'Semionotiformes' and Macrosemiiformes (Grande, 2010). Lepisosteiformes and Macrosemiiformes are well characterized by osteological characters, but the 'Semionotiformes' are still poorly defined (Cavin 2010, Cavin et al. in press). In these studies, the 'Semionotiformes' are positioned as stem taxa to the Lepisosteiformes, but show poorly resolved intrarelationships. For more than a century, only a few species of wellpreserved 'Semionotiformes' have been described, mostly from Europe, and numerous taxa have been defined on the basis of incomplete and often fragmentary material. During the last few decades, however, re-examination of old specimens and new taxa found worldwide have greatly improved our knowledge of the group. Without evidence supporting the monophyly of 'Semionotiformes' in the present analysis, we do not retain this term, and we use instead Ginglymodi, which represents a broader monophyletic group. Recently, López-Arbarello (2012) provided important new results about ginglymodian relationships, showing that Lepisosteiformes includes Lepisosteidae and several stem groups, i.e. the Obaichthyidae, *Pliodetes*, *Araripelepidotes*, *Lepidotes* (with a new definition, and including three Early Jurassic species), *Scheenstia* (with a new definition, and including seven species from the Late Jurassic and Early Cretaceous) as well as *Isanichthys palustris*. Importantly, a clade called Semionotiformes is resolved: it comprises the Semionotidae, the Callipurbeckiidae, and the Macrosemiidae. The set of characters used in López-Arbarello's analysis (2012) differs from the set of characters used in analyses of Cavin (2010), Cavin et al. (in press) and in the present study. We discuss and compare our results with those of Lopez-Arbarello (2012).

In Thailand, ginglymodians constitute the most common fish remains in the continental Mesozoic deposits of the Khorat series in the northeastern part of the country, and well-preserved material has been uncovered since the 2000s (Cavin et al. 2009). The most productive locality, Phu Nam Jun, located in Tambon LaoYai, Kalasin province, exposes the Late Jurassic – Early Cretaceous Phu Kradung Formation (Cavin et al. 2004). It has yielded *'Lepidotes' buddhabutrensis* (Cavin et al. 2003), a ginglymodian that was recently referred to a new genus (Cavin et al. in press). While *'Lepidotes' buddhabutrensis* is represented in this locality by several hundreds of complete and subcomplete individuals (Deesri et al. 2009), a single specimen has been referred to another taxon by Cavin and Suteethorn (2006). In September 2008, a new excavation at the Phu Noi locality was opened in Kalasin District, approximately 75 km NW of Phu Nam Jun (Fig. 1). Although also exposing the Phu Kradung Formation, the new locality is at an older stratigraphical level than Phu Nam Jun. Phu Noi has yielded an array of tetrapods, as well as isolated shark teeth and some ginglymodian remains. The latter material is described in this paper.

Institutional abbreviations. CDUT, Palaeontological Museum of the Chengdu University of Technology, China; KS, Sirindhorn Museum, Sahat Sakhan, Kalasin Province; NHMUK, Natural History Museum, London.

Material and methods

The specimens have cracks filled with sediment caused by roots from the soil, and were coated with a few cm of calcareous sandstone. We extracted the fossils from the field with the plaster jacket technique in order to preserve their delicate and fragile fins. Preparation was performed using an air pen in the laboratory of the Sirindhorn Museum, Sahat Sakhan, Kalasin Province, where the specimens are housed. In the laboratory, the upper part of the jackets was sawed in order to free the upper side of the specimens, which were visible in the field. Details of the skulls were prepared under a binocular microscope. The available sample comprises four specimens in total. Nomenclature in the anatomical description follows Grande (2010).

Geological setting

The Phu Noi locality is located on the flank of a small hill at Ban Din Chi, Kam Muang District, Kalasin Province (Fig. 1B). Stratigraphically, it is in the lower part of the Phu Kradung Formation, which is characterized by sandstone beds alternating with silty to sandy claystones. This formation is low in the Khorat Group as currently defined, above the Upper Nam Phong Formation (Racey 2009). The Khorat Group comprises post-Triassic deposits on the Khorat Plateau and adjacent areas, and it has long been regarded as Late Jurassic, but palynological studies now suggest Early Cretaceous ages for most of the vertebrate-bearing horizons, i.e. the Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations (Racey et al. 1994, 1996). The dating of the Phu Kradung Formation is still problematic, but a recent synthesis suggests a Late Jurassic age for its lowermost part, in which the Phu Noi locality is located, and a basal Cretaceous (Berriasian) age for the upper part (Racey 2009).

The sediments of the Phu Kradung Formation are fluviatile and lacustrine in origin, and the main palaeocurrents are oriented towards the SW (Racey 2009). At Phu Noi, greenish grey sandy deposits are interbedded with maroon siltstones, which are mica rich and contain laminated plant debris. The fish remains have been found in two main layers. The upper layer consists of an accumulation of dinosaur skeletons, approximately 3 m thick and dips approximately 10 degrees towards the SE. The fossil assemblage consists of fragments of skeletons of sauropod dinosaurs, isolated theropod bones, fragments of skeletons of crocodiles, turtle and shark remains, and includes two specimens of ginglymodian fishes. The lower layer is approximately 2 m below the dinosaur assemblage, and has yielded the other two ginglymodian specimens. However, there are no visible differences in terms of sediment deposition between the two layers.

Systematic palaeontology

Superdivision Holostei sensu Grande, 2010
Division Ginglymodi sensu Grande, 2010
Order Lepisosteiformes sensu López-Arbarello, 2012
Genus *Isanichthys* Cavin & Suteethorn, 2006

Type species.–Isanichthys palustris Cavin and Suteethorn, 2006
Emended diagnosis.–Ginglymodian fish with skull roof bones strongly ornamented, with no continuous ganoin cover; frontals slightly narrower anteriorly than posteriorly; ratio of frontal length to parietal length less than 2.5; ratio of skull length to orbit length more than 6, closed orbital ring; two anterior infraorbitals not in contact with the orbit, anteriormost infraorbital deeper than long; two supraorbitals, the anterior one generally elongated with anterior margin contacting the first and/or the second infraorbital; cheek region completely covered by bones, quadrate lies below the orbit; preopercle slightly curved; maxilla formed by a posterior rounded plate-like part and a thin anterior part, which precedes the articular process; one supramaxilla; epiotic with a short and simple posteriorly directed process; posttemporal fossa present; intercalar absent; basisphenoid present; presence of an oral sensory canal; 25 rays in caudal fin, 12 in upper lobe; 50 to 53 rows of ganoid scales along the flank and approximately 20 scales in the transverse row at the deepest level of the body.

ginglymodians (see Cavin et al. in press for a review). In gars the sphenotic is visible laterally and separated from the dermosphenotic (Grande 2010). In *Isanichthys lertboosi* the tip of the lateral process of the sphenotic is separated from the orbit by a gap, but it is closely associated with the dermosphenotic. In obaichthyids, sphenotic and dermosphenotic are fused together (Grande 2010).

In KS34-380, the basisphenoid, pterosphenoid and orbitosphenoid surround the orbital cavity, with only a gap on the ventral margin that was occupied by the parasphenoid, as confirmed by the presence of attachment areas on the ventral surface of the basisphenoid and orbitosphenoid (Fig. 8). The basisphenoid is the smallest bone of the preserved series and is situated at the posteroventral edge of the orbit cavity. The posterior margin is covered with matrix, but we can estimate its shape. It is approximately triangular with a slightly curved anterodorsal margin, while the other margins are straight. Along the posterior margin runs a narrow groove that reaches the pterosphenoid. Although in KS34-380 the pterosphenoid has slightly shifted, it is clear that the pterosphenoid was sutured to the basisphenoid ventrally and to the orbitosphenoid anteriorly. The pterosphenoid is wing-shaped with its dorsal margin forming a rounded rim and its ventral margin marking a broad angle, almost at its mid-length. The lateral surface of the bone presents alternating ridges and grooves. The orbitosphenoid has an irregular shape and is located anteriorly to the orbit. Its posterior margin has a deep notch. It bears a blunt process on the posteroventral corner, which almost reaches the basisphenoid, while the posterodorsal extremity sutures with the pterosphenoid. Laterally, two grooves run anteriorly from the centre of ossification. The anterior margin forms a slightly concave line and the dorsal margin is satured with the ventral side of the frontal. The basisphenoid is absent in gars and in *'Lepidotes' buddhabutrensis*, while it is present in most other ginglymodians in which this region is known (*Araripelepidotes*, *Scheenstia mantelli*, *Callipurbeckia minor*, *Lepidotes semiserratus*).

Circumorbital and suborbital series.–The circumorbital ring is complete. It is composed of a large dermosphenotic forming the posterodorsal edge of the orbit, two supraorbitals above the orbit and six to eight infraorbitals located posteriorly, ventrally and anteriorly to the orbit. The number of infraorbitals is generally eight but KS34-281 contains six large infraorbitals only (Fig. 5A). Two infraorbitals anteriorly are not in contact with the orbit. The first, anteriormost, infraorbital is deep and irregular in shape with a dorsal margin shorter than the ventral margin, which is gently convex (Fig. 3B). The second infraorbital is approximately rectangular or ovoid in shape, slightly deeper than long. The third infraorbital, which forms the anteroventral corner of the orbit, and the remaining ones, situated below and behind the orbit, are deeper than long. On the left side of KS36-3, the infraorbitals are ornamented with strong knobs and grooves in the centres of all ossifications, except the large posteroventral one, which lacks ornamentation (Fig. 4A). The shape of the dermosphenotic varies: it is elongated and trapezoidal in KS36-2, large and rectangular in KS36-3 and narrow and rectangular in KS34-281. The supraorbitals consist of two large bones. The anteriormost is elongate and rectangular in shape, tapers anteriorly, and the posterior one is smaller and deeper than long. In the holotype (KS36-2), there are six suborbitals arranged in one row located between the dermosphenotic, the infraorbitals and the preopercle. In some specimens (KS36-3, KS34-281) four suborbitals only are present (Figs. 4, 5). The largest one, situated anteroventrally, is irregular in shape with its dorsal margin straight, and its ventral margin slightly undulating. It articulates posteriorly to the adjacent suborbital and dorsally to the infraorbitals, and contacts posteroventrally the blunt extremity of the preopercle. The dorsalmost suborbital is large and rectangular, longer than deep and articulates with the dermopterotic dorsally, the dermosphenotic anteriorly, the dorsal portion of the preopercle posteriorly and the adjacent suborbital ventrally. The remaining suborbitals are deeper than long (Fig. 4). On its right side, KS36-2 presents a small triangular suborbital located at the anterior end of the series (Fig. 3B).

Jaws.–There are some variations in the arrangement of jaw bones and in tooth morphology. The maxilla is best preserved on the left side of KS 34-281. It is an elongate bone with a thin, slender anterior part and a plate-like, rounded posterior part. Its narrow anterior portion is edentulous (Figs. 5A, 12). The anterior articular process, prolonging the anterior thin part and corresponding to one third of the length of the bone, is inwardly curved. A supramaxilla rests on the dorsal margin of the posterior plate. Its depth is nearly half the depth of the maxilla, and it has a curved dorsal margin and a straight ventral margin that borders the maxilla. The nasal process of the premaxilla extends posterodorsally under the nasal and the frontal, and the alveolar portion extends laterally as blunt processes. Only one tooth is preserved on the premaxilla of KS 34-281 but the exact number of teeth on the anterior transversal margin of the bone is unknown. The tooth is similar in shape and size to the teeth borne by the dentary and ectopterygoid. It is well developed, about 4 mm in height with an acrodine tip, which is about 0.5 mm high (Figs. 12, 13).

The lower jaw is massive. The visible ossifications are a dentary, one or two coronoids, a large angular, and a surangular located on the posterodorsal edge of the mandible and visible just anterior to the coronoid process in lateral view (Fig. 5A). The angular forms most of the posterior part of the mandible, it contacts the dentary along a suture, whose pattern varies within the set of available specimens. An elongated posterior process of the dentary is present on the holotype. The dentary is robust and slightly tapering at its anterior extremity, which bears a row of approximately 13 conical teeth with bulbous and pointed acrodine caps. Each tooth is composed of a high cylindrical base, approximately 4 mm in height and 1 mm in width, topped by a bulbous cap that is shallow (0.5 mm) compared to its base. All teeth are held on a single row along the anterior portion of the dorsal rim of the dentary. A second row of teeth, similar in both shape and size to the dentary teeth, lies behind the anterior marginal teeth. These teeth are regarded as coronoid teeth. A second coronoid (or the posterior part of the anterior one) is visible as a thin blade of tooth-bearing bone wedged in a notch of the dentary, anteriorly to the coronoid process and visible on both sides of KS34-281 (Figs. 11, 12).

The holotype, KS 36-2 (Figs. 14, 15), shows a different arrangement of its jaws. The premaxillae have no preserved teeth. Posteriorly, the narrow and elongate nasal process of the premaxilla extends under the frontal, and anteriorly the bone extends transversely to form the alveolar processes (Figs. 15A-B). On this specimen, the lower jaw is broken but we observe a piece of mandible shifted close to the skull. This piece of bone bears two rows of crushing teeth. The teeth, approximately 5 mm high, have a cylindrical base with a bulbous acrodine cap, which is 2.5 mm high, 2 mm wide (this morphology corresponds to the 'moderately tritorial dentition' as defined by Cavin 2010). The teeth are not attached to the dentary, and we regard them as coronoid teeth (Figs.15C-D). Based on the location of the articulation between the lower and upper jaws, it seems that this fish had a wide gape.

Hyopalatine series.–The suspensorium is visible on both sides of the holotype (KS36-2), but it is poorly preserved and identification of the ossifications remains uncertain. The hyomandibula is partially exposed: the anteroventral part only is visible, while the rest is hidden by the opercle and subopercle. Based on the surface of the exposed region, it seems that the bone is a massive and relative large ossification. The metapterygoid (Fig. 3A) is irregular in shape, with its posterior part expanding and with a tapering anterior extremity. It contacts the hyomandibula posteriorly and the entopterygoid anteriorly, but we cannot see if there was a contact with the quadrate. The entopterygoid is a triangular bone wedged between the metapterygoid dorsally and the ectopterygoid anteriorly. The ectopterygoid is preserved as a crescent-shaped ossification suturing posteriorly with the entopterygoid. The anterior portion of the ectopterygoid bears at least 7 small cylindrical-based teeth along its ventral border. Each of these teeth is tipped with a bulbous cap. In KS36-2, the dermopalatine is covered with teeth (Fig. 14). The teeth are variable in size and irregularly arranged, but two main rows of crushing teeth appear to be present. In KS34-281, the right ectopterygoid is also visible as a thin bone lying under the infraorbitals (Figs. 11, 12). It bears 6-7 conical teeth restricted to its anterior margin. The arrangement of the palatine dentition is unknown in other specimens.

Opercular series.–The opercular series is complete, formed by the preopercle, opercle, subopercle and interopercle.

In the holotype, KS36-2, the preopercle (Figs. 3-5) is preserved only on the right side. It is narrow with a poorly developed ventral limb, and is slightly bent forward. The ossification is crescent-shaped, with no marked angle between both limbs. In KS34-281, the preopercle of the right side shows two limbs forming a more closed angle than in the holotype, and the horizontal limb is shorter than the vertical (Fig. 5B), but it is unclear if this arrangement is genuine or caused by preservation. The vertical branch has parallel margins that do not converge dorsally, and the ossification ends anteriorly as a blunt spine. The extremity of the horizontal branch slightly widens in its anterior part before the blunt spine The preopercular sensory canal extends enclosed within the thickened anterior margin of the ossification. The opercle (Fig. 3) is roughly quadrangular and slightly deeper than long, but in one specimen (KS34-281) the ossification is more rounded (Fig. 5A). The anterior border is straight, while the posterior border is strongly convex and widely overlaps the supracleithrum. The dorsal border reaches the dermal skull roof. The surface is smooth in KS 36-2 (holotype) but in some specimens, such as KS36-3, the external surface is ornamented with fine grooves, and in KS34-281 rough tubercles are present. The subopercle is well developed with a vertical limb reaching half the depth of the opercle. The anterior margin of the bone is vertical and straight, and contacts the posterior border of the interopercle. The ventral margin of the bone is convex. The interopercle is visible as a triangular bone wedged between the subopercle and the posteroventral edge of the preopercle (Fig. 3B). The anterior tip tapers and it runs toward the ventral extremity of the preopercle. In KS36-3, however, the interopercle is visible as a narrow bone along the ventral margin of preopercle (Fig. 4A).

Hyoid arch and branchiostegal rays.–Six thin and elongated branchiostegal rays are preserved on the left side of holotype, KS36-2 (Fig. 3A): the posteriormost one is the shortest but the widest. The four anterior rays articulate with the anterior ceratohyal and the two posterior ones with the posterior ceratohyal. The anterior ceratohyal is hourglass-shaped, with a slightly convex posterior border There is a weak groove running on the median region of the lateral surface of the bone The posterior ceratohyal is roughly triangular in shape, with a regularly curved margin contacting the anterior ceratohyal

Pectoral girdle.–The posttemporal is visible as a crescent-shaped ossification with a notch along its posterolateral margin for the exit of the sensory canal (Fig. 4). The supracleithrum is an ovoid ossification and its dorsal border articulates with the posterior margin of the posttemporal. The path of the sensory canal is indicated by three pores that open adjacent to the exit of the sensory canal. The cleithrum is a long and curved ossification, proportionally narrow on its exposed part, which is overlapped by the opercular series. The lateral face of the cleithrum bears traces of enamel. The posterior margin of the bone is curved. In KS34-281, the ventral margin of the cleithrum shows a concavity for the insertion of the pectoral fin (Fig. 5A). The horizontal limb of the cleithrum is rather short and deep, with its lateral face marked by a smooth ridge. One gently curved postcleithrum is visible.

Cephalic sensory canal.–The anterior part of the lateral line is indicated by a series of pores located on the dorsal margin of the supracleithrum, then by a pore located in the concavity of the middle part of the posttemporal and by one on the anteroventral edge of this ossification. The occipital sensory canal (forming the supratemporal commissure) is indicated by a series of pores that open along the posterior edges of extrascapular ossifications. The supraorbital canal marks an angle at the level of the posterodorsal corner of the orbit, and several pores along the lateral margin of the frontal and along the lateral margin of the parietal. The canal passes through the nasal along the longitudinal axis of the bone. There is one pore visible on the anterior tip of the nasal in specimen KS 36-2 and KS34-281. The middle pit line is indicated by a groove and pores opening between parietal and dermopterotic close to the posterior edge of these bones. The supratemporal sensory canal extends along the dermopterotic through the dermosphenotic, which marks the connection with the infraorbital sensory canal. The infraorbital sensory canal runs in the centre of the infraorbital ossifications, and gives off openings located near the ventral and posterior margin of the infraorbitals located respectively ventrally and posteroventrally to the orbit. There is no evidence of a sensory canal running within the supraorbital bones. The preopercular sensory canal presents several pores along the horizontal and vertical branches of the ossification: three elongate pores open in the curvature of the bone near its ventral margin and two smaller pores open more dorsally (KS36-3), and two pores are visible close to the dorsal margin of the preopercle in KS34-281. The mandibular sensory canal gives off two or three pores in the angular, and approximately six pores in the dentary arranged in two lines in KS34-281, the dorsal one corresponding to the oral canal.

Pectoral fins.-The pectoral fin of KS36-2 is composed of three basal fulcra - the anterior one, unpaired, is followed by two elongate and paired ones - and two fringing fulcra (only two basal fulcra are visible in Fig. 17A because of the angle). The unsegmented basal portions of ten rays are visible in KS36-2.

Pelvic fins.–The pelvic fin consists of two basal fulcra, the anterior of which is unpaired and the second paired (both halves of the paired fulcrum are visible in Fig. 17B), five thin fringing fulcra and five rays. The rays are very long, representing 47% of the head length (KS36-2, fin length = 90 mm, head length = 190 mm)

Unpaired fins.–The dorsal fin is visible on KS36-2 and more completely on KS36-3 (Fig. 18) while the anal fin is lacking in all specimens. The dorsal fin is composed generally of four basal fulcra (the anterior one is unpaired and the other are paired on KS36-2), approximately eight fringing fulcra and 12 rays (KS36-3, Fig. 18C). The fringing fulcra are slightly curved and very elongated, the first one being equal to half the length of the first ray. The first third of the length of the rays is not segmented. A first longitudinal division of the ray occurs at mid-length, and a second division occurs approximately at the third quarter of the length of the rays. Although the very tips of the rays are usually not preserved, the outline of the fin observed in KS36-3 seems to indicate that the distal margin of the fin was straight.

As for the other fins, the caudal fin is poorly preserved (Fig. 19). The dorsal lobe is preceded by an indeterminate number of fulcra, whose arrangement cannot be exactly described. The ventral lobe is preceded by at least two basal fulcra and 12 small and thin fringing fulcra. There are probably 25 rays, 12 in the ventral lobe separated by a deep fork in the squamation from the 13 in the dorsal lobe. Each ray divides three times. The ventral lobe of the caudal fin equals approximately 60% of the head length and we can infer that the dorsal lobe, poorly preserved on the available material, was similar in size (the tail is usually externally homocercal in ginglymodians).

Squamation.– Based on the general outline, we can estimate the number of scales along the lateral line as approximately 53, 12 scales along a row from the anterior extremity of the dorsal fin to the lateral line and 25 scales in the mid-line between the head and the dorsal fin. The shape of the scales varies depending on position on the body. The anterior margin of individual scales bears a peg articulation as in most ginglymodians (see Cavin et al. [2009] and López-Arbarello [2012] for a discussion of this character). The lateral line scales are marked with a small pore on their surface. The posterior extremity of the scales forms a blunt spine, sometimes more acute, especially in the posterior part of the trunk. In KS36-2, the median dorsal scales are longer than broad, rhomboidal in shape and have a slightly concave surface. There are very elongate spines in KS36-3.

Isanichthys palustris Cavin and Suteethorn, 2006
Emended diagnosis. *Isanichthys* with the body elongated and slender, with the total length 5.5 times the estimated maximum depth, and 4.5 times the head length (including the opercular series); 8-9 suborbitals arranged in a mosaic pattern; no dermal component of the sphenotic; infraorbital and suborbital bones strongly ornamented, median dorsal row of scales without posterior spine; two pairs of extrascapulars, toothed maxilla; dentary bearing approximately 12 small cylindrical teeth.

Remark.–Isanichthys palustris Cavin and Suteethorn, 2006 was identified on the basis of a single specimen from the Phu Nam Jun locality, Thailand. Although from the same formation, i.e. the Phu Kradung Formation, the Phu Nam Jun locality is stratigraphically higher in the formation, close to its top, and consequently the fish assemblage of this locality is likely younger than the assemblage from the Phu Noi locality.

Isanichthys latifrons (Woodward, 1893)
Emended diagnosis. -Isanichthys with most of the dermal ossifications of the skull ornamented with tubercles of ganoin; skull root proportionally short, being approximately 1.5 times longer than wide; parietals asymmetrical; preorbital region reduced; circa 12 suborbitals arranged in a mosaic pattern; semi-tritorial dentition; two pairs of extrascapulars; toothed maxilla.

Remark.–Isanichthys latifrons (Woodward, 1893) was originally described as *Lepidotes latifrons* by Woodward (1893) on the basis of material from the Oxford Clay of Northamptonshire, UK. Woodward compared the skull of this species to the Early Jurassic *Dapedius* (=*Dapedium*), to which it was thought to be closely related. Later, Jain (1983) discussed some characters of this species.

Isanichthys latifrons possesses characters of the genus *Isanichthys* such as the strongly ornamented bones of the skull roof, the frontal only slightly narrower anteriorly than posteriorly, the frontal less than 2.5 times longer than the parietal, two supraorbitals, the cheek region completely covered by bones, the preopercle slightly curved, the maxilla forming a thin blade with a posterior rounded plate-like part, a posttemporal fossa and an oral sensory canal, ratio of skull length to orbit length greater than 6, and the quadrate situated below the orbit. Moreover, based on the proportions of the skull and the reconstruction figured by Jain (1983), the anterior infraorbital would have been deep, and the anterior supraorbital would have closed the orbit anteriorly and should have contacted two infraorbitals, three other characters diagnostic of *Isanichthys*. In contrast to the other *Isanichthys* species, *I. latifrons* bears small tubercles of ganoin of its dermal skull bones, and other specific characters mentioned in the diagnosis above.

Isanichthys luchowensis (Wang, 1974)
Fig. 20
Emended diagnosis. *Isanichthys* with preorbital region reduced; no tritorial dentition; few infraorbitals (7) and few suborbitals (6) arranged in one row; dentary and premaxilla bearing strong teeth with vertical shaft and conical cap; no conspicuous dorsal median ridge scale.

of new ginglymodians by Schröder et al (2012) from the Late Jurassic of Europe. On the basis of this study, we included in the analysis a new taxon from the Solnhofen locality, *Macrosemimimus fegerti*, we altered the coding of some characters of *Macrosemimimus lennieri* (previously referred to *'Lepidotes' lennieri*, with *'L.' toombsi* as a junior synonym), and we added a new state for a character discussed in Schröder et al. (2012) concerning the arrangement of suborbital ossifications: 'two suborbitals, the ventral one much larger than the dorsal one' (char. 29). We also completed the data matrix from Cavin et al. (2010) for *Isanichthys latifrons* with information from Woodward (1893). Several states of characters for this species are based on the specimen NHMUK P.6841. It consists of a completely disarticulated skull and postcranial elements. The dermal ossifications of the skull are well preserved and fit to each other, which permitted its reconstruction in 3D. The coding of some of the characters is based on this reconstruction. We altered the names of some of the terminal taxa used in the Cavin et al.'s analysis following the recent phylogenetic analysis by López-Arbarello (2012). Finally, we added to the previous analysis *Lepidotes luchowensis*, from the Early or Middle Jurassic of Sichuan, on the basis of direct examination of the single known specimen. We are aware that other Chinese species of ginglymodians represent interesting candidates for this analysis, but a review of all this material is beyond the scope of this paper. Appendix 1 shows the list of characters and the data matrix.

The parsimony analysis was run in PAUP* 4.0b10 (Swofford 2001). A heuristic search (using random addition sequence, 2,000 replications, 10 trees held at each iteration, and tree bisection and reconnection branch swapping) was carried out to try to avoid the 'islands of trees' problem (Maddison 1991). Figure 21 shows the strict consensus tree of the 24 most parsimonious trees produced by PAUP (83 characters informative; consistency index 0.38; retention index 0.65). The main pattern of the consensus tree is similar to that obtained by Cavin et al. (in press), except for the position of the genus *Sangiorgioichthys*, which is located in a slightly more derived position than in the former cladogram, and some other minor differences, such as the position of *Lepidotes gloriae*, which was resolved in a broad polytomy gathering several taxa and the Lepisosteiformes, while it is here resolved as the sister-group of this large clade. Although based on different sets of characters, López-Arbarello's phylogenetic analysis (2012) and the present one show similar relationships for the genus *Isanichthys*, which is resolved together with the genera *Scheestia* and *Lepidotes* as stem Lepisosteiformes. The genus *Lepidotes* includes in our cladogram *L. elvensis* (regarded here as a synonym of *L. gigas*) and *L. semiserratus*, as in López-Arbarello's analysis (2012), but also *L. piauhyensis*, a taxon not included in the latter study. Other parts of the cladograms differ significantly between both studies. In particular our analysis did not resolve the Semionotiformes and the Callipurbeckiidae as clades. However, it should be mentioned that most branches of this part of our phylogenetic analysis are weakly supported, as also in López-Arbarello's analysis (2012).

The aim of this paper, however, is not to discuss the hypothesis of relationships within the set of ginglymodian taxa, but to focus on the inter- and intrarelationships of the genus *Isanichthys*. *I. palustris* and *I. latifrons* are grouped together, as already noticed by Cavin (2010) and Cavin et al. (in press) (although they did not remove *L. latifrons* from the genus *'Lepidotes'*). To both species are added here two other species, *I. luchowensis* and *I. lertboosi*, but the relationships between the four taxa are not resolved. Because few characters can be coded for *I. luchowensis* in this phylogenetic analysis (40%), we conducted another analysis without this species. The strict consensus tree (Fig. 21, right) is similar to the tree with all taxa, except that *Isanichthys* is resolved as the sister group of *Scheenstia mantelli* – Lepisosteoidei sensu López-Arbarello (2012) (instead in a trichotomy with *Lepidotes*), and the relationships between the three species of *Isanichthys* are now resolved. *Isanichthys lertboosi* is the sister-group of the pair *I. palustris* – *I. latifrons*. In this new analysis, *Isanichthys* is characterized by six homoplasies, with two observed in all three species: the frontal as broad, or almost as broad, anteriorly as posteriorly (char. 19) and the ratio of skull length to orbit diameter greater than 6 (char. 36). A third character, presence of a moderately tritorial dentition between palate and coronoids (char. 47) is present in *I. lertboosi* and *I. latifrons*, but unknown in *I. palustris*. Other characters are known in one of the three species, or show a reversed state in one of the species. Based on our analysis, *I. palustris* and *I. latifrons* share a mosaic pattern of suborbitals (char. 29) and the absence of scale with posterior spine along the dorsal midline (char. 85).

Conclusions

The ginglymodian specimens from Phu Noi can be referred to a distinctive new species with confidence. However, the absence of completely preserved specimens and the polymorphic condition observed for several of its characters make its assignment to the genus *Isanichthys* still uncertain. In particular, new material will be necessary to assess if there is more than a single species in this assemblage, and if all are referable to the genus *Isanichthys*. The cladistic analysis provides interesting results with the grouping of three species, Middle Jurassic to basal Cretaceous in age, discovered in freshwater deposits of South-East Asia and South China. The inclusion in this clade of a species, *I. latifrons* from a Middle Jurassic marine assemblage from Europe, is more unexpected. The results obtained here should be interpreted with caution because this clade is weakly supported and might easily be challenged by new discoveries. However, if true, affinities between species from Eastern Asia with one from Europe are not so surprising if we consider the direct connection between both areas along the northern margin of the Tethys during most of the Mesozoic. As early as the Triassic, marine actinopterygian species belonging to same genera are known in Europe and China (for instance Tintori et al. 2008; López-Arbarello et al. 2011; Lombardo et al. 2011). *Isanichthys lertboosi* is the third ginglymodian species from the Phu Kradung Formation to be properly characterised. Other material from this formation, still under study, indicates that at least two other ginglymodian taxa are present. Remains of other actinopterygian clades are extremely rare in the Phu Kradung Formation, and the single known recognized taxon is an isolated spine referred to an indeterminate actinopterygian from the Chong Chat locality and fragments of articulated fishes from Khok Sanam referred to cf. *Ptycholepis* (Cavin et al. 2009). The abundance of ginglymodian remains in the Phu Kradung Formation, as well as in the overlying formations of the Khorat Group deposited mostly in freshwater environments, is certainly caused partly by taphonomic biases. Ganoid scales and thick dermal ossifications of the skull are more prone to fossilize than more fragile bones of most other ray-finned fishes, in particular teleosts.

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Figure captions

Fig. 1. **A**. Silhouette of Thailand with a schematic map of the Isan region (frame) showing the outcrops of the Phu Kradung Formation in black and the localisation of the site of Phu Noi. **B**. landscape showing the localization of the Phu Noi excavation site (circle) in the hilly lanscape surrounded by rice pads. **C** and **D.** Views of the excavations in Phu Noi in February 2010.

Fig. 2. Holotype of *Isanichthys lertboosi* sp. nov. (KS36-2) in left lateral view. **A.** photograph. **B.** semi-interpretative line drawing.

Fig. 3. Photographs and semi-interpretative line drawings of the skull of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2 (holotype), Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left (**A**) and right (**B**) lateral views.

Fig. 4. Photographs and semi-interpretative line drawings of the skull of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-3, Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left (**A**) and right (**B**) lateral views.

Fig. 5. Photographs and semi-interpretative line drawings of the skull of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-281, Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left (**A**) and right (**B**) lateral views.

Fig. 6. Photographs and semi-interpretative line drawings of the skull roof of the ginglymodian fish *Isanichthys lertboosi* sp. nov. in dorsal views. Phu Kradung Formation, Late Jurassic, Kalasin Province, Northeastern Thailand. **A.** KS34-380. **B.** KS36-3.

Fig. 7. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-380 in ventral view. **A**. Photograph. **B**. semi-interpretative line drawing

Fig. 8. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-380 in left ventrolateral view (the dorsal side faces down). **A**. Photograph. **B**. semi-interpretative line drawing.

Fig. 9. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-380 in left posteroventral view. **A**. Photograph. **B**. semi-interpretative line drawing.

Fig. 10. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-380 in posterior view. **A**. Photograph. **B**. semi-interpretative line drawing

Fig. 11. Part of suspensorium and mandible of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-281 in right lateral view. **A**. Photograph. **B**. semi-interpretative line drawing.

Fig. 12. Snout region and mandible of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-281 in left lateral view. **A**. Photograph. **B**. semi-interpretative line drawing.

Fig. 13. Snout of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS34-281 in anterior view. **A.** Photograph. **B.** semi-interpretative line drawing. **C.** photograph of the teeth on dentary.

Fig. 14. Ventral views of the snout of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS36-2 show vomerine and ectopterygoid teeth. **A, B.** Photograph. **C.** semi-interpretative line drawing.

Fig. 15. Snout region and coronoid dentition of the ginglymodian fish *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. KS36-2. Photograph (**A**) and semi-interpretative line drawing (**B**) of the snout region in ventral view. Photograph (**C**) and semi-interpretative line drawing (**D**) of the coronoid dentition in left lateral view.

Fig. 16. *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. Reconstruction of the skull with the path of sensory canals. **A.** KS36-3; **B.** KS34-281.

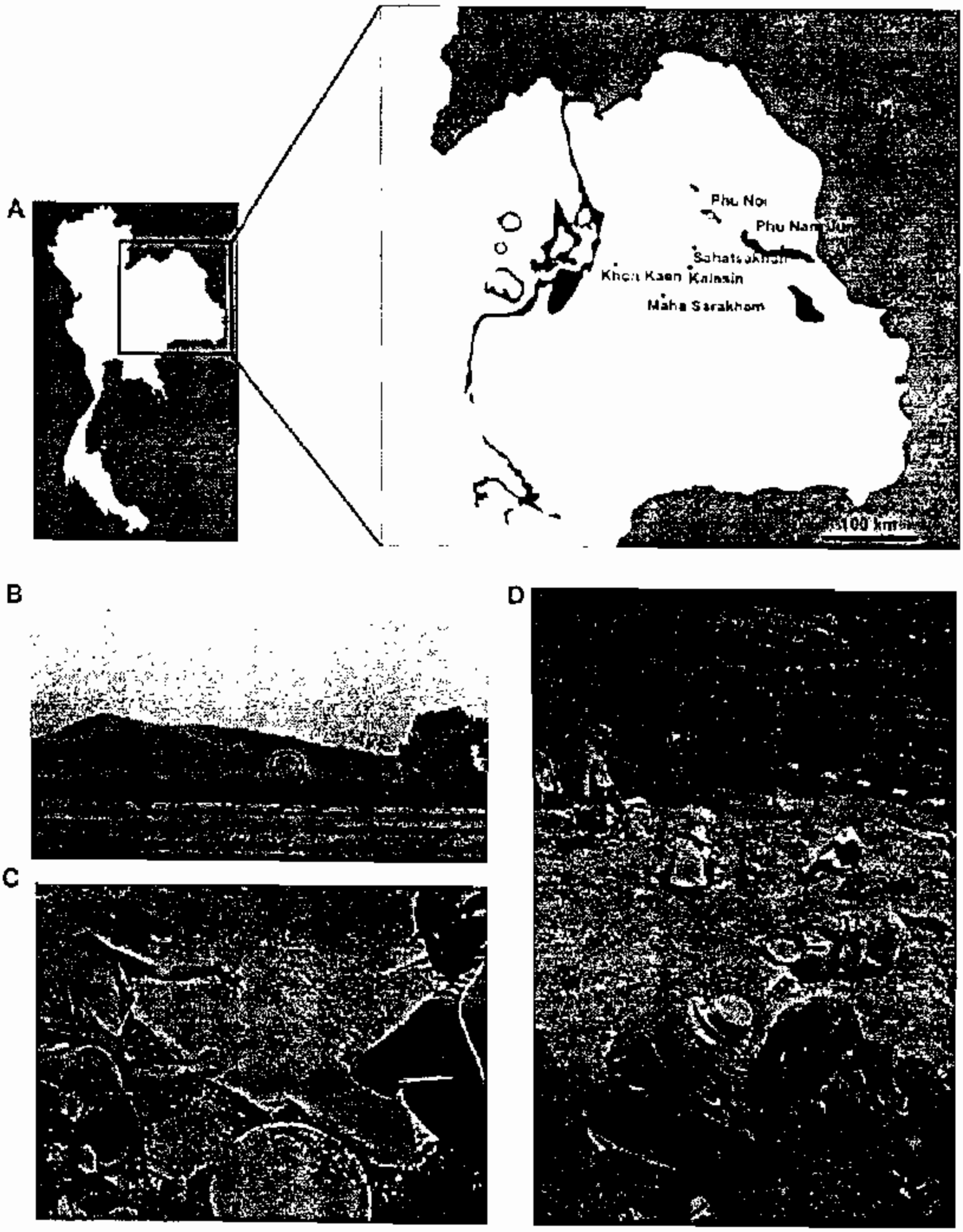
Fig. 17. *Isanichthys lertboosi* sp. nov. KS36-2 (holotype). Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. **A.** pectoral fin. **B.** pelvic fin.

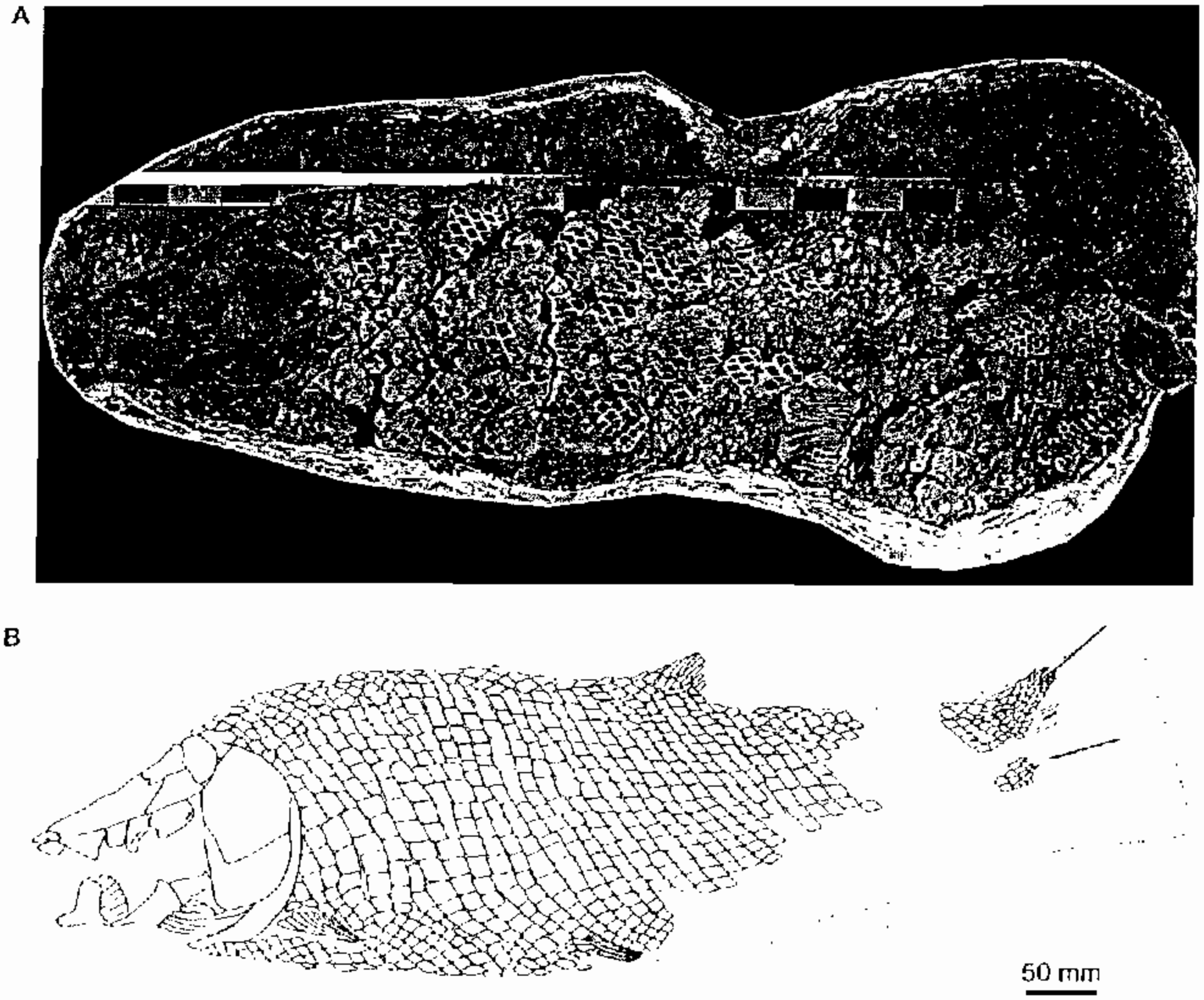
Fig. 18. *Isanichthys lertboosi* sp. nov. Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. **A.** KS36-2, dorsal fin in dorsal view. **B.** KS36-2, dorsal fin in lateral view. **C.** KS36-3, dorsal fin in lateral view (all branchings and segmentations of the rays are not drawn, although present, because they are hardly visible on the specimen).

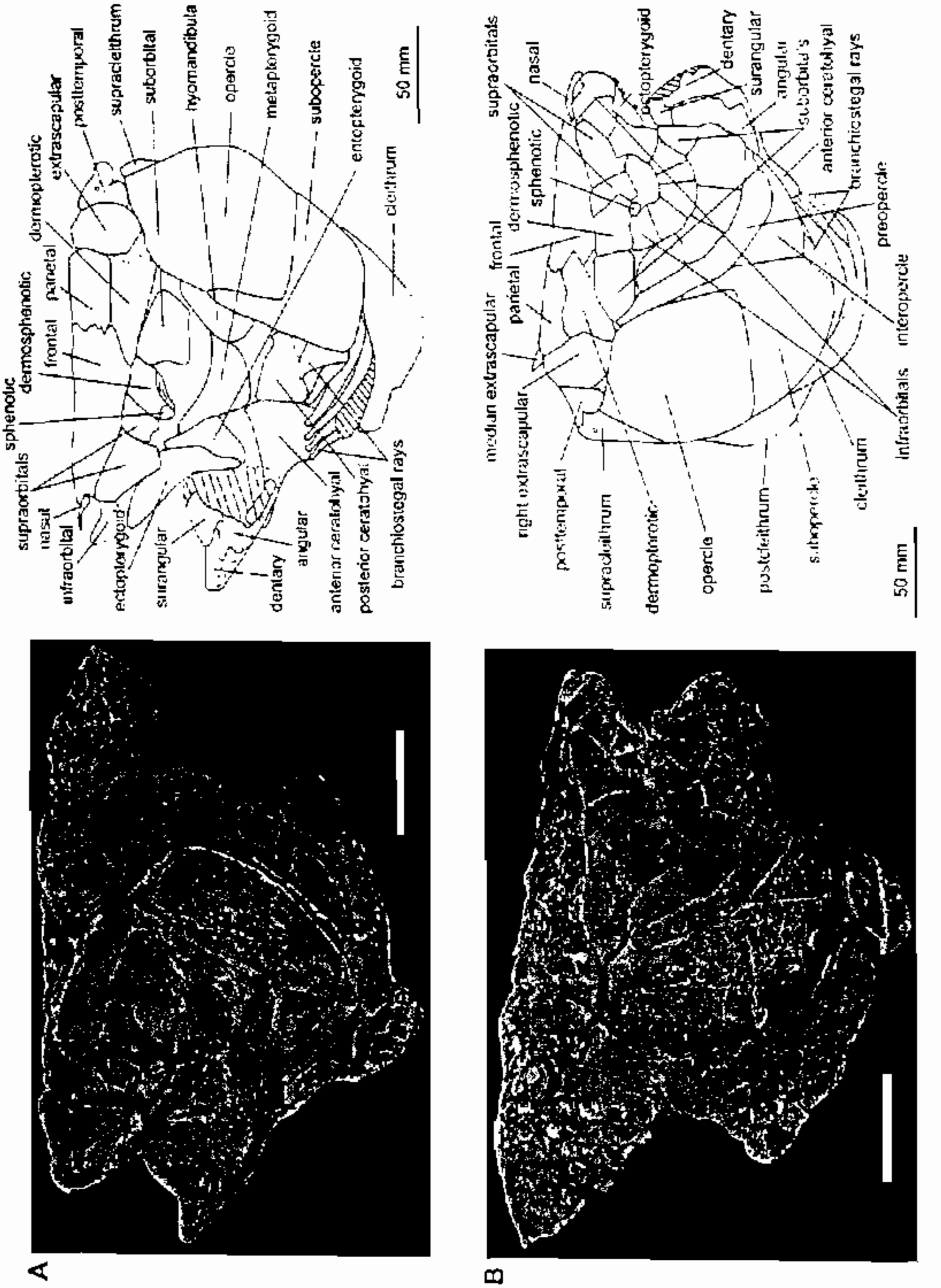
Fig. 19. *Isanichthys lertboosi* sp. nov. KS36-2 (holotype). Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. Caudal fin in right view (all branchings and segmentations of the rays are not drawn, although present, because they are hardly visible on the specimen).

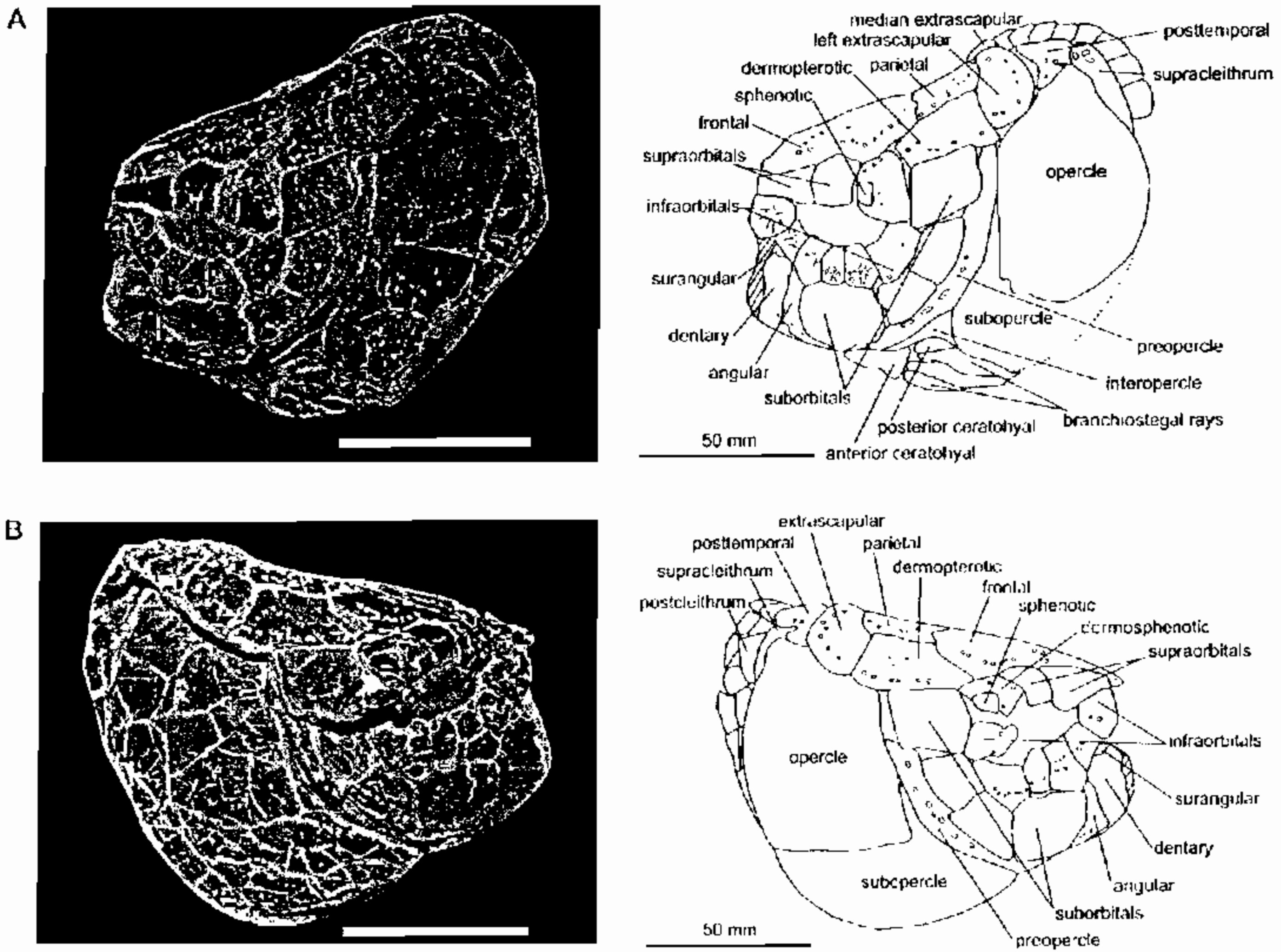
Fig. 20. Skull of *Isanichthys luchowensis* sp. nov., cv 002, Early or middle Jurassic of Sichuan, China. **A.** Photograph. **B.** semi-interpretative line drawing. Scale bar = 20 mm.

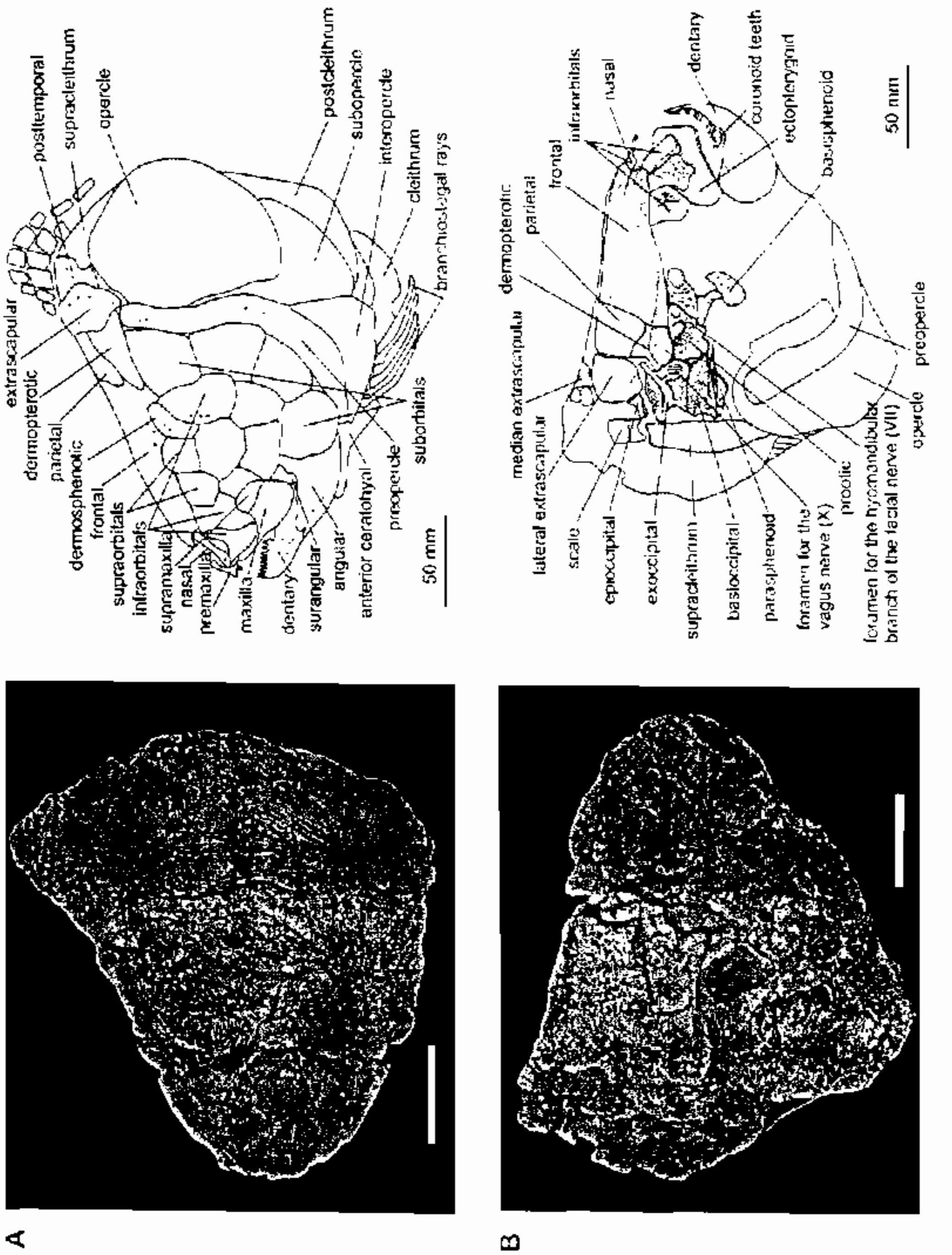
Fig. 21. Strict consensus tree of the 24 most parsimonious tree (305 steps; consistency index = 0.38; retention index = 0.65). All characters are unordered and have equal weight. In brackets are the bootstrap values of the nodes if superior to 50 (3840 replicates) and the Bremer supports if superior to 1. On the right side of the cladogram are figured the relationships between the species of *Isanichthys* if *I. luchowensis* is removed from the analysis (strict consensus of three trees, 303 steps, CI = 0.38, RI = 0.65). The rest of the cladogram is similar to the left side.

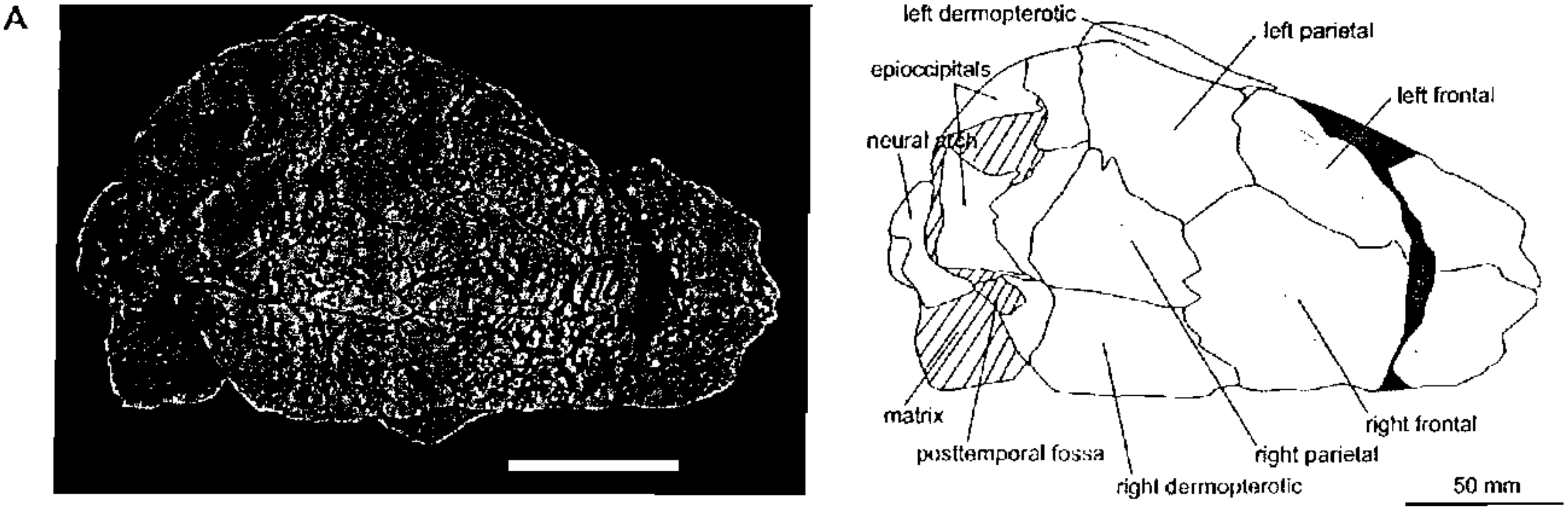

A
Phu Noi
Phu Nam
Sahatsakhan
Khon Kaen
Kalasin
Maha Sarakham
100 km
B
C
D

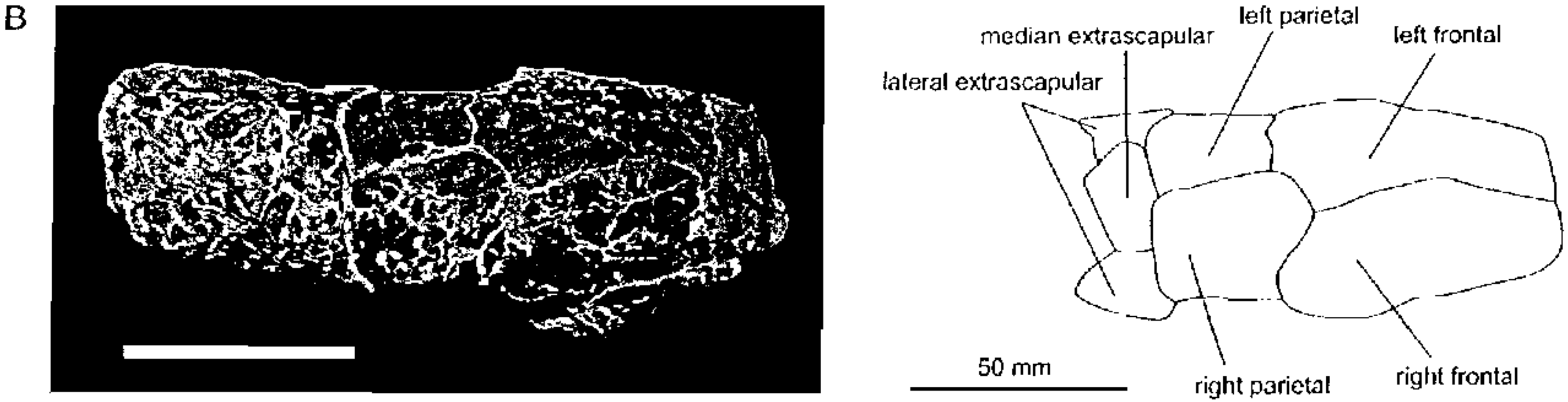

A
B
50 mm

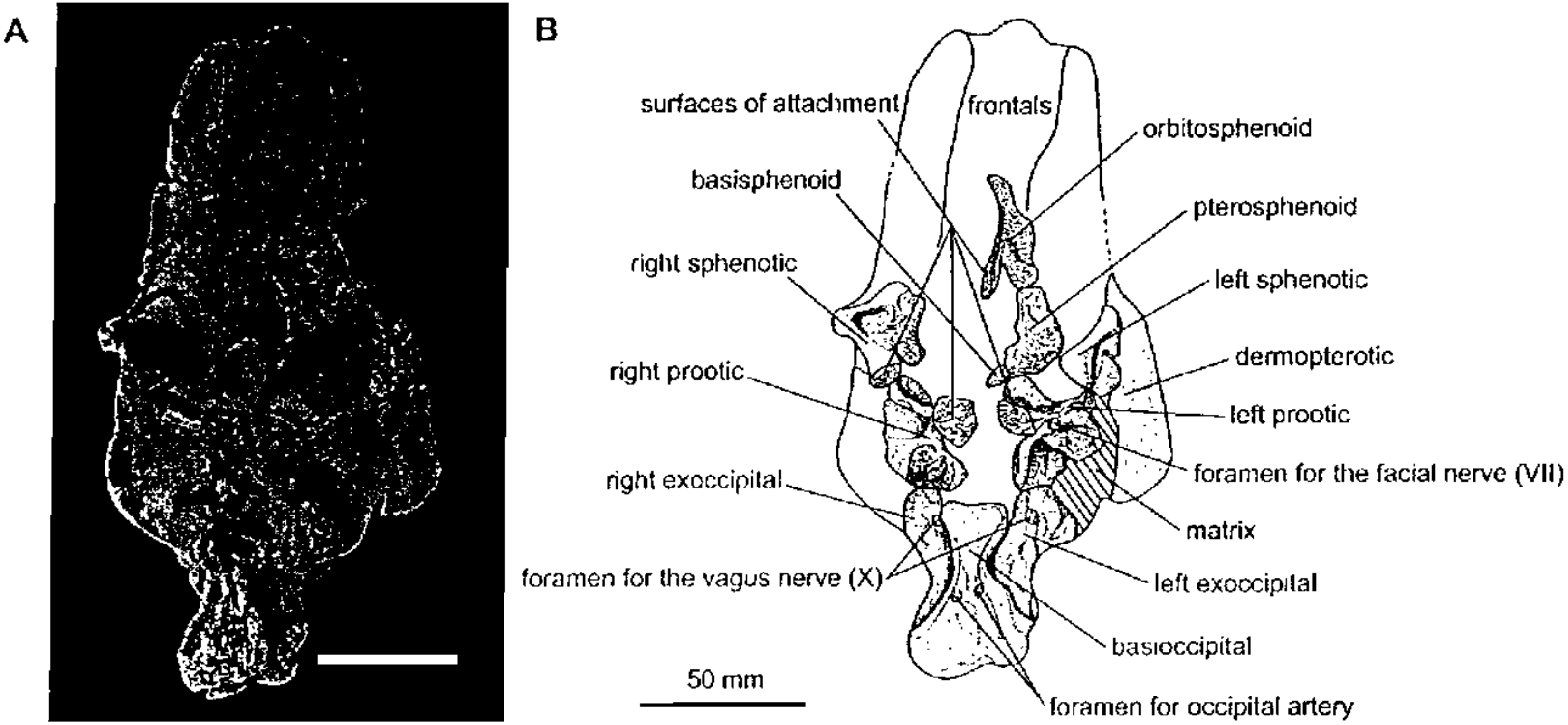

A
supraorbitals
nasal
infraorbital
sphenotic
dermosphenotic
frontal
parietal
dermopterotic
extrascapular
posttemporal
supracleithrum
suborbital
hyomandibula
opercle
metapterygoid
subopercle
entopterygoid
cleithrum
50 mm
ectopterygoid
surangular
dentary
angular
anterior ceratohyal
posterior ceratohyal
branchiostegal rays
B
median extrascapular
right extrascapular
posttemporal
supracleithrum
dermopterotic
opercle
postcleithrum
subopercle
cleithrum
50 mm
parietal
frontal
dermosphenotic
sphenotic
supraorbitals
nasal
ectopterygoid
dentary
surangular
angular
suborbital's
anterior ceratohyal
branchiostegal rays
preopercle
interopercle
infraorbitals

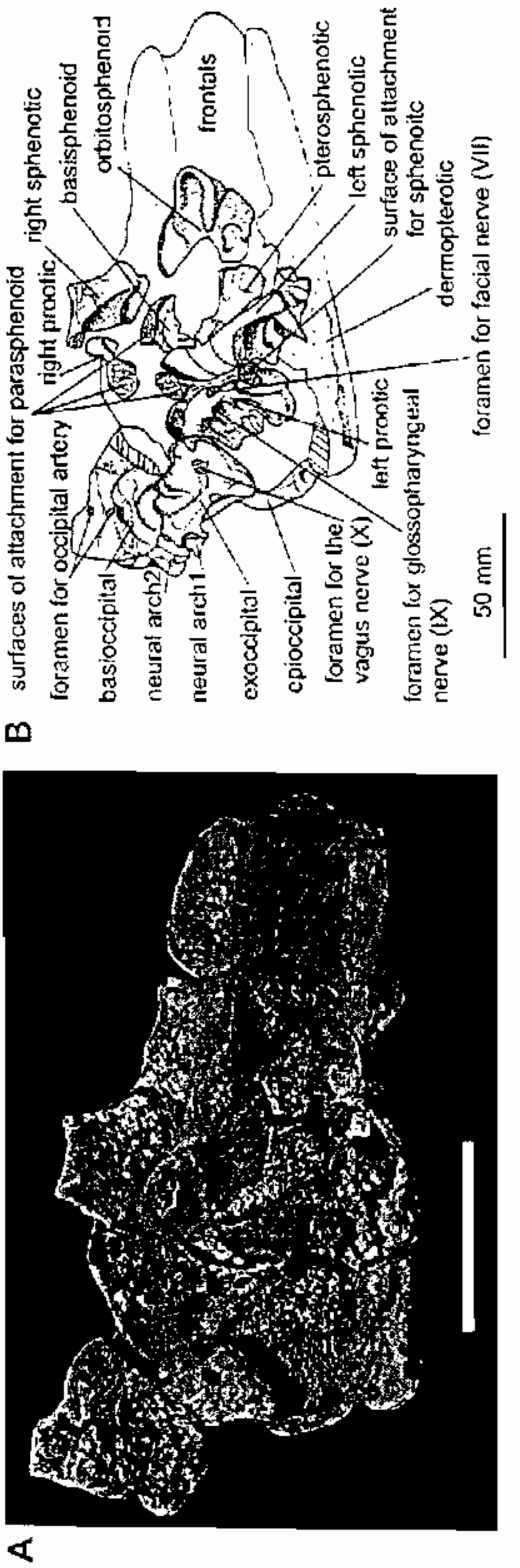

A
median extrascapular
left extrascapular
postlemporal
supracleithrum
dermopterotic
parietal
sphenotic
frontal
supraorbitals
infraorbitals
opercle
surangular
dentary
angular
suborbitals
subopercle
preopercle
interopercle
branchiostegal rays
posterior ceratohyal
anterior ceratohyal
50 mm
B
extrascapular
postlemporal
parietal
supracleithrum
dermopterotic
postcleithrum
frontal
sphenotic
dermosphenotic
supraorbitals
opercle
infraorbitals
surangular
dentary
subopercle
angular
suborbitals
preopercle
50 mm

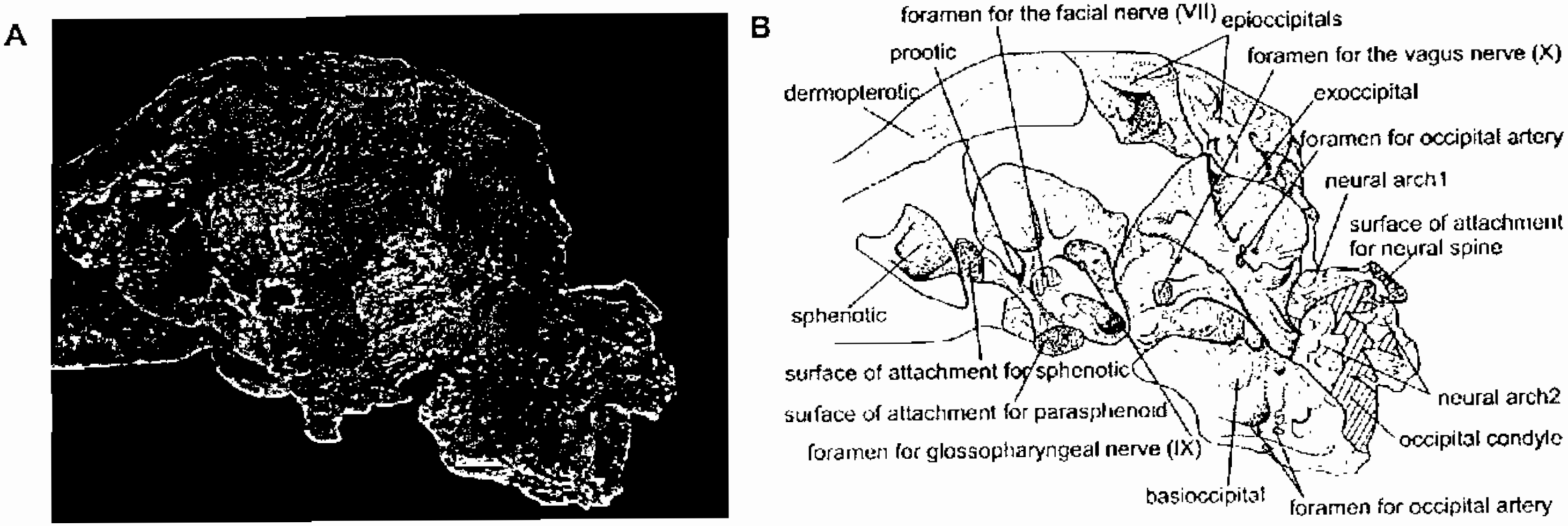

A
extrascapular
dermopterotic
parietal
dermosphenotic
frontal
supraorbitals
infraorbitals
supramaxilla
nasal
premaxilla
maxilla
dentary
surangular
angular
anterior ceratohyal
preopercle
suborbitals
branchiostegal rays
cleithrum
interopercle
subopercle
postcleithrum
opercle
supracleithrum
posttemporal
50 mm
B
median extrascapular
lateral extrascapular
scale
epioccipital
exoccipital
supracleithrum
basioccipital
parasphenoid
foramen for the vagus nerve (X)
prootic
foramen for the hyomandibular branch of the facial nerve (VII)
opercle
preopercle
dermopterotic
parietal
frontal
infraorbitals
nasal
dentary
coronoid teeth
ectopterygoid
basisphenoid
50 mm

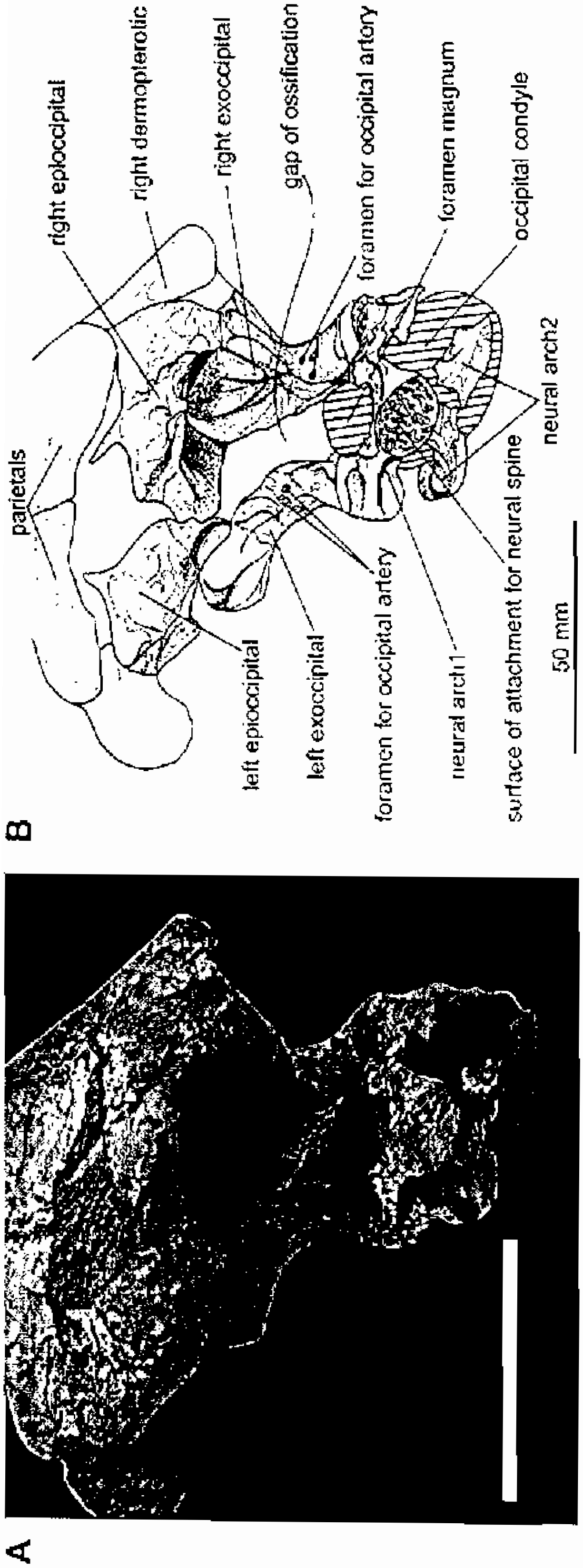

A
left dermopterotic
left parietal
epioccipitals
left frontal
neural arch
matrix
right frontal
posttemporal fossa
right parietal
right dermopterotic
50 mm

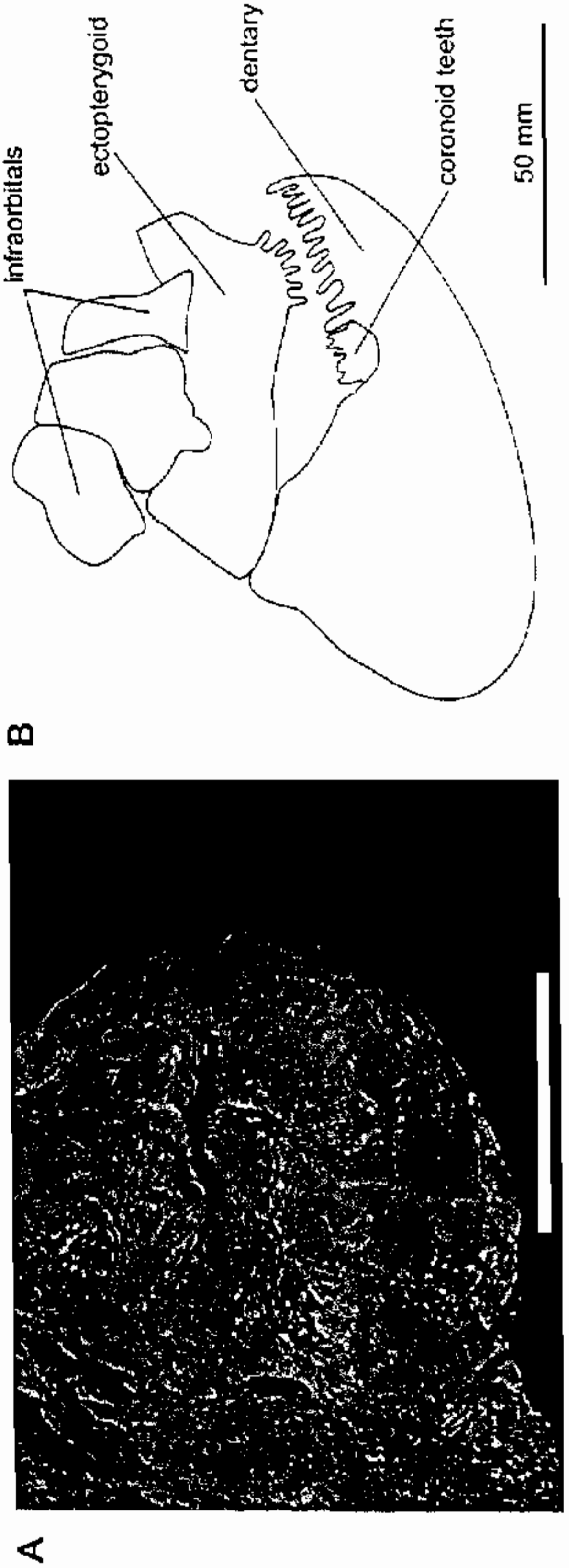

B
left parietal
median extrascapular
left frontal
lateral extrascapular
50 mm
right parietal
right frontal

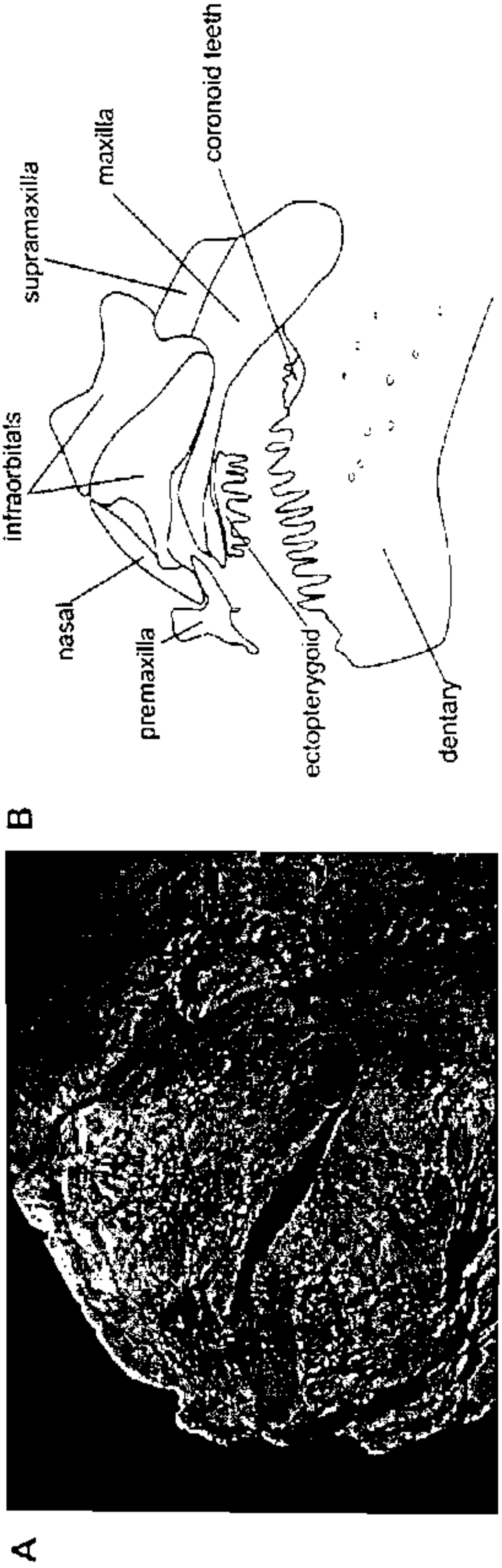

A
B
surfaces of attachment
frontals
orbitosphenoid
basisphenoid
pterosphenoid
right sphenotic
left sphenotic
right prootic
dermopterotic
left prootic
foramen for the facial nerve (VII)
right exoccipital
matrix
foramen for the vagus nerve (X)
left exoccipital
basioccipital
50 mm
foramen for occipital artery

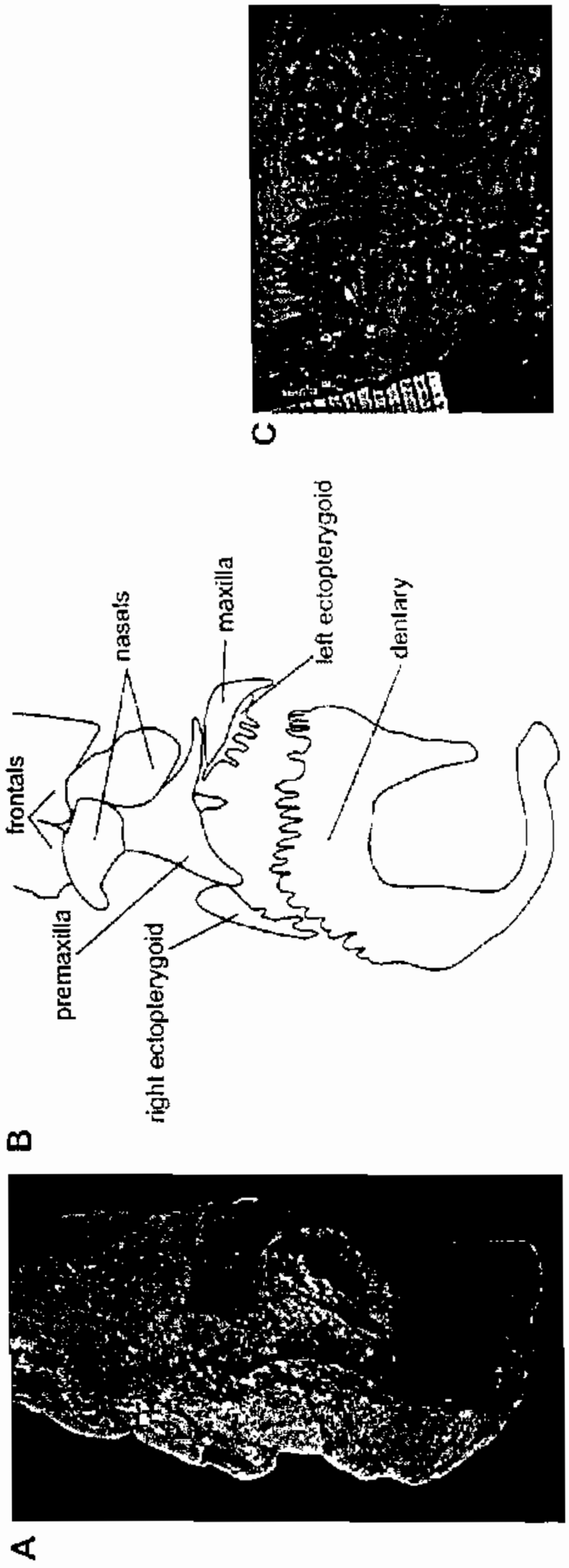

A
B
surfaces of attachment for parasphenoid
foramen for occipital artery
basioccipital
neural arch2
neural arch1
exoccipital
epioccipital
foramen for the vagus nerve (X)
foramen for glossopharyngeal nerve (IX)
50 mm
right prootic
right sphenotic
basisphenoid
orbitosphenoid
frontals
pterosphenotic
left sphenotic
surface of attachment for sphenoitc
dermopterotic
foramen for facial nerve (VII)
left prootic

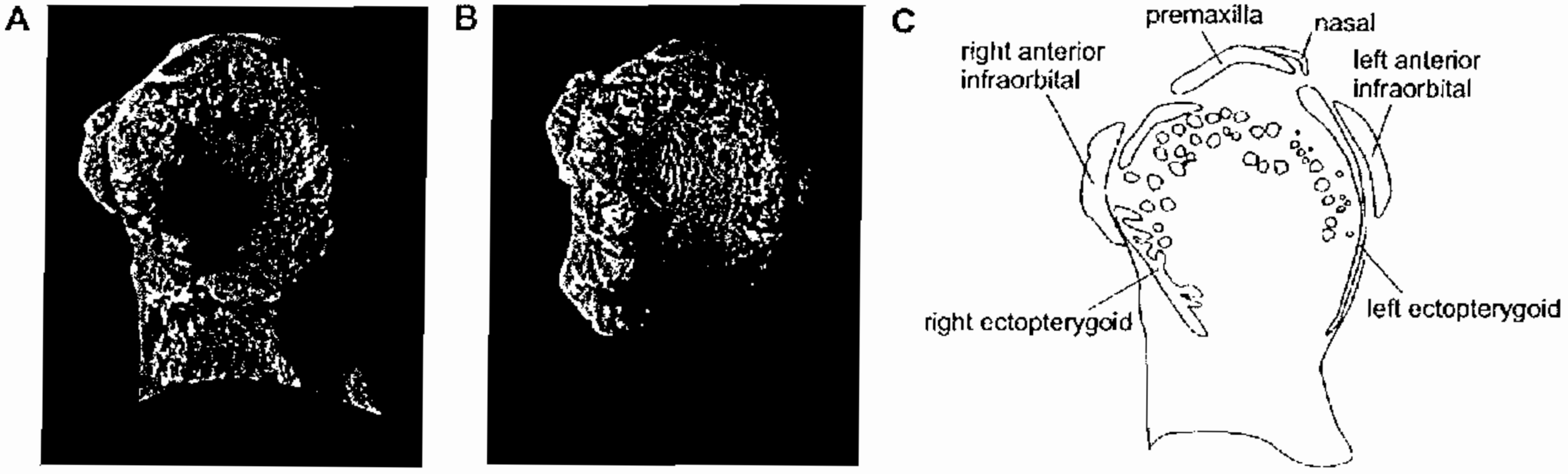

A
B
foramen for the facial nerve (VII)
epioccipitals
prootic
foramen for the vagus nerve (X)
dermopterotic
exoccipital
foramen for occipital artery
neural arch1
surface of attachment for neural spine
sphenotic
surface of attachment for sphenotic
surface of attachment for parasphenoid
foramen for glossopharyngeal nerve (IX)
neural arch2
occipital condyle
basioccipital
foramen for occipital artery

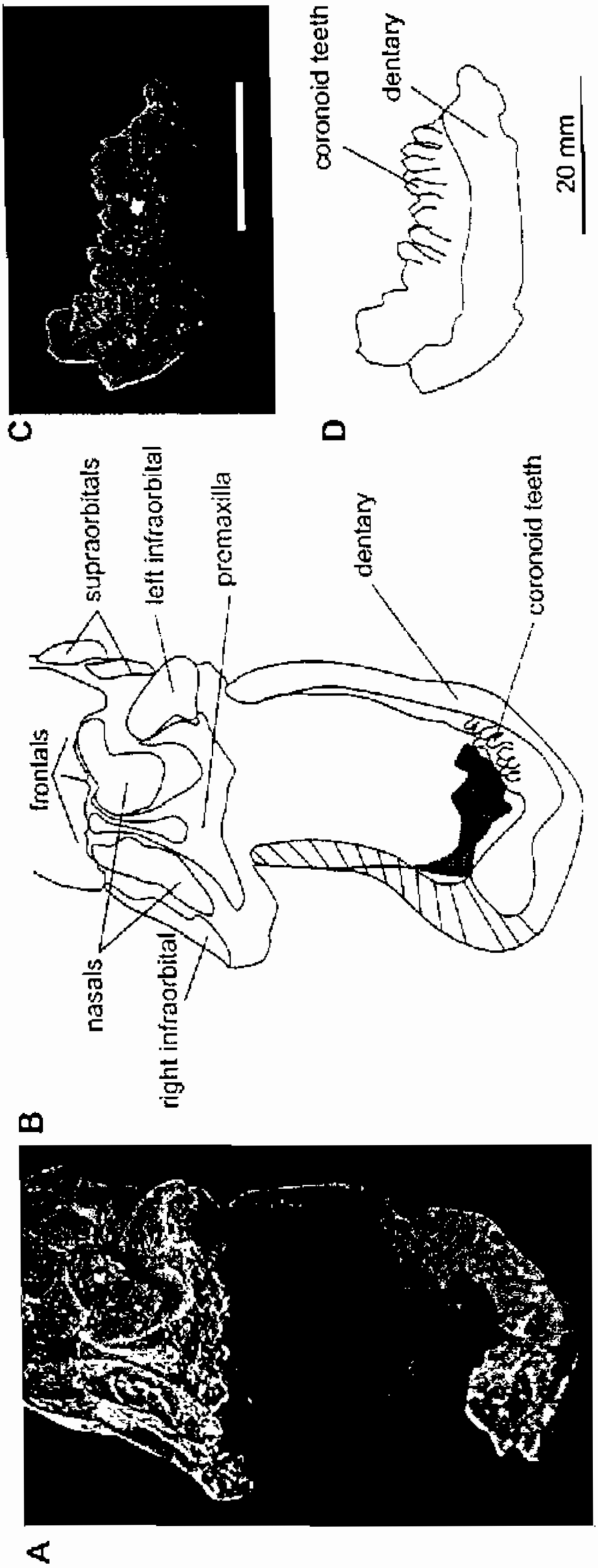

A
B
parietals
right epioccipital
right dermopterotic
right exoccipital
gap of ossification
foramen for occipital artery
foramen magnum
occipital condyle
neural arch2
left epioccipital
left exoccipital
foramen for occipital artery
neural arch1
surface of attachment for neural spine
50 mm

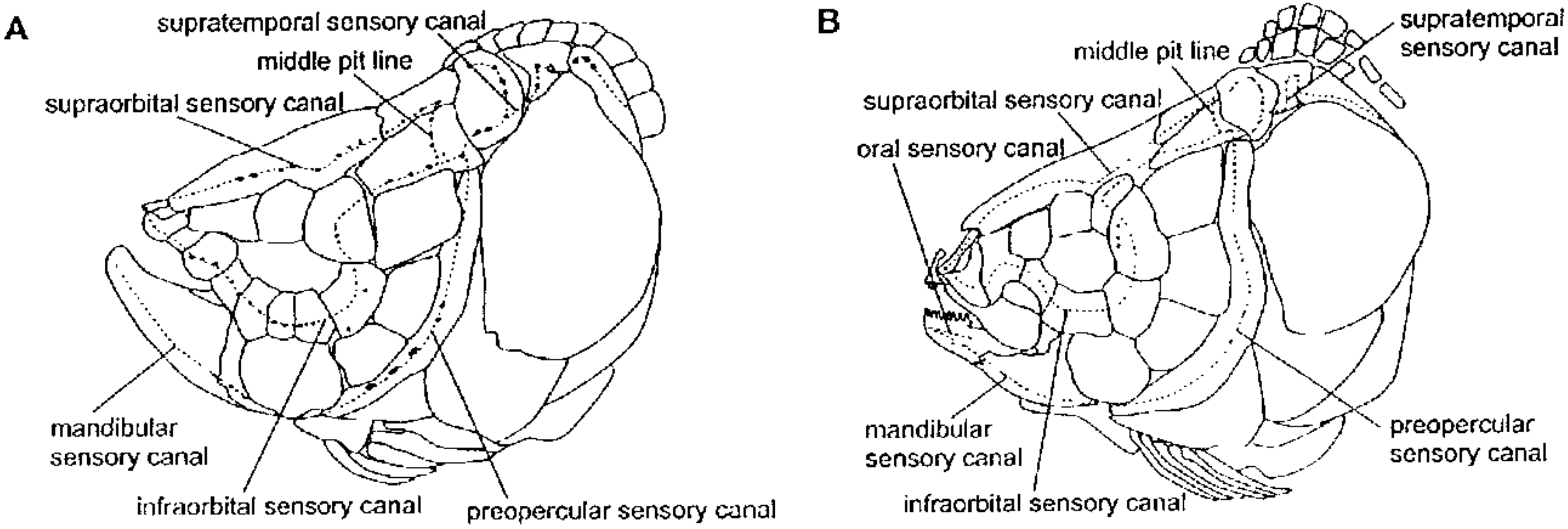

A
B
infraorbitals
ectopterygoid
dentary
coronoid teeth
50 mm

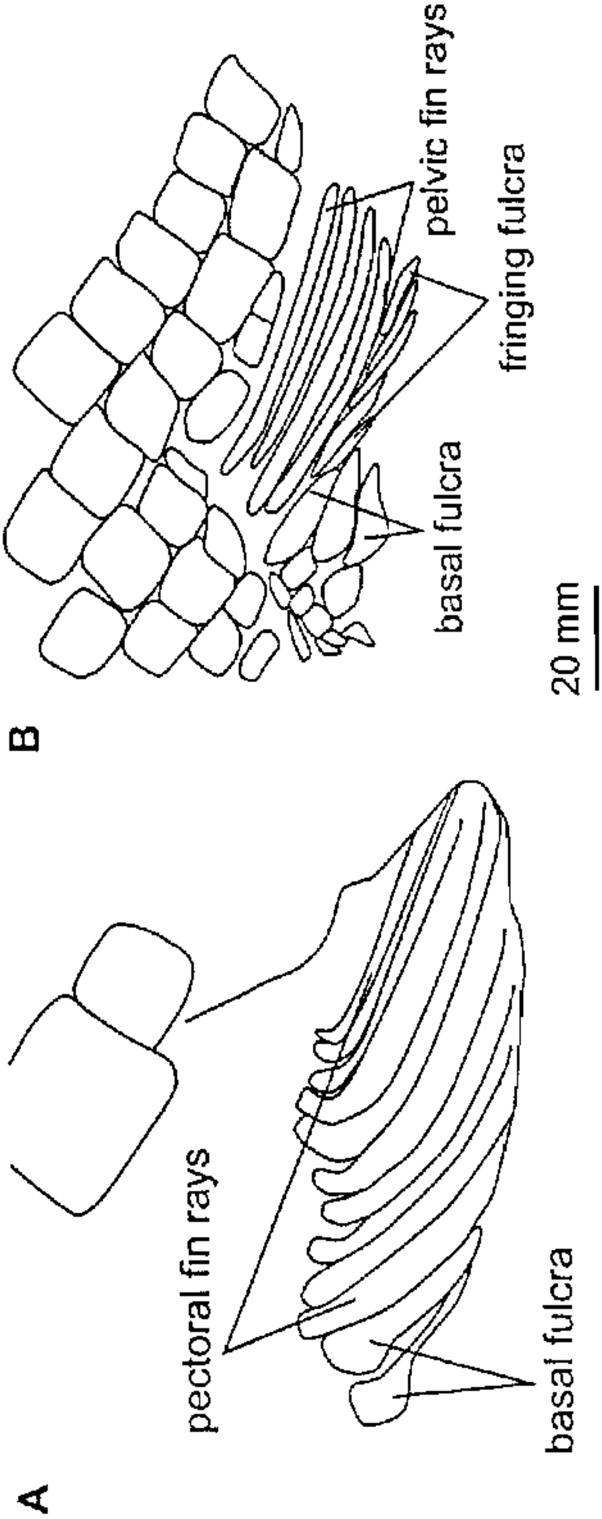

A
B
infraorbitals
supramaxilla
maxilla
coronoid teeth
nasal
premaxilla
ectopterygoid
dentary

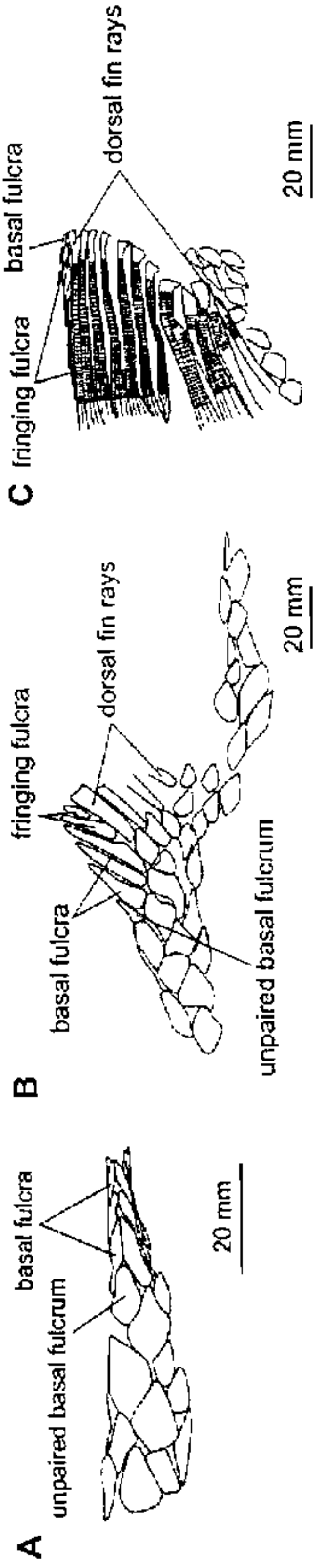

A
B
C
frontals
nasals
maxilla
left ectopterygoid
dentary
premaxilla
right ectopterygoid

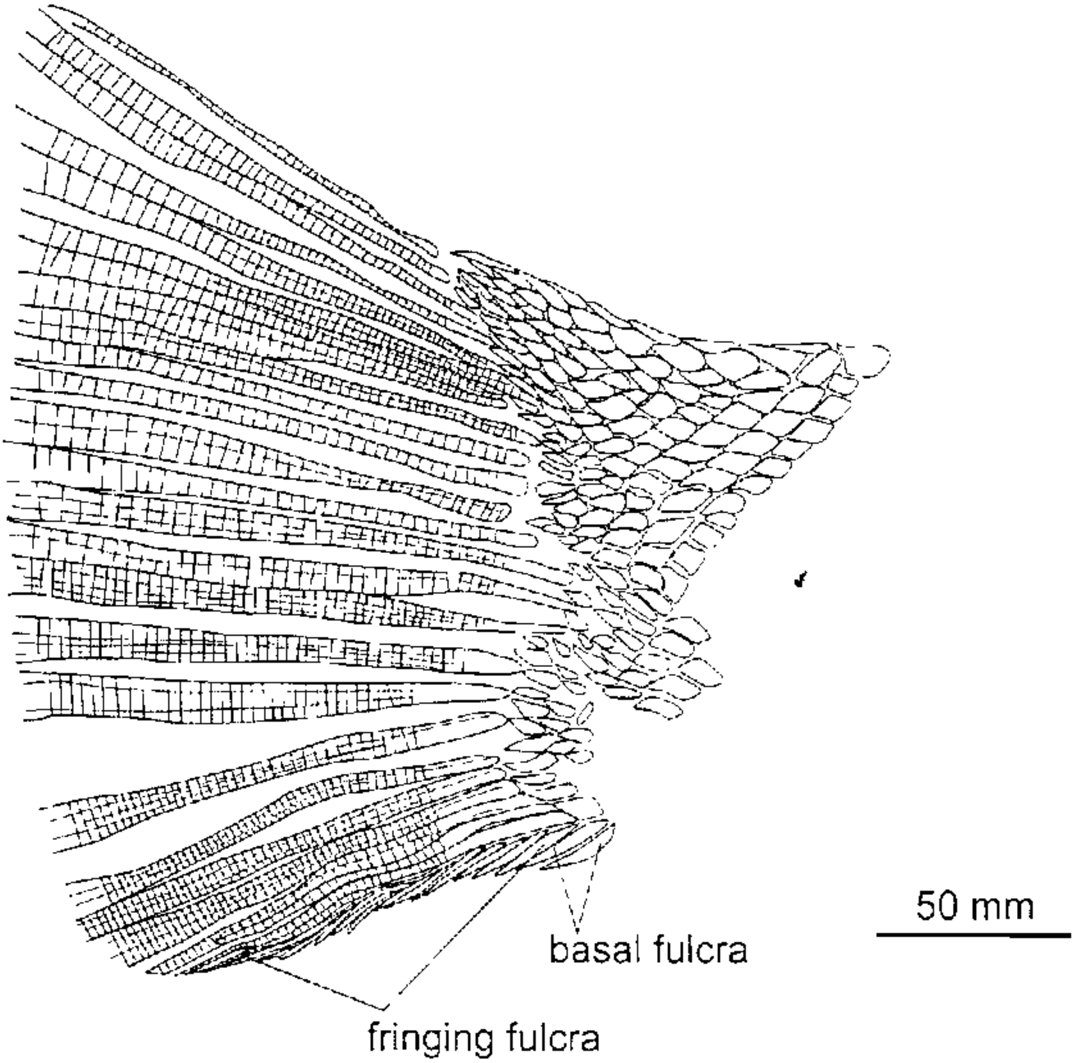

A
B
C
premaxilla
nasal
right anterior infraorbital
left anterior infraorbital
right ectopterygoid
left ectopterygoid

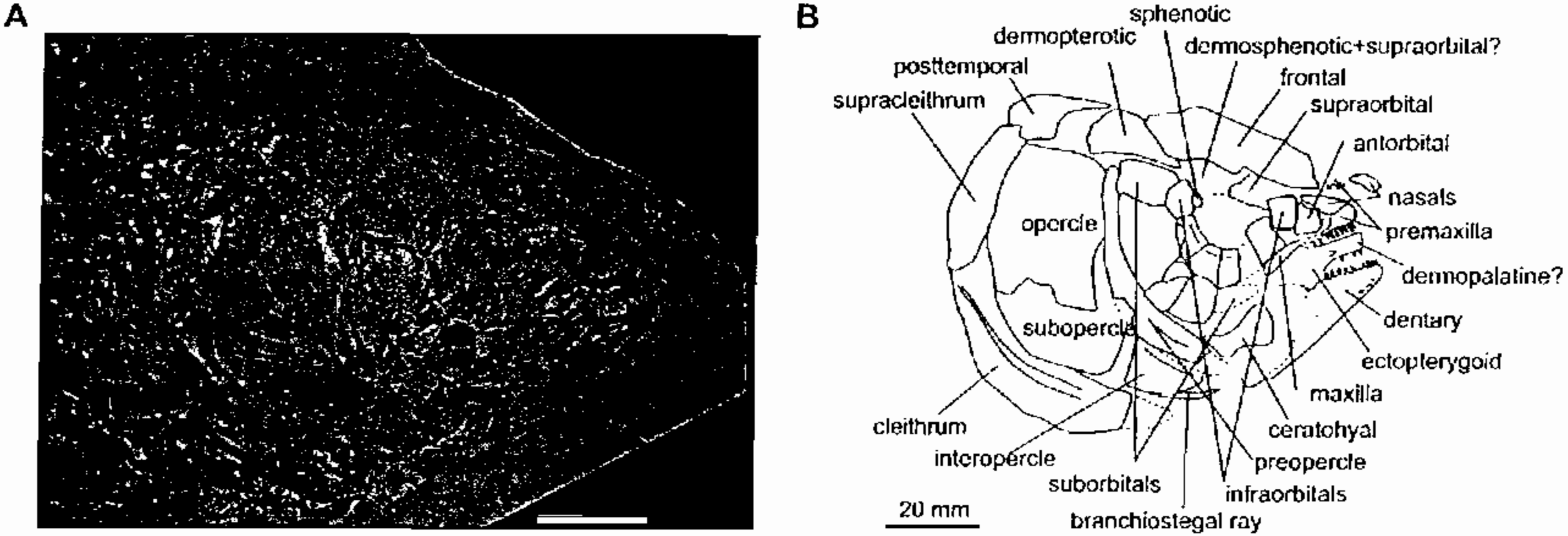

A
B
frontals
supraorbitals
left infraorbital
premaxilla
nasals
right infraorbital
dentary
coronoid teeth
C
D
coronoid teeth
dentary
20 mm

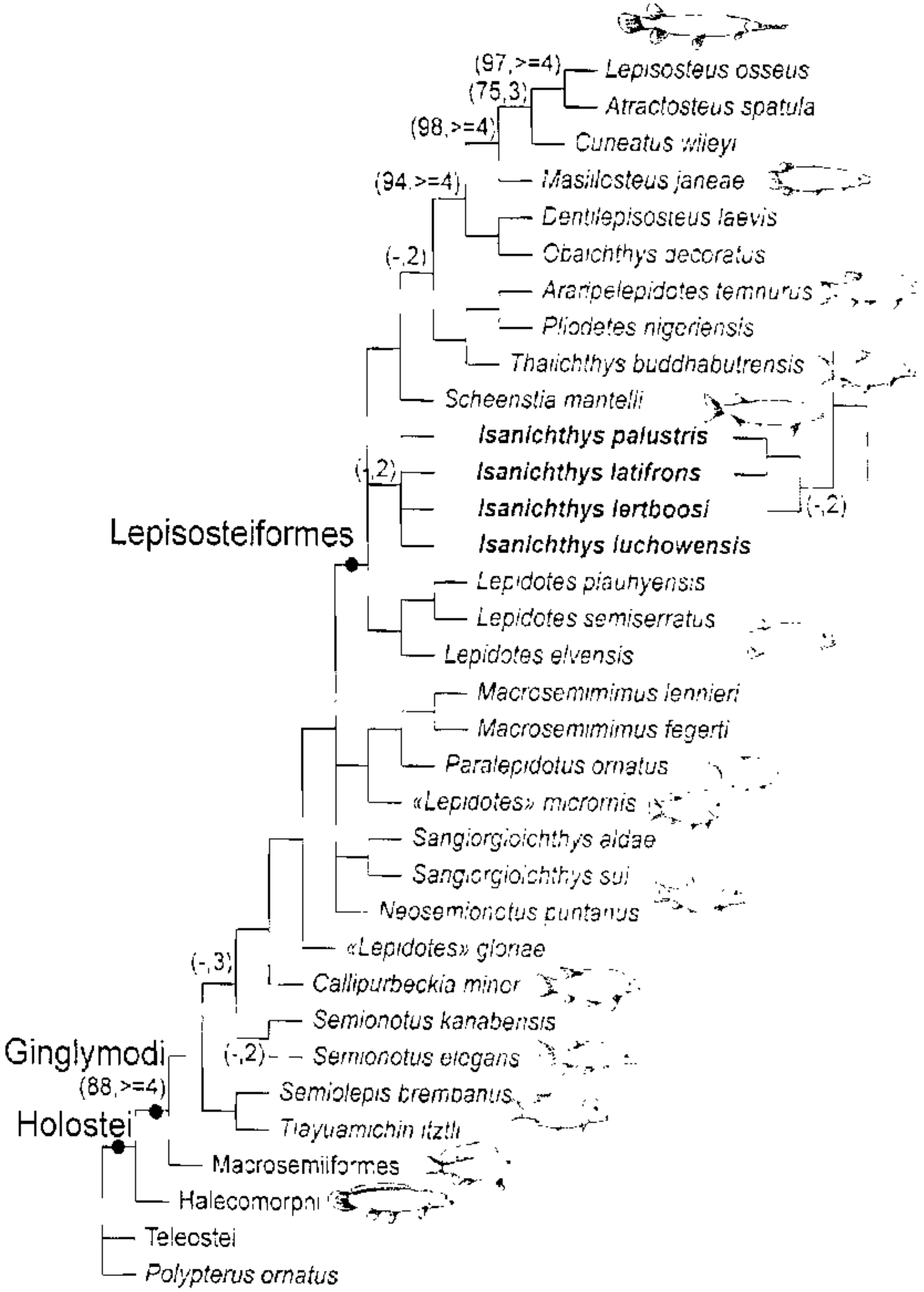

A
supratemporal sensory canal
middle pit line
supraorbital sensory canal
mandibular
sensory canal
infraorbital sensory canal
preopercular sensory canal
B
middle pit line
supratemporal
sensory canal
supraorbital sensory canal
oral sensory canal
mandibular
sensory canal
infraorbital sensory canal
preopercular
sensory canal


A
pectoral fin rays
basal fulcra
B
pelvic fin rays
fringing fulcra
basal fulcra
20 mm


A
unpaired basal fulcrum
basal fulcra
20 mm
B
basal fulcra
fringing fulcra
dorsal fin rays
unpaired basal fulcrum
20 mm
C
fringing fulcra
basal fulcra
dorsal fin rays
20 mm


basal fulcra
fringing fulcra
50 mm


A
B
sphenotic
dermopterotic
dermosphenotic+supraorbital?
posttemporal
frontal
supracleithrum
supraorbital
antorbital
nasals
opercle
premaxilla
dermopalatine?
subopercle
dentary
ectopterygoid
maxilla
cleithrum
ceratohyal
interopercle
preopercle
suborbitals
infraorbitals
20 mm
branchiostegal ray


(97,>=4)
Lepisosteus osseus
(75,3)
Atractosteus spatula
(98,>=4)
Cuneatus wileyi
(94,>=4)
Masillosteus janeae
Dentilepisosteus laevis
Obaichthys decoratus
(-,2)
Araripelepidotes temnurus
Pliodetes nigeriensis
Thaiichthys buddhabutrensis
Scheenstia mantelli
Isanichthys palustris
(-,2)
Isanichthys latifrons
Isanichthys lertboosi
(-,2)
Lepisosteiformes
Isanichthys luchowensis
Lepidotes piauhyensis
Lepidotes semiserratus
Lepidotes elvensis
Macrosemimimus lennieri
Macrosemimimus fegerti
Paralepidotus ornatus
«Lepidotes» minor
Sangiorgioichthys aldae
Sangiorgioichthys sui
Neosemionotus puntanus
«Lepidotes» gloriae
(-,3)
Callipurbeckia minor
Semionotus kanabensis
Ginglymodi
(-,2)
Semionotus elegans
(88,>=4)
Semiolepis brembanus
Holostei
Tlayuamichin itztli
Macrosemiiformes
Halecomorphi
Teleostei
Polypterus ornatus

APPENDIX IV

The article has been published in the Palaeontogy Journal.

Osteology and relationships of *Thaiichthys* nov. gen.: A ginglymodi from the Late Jurassic-Early Cretaceous of Thailand.

LIONEL CAVIN, UTHUMPORN DEESRI and VARAVUDH SUTEETHORN

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incertae sedis (Patterson 1994; Grande and Bemis 1998), to Halecostomi *incertae sedis* (Patterson 1973; Wenz 1999), regarded as the sister group of the teleosts (Véran 1988) or gathered with the Lepisosteidae and the Macrosemiidae into the Semionotiformes (Olsen and McCune 1991). Recently, Grande (2010) drew attention on the Holostei, throughout a study in which the Semionotiformes, represented by *Semionotus elegans*, and Lepisosteiformes form a monophyletic group (Grande's section B), which together is the sister group of Macrosemiiformes (Grande's section A) constituting the clade Ginglymodi. The Ginglymodi and its sister group, the Halecomorphi, constitute the Holostei.

In 2001, one of us (VS) observed fossil fish remains kept in showcases in the Wat (temple) Buddhabutr in Kalasin province, north eastern Thailand. The fragments were collected by local people. Then, because of supposedly curse associated with the fossils and responsible of the death of several of the people involved in the excavation, the specimens were re-buried in the original site or brought to the temple Buddhabutr, where they have been kept under the supervision of the head of the monastery, Phra Sakda Thammaratho. On the basis of these fragmentary remains including some skulls and pieces of squamation, and to preliminary field observations in the spot where the specimens were originally discovered, the species *Lepidotes buddhabutrensis* Cavin, Suteethorn, Khansubha, Buffetaut, Tong, 2003 was erected. Since 2002, systematic excavations have been regularly conducted at the place where villagers found the first specimens, *c.* 2.5 km south of the Wat Buddhabutr (Cavin *et al.* 2004). The locality, called Phu Nam Jun ('Hill of the Spring' in Thai language), is located in Tambon LaoYai, Amphoe Kuchinarai, Kalasin Province (Fig. 1). Up to now, more than 300 specimens have been excavated using the plaster-jacket technique. The material was mechanically prepared and stored in the Sirindhorn Museum, Tambon Sahat Sakan, Kalasin Province. The aim of this study is to describe the osteology of this fish and to explore its phylogenetic relationships.

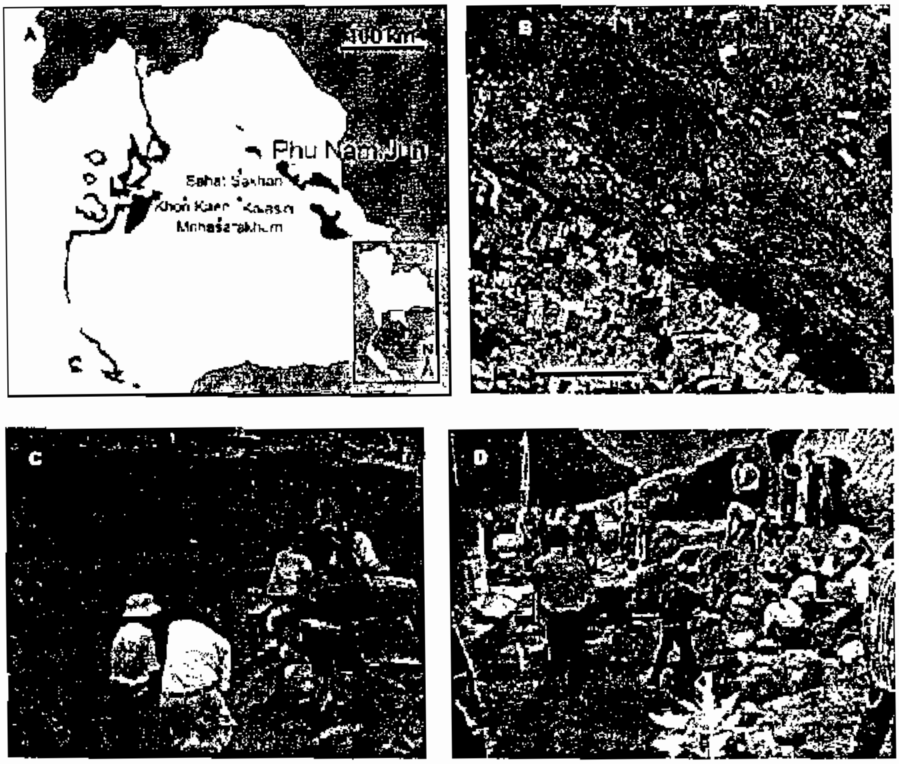

FIG. 1. Localization of the site of Phu Nam Jun. A, schematic map of the Isan region (NE Thailand) with outcrops of the Phu Kradung Formation in black. B, satellite view (Google Earth) showing the localization of the site of Phu Nam Jun (circle) in a hilly region surrounded by rice pads. C–D, views of the excavation in 2002 (C) and 2005 (D).

GEOLOGICAL AND TAPHONOMICAL SETTINGS

The fossil fish-bearing strata of Phu Nam Jun outcrops in the upper part of the Phu Kradung Formation, a Late Jurassic – Berriasian geological unit, constitute the base of the Khorat Group as currently defined (Racey 2009). The Khorat Group comprises post-Triassic Mesozoic deposits of the Khorat Plateau and adjacent areas. This sedimentary series has long been regarded as Late Jurassic in age, but palynological studies suggest now Early Cretaceous ages for most of the vertebrate-bearing formations of that Group, that is, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations (Racey *et al.* 1994, 1996). The dating of the Phu Kradung Formation is still problematic, but recent synthesis suggests a Late Jurassic age for the lowermost part of the Phu Kradung and a early Cretaceous (Berriasian) age for the upper part (Racey 2009), which contains the Phu Nam Jun fish assemblage.

The sediments of the Phu Kradung Formation are fluviatile and lacustrine in origin, and the main paleocurrents tend to be oriented towards the south-west (Racey 2009). The upper part of the formation, sometimes regarded as a distinct formation – the Wantchaphum Formation – is considered as deposited in a wetter climate than the underlying part of the formation because of the presence of silicified woods in the latter and its near-absence in the former (Philippe *et al.* 2004).

Deposit at the Phu Nam Jun consists of greenish sand at the bottom of the excavated area and maroon-coloured mudstone at the top. The mudstone contains lens of sandstone composed of 70–80 per cent clay and 20–30 per cent silt, mica as well as concretions that enclose most of the specimens. The fish accumulation is *c.* 1 m thick and dips *c.* 12 degrees towards the SE. Ninety-nine per cent of the specimens belong to *Thanichthys buddhabutrensis*. The remaining specimens consist of the 'semionotiform' *Isanichthys palustris* Cavin and Suteethorn, 2006 and of the lungfish *Ferganoceratodus martini* Cavin, Suteethorn, Buffetaut and Tong, 2007. The preservation mode of the specimens of *T. buddhabutrensis* varies, but statistical analyses showed that a single population occurs in the site and no significant differences in the mode of preservation have been observed within the thickness of the fish layer (Deesri *et al.* 2009). Cavin *et al.* (2004) suggested four lines of evidence that indicate that most of the fish carcasses are likely to have dried in open air before burial. In particular, several specimens show decayed squamations, with the rows of ganoid scales remaining articulated, but with the individual rows parting from each other (Fig. 2A). This particular manner of disarticulation was observed by Weigelt (1927) on carcasses of gars carried ashore by a storm and lying along the shoreline at Smithers Lake in Texas, USA. A similar mode of preservation was figured by Grande (2010, fig. 408A) for a specimen of the Eocene gar *Cuneatus cuneatus* from the 'Manti shales' in Utah. Other carcasses from Phu Nam Jun show the body completely bent ventrally (Fig. 2C) – in contrast to carcasses with the anterior part of the column dorsally bent in specimens from marine Lagerstätten – indicating that the fishes were in open air when they died. One specimen has been found vertical in the sediment in the lowest part of the fossiliferous layer (Fig. 2D). This location, and its posture with the posterior part of its body bent, may indicate that the fish was in a burrow when it died. A similar interpretation was postulated for the lungfish found in the same locality (Cavin *et al.* 2007). Finally, several specimens show one or two folds in their squamation at the level of the abdominal cavity (Fig. 2B) probably caused by expulsion of gases during decay.

FIG. 2. Mode of preservation of specimens of *Thanichthys buddhabutrensis* in the site of Phu Nam Jun. Arrows indicate features described in the text. A, KS12-26. B, KS12-238. C, KS12-128. D, KS12-168. Scale bars represent 10 mm.

MATERIAL AND METHOD

Because most of the specimens have their fins preserved as very delicate and fragile structures, the mechanical preparation does not aim at removing completely the matrix from the fossil. Once extracted from the field, the lower part of plaster jackets was sealed with plaster. In the laboratory, the upper parts of the jackets were sawed to free the upper side of the specimens, that is, the side that was visible in the field. The preparation was performed using air pens. Some skulls were prepared under the binocular microscope. Several thousands of hours of preparation, mainly performed by UD, were necessary for preparing 288 specimens. This sample comprises different kinds of preservation, ranging from complete individuals with all the fins preserved to isolated 3D-preserved braincases (Deesri *et al.* 2009). The list of the referred specimens is available in Appendix S1 of the Additional Supporting Information.

The nomenclature used in the description follows Grande (2010), except for the infraorbital series. The lacrimal is generally defined as the anteriormost ossification of the infraorbital series, but Grande considers that gars possess several lacrimals, the anteriormost ones being fused to a series of 'maxillaries' (the 'lacrimomaxillia'). This author also distinguishes infraorbitals posterior to the orbit ('postinfraorbitals') and those inferior to the orbit ('subinfraorbitals'). When describing ginglymodian fishes, we face situations in which these distinctions are not obvious, for instance if lacrimals are not fused with maxillae (Grande 2010, p. 49) or if the distinction between sub- and postinfraorbitals is ambiguous when a large infraorbital bone occurs in the posteroventral corner of the orbit. These uncertainties may affect the recognition of supposedly primary homologies and influence the definition of characters in the search of phylogenetic relationships. Consequently, following Wenz (1999), we prefer here to retain only the term 'infraorbitals', and we distinguish within the series only those which have no direct contact with the orbit, because this definition rests only on topographic grounds (Cavin's (2010) character 16). In doing so, we follow Grande's (2010, p. 820) recommendation in his discussion about terminology.

Because the 'semionotiformes' do not constitute a clade in our phylogenetic analysis, we use throughout the text the term 'semionotiformes' to designate an informal group gathering non-Lepisosteiformes and non-Macrosemiiformes Ginglymodi (i.e. most species of '*Lepidotes*', '*Semionotus*' and some related taxa).

Anatomical abbreviations. at, articular facet; an, anus; Ang, angular; Ao, antorbital; ar, ascending ramus of the parasphenoid; Art, articular; Bb, basibranchial (numbered); bhc, opening for the bucco-hypophysial canal; Bo, basioccipital; br, branchiostegal ray; ca, abdominal centrum; Cb, ceratobranchial (numbered); Cha, anterior ceratohyal; Cl, cleithrum; D, dentary; Dpl, dermopalatine; Dpt, dermopterotic; Dsp, dermosphenotic; Ecp, ectopterygoid; Enp, entopterygoid; Epo, epioccipital; Es, extrascapular; Exo, exoccipital; focn, foramen for spinal nerves; Fr, frontal; fri, facet for cranial rib; fub, basal fulcra; fufr, fringing fulcra; fuub, unpaired and forked basal fulcra; ha, haemal arch; Hb, hypobranchial (numbered); hb, horizontal blade; Hh, hypohyal; Hm, hyomandibula; Ic, intercalar; Io, infraorbital; iocn, infraorbital sensory canal; Iop, interopercle; Le, lateral ethmoid; mcn, mandibular sensory canal; Mx, maxilla; mr, middle radial; N, nasal; na, neural arch; naa, anterior external naris; nap, posterior external naris; ocn, occipital sensory canal; Op, opercle; osc, oral sensory canal; Pa, parietal; Par, prearticular; Pas, parasphenoid; Pb, pelvic bone; Pcl, postcleithrum; plm, middle pit line; Pmx, premaxilla; pmxnp, nasal process of the premaxilla; Pop, preopercle; popcn, preopercular sensory canal; pr, proximal radial; prc, process; Pro, prootic; ptf, post-temporal fossa; Ptg, propterygial ossification; Ptt, post-temporal; Q, quadrate; Qj, quadratojugal; R, ray; Ra, radial; Ro, rostral; Sag, supraangular; Sc, scapula; Scl, supracleithrum; Sct, scute; sn, supraneural; So, supraorbital; Sob, suborbital; socn, supraorbital sensory canal; Sop, subopercle; Spo, sphenotic; stcn, supratemporal sensory canal; stt, subtemporal fossa; Sy, symplectic; Vo, vomer; I, olfactory foramen; VII, foramen for the facial nerve; VIIpr, foramen for palatine ramus of the facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for the vagus nerve.

SYSTEMATIC PALAEONTOLOGY

Super Division HOLOSTEI *sensu* Grande, 2010
Division GINGLYMODI *sensu* Grande, 2010
Order LEPISOSTEIFORMES *sensu* Grande, 2010

Genus THAIICHTHYS gen. nov.

Type species. Thaiichthys buddhabutrensis (Cavin, Suteethorn, Khansubha, Buffetaut and Tong, 2003).

Derivation of name. From *Thailand* and Greek, *ichthys*, fish.

Diagnosis. The same as the single known species.

Thaiichthys buddhabutrensis (Cavin, Suteethorn, Khansubha, Buffetaut and Tong, 2003)

Figures 2–19

Holotype. KS12-2, an isolated skull (Fig. 3).

Locality and horizon. Phu Nam Jun, Tambon Lao Yai, Amphoe Kuchinarai, Kalasin Province, NE Thailand. Top of the Phu Kradung Formation, probably Berriasian (Early Cretaceous).

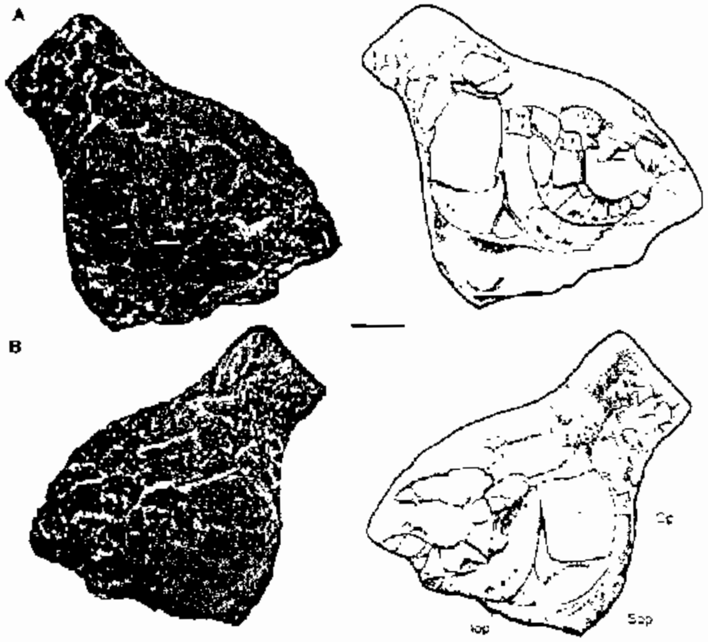

FIG. 3. *Thaiichthys buddhabutrensis*, holotype (KS12-2). Scale bar represents 20 mm.

Diagnosis (emended). Body deep, *c.* 2.6 times longer than high; preorbital region reduced; skull roof slightly concave in lateral view; frontal short, almost quadrangular in shape; more than one pair of extrascapulars; large dermosphenotic; few infraorbitals (circa 9 or 10) and few suborbitals (generally 2); cheek region completely covered by bones, with an enlarged infraorbital, which contacts the preopercle; numerous (circa 10), strong, slightly recurved teeth on the well-developed premaxilla; maxilla reduced with 4–6 small cylindrical teeth; no supramaxilla; mandible with an horizontal blade of bone at the symphysis that extends laterally; dentary bears *c.* 18 small teeth held horizontally with their acrodine apex upwards oriented; preoperculum with two limbs arranged at an approximately right angle, the horizontal branch is slightly shorter than the vertical one; 10 rays in the pectoral fin, 6 rays in the pelvic fin, 12 rays in the dorsal fin, 12 rays in the anal fin, 19 or more rays in the caudal fin; 46 scales along the lateral line.

Comparative description and interpretation

General body features and proportions. *Thaiichthys buddhabutrensis* is a moderate-sized 'semionotiform' fish (403 mm of average standard length), with a proportionally deep body (154 mm of average depth of the body; length/depth ratio = 2.6) and proportionally long fins. For further morphometric details, see Deesri *et al.* (2009).

General features and proportions of the skull. The head is 126 mm in average length (including the opercular series) and 68 mm in average depth (Deesri *et al.* 2009). The dorsal outline of the skull roof is sinusoidal in lateral view, with a concavity above the otic region and a convexity in the snout region (Figs 2–4). The antorbital region of the head is short and the gape is small. The ossifications of the head have no ganoin cover, and most of them are smooth, except faint tubercles in the posterior region of the skull roof (parietals, extrascapulars) and on the supraorbitals, as well as radiating ridges from centres of ossification of the frontals (Fig. 5).

Skull roof. The frontal is roughly rectangular in shape, without tapering anteriorly. The situation is similar in *Pliodetes nigeriensis* (Wenz 1999), *Neosemionotus puntanus* (López-Arbarello and Codorniu, 2007) and in some species of *Lepidotes*, such as *L. microrhis* (Wenz 2003), *L. pankowskii* (Forey *et al.* 2011), *L. latifrons* and *L. minor*. In most other 'semionotids' (*L. elvensis* (Wenz 1967), *L. leedsi* (NHM P10907), *L. mantelli* (NHM P 6933), *L. semiserratus* (NHM P69239), *L. tanyrhis* (Wenz 2003), *Semionotus capensis* (NHM P6861), *S. bergeri* (López-Arbarello 2008), *S. elegans* (Olsen and McCune 1991) and *Tlayuamichin itztli* (López-Arbarello and Alvarado-Ortega 2011)), the frontal regularly tapers anteriorly. In gars, the frontal tapers anteriorly, although it is still proportionally wider in basal forms, such as *Obaichthys*, *Dentilepisosteus*, *Cuneatus* and *Masillosteus* (Grande 2010, fig. 520). In some specimens (KS12-166, KS12-201), the suture between both frontals is not aligned with the suture between both parietals, but in other specimens, the sutures between both pairs are almost aligned. Similarly, the shape of the suture between these two pairs of ossifications is variable

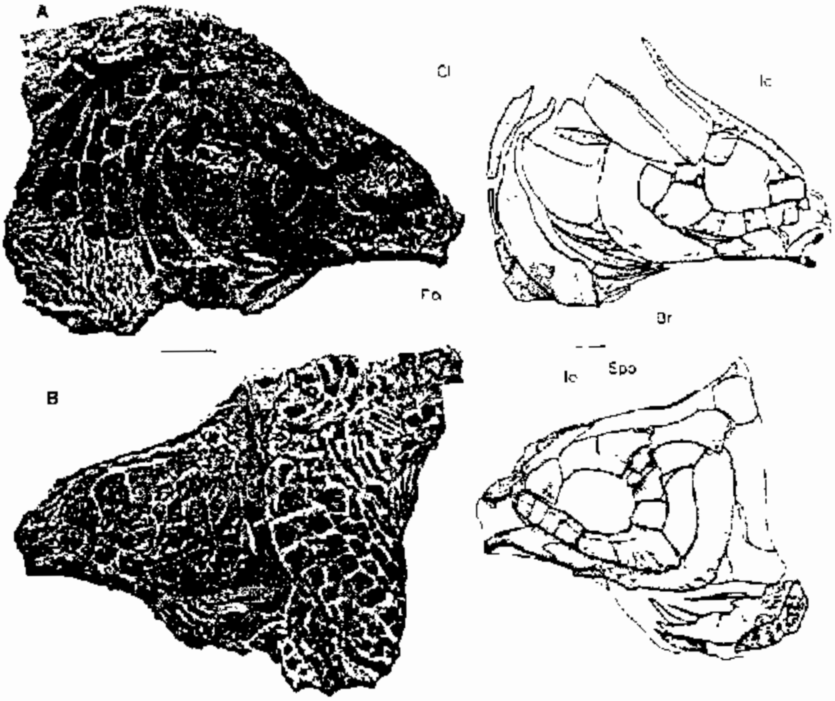

FIG. 4. *Thaiichthys buddhabutrensis*, skull of KS12-168. Scale bars represent 20 mm.

among the population, with a marked zigzag line in some specimens (Figs 5B and 6) or an irregular but smooth line in others (Fig. 5A). The lateral margin of the frontal shows a pair of weak concavities at the level of the orbit corresponding to the location of the supraorbital and of the dermosphenotic, but there is no marked interorbital constriction. A well-marked constriction is observed in a majority of 'semionotiformes' and Recent gars, but not in most fossil gars such as *Obaichthys*, *Dentilepisosteus* and *Cuneatus* (Grande 2010, fig. 528). The frontal ends anteriorly not far from the level of the anterior margin of the orbit. Anteriorly, the frontal extends as a thin ventral lamina of bone on which rests the nasal (KS12-126, KS12-275), and medially the bone develops a blunt process which forms with its counterpart a median prominence. A ridge extends laterally from the median prominence and defines a shallow notch at the level of the exit of the supraorbital sensory canal. The premaxilla extends apparently under the frontal (Fig. 7B) as in other 'semionotiformes', but it does not participate to the dermal skull roof cover as in gars and in some specimens of *Pliodetes* (Wenz 1999). The nasal has two wings, reminiscent of a 'half butterfly' (Fig 5A, KS12-275). The lateral concavity between the two wings marks the opening for the posterior external naris, while the anterior external naris probably opened in the gap between the nasal and the antorbital. The antorbital is a narrow curved rod of bone that connects the arched and tubular median rostral anteriorly and the anteriormost infraorbital (lacrimal) posteriorly (Figs 5A, 10C; KS12-262, KS12-275).

The parietal is about 1.5 times longer than wide. The medial, posterior and lateral margins are irregular but smooth, while the anterior margin is digitated, at least in some individuals (compare Fig. 5A and 5B). A small notch is located at the posterior third of the lateral margin for the path of the middle pit line. The dermopterotic, about 1.5 times longer than wide, is a large bone roughly rectangular in shape that extends posterolaterally along the frontal. The dermopterotic extends along the posterolateral edge of the frontal. The length of the contact between both ossifications varies within the population. In ventral view, the dermopterotic has no ventral flange as in *Amia* (Grande and Bemis 1998). There are generally three extrascapulars on each side of the skull (Fig. 5B, KS12-201), but some specimens have two pairs only plus a medial one (Fig. 5A, KS12-275) and others possess supernumerary small extrascapulars posteriorly wedged between the main ossifications (KS12-279). In *Obaichthys decoratus*, a third extrascapular is wedged between the lateral and the medial extrascapular on each side of the skull (Grande 2010), but the ossification is present anteriorly to the series, not posteriorly as in KS12-279. The lateralmost one is the largest and is roughly circular in shape, with an irregular anterior margin contacting the dermopterotic (Fig. 6, KS12-9). The other extrascapulars are smaller and irregular in shape, but their posterior margin draws a regular forwardly curved line, against which abuts the first row of scales (Fig. 5). Most Cretaceous 'semionotiformes' and Lepisosteiformes have more than two pairs of extrascapulars, while a single pair is generally present in Jurassic taxa (Cavin 2010).

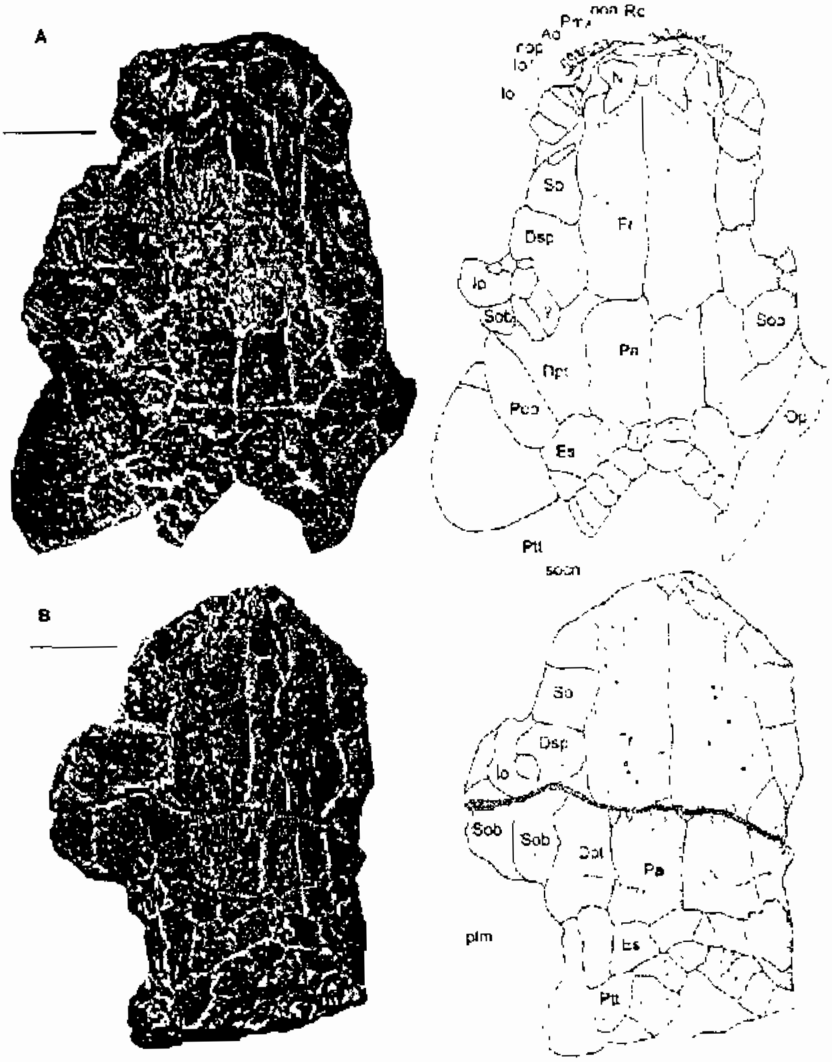

FIG. 5. *Thaiichthys buddhabutrensis*, skull roof in dorsal views. A, KS12-275; B, KS12-201. Scale bars represent 20 mm.

Endocranial braincase and parasphenoid. The occipital region forms an ossified block separated from the otic region by a gap – the metotic fissure – that was filled with cartilage during life (Fig. 8, KS12-41, KS12-134, KS12-287, KS12-288). The gap is wider than in *L. toombsi*, in which the exoccipital touches the prootic (Patterson 1975), but reminiscent of the situation observed in taxa belonging to the gar lineage (Grande 2010). The basioccipital is visible in KS12-287, KS12-134 and KS12-288. Its lateral face is excavated. On the left side of KS12-288, a rounded process situated near the posteroventral corner of the lateral face of the basioccipital is regarded as the facet for a cranial rib (Fig. 8D), as described in *L. toombsi*, and may indicate the occurrence of at least one fused vertebral centrum with the braincase (Patterson 1975). The exoccipital meets its counterpart above the foramen magnum. It comprises a laterally oriented face, extending above the basioccipital, and a horizontally oriented dorsal face. Both faces are separated by a rounded ridge that spreads out laterally. There is no evidence for paired series of foramens for the dorsal and ventral roots of spinal nerves, but instead a single small foramen opens at this place. In the specimen KS12-287, no vagus canal crosses the exoccipital, indicating that the vagus nerve (X) should have exit in the metotic fissure (Fig. 8C), that is, the condition coded for *T. buddhabutrensis* in Cavin's (2010) analysis. On the right side of KS12-134,

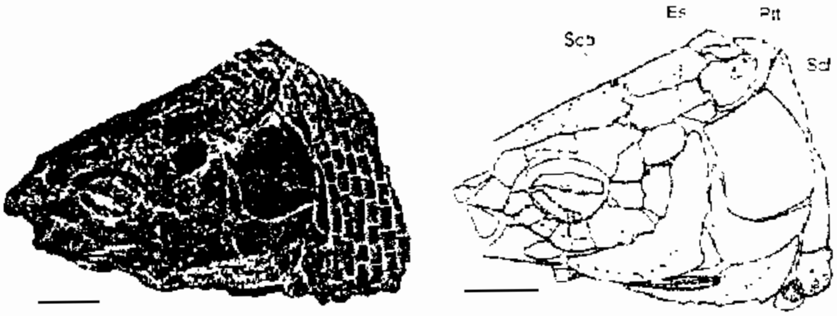

FIG. 6. *Thaiichthys buddhabutrensis*, skull of KS12-9. Scale bars represent 20 mm.

and apparently in KS12-288 (Fig. 8D); however, a notch is present at the anterior margin of the exoccipital for the exit of the vagus nerve, and in KS12-41 the foramen seems to be completely enclosed by the intercalar (Fig. 8B). Although this part of the braincase is poorly preserved on the available material, we consider that this character – vagus nerve completely enclosed by exoccipital', regarded by Olsen and McCune (1991) as important to characterize the 'semionotiformes' – is variable within the population of *T. buddhabutrensis*. A similar situation, the vagal foramen partly or completely enclosed by bone, has been described in *Lepisosteus* and *Atractosteus* (Grande 2010). In *Obaichthys* and *Dentilepisosteus*, the vagus foramen is completely enclosed in the exoccipital (Grande 2010, figs 476C, D and 488C, D, respectively). In the specimen KS12-287, the exoccipital develops a posterodorsal articular facet for the first neural arch, and a lateral articular facet that articulates with the dorsal part (basidorsal) of the first centrum (Fig. 8C). In KS12-288, the lateral process is still visible, but the contact with the first centrum is tight, and the suture is barely discernible (Fig. 8D). This structure corresponds to a partial fusion of the centrum with the occipital condyle. We have not observed the situation in larger individuals, and consequently, we cannot establish whether the centrum became completely fused with the basi- and exoccipital during ontogeny, eventually forming a structural part of the neurocranium. The occurrence of an articular facet for cranial rib, which indicates a possible phylogenetic fusion of a centrum (see above), and the occurrence of a tightly associated centrum in KS12-288 are the evidence of partial and/or complete fusion of two vertebrae to the occiput. Grande (2010) observed the fusion of two vertebrae in *Lepisosteus osseus* and *Atractosteus spatula*, while Britz and Johnson (2010) observed two vertebrae fused in *Lepisosteus* sp., but only one in *Atractosteus* sp. In both studies, the fusion is testified by the fusion of the neural arches, but the centra of the two vertebrae are never present during the development, to the contrary of the situation observed in *T. buddhabutrensis*.

Prolonging anterolaterally the ridge of the exoccipital is a separated ossification visible in KS12-134, KS12-287 and KS12-288 (Fig. 8C–E), and regarded here as an individualized intercalar. The bone forms a well-developed rounded lateral process, on which probably rested the ventral limb of the post-temporal (not observed). Its anterior margin is curved and delimitates, with the ventral margin of the epioccipital (following Grande's (2010) discussion about the homology and terminology of this bone in Holostei), a gap that was filled with cartilage. An intercalar has been described in several '*Lepidotes*' species. Patterson (1975), however, observed no intercalar in *L. toombsi* and concluded that previous observations of this bone in *Lepidotes* were

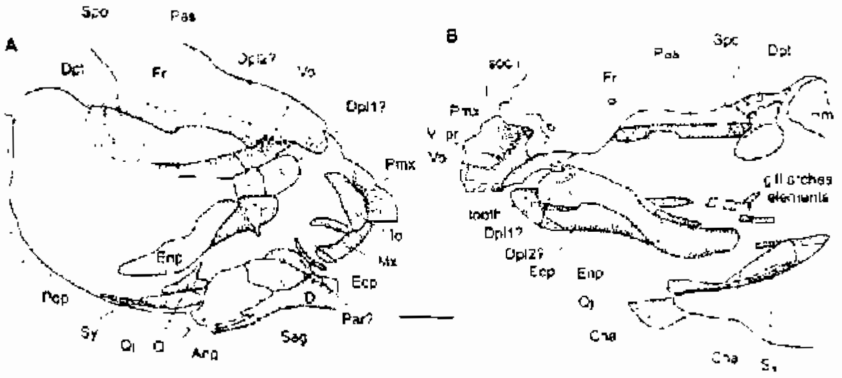

FIG. 7. *Thaiichthys buddhabutrensis* KS12-266. Snout region and part of the suspensorium in right (A) and left (B) lateral views. Scale bar represents 10 mm.

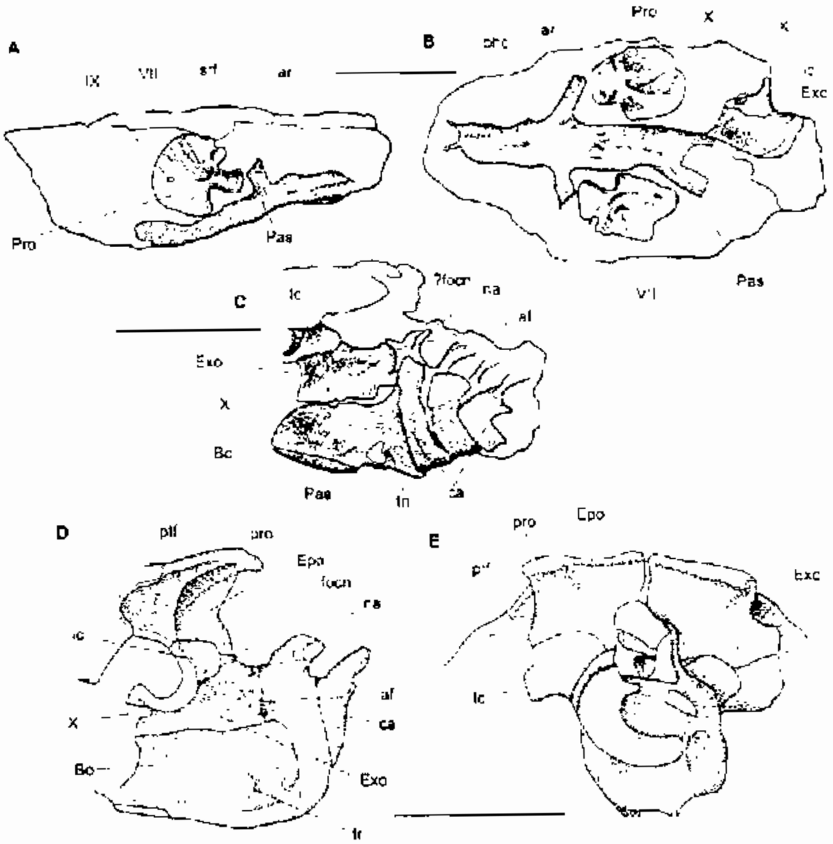

FIG. 8. *Thaiichthys buddhabutrensis*, endocranial braincase and parasphenoid. A–B, KS12-41; A, right lateral view; B, ventral view; C, KS12-287, left lateral view; D–E, KS12-288; D, left lateral view; E, posterior view. Scale bars represent 20 mm.

wrong (p. 452). We agree with Patterson's argument for questioning the observation made by Woodward (1916) in *L. mantelli* and in *L. latifrons*, and by Rayner (1948) in *L. semiserratus*, but we see no reason to refute the previous observations of an intercalar in *L. semiserratus* by Stensio (1932) and in *L. mantelli* by Gardiner (1960). Accordingly, we regard the occurrence of an intercalar in *L. mantelli*, *L. semiserratus* and *T. buddhabutrensis*, at least, as likely. An intercalar, fused to the exoccipital and termed 'intercalar process', is present in *Dentilepisosteus laevis* (Grande 2010). The situation is unknown in *Obaichthys*. The epioccipital is well visible on KS12-288 (Fig. 8D–E), but no detached ossification allows us to see the internal morphology of this ossification, which bears important features for 'semionotiformes' (Patterson 1975; Thies 1989*a*). The bone bears on its posterolateral edge a process (KS12-41 and KS12-288 left, KS12-134 right), which is less developed and not digitated as in *L. toombsi* and *L. gloriae*, but reminiscent of the structure present in gars, except in *Dentilepisosteus* in which the process is large and slightly digited (Grande 2010, fig. 487). Laterally, the epioccipital forms a shallow post-temporal fossa. A post-temporal fossa is present in 'semionotids', in which this part of the braincase is visible, but absent in Recent and extinct gars. Both epioccipitals are separated posteriorly by a narrow gap. There is no trace of opisthotics, supraoccipital or supraotic.

Both prootics are visible in KS12-41 (Fig. 8A–B) and KS12-134 and partly in KS12-288. The ossification is reminiscent of the prootic of *L. toombsi* and of the members of the gar lineage. There is apparently no contact between the intercalar and the prootic, as in *Lepidotes semiserratus* (*L.* sp.) figured by Stensio (1932) and in *Dentilepisosteus* (Grande 2010), but unlike *Amia* and basal teleosts. The prootic has a regularly curved posterior border that was embedded in cartilage. It extends as a wing-like structure that contacts the ascending ramus of the parasphenoid anteriorly, the sphenotic dorsally and the parasphenoid ventrally (in *Amia*, the prootic does not reach the sphenotic). An empty space between the prootic dorsally and the parasphenoid ventrally housed the internal carotid artery (or orbital artery, Grande 2010). Almost in the centre of the ossification opens a pore for the nerve (VII) and the jugular canal. Posterior to that large opening opens a small foramen for the glossopharyngeal nerve (IX). A shallow subtemporal fossa is excavated in the dorsal part of the ossification (Fig. 8A). The prootic contacts anteriorly the ascending ramus of the parasphenoid, as in *L. toombsi,* but does not form with it the typical basipterygoid process of gars. The anterior face of the prootic is not visible, and we cannot observe whether a posterior myodome is present.

The sphenotic is sutured to the ventral side of the dermopterotic. It develops a lateral blunt process which is visible on the cheek in a concavity of the dermosphenotic (Figs 4B, 7 and 9). A small ossification in a similar position, probably the tip of the sphenotic process, is also visible in some specimens of *Lepidotes mantelli* (Woodward 1916, pl. IX), *Araripelepidotes* (Thies 1996, fig. 2A), *L. elvensis* (Wenz 1967, pl. XXI; Thies 1989*b*, fig. 2) and *L. semiserratus* (BMNH P.62939) and has been described in *Tlayuamichin itztli,* in which it shows a dermal ornamented component (López-Arbarello and Alvarado-Ortega 2011). In all extant species of gars, the sphenotic is visible laterally on the cheek in the form of a minute ossification wedged between the dermopterotic dorsally and suborbital ventrally, and consequently, the bone is separated from the dermosphenotic (Grande 2010). In *Thanichthys* the tip of the sphenotic is separated by a gap from the skull roof, and it is closely associated with the dermosphenotic. In obaichthyids, sphenotic and dermosphenotic are fused together (Grande 2010).

The endocranial ethmoid region is poorly ossified. No lateral ethmoid has been observed. Patterson (1975, p. 499) described in the ethmoid region of *L. mantelli* paired ossifications 'more economically interpreted as lateral ethmoids'. A lateral ethmoid with a large lateral process was described in *Scheenstia zappi* by López-Arbarello and Sferco (2011), and the ethmoid region is well ossified in *Araripelepidotes* (Wenz and Brito 1996) and possibly in *Pliodetes* (see below). Gars do not possess lateral ethmoid (Grande 2010). In *Tlayuamichin itztli,* a series of endochondral bones aligned in correspondence with the anterior infraorbital bones have been named parethmoids by López-Arbarello and Alvarado-Ortega (2011), and in *Semiolepis brembanus* an ethmoid ossification has also been figured by Lombardo and Tintori (2008, fig. 2). The vomer has been described by Cavin *et al.* (2003) as a paired ossification. In KS12-288, however, no suture is visible, but the ossification is partly covered with matrix. This feature – paired vs unpaired vomer – is possibly related to ontogeny. KS12-288 also shows the occurrence of at least five teeth transversally arranged along the anterior wide part of the vomer plus some other teeth (at least three) on the posterior part of the bone. The teeth are stout and conical, smaller than the premaxillary teeth. The teeth arrangement looks similar in *L. microrhis* (Wenz 2003), *L. gloriae* (Thies 1989*a*), *L. deccanensis* (Jain 1983), *Semionotus elegans* (Olsen and McCune 1991) and in the extinct gar *Dentilepisosteus laevis* (Grande 2010), although in the latter three species the vomers are paired. In *L. mantelli* and *L. maximus,* two species with crushing dentitions, the button-like teeth are more numerous, more densely arranged and extend more posteriorly on the unpaired vomer (Woodward 1916 and Jain 1985, respectively). In Recent gars, the paired vomers are extremely elongated and bear patches of fine teeth and some fangs anteriorly, except in *Lepisosteus osseus* which has no fangs (Grande 2010).

The posterior forked extremity of the parasphenoid sutures to the ventral side of the basioccipital and forms a V-shape notch that delimitates a groove for the dorsal aorta similar to the one described in *L. toombsi* (Patterson 1975). A small foramen for the bucco-hypophysial canal opens on the ventral face of the parasphenoid at the posterior level of the orbit (Fig. 8B). Well-developed ascending rami extend from the main body of the parasphenoid at the posterior level of the orbit. No basipterygoid processes are present. In *L. toombsi,* both ascending rami and basipterygoid process (formed by the parasphenoid only) are present, while in gars, the ascending rami are absent and the basipterygoid processes are present, but modified with a participation of the anterior edge of the prootic. In the orbital region, the parasphenoid bears lateral flanges. Posterior to the ascending

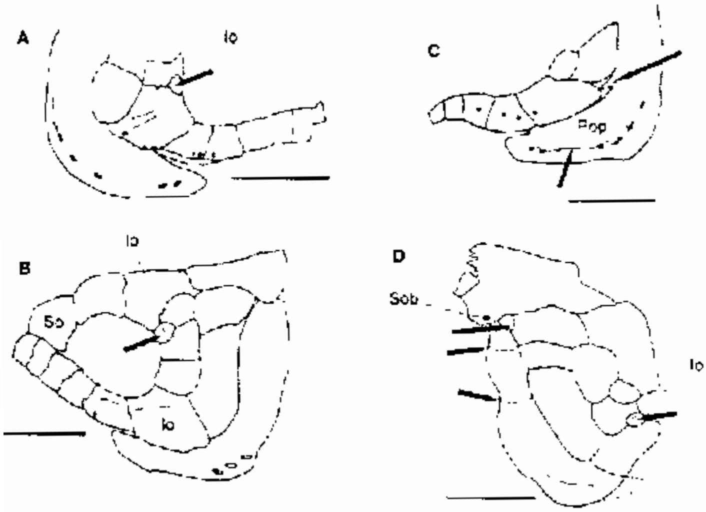

FIG. 9. *Thanichthys buddhabutrensis,* cheek patterns. A and B, KS12-166; C, KS12-60; D, KS12-26. Arrows show features discussed in the text. Scale bars represent 20 mm.

rami, shallow ridges are present at the surface of the parasphenoid, but no teeth are visible in that area by contrast to *L. toombsi* and *S. elegans*, but like *L. gloriae*. The basisphenoid is not visible in specimens where the sphenoid region is preserved (KS12-41, KS12-134), and consequently, we consider that this ossification is absent.

Circumorbital and suborbital series. The number and pattern of cheek bones of the circumorbital series varies within the population of Phu Nam Jun. The circumorbital ring is complete. It is composed of a large dermosphenotic forming the posterodorsal edge of the orbit, two large supraorbitals above the orbit and nine or ten infraorbitals located posteriorly, ventrally and anteriorly to the orbit. One or two infraorbitals border the posterior margin of the orbit: a large one is located in the posteroventral edge of the orbit, and the remaining ones, which are deeper than long, are situated below and anterior to the orbit. The three or four anteriormost infraorbitals are small and have no contact with the orbit. The first, anteriormost, infraorbital (lacrimal) is triangular or L-shaped (Figs 5A, 10A; KS12-80, KS12-262). The infraorbital forming the posteroventral corner of the orbit is the largest one of the series and extends posteriorly to reach the preopercle (Fig. 9), as in *Araripelepidotes* (Maisey 1991) and in gars among others. The infraorbitals bordering the posterior margin of the orbit are generally large, deeper than long. A supplementary small rounded ossification is often present in the anteroventral and sometimes in the anterodorsal corner of the large posterior infraorbital(s). Both patterns – one small ossification wedged in dorsal and one in ventral position – may occur in a single specimen (Figs 4, 9A–B; KS12-168). The shape of the dermosphenotic varies, but its general outline is always L-shaped. The posteroventral margin embraces the lateral extremity of the sphenotic. As mentioned above, a rather similar pattern occurs in *Lepidotes mantelli* and *Tlayuamichin*. In *Obaichthys* and *Dentilepisosteus*, the dermosphenotic is fused with the sphenotic, and the compound ossification is excluded from the orbital ring. The supraorbitals of *Thaiichthys* are large. The posterior one is almost square in shape, and the ventral margin of the anterior one extends above two or three infraorbitals (Fig. 9B), as in gars and in some *Lepidotes* and closely allied taxa.

Most specimens of *T. buddhabutrensis*, including the holotype, have two suborbitals vertically arranged between the posterior infraorbitals and the preopercle (Figs 3–6, 9). In some specimens, a third and even a fourth (Fig. 9D) suborbital are apparently present.

The circumorbital and suborbital bone pattern is variable among 'semionotiformes' and may also vary within a single species as shown here. The features of the cheek of *T. buddhabutrensis* comparable with other 'semionotiformes' and that contain potential phylogenetic signals are the following ones: a series of

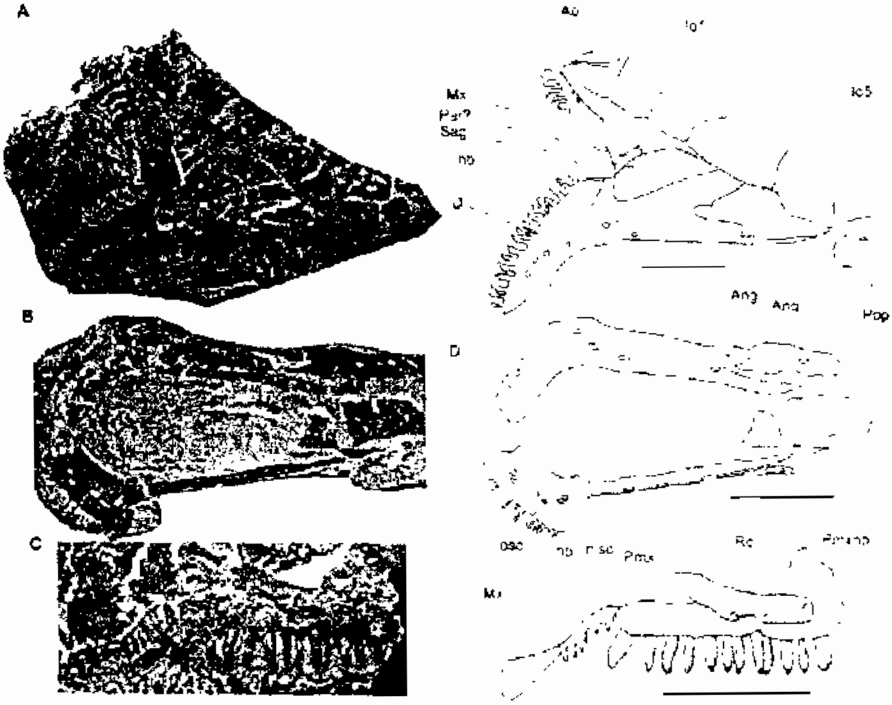

FIG. 10. *Thaiichthys buddhabutrensis*, jaws. A and C, KS12-262, A, left lateral view, C, anterior view; B, KS12-168, ventral view. Scale bars represent 20 mm.

anterior infraorbitals with no contact with the orbit, a synapomorphy of 'semionotiformes' as defined by Cavin and Suteethorn (2006); a few suborbitals arranged in a single row, a character found in most *Lepidotes* spp. and closely allied taxa and in obaichthyids (Grande 2010); and the cheek completely covered with dermal bones and circumorbital ring complete, both characters also present in some *Lepidotes* spp. and closely allied taxa as well as in all gars.

Hyopalatine series. The suspensorium is visible on both sides of KS12-266, but it is poorly preserved and identification of the ossifications is still uncertain (Fig. 7). Of the hyomandibula, only a poorly preserved fan-shaped articular head is visible on the left side of the specimen. The quadrate is visible as fragments only. The quadratojugal rests along the dorsal border of the horizontal limb of the preopercle and contacts the condyle of the quadrate, in a similar arrangement to *Semionotus elegans* (Olsen and McCune 1991) and gars. The symplectic is a thin rod of bone located posteriorly to the quadratojugal and rests against the preopercle. This ossification appears to have no contact with the quadrate. The entopterygoid is a twisted sinusoid ossification, under which rests the curved ectopterygoid. On the right side of KS12-266, the anterior extremity of the ectopterygoid shows a complex morphology, reminiscent of the arrangement present in *Semionotus elegans*: a medially directed lamina articulates with the entopterygoid, and the anterior extremity shows a bowl-shaped surface for the autopalatine (Olsen and McCune 1991, p. 278). The latter bone, however, has not been identified in our material. Anteromedially to the ectopterygoid are two flat ossifications, visible on both sides, which are interpreted with caution as two dermal palatines. A single tiny tooth is visible on the left side of the anterior dermopalatine. The metapterygoid is not preserved.

The suspensorium of *T. buddhabutrensis* is more reminiscent to the suspensorium of 'semionotid' taxa, such as *Semionotus elegans*, *Lepidotes piauhyensis* or *Tlayuamichin itztli* (Olsen and McCune 1991; Gallo 2005; López-Arbarello and Alvarado-Ortega 2011, respectively), than to the very specialized suspensorium of gars (Grande 2010).

Jaws. The anatomy of the jaws shows several specializations (Fig. 10). The jaws are fragile and are proportionally small compared to the skull, except the premaxillae that are robust ossifications. The maxilla is preserved on few specimens only (KS12-80, KS12-97, KS12-168, KS12-262). Its posterior half is an edentulous thin blade of bone, with almost straight and parallel dorsal and ventral margins. Its anterior half, which is thinner than the posterior portion, bears between four and six teeth. Although not clearly visible, the arrangement of the anterior extremity of the maxilla indicates that a medial articular process is present (KS12-262). The teeth are 2–2.5 mm long, have a cylindrical base and a tip of acrodine, which marks an open angle with the base, thus forming an internally curved hook (Fig. 10A). No supramaxilla is observed, and this ossification was probably absent. The teeth-bearing portion of the premaxilla is held transversally to the long axis of the head. On the basis of a specimen with only the bases of the teeth preserved (KS12-6), nearly 12 teeth were initially suspected to be borne by each premaxilla (Cavin *et al.* 2003). It appears that the number of functional teeth at the same time is slightly less, *c.* 10 (KS12-176, KS12-275). The premaxillary teeth are strong, bigger than the maxillary and dentary teeth (*c.* 5 mm in height) and only slightly recurved inwards. The lateralmost tooth is slightly bigger than the other teeth (Fig. 10C). A second row of teeth, smaller and more acute, is present behind the anterior row of strong teeth (KS12-80, KS12-262). The premaxilla extends posteriorly forming a well-developed nasal process, which is dug by a concavity where opens the large olfactory foramen and more anteriorly a small foramen for the palatine ramus of the facial nerve (Fig. 7B). The suture with the frontal appears to be interdigitated (KS12-80).

The lower jaw is highly specialized, as in several Early Cretaceous freshwater 'semionotiformes' (Cavin 2010). It has a deep and well-developed coronoid process and a dentigerous portion composed of a horizontal blade of bone that bears horizontally oriented teeth (Fig. 10). This peculiar morphology is not owing to preservation, because it is visible on several well-preserved specimens (KS12-80, KS12-97, KS12-165 and KS12-168). The surangular forms most of the coronoid process in lateral view. A fragment of prearticular is apparently visible along the anterior margin of the coronoid process in KS12-262 and KS12-266 (Figs 7A, 10A). The angular forms most of the posterior part of the mandible and contacts the dentary through a double V-shaped suture. Independent retroarticular and coronoid ossifications have not been observed. The dentary develops a thin posterior process. This process, which appears to reach the articular region of the mandible, was regarded as an important character to resolve the phylogeny of 'semionotiformes'. In gars, the dentary develops a dorsal process above the angular (Cavin 2010, character 31). A detailed description of Recent gars by Grande shows that the dentary reaches the posterior margin of the mandible in some species (in *Lepisosteus osseus*, *L. spatula* (although a tiny piece of articular is still visible posteriorly in lateral view)), but not in others in which the supraangular and angular meet, preventing the dentary to reach the posterior margin (*L. platostomus*, *L. oculatus*, *Atractosteus platyrhincus*, *A. tristoechus* and *A. tropicus*). It is unclear whether this difference is related to the species and/or to the size of the specimen. In *Thaiichthys buddhabutrensis*, a process above the angular seems to be present in some specimens only (compare Fig. 10A, KS12-262 and Fig. 7A, KS12-266). Consequently, we regard this pattern as uncertain now. In the data matrix, we coded for *T. buddhabutrensis* the most common pattern, that is, a process extending below the angular only.

Anterior to the coronoid process, the dentary forms with its counterpart a horizontal blade of bone that protrudes laterally off the mandible. C. 18 small teeth, 2–2.5 mm, are borne along the anterior margin of the blade (Fig. 10A–B, KS12-80, KS12-97, KS12-165, KS12-168, KS12-262). Each tooth is composed of a cylindrical base held horizontally and a bulbous cap of acrodine, which stands at right angle with the cylindrical base. There is no evidence for the presence of tritoral teeth on the mandible and on the palate.

The jaw and the dentition of Ginglymodi show a wide range of specializations, such as the development of moderately or strongly tritoral dentition in various Triassic to Cretaceous taxa, predatorial dentition in Recent gars and reduction in the dentition in several forms from the 'mid-' Cretaceous (*Araripelepidotes*, *Pliodetes*, obaichthyids). *T. buddhabutrensis* belongs to the latter group. In particular, it shares with *Masillosteus*, *Obaichthys* and *Dentilepisosteus* the teeth arranged in a single row and concentrated in the anterior portion of the mandible.

Opercular series. The preopercle shows variations within the population. It has a horizontal limb slightly shorter than the vertical one. The vertical branch has parallel vertical margins with a slight tapering dorsally (Fig. 6). One specimen at least shows a hook-like process located on the anterior margin of the bone, just below the mid-depth of its height (Fig. 9C; KS12-214). The posteroventral margin of the preopercle is gently curved (Fig. 9). Some specimens, however, bear at this level a rounded process protruding posteriorly (Fig. 6; KS12-9, KS12-48). The ventral margin of the horizontal limb is gently curved, and the ossification ends anteriorly as a blunt spine. The specimen KS12-26, which is large in size, shows fracturings of the cheek bones: in addition to the presence of a supplementary small infraorbital and suborbital (see above), there is another ovoid bone wedged between the dermopterotic and the lateral most extrascapular and, interestingly, the vertical branch of the preopercle appears to be divided by two supplementary sutures (Fig. 9D). Although the cheek ossifications of this specimen are damaged by several fractures, the sutures delimitating the bones described above appear to be genuine according to detailed observations of the margin of the bones. Two ossifications filling the space of the preopercle have been described in a specimen of *Semionotus bergeri* by López-Arbarello (2008), but it is unclear whether this pattern represents a character of the taxon or is an abnormal condition. In KS12-26, the small ossification present at the dorsal tip of the preopercle corresponds to the position of the dermohyal and/or suprapreopercle present in gars (Grande 2010), but we have no other evidence to test this possible homology. The path of the preopercular sensory canal is described below, but mention is made here of a ridge running above the exits of the sensory canal present in some individuals only (Fig. 9C). The opercle is squarish in shape, with its anterior and posterior margins slightly curved. Some specimens (KS12-26, KS12-208) have an opercle proportionally deeper than the squarish opercle of the type specimen (compare Figs 2A, 3). The dorsal margin of the opercle is straight, the posterior margin is fringed by fine grooves visible on well-preserved specimens only, and the ventral margin is slightly convex. The subopercle is well developed with a vertical limb almost reaching the articular process of the opercle. The dorsal margin of the bone has a proportionally large crescent-shape area that is covered with the opercle on articulated specimens (Fig. 4A2). The interopercle is visible as a triangular bone wedged between the subopercle and the posteroventral edge of the preopercle.

Branchial apparatus and branchiostegal rays. Six thin and elongated branchiostegal rays are preserved on the right side of KS12-168 (Fig. 4A). Some elements of the branchial apparatus are visible in specimens KS12-201, KS12-176 and KS12-287 (Fig. 11). The anterior ceratohyal is hour-glass-shaped, with a broad posterior extremity and a much narrow anterior extremity. The posterior ceratohyal (not visible in Fig. 11) is roughly triangular in shape, with a margin contacting the anterior ceratohyal regularly curved. In KS12-287, a pair of half-circular hypohyals is sutured to the anterior extremity of the ceratohyals. The first hypobranchial is visible in this specimen as a rod of bone slightly wider distally than proximally. Several specimens show ceratobranchials, which are well developed and dug by a deep gutter on the ventral side. Their number cannot be determined, but we can suppose that there were four pairs of hypobranchials and five pairs of ceratobranchials as in gars, *Amia* and *Semionotus* sp. (Olsen and McCune 1991). In KS12-287, a thin median rod of bone is visible just posterior to the first pair of hypobranchials. Although this part is poorly preserved, this element is regarded as the ossified anterior part of the second basibranchial. In *Lepisosteus osseus* and *Atractosteus spatula*, the second basibranchial is cartilaginous, except a section situated

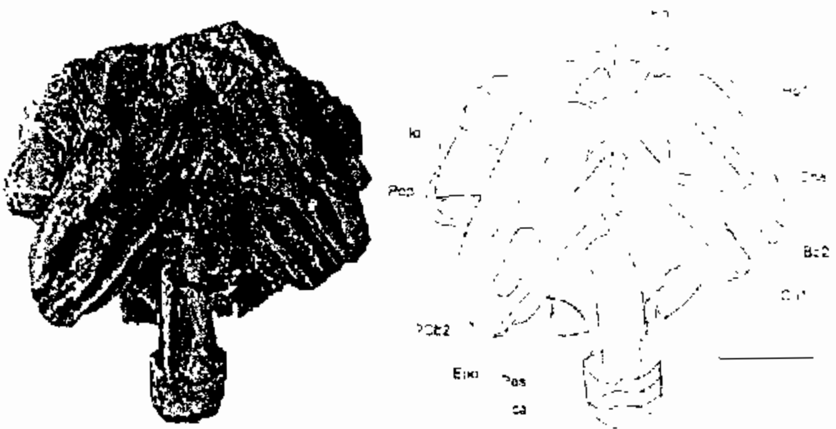

FIG. 11. *Thaiichthys buddhabutrensis*, KS12-287, ventral view of the skull with elements from the branchial apparatus. Scale bar represents 20 mm.

between the second and the third pairs of branchial arches (Grande 2010), while in *Thaichthys buddhabutrensis*, the ossified section seems to be located more anteriorly, between the first and second pairs. In KS12-176, elements of the dorsal part of the gill arches are apparently preserved, but their determination remains dubious.

Pectoral girdle. The post-temporal is a crescent-shape ossification bordering the posterior margin of the lateralmost extrascapular (Figs 5, 6). The visible part of the supracleithrum has a dorsal border that lines the posterior margin of the post-temporal (Fig. 6). There is no supracleithral process on the internal side of the bone (KS12-208), and the posterior margin is marked by a shallow concavity and some faint ridges running on the lateral face (Fig. 6). The cleithrum (Fig. 4A) has a long, proportionally narrow and slightly curved vertical limb that ends dorsally with a short inversely curved process. The lateral face of the vertical limb is ornamented with ridges bearing faint traces of enamel. The posteroventral margin of the bone is straight, and the surface bears a triangular area of ganoin. This area was exposed on the surface of the body on the living fish, to the contrary of other parts of the cleithrum that were covered by the opercular series. There is no trace of a serrated organ. The horizontal limb of the cleithrum is rather short and deep, with its lateral face marked by a smooth ridge. On KS12-202 and KS12-146, the cleithrum is visible in internal view (Fig. 12). It shows a well-developed curved internal lamina that delimitated the gills chamber. Grande (2010, p. 786) regards the lamina of the cleithrum in *Macrosemius* – observed by Bartram (1977) using X-rays – as homologous to the one of gars. The morphology present in *T. buddhabutrensis* is very similar, and in consequence, we consider it as homologous to the internal lamina of gars. In *Amia*, the cleithrum is a simple L-shaped blade of bone. There are four postcleithra (Fig. 4A). The dorsalmost postcleithrum is a ganoin-free elongated slightly curved and rectangular ossification with a short dorsal process. The three ventral ones are smaller and bear ganoin in some specimens.

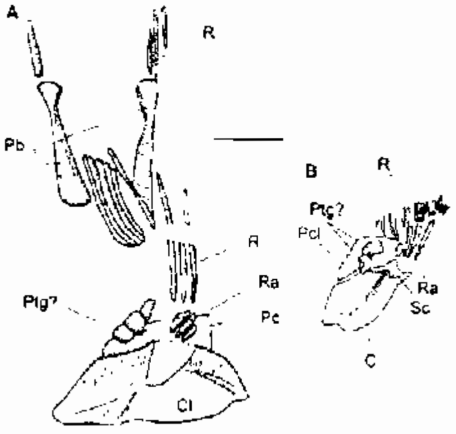

FIG. 12. *Thaichthys buddhabutrensis*. A, KS12-202, portion of the pectoral girdle in internal view and pelvic girdle; B, KS12-146, portion of the pectoral girdle. Scale bar represents 20 mm.

Chondral elements of the pectoral girdle are visible as trace of bone in KS12-202 and in better condition in KS12-146 (Fig. 12). The scapula is an irregular shaped bone with a ventral arm that delimitates the scapular foramen (actually a 'scapular notch'). There are at least four radials increasing in size anteriorly (because the left pectoral girdle has shifted, the radials are visible in a reversed alignment in KS12-146). Two (KS12-146) or 3 (KS12-202) rounded ossifications located in the ventroposterior edge of the cleithrum are possibly propterygial ossifications. The arrangement and shape of bones of the pectoral girdles are reminiscent of the situation described in *Semionotus elegans* (Olsen and McCune 1991) and, to a lesser degree (in particular in the shape of the cleithrum), in gars (Grande 2010).

Cephalic sensory canal. The supratemporal sensory canal is barely visible on the specimens (Fig. 13), except the exit for the connection with the preopercular canal. This canal exits the cephalic system posteriorly through a pore located in the concavity of the posterior margin of the supracleithrum (Fig. 6). The presence of the occipital sensory canal (or supratemporal commissure) is indicated by a series of pores that open along the posterior margin of the extrascapulars. The supraorbital branch gives off a couple of pores on the dermopterotic near the connection with the frontal. On the frontal, several pores are arranged along a curved line. One or two pores open laterally in the anterior portion of the frontal, and the canal passes through the nasal via a pore located in a small notch of the frontal. The supraorbital canal runs along the longitudinal axis of the nasal. No pore is visible on the nasal of several specimens (KS12-275), but in others, one or several (KS12-168) pores open in the ossification. A posterior pit line runs transversally through the suture between parietal and dermopterotic (KS12-9, KS12-201).

No opening is visible on the posterior one or two infraorbitals. In the infraorbitals located ventrally and posteroventrally to the orbit, the infraorbital sensory canal runs close to the orbital margin of the infraorbital ossifications. It gives off diverticula that open near the ventral margin of the bones. The number of openings along the infraorbital canal varies according to individuals, but the most common pattern seems to be the following one: there are four pores near the ventral margin of the large posteroventral infraorbital, three small pores on the ventral margin of the anterior next infraorbital and two pores located along a line situated in the middle depth of the next anterior infraorbital. On the anteriormost infraorbitals, the openings run along a line located in the dorsal half of ossifications. The canal enters the antorbital via a pore located at the angle of this crescent-shape bone and gives off two more small exits along the ventral limb of the ossification (KS12-9, KS12-80). The ethmoid commissure crosses the tubular rostral (KS12-275). There is no evidence of a sensory canal running within the supraorbital bones. The preopercular sensory canal has few pores along the vertical branch of the preopercle, and three or four supplementary pores open in the curvature of the bone near its posterior margin. Three or four pores open along the horizontal branch. In some specimens (KS12-168, KS12-201), these openings are separated of the posterior ones by a gap. The mandibular sensory canal gives off at least two elongated pores in the angular and –8

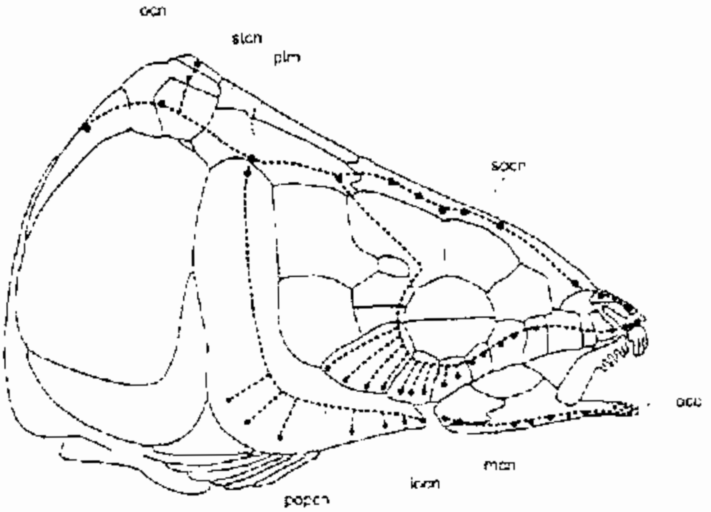

FIG. 13. *Thaiichthys buddhabutrensis*, reconstruction of the skull with the path of the sensory canals.

pores in the dentary along a line located at the ventral margin of the bone and extending anteriorly on the ventral side, in the middle of the horizontal blade of bone. A few pores open above the anterior portion of the mandibular canal, indicating the presence of an oral sensory canal (Fig. 10; see Cavin and Suteethorn 2006 for a discussion of this feature). An oral sensory canal is present in several 'semionotids' and in the gar *Masillosteus janeae* (Grande 2010, p. 654).

One or two pores are visible in the maxilla of KS12-60 and KS12-262. It is still unclear whether these openings are related to the sensory system, as it was described in a specimen of *Lepidotes elvensis* by Thies (1989*b*), or whether they accommodated nerves as the foramens accommodating rami of the trigeminal nerve described in *Amia calva* (Grande and Bemis 1998, fig. 42J).

Axial skeleton. The first three centra at least are ossified in KS12-287 (but only this part of the column is preserved on that specimen, Figs 8D, 11) and apparently the first four centra at least in KS12-176 (Fig. 14A). Posteriorly, the centra are not more ossified. In KS12-288, the first free centrum appears to be restricted to its basidorsal element (Fig. 8D–E). The first neural arch is wedged between the first centrum and the paired articular facets of the exoccipitals (Fig. 8C). The neural arches of the first three vertebrae do not extend high, but this may be an artefact of preservation. It is unclear whether these neural arches are fused to their corresponding centrum. In the anteriormost vertebrae (c. the first 6 ones), the neural arches expand dorsally as posteriorly curved processes with an enlarged distal extremity. In the more posterior vertebrae, the neural arches are more elongated and taper distally. The neural arches are apparently paired in the abdominal region and certainly paired in the caudal region. The supraneurals are elongated and slightly curved, with a distally enlarged extremity for the first ones (Fig. 14A). Fifteen supraneurals are visible on KS12-176 and 17 on KS12-201. At the level of the dorsal fin, the supraneurals are not more present, and the neural arches are close to, but not articulating with, long and proportionally wide proximal radials (pterygiophores). Posterior to the dorsal fin, the neural arches are thin.

There are a few ossified ribs visible in some specimens (KS12-45, KS12-162, KS12-180, KS12-214 and KS12-176), but their number and arrangement cannot be determined. They appear to be slimmer than the neural spines. In KS12-176, the last preserved caudal elements are twisted and the vertebral series points forward. The visible elongated and arched elements associated with the vertebrae are probably haemal arches (Fig. 14A). At least 32 vertebrae are present in this specimen, but the total number was higher. On the basis of our reconstruction, we estimate that the total number of vertebrae was c. 54.

Centra are generally not ossified in 'semionotids', while they are always strongly ossified and opisthocoelous in gars. In *Pliodetes*, abdominal vertebrae have a complete ossified ring around the notochord (Wenz 1999), and in *L. mantelli*, the anteriormost vertebrae at least show some degree of ossification (Woodward 1916, fig. 18).

Pectoral fins. The pectoral fin has 3 basal fulcra (KS12-97), at least 10 fringing fulcra (KS12-45, KS12-63 and KS12-221) and 10 rays (KS12-27, KS12-33). It is elongated, representing 70 per cent of the head length in one specimen (KS12-165: fin length = 70 mm, head length = 100 mm) and 78 per cent in another (KS12-156: fin length 90 mm, head length 115 mm).

Pelvic girdle and fin. Several specimens show portions of their squamation visible in internal view, and their pair of pelvic bones (KS12-213, KS12-202 and KS12-180). The pelvic bones are elongated bones with an enlarged proximal extremity situated in the horizontal plan (Fig. 12A). Posteriorly, the shaft of the bone thinners and twists, and its posterior extremity widens in the vertical plan. This rounded extremity bears the rays,

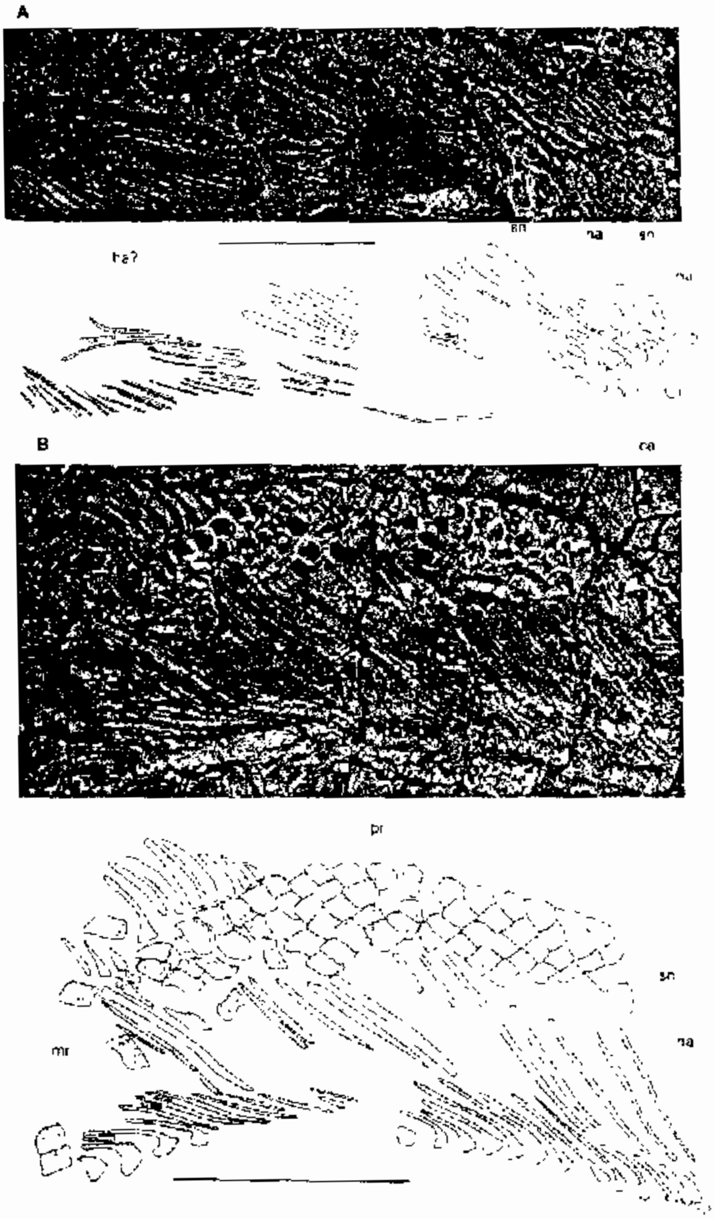

FIG. 14. *Thaiichthys buddhabutrensis*, axial skeleton. A, KS12-176 in left lateral view. B, KS12-201 in left lateral view. Scale bars represent 50 mm.

three of them being visible on KS12-202. The pelvic fin has three basal fulcra, six or more fringing fulcra (KS12-238), the basal most being slightly longer than half the fin length (KS12-72: 18 and 30 mm, respectively), and six rays (KS12-97, KS12-168). The length of the pelvic fin represents 47 per cent of the head length (KS12-97: fin length = 42 mm, head length = 90 mm).

Unpaired fins. The specimen KS12-201 shows the first five proximal radials (pterygiophores) and some more posterior ones supporting the dorsal fin (Fig. 14B). They are anteriorly oriented, robust and very elongated ossifications (Fig. 14B). In KS12-201, the distal extremities of the proximal radials show enlarged heads that articulate with hour-glass-shaped middle radials. In most specimens, the unpaired fins are incomplete.

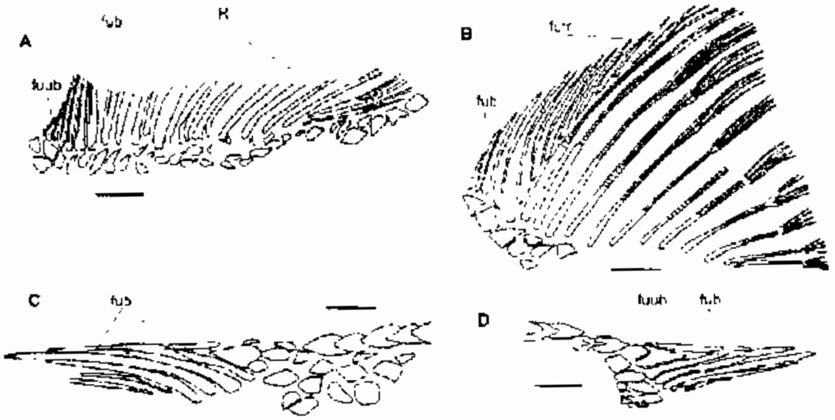

FIG. 15. *Thaiichthys buddhabutrensis*, dorsal fin. A, KS12-75 in left lateral view. B, KS12-190 in left lateral view. C, KS12-176 in right anterolateral view. D, KS12-224 in left anterolateral view. Scale bars represent 20 mm.

This is why only the basal length of dorsal and anal fins was used in the morphometric analysis of the population (Deesri *et al.* 2009). However, rare specimens show rather complete fins allowing general description for the species (Fig. 15). The dorsal fin is proportionally high, representing 76 per cent of the head length (KS12-190: fin length = 80 mm, head length = 105 mm). It is composed generally of four paired basal fulcra (6 are apparently visible on KS12-44), c. 10 fringing fulcra and 12 rays (KS12-190, KS12-75). In lateral view, a structure similar to a basal fulcrum is present anteriorly to the four true basal fulcra in some specimens. In KS12-224 and KS12-237, which have a slightly twisted body, this structure appears to be unpaired but proximally forked (Fig. 15D). It is regarded as an unpaired basal fulcrum according to Arratia's (2009) definition. The basal fulcra, which articulate with radials, are homologous with the 'rudimentary rays' described by Grande (2010, p. 128) in gars. The fringing fulcra are slightly curved and very elongated, the first one being equal to half the length of the first ray. The first third of the length of the rays is not segmented. A first longitudinal division of the ray occurs at mid-length, and a second division occurs at the third quarter of the length of the rays approximately. Although the very tips of the rays are usually not preserved, the outline of the fin observed in KS12-190 shows that the distal margin of the fin was straight.

As for the dorsal fin, the anal proximal radials are robust and elongated, the first one reaching 55 per cent of the head length (KS12-45: pterygophore length = 55 mm, head length = 100 mm). The anal fin has four basal fulcra (KS12-23, KS12-27, KS12-82 and KS12-272; but we cannot assess whether the first one is unpaired and forked), 12 fringing fulcra (KS12-272) and 12 rays (Fig. 16). Segmentation and division are similar than for the dorsal fin. According to the observation on KS12-38, the external margin of the anal fin was probably straight, and its depth was c. 46 per cent of the head length (KS12-38: fin length = 36 mm, head length = 78 mm).

Caudal fin. As for the other fins, the caudal fin is generally poorly preserved. The caudal lobe is preceded by an indeterminate number of fulcra. The ventral lobe is preceded by a scute (KS12-192), three unpaired and probably forked basal fulcra, four paired basal fulcra (the specimen KS12-272 shows a supernumerary small basal fulcrum wedged between two large fulcra, Fig. 17B) and at least 11 fringing fulcra (KS12-101, KS12-272). There are usually 19 rays, 9 in the ventral lobe separated by a slightly larger gap and 10 in the dorsal lobe, but some specimens apparently have more rays in their ventral lobe (Fig. 17C; KS12-101). Each ray divides three times. The ventral lobe of the caudal fin equals approximately 90–95 per cent of the head length (KS12-67, KS12-136), and we can suspect that the dorsal lobe poorly preserved on the available material had approximately the same size (the tail is usually externally homocercal in 'semionotids'). Some specimens (KS12-67, KS12-136, KS12-139139) indicate that the posterior margin of the caudal fin was regularly concave but not deeply forked.

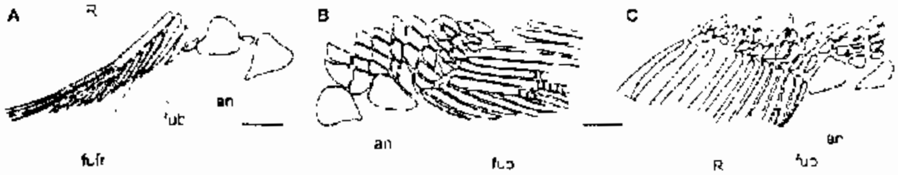

FIG. 16. *Thaiichthys buddhabutrensis*, anal fin. A, KS12-272 in right lateral view. B, KS12-192 in left lateral view. C, KS12-264 in right lateral view. Scale bars represent 10 mm.

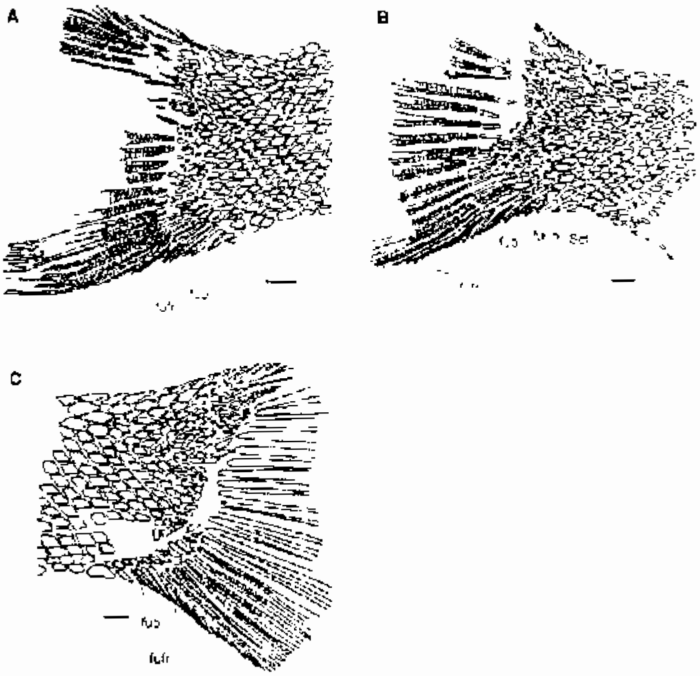

FIG. 17. *Thaiichthys buddhabutrensis*, caudal fin. A, KS12-67; B, KS12-272; C, KS12-101. Scale bars represent 20 mm.

Squamation. According to Deesri *et al.* (2009), there are on average 46 scales along the lateral line, 25 scales along a row from the anterior extremity of the dorsal fin to the lateral line and 16 scales from the anterior extremity of the anal fin to the lateral line. Twenty-three (21–25) scales are located on the lateral line between the head and the dorsal fin. The flank scales bear a pair of processes (pegs) located on the dorsal and ventral corners of the anterior margin, as in most 'semionotiformes' (see Cavin *et al.* 2009 for a discussion of this character). The posterior extremity of the scales forms a blunt spine, sometimes more acute, especially in the posterior part of the trunk (KS12-54). The median dorsal scales are longer than broad, lozangic in shape and sometimes with a slightly concave surface (Fig. 18; KS12-227). Some specimens show a morphology of the median dorsal scales that fits the definition proposed by Olsen and McCune (1991) for the 'Semionotidae', while other specimens show morphology that do not. Consequently, we regard this character as polymorphic in the phylogenetic analysis below. Scales similar to the dorsal mid-line scales, with a rather well-developed spine, are also present along the ventral mid-line of the body between the pelvic and the anal fins (KS12-97, KS12-22b), but we cannot ascertain whether this feature is present in all specimens. The pattern of the squamation is regular showing the typical caudal inversion in the caudal peduncle (Fig. 19), with the exception of the base of the unpaired fins. Scales from the first row under the dorsal fin have an irregular morphology, with the anteriormost ones showing a small process on their dorsoposterior edge (Fig. 15). The first two rows of scales at the base of the anal fin are also irregular (Fig. 16). The anus is surrounded by larger scales, but their precise arrangement is unclear (Fig. 16). In gars, there are an anterior medial anal scale and paired large lateral anal scales, and we suspect that the pattern is similar in *T. buddhabutrensis*.

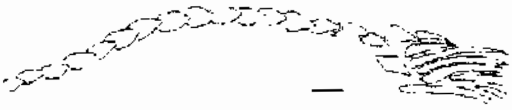

FIG. 18. *Thaiichthys buddhabutrensis*, dorsal ridge scales. KS12-227. Scale bar represents 10 mm.

PHYLOGENETIC ANALYSIS

Morphometric parameters of the specimens of *T. buddhabutrensis* from the locality of Phu Nam Jun indicate the occurrence of a single population representing a single species (Deesri *et al.* 2009). Osteological variations are observed within this population. These are: (1) pattern of sutures running between both frontals and both parietals, and of the suture separating these two pairs of ossifications, (2) length of the contact between the dermopterotic and the frontal; (3) number and arrangement of the extrascapulars, (4) location of the exit of the vagal nerve from the braincase; (5) pattern and number of infraorbitals; (6) outline of the posterior margin of the preopercle;

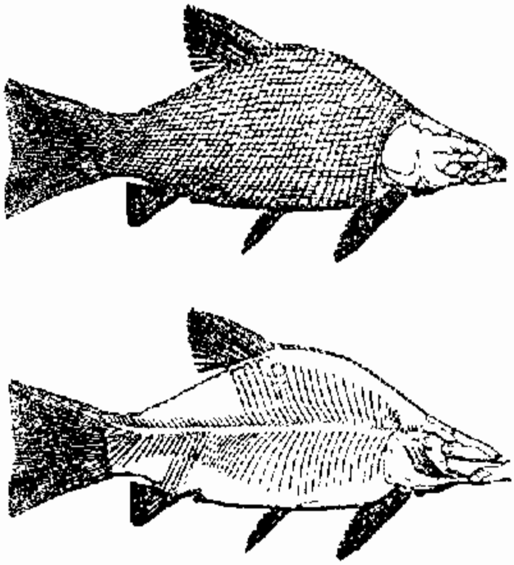

FIG. 19. *Thaiichthys buddhabutrensis*, reconstructions. Top, external view; bottom, view with no scales, and cheek and opercular ossifications.

(7) presence or absence of a ridge along the horizontal arm of this bone; (8) morphology of the median dorsal scales before the dorsal fin; and (9) little variations in fins' rays counts. Consequently, caution should be taken when these features are used in the phylogenetic analysis.

Cavin (2010) suggested that the gar lineage roots in a clade of Mesozoic 'semionotids' by using a set of 43 characters. In the meantime, Grande (2010) published an extensive description of Recent and extinct gars and defined 105 morphological characters to explore their phylogenetic relationships. Grande used *Semionotus elegans* as the single representative of 'semionotids' and found gars (Lepisosteiformes) as the sister group of Semionotiformes (*S. elegans*), a clade named section B. Section B is gathered with Macrosemiiformes in the clade Ginglymodi. The Giglymodi form with the Halecomorphi a monophyletic group, the Holostei

The description of *T. buddhabutrensis*, together with recent studies of new 'semionotiformes' taxa and revisions of several species, is an opportunity to re-evaluate the relationships between Lepisosteiformes and 'semionotiformes' using a combination of characters employed by Grande (2010) and Cavin (2010).

The characters used in the cladistic analysis are those used by Cavin (2010) with the addition of characters used by Grande (2010) for gars when they are relevant for our set of taxa. We cut off Cavin's (2010) character 2 (vagus nerve exits through the metotic fissure versus forward extension of exoccipital around vagus nerve) because the pattern is polymorphic (see above). Polymorphic characters can be used in phylogenetic studies, but this one is known in too few specimens among the compared species to be properly evaluated. We also deleted Cavin's (2010) character 7 (absence vs presence of a posterior myodome) following the discussion of Grande (2010, p. 806) on that feature.

Some of Grande's (2010) characters are not used in the analysis because: (1) in most cases they are not visible on fossil material (Grande's characters 3, 78–81, 83–86, 99, 103, 104); (2) the set of compared species do not show the concerned features or the character is uninformative (11, 54, 76); (3) they are regarded as related to other characters (31 (see discussion of character 8 in Cavin (2010)), 17 (see discussion of character 37 in the appendix), 37 (see discussion of character 3 in Cavin and Suteethorn (2006) and 27 in Cavin (2010)), and 72); or (4) there are too many uncertainties in the recognition of character state (27, 29, 40, 64, 65). Grande's (2010) characters 62 – length of ectopterygoid relative to entopterygoid – and 63 – ectopterygoid participation in palatal surface area – are regarded here as linked, as mentioned by Grande himself. In his data matrix, the distribution of character states for these two characters is similar for all taxa (when characters are known and applicable), except for the obaichthyids which show the plesiomorphic conditions for character 62 only (but the limit between both states rests on an arbitrary value for both characters). Consequently, we prefer here to retain a single character, that is, Grande's character 62 which is a character previously used in phylogenetic studies of gars and 'semionotiformes'. The 69 retained characters, including comments about their origin and definition, and the data matrix are listed in the Appendix S2 of the Additional Supplementary Information.

The taxa included in the phylogenetic analysis are those used in the second analysis of Cavin, that is, the analysis without the taxa containing too much question marks. Contrary to the previous study, we did not use a theoretical outgroup here, but we included *Polypterus ornatus* as outgroup with data collected from Grande (2010). We modified Cavin's former set of data according to a new description of *Obaichthys decoratus* by Grande (2010). On the basis of the latter study, we deleted *'Oniichthys' falipoui*, regarded now as an *Atractosteus*, and we included the type species of *Atractosteus*, *A. spatula*, and the type species of *Lepisosteus*, *L. osseus*, instead of *Lepisosteus* spp. in Cavin (2010). We also added recently described taxa, including *Cuneatus wileyi*, *Masillosteus janeae*, *Dentilepisosteus laevis* according to Grande (2010); *Sangiorgioichthys sui* according to Lopez-Arbarello *et al.* (2011), *Tlayuamichin itztli* according to Lopez-Arbarello and Alvarado-Ortega (2011), and *Semiolepis brembanus* according to Lombardo and Tintori (2008). The list of the examined fossil material and of the consulted references is available in Cavin (2010) including the electronic supplementary material.

In complement to the description of *T. buddhabutrensis*, we examined two acid-prepared *Araripelepidotes temnurus* specimens and several mechanically prepared specimens of *Pliodetes nigeriensis* kept in the Muséum national d'Histoire Naturelle, Paris. These observations led us to add new coding or to alter coding in the data matrix used in the 2010 analysis. For *A. temnurus*, these new observations are the following (Fig. 20). Thies (1996) suggested that the angular and 'surangular' (='supraangular') in this species are either lacking or strongly reduced, the lower jaw being formed mainly by the dentary. In BCE 336, however, a small rounded ossification is visible on the left mandible posterior to the dentary and is regarded here as an angular. Moreover, an articular and a supraangular are also apparently present, although their identification is still uncertain. Consequently, the character 'long posterior process on the dentary in lateral view' – which was regarded as inapplicable in the 2010 analysis – is regarded here as 'absent' (character 56). Moreover, we noticed that the dentary of *A. temnurus* forms anteriorly a 'horizontal blade' reminiscent of the dentary morphology of *T. buddhabutrensis*. This character, not coded in our analysis, adds further weight to possible affinities between both species. The presence versus absence of a prearticular and supraangular (characters 60 and 61, respectively, in the present analysis) was coded as 'absent' in the 2010 analysis. On the basis of the comment above, we prefer here to code both characters with question marks. A medial wing on the cleithrum is present in BCE 336 (character 75), and conspicuous large prominent posteriorly pointing spines are present on the flank scales in BCE 335 (character 87). For *Pliodetes nigeriensis*, the modified characters are the following (Fig. 21). In GDF 1314, an endochondral ethmoid ossification – possibly a lateral ethmoid – is present. Consequently, we coded the character concerning the state of ossification of the ethmoid region (Character 9) as uncertain (question mark). As mentioned by Wenz (1999), the posterior extremity of the nasal process is ornamented with the typical odontodes present on the skull roof in some specimens only. We confirm this observation and modified the coding of the character 'participation of the premaxilla to dermal skull roof cover' (character 15) as 'polymorphic' (and not as 'present' as coded in the 2010 study). We observed a small dermal component of the sphenotic in GDF 1275, GDF 1319 (character 34) and the absence of participation of the dorsal surface of the ectopterygoid forming part of the skull roof in GDF 1275 (character 44). The presence versus absence of a prearticular is unclear (character 60, coded '?' instead of '1'), and a supraangular was observed in GDF 1275 (character 61, coded '1' instead of '0'). Eventually, we also observed the occurrence of conspicuous large prominent posteriorly pointing spines on the flank scales (character 87). The data matrix is shown in Appendix S2.

The parsimony analysis was run in PAUP* 4.0b10 (Swofford 2001). A heuristic search (using random addition sequence, replicate 2000 times, 10 trees held at each iteration, and tree bisection and reconnection branch swapping) was carried out to try to avoid the 'islands of trees' problem (Maddison 1991). Figure 22 shows the strict consensus tree of the 142 most parsimonious trees produced by PAUP (82 characters informative; consistency index 0.42; retention index 0.67). The gars' interrelationships obtained here are similar to those obtained by Grande (2010) and Cavin (2010), keeping in mind that in

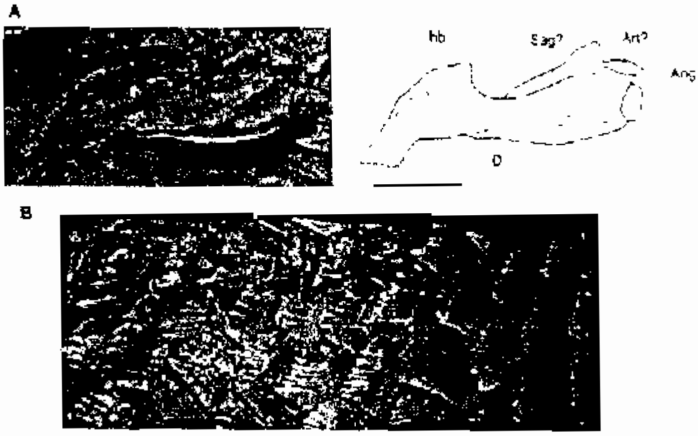

FIG. 20. *Araripelepidotes temnurus.* A, BCE 336, left lower jaw in lateral view; scale bar represents 50 mm. B, BCE 335, squamation of the flank; scale bar represents 30 mm.

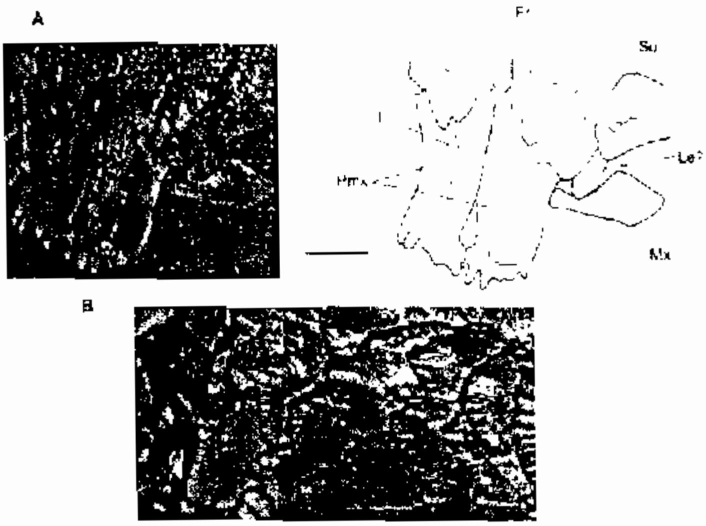

FIG. 21. *Pliodetes nigeriensis*. A, GDF 1314, snout in anterodorsal view. B, GDF 1312, squamation of the flank. Scale bars represent 30 mm.

the later study, *Oniichthys* was regarded as a valid taxon (it was synonymized with *Atractosteus* by Grande (2010)) and that the genus *Dentilepisosteus* was not yet erected.

Holostei, resolved at node 1, are moderately well supported by characters (bootstrap value equals 56, but Bremer support equals 1). Four characters, premaxilla immovably attached to the braincase by means of a long nasal process tightly sutured to the frontals (char. 13), anterior portion of premaxilla lining the nasal pit and pierced by a large foramen for the olfactory nerve (char. 14), presence of a tubular canal bearing anterior arm of the antorbital (char. 26, ci = 1) and compound coronoid process (char. 59, ci = 1, a second derived state is present in *Araripelepidotes + Pliodetes*), are found here and in Grande's analysis. Other characters defining the clade here differ a little from those found by Grande, mainly because of the inclusion of more 'semionotid' taxa. In the present analysis, a tubular rostral (char. 12, Grande's character 5) characterized the Macrosemiiformes and unambiguously supports the node gathering *Semionotus* and more derived taxa. But this character state is plesiomorphic in *Semiolepis* and *Sangiorgioichthys* and consequently does not support the node Holostei in our cladogram. Moreover, the shape of the rostral is polymorphic in halecomorphs (Grande and Bemis 1998), and consequently, we do not retain it in the diagnosis of Holostei. Other characters defining Holostei by Grande show other distribution in our analysis because of their uneven occurrence in the set of compared 'semionotids' (char. 81, Grande's character 87; char. 88, Grande's character 90, char. 34, Grande's character 23). Other differences with the list of characters found by Grande are due to characters not retained in our analysis for reasons explained above (Grande's char. 29, 85, 99), to characters defined in a different way (Grande's char. 37, 96) or to different optimization of character transformations (Grande's char. 53, presence of a supraangular, is better resolved in our analysis as a primitive state lost in the outgroup and in *Araripelepidotes + Pliodetes*). Finally, state 1 of characters 5 and 24 supports the Holostei in our analysis only, but these are homoplasic and the recognition of character 24 in fossil forms is often dubious.

The node 2 corresponds to the Ginglymodi as defined by Grande (2010), that is, the Macrosemiiformes, the Semionotiformes and the Lepisosteiformes. This node is well supported (bootstrap value equals 88, Bremer support is equal or superior to 4) and is defined mainly by the same characters than in Grande's analysis: a series of infraorbitals anterior to the circumorbital ring (char. 22, ci = 1, Grande's character 20 and 21); the size proportion of the lower jaw (char. 55, Grande's character 80); the loss of the gular bone (char. 66, ci = 1, Grande's character 75); the shape of the subopercle (char. 67, ci = 1, Grande's character 71), and a medial wing on the cleithrum (char. 75, ci = 1, Grande's character 94). Differences in characters defining Ginglymodi with Grande's analysis concern: the size proportion of the ethmoid region (char. 8, Grande's character 1) because the defined states of this character are not similar in our study to be applicable to a different set of species; the quadrate in front of the orbit (char. 37; Grande's character 45) because of a different coding in macrosemiids between both studies (see Grande's comment on this character p. 780); the absence of mentomeckelian bone (char. 63,

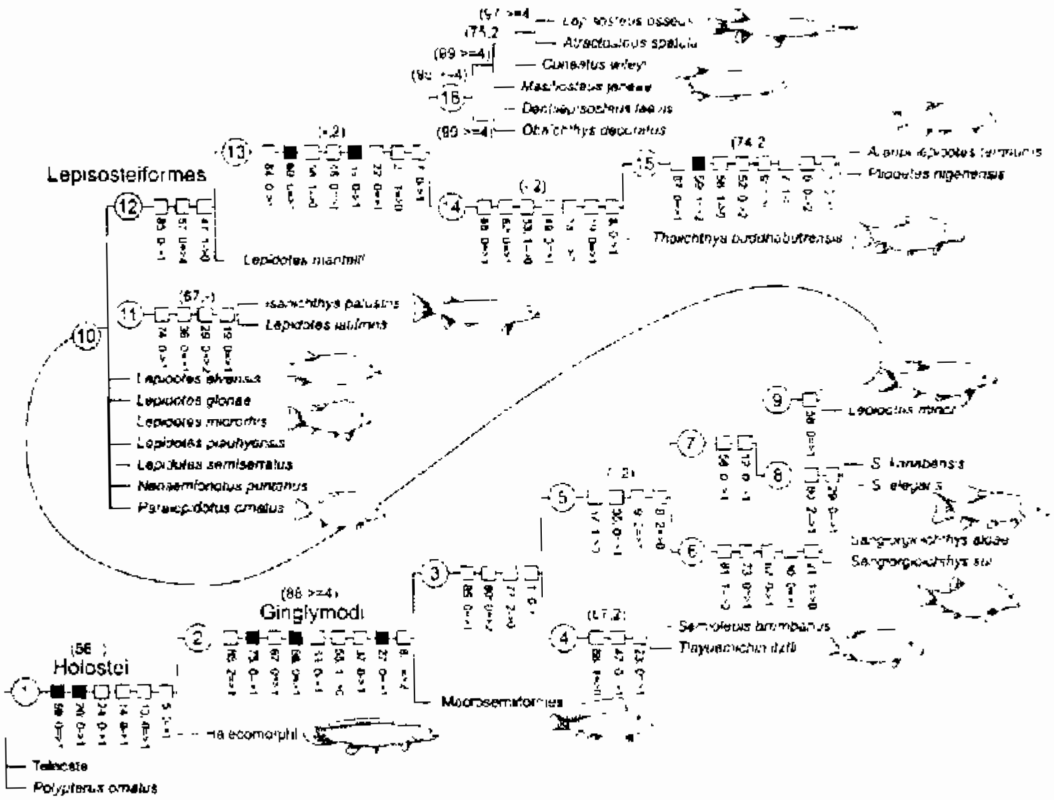

FIG. 22. Strict consensus tree of the 142 most parsimonious tree (length = 277; consistency index 0.41; retention index 0.67). All characters are unordered and have equal weight. ACCTRAN optimization of characters is given below nodes (single-lined arrows mean that the transformation is ambiguous and could be different on alternative equally parsimonious trees or different under the DELTRAN option, double-lined arrows mean the change is unambiguous). Black boxes indicate characters with ci = 1. Characters supporting node 16 and more derived Lepisosteidae, as well as characters supporting terminal taxa, are not figured. In brackets above the node are the bootstrap values if superior to 50 (4000 replicates) and Bremer supports if superior to 1.

Grande's character 58) but this transformation is ambiguous because the state of the character is unknown in most of the fossil forms; enlarged fulcra (char. 88; Grande's character 90 in part) because of different definitions of these character states between both studies. Other differences between both studies are caused by characters not used in the present analysis (Grande's character 31); by a different optimization (char. 44, Grande's character 70); or by the inclusion of new taxa in the present analysis (char. 82, Grande's character 88).

The section B defined by Grande (2010) gathers the Semionotiformes (represented by *Semionotus elegans* only in his analysis) and the Lepisosteiformes. Because we included more 'semionotiform' taxa in our analysis, section B may correspond to three different nodes in our cladogram, that is, nodes 3, 5 and/or 7. In Grande's analysis, the section B is supported by the loss of the ethmoid ossification (char. 9, Grande's char. 35), a character that we found at node 5, with a reversion in *Araripelepidotes* and possibly in *Pliodetes*. In *Tlayuamichin*, the ethmoid region shows a series of ethmoid ossifications (the 'paraethmoid bones' of López-Arbarello and Alvarado-Ortega, 2011), and in *Semiolepis*, the ethmoid region also shows some kind of ossification (Lombardo and Tintori, 2008, fig. 2). Another character found by Grande at this node is the structure of the symplectic, which is separated from the quadrate by the quadratojugal (char. 46; Grande's char. 69). In our analysis, this character supports the node 13 and is present in parallel in *Semionotus elegans*, but it is absent from several *Lepidotes* species. The symplectic is located posteriorly to the quadrate in *Araripelepidotes* (Wenz and Brito 1996, p. 157) and in *Thaiichthys* *buddhabutrensis*. In *Semionotus elegans*, the structure is different because the symplectic, although separated from the quadrate by the quadratojugal, extends ventrally and reaches the level of the quadrate. This character is generally difficult to observe on fossil material, and it will deserve further examination. Other characters supporting this node in Grande's study are uncertain because they are also equally parsimoniously located at the node supporting the Holostei (his characters 6, 8 and 23) or the Ginglymodi (his character 32)

In Figure 22, the node 3 is supported by four homoplasic characters (1, 77, 80 and 85), the node 5, better supported with a Bremer index of 2, is characterized by four homoplasies (8, 9, 35 and 37), including character 9 (ossification of the ethmoid region) discussed above, and node 7 is supported by two character (12 and 56). State 1 of character 56 – a long posterior process on the dentary ventral to the angular – was discussed by Thies (1989*a*) in his search of features characterizing the family Semionotidae. In Figure 22, this state is present in all the terminal taxa including *Semionotus* and more derived species, except in *Pliodetes* and *Araripelepidotes* which show a reversion (but the mandible is much derived in this species). Gars show a second derived state, that is, a long posterior process on the dentary dorsal to the angular.

Node 4, rather well supported with a Bremer support of 2 and a bootstrap value of 67, defines an interesting clade gathering the Late Triassic *Semiolepis* and the Early Cretaceous *Tlayuamichin*. It is supported by three homoplasic characters, which are known in both genera: more than 2, subrectangular extrascapulars (char. 23, state 1), moderately tritorial teeth between palate and coronoids (char. 47, state 1) and small basal and fringing fulcra of the fins (char. 88, state 0). Both genera are actually very similar and share numerous other characters, either plesiomorphic or derived for 'semionotiformes', which are not included in our analysis: the ornamentation of the dermal bones is restricted to the posterior part of the skull roof, the frontals are thin and elongated, the shape and pattern of the infraorbitals are rather similar, the opercular series is short, the postcleithra have similar shape, serrations occur on the posterior margin of some scales, etc. Each taxon shows diagnostic characters that allow distinguishing both species, but we question here the generic status of *Tlayuamichin*, that might be a junior synonymous of *Semiolepis*. Further comparisons are necessary to test this hypothesis

Node 6 supports the genus *Sangiorgioichthys*, and node 8 supports two species of *Semionotus*. The type species of *Semionotus*, *S. bergeri*, has been recently re-described by López-Arbarello (2008). It is, however, too incompletely known to be included in our analysis, and consequently, we cannot ascertain whether both '*Semionotus*' species used here actually belong to this genus. Node 9 groups *L. minor* and the more derived Ginglymodi. It is supported by a single homoplastic character (58). Node 10 gathers a large polytomy, and consequently, the characters supporting it are highly variable among the set of most parsimonious cladograms and not detailed here. Node 11, already found in Cavin (2010) and rather well supported (bootstrap value of 67), groups the Asian Late Jurassic – Early Cretaceous *Isanichthys palustris* and the European Middle Jurassic *Lepidotes latifrons*. Characters supporting this node and observed in both taxa are a frontal as broad anteriorly than posteriorly (char. 19); a mosaic of suborbitals (char. 29, state 2); a proportionally small orbit (char. 36); and presence of a medial process on the supracleithrum (char. 74 state 1, unknown in *Isanichthys*). The character 'elongated body with the dorsal and anal fins located posteriorly' (char. 80) is present in *Isanichthys* and coded as a question mark in *L. latifrons*. A specimen of *L. latifrons* housed in The Natural History Museum, London, (BMNH P.6838) consists of a subcomplete body. Although incomplete, the body appears to have been elongated and the anal fin is located posteriorly (the dorsal fin is not visible). If confirmed, this feature may represent another character shared by both taxa. Node 12 is weakly supported by three homoplasic characters: no tritorial dentition (char. 47); dentary teeth form a single row and are all of similar size, concentrated at the anterior extremity of the mandible (char. 52, state 4) and dorsal ridge scale is present (char. 85). Node 13 is rather well supported compared to other nodes (Bremer support of 2). It is characterized by two uniquely derived characters: no contact or close association between the metapterygoid and the quadrate (char. 39) and the angle between both arms of the preopercle are equal or inferior to 110 degrees (char. 69). The first of this character was not observed in most fossil representatives of that clade, in particular in taxa gathered under node 14, but the second character related to the shape of the preopercle was observed in almost all the species included in the phylogenetic analysis and is regarded as strong for defining this node.

Node 14 is supported by 7 homoplastic characters. Among these characters, one, a maxilla free with posteriorly a constant depth (char. 49, state 1), is known in this clade only within the Ginglymodi (Wenz 1999, fig. 6, Fig. 2, here for *Pliodetes*; Thies 1996, fig. 2 for *Araripelepidotes* and present study for *Thaiichthys*) and is present in parallel in Teleostei. In all other Ginglymodi in which this ossification has been observed, the posterior plate of the maxilla shows a rounded outline, except in Lepisosteidae which have an atrophied maxilla fused with the infraorbitals (state 2). The well-supported node 15 (bootstrap value equals 73, Bremer support equals 2) supports the sister genera *Araripelepidotes* and *Pliodetes*. The node is characterized by seven homoplastic characters and one uniquely derived character. Three of these characters are related to the jaw apparatus: no teeth on the maxilla (char. 52); no posterior process of the dentary (char. 56), and no coronoid process (char. 58, ci = 1). Node 16 and inclusive nodes are similar to those found by Grande (2010) and are not discussed here.

Grande (2010) defined the Lepisosteiformes for gathering the Lepisosteidae and the Obaichthyidae. This clade is supported by several characters, most of them located in node 16 of our cladogram: participation of the premaxilla in the dermal skull roof cover (char. 15, Grande's character 7 (as noted above, some specimens of *Pliodetes* also show this character)), supraorbital canal on the premaxillary process (char. 18, ci = 1, Grande's character 24), junction of supraorbital canal with infraorbital canal in the dermopterotic bone (char. 24, Grande's character 25), a series of paired primary basihyal toothplates supported by a spatulated tongue (char. 64, Grande's character 77), opisthocoelous vertebral centra (char. 77, Grande's character 82), and possibly the absence of post-temporal fossa (char. 2, Grande's character 32) and L-shaped symplectic (char. 45, Grande's character 68).

Because of the inclusion of several 'semionotiform' taxa in the present analysis, the transformation of some characters regarded as supporting Lepisosteiformes in Grande's analysis occurs in other locations on our cladogram: more than two, subrectangular extrascapulars (char. 23, Grande's character 13), laterally sliding articulation between metapterygoid and the basipterygoid process (=parasphenoid-prootic process) in adults (char. 38, Grande's character 59), no quadrate/metapterygoid contact or close association (char. 39, Grande's character 60). Other characters defining the Lepisosteiformes in Grande's analysis have not been taken into account in the present study for reasons explained above (Grande's characters 17, 34, 48, 63, 64, 55).

The 'Semionotiformes' do not constitute a clade in our analysis, and consequently, all 'semionotiformes' should be regarded as stem Lepisosteiformes if we consider a node-based definition for clades. However, because we obtained a bad resolution for most of these taxa (node 10 in Fig. 22), we prefer here: (1) to temporary fix the clade Lepisosteiformes at node 12 keeping in mind that it might also be fixed at node 13 – which is better supported – depending on future studies including new data, and (2) to consider the 'Semionotiformes' as an unresolved group, pending further studies.

The phylogenetic position of *Thaiichthys buddhabutrensis* found in this study differs slightly from the one found in Cavin (2010): it is here resolved as the sister group of *Araripelepidotes* + *Pliodetes*, while it was resolved as the sister group of (*Araripelepidotes* + *Pliodetes*) + (Obaichthyidae + Lepisosteidae) in Cavin (2010) (these family names were not used then). Moreover, *Lepidotes microrhis* and *Neosemionotus puntanus* were resolved as stem Lepisosteiformes, while they are resolved in a polytomy in the present study. These differences are due to the distinct datasets used in both studies, and to variation in the distribution of character transformations. However, although the resolution differs between both studies, common patterns are discernable: (1) *Araripelepidotes* + *Pliodetes* is the sister group to Obaichthyidae + Lepisosteidae and (2) *Thaiichthys buddhabutrensis* and possibly *Lepidotes mantelli* are stem Lepisosteiformes.

CONCLUSION

'Semionotiformes' fishes have always been reluctant to unveil their intrarelationships and their affinities with other neopterygians because their general gross morphology is conservative. Moreover, studies based on large samples show that several of their cranial characters are polymorphic, making difficult the recognition of diagnostic characters and of characters useful for phylogenetic analysis. As noticed since the first studies of this group, important features for understanding the relationships are related to the dentition and to the jaw apparatus. The characters associated with the jaw may be considered as dubious for being used in phylogenetic analyses because they are directly related to the mode of feeding, which can be highly homoplasic. However, their use in combination with characters of the skull roof and of the cheek allows drawing some trends in the evolutionary history of this group. The present analysis is far from being completely satisfying because a large part of the tree is still unresolved and because of the weak support of most of the nodes. However, it provides a preliminary step which needs to be tested using new material and new discussions of the characters defined for the phylogenetic analysis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Appendix S1. List of the referred material.

Appendix S2. Characters and data matrix used in the phylogenetic analysis.

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APPENDIX V

The article has been published in the Late Palaeozoic and Mesozoic Continental Ecosystems in SE Asia, Geological Society special Publication 315.

The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand.

LIONEL CAVIN, UTHUMPORN DEESRI and VARAVUDH SUTEETHORN

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The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand

LIONEL CAVIN[1]*, UTHUMPORN DEESRI[2] & VARAVUDH SUTEETHORN[3]

[1]*Department of Geology and Palaeontology, Muséum d'Histoire naturelle, CP 6434, 1211 Genève 6, Switzerland*

[2]*Phu Kum Khao Dinosaur Research Centre, The Sirindhorn Museum, Sahat Sakhan District, Kalasin 46140, Thailand*

[3]*Bureau of Palaeontological Research and Museum, Rama VI Road, Bangkok 10400, Thailand*

**Corresponding author (e-mail: lionel.cavin@ville-ge.ch)*

Abstract: This first overview of the bony fish record from the Jurassic and Cretaceous continental deposits of Thailand reveals a significant diversity, with 16 taxa in four formations (the Khlong Min, Phu Kradung, Sao Khua and Khok Kruat Fms). Four of these taxa have already been diagnosed and described, and a couple of others are sufficiently well preserved to be diagnosed in the future. The other taxa are represented at present by fragmentary and isolated remains. The highest diversity is observed among 'semionotids', which occur in the four formations. Sinamiids are represented by at least three taxa that occur only in the Sao Khua and the Khok Kruat Formations. Pycnodont fishes are known by rare and isolated dentitions and teeth in the Khlong Min and Sao Khua Formations, and lungfishes referred to *Ferganoceratodus* occur in the Khlong Min and the Phu Kradung Formations. The assemblages provide few palaeogeographical indications at present, except for evidence of relationships with China and Central Asia. However, it is expected than once the phylogenetic relationships of these taxa are resolved, we will be able to reconstruct precise palaeogeographical scenarios.

Bony fish remains represent an important part of the fossils discovered during palaeontological field work conducted in the continental Jurassic and Cretaceous deposits of Thailand for more than 25 years. They have been mentioned in several publications as a component of the vertebrate assemblages, but have rarely been properly described, except for a handful of taxa known from more complete material. No overview of the succession of the fish assemblages throughout the Mesozoic deposits of Thailand has yet been published. Here we describe the fossil record of bony fishes from the Middle–Late Jurassic of the Khlong Min Formation in the peninsula of Thailand to the Early Cretaceous Khok Kruat Formation in the Khorat Plateau. Triassic fishes are known in Thailand, but they are not reviewed here because they belong to assemblages separated from the Jurassic assemblages by a large stratigraphic gap. All specimens described here, unless specified otherwise, are housed in the Sirindhorn Museum, Sahat Sakhan, Kalasin Province.

Geological setting

The bony fish remains described below were found in several localities of the Khorat Plateau in NE Thailand and in one locality in southern Thailand, Mab Ching. The main tectonic units in Thailand comprise two continental blocks or microcontinents (Fig. 1): the eastern part (including the Khorat Plateau) belongs to the Indochina block, and the western part (including the southern peninsula) is part of a block called 'Shan-Thai' or 'Sibumasu'. The stratigraphy of the non-marine sediments in southern peninsular Thailand has been recently reviewed (Teerarungsigul *et al.* 1999). These clastic red beds are known as the Trang Group, which is now subdivided into a basal Khlong Min Formation, overlain by the Lam Thap, Sam Chom and Phun Phin Formations (Meesook *et al.* 2002). The Mab Ching locality in the Khlong Min Formation has yielded hybodont sharks (Cuny *et al.* 2009), lungfishes (Martin *et al.* 1997), temnospondyls (Buffetaut *et al.* 1994), mesosuchian crocodiles and the turtle *Siamochelys* (Tong *et al.* 2002). This formation was dated to the Middle or Late Jurassic on the basis of charophytes and palynomorphs (Lei 1993; Buffetaut *et al.* 1994), an age confirmed by the turtles (Tong *et al.* 2002; see also Cuny *et al.* 2009). The occurrence of a euhelopodid sauropod in the Khlong Min Formation indicates a continental connection with mainland Asia (Buffetaut *et al.* 2006).

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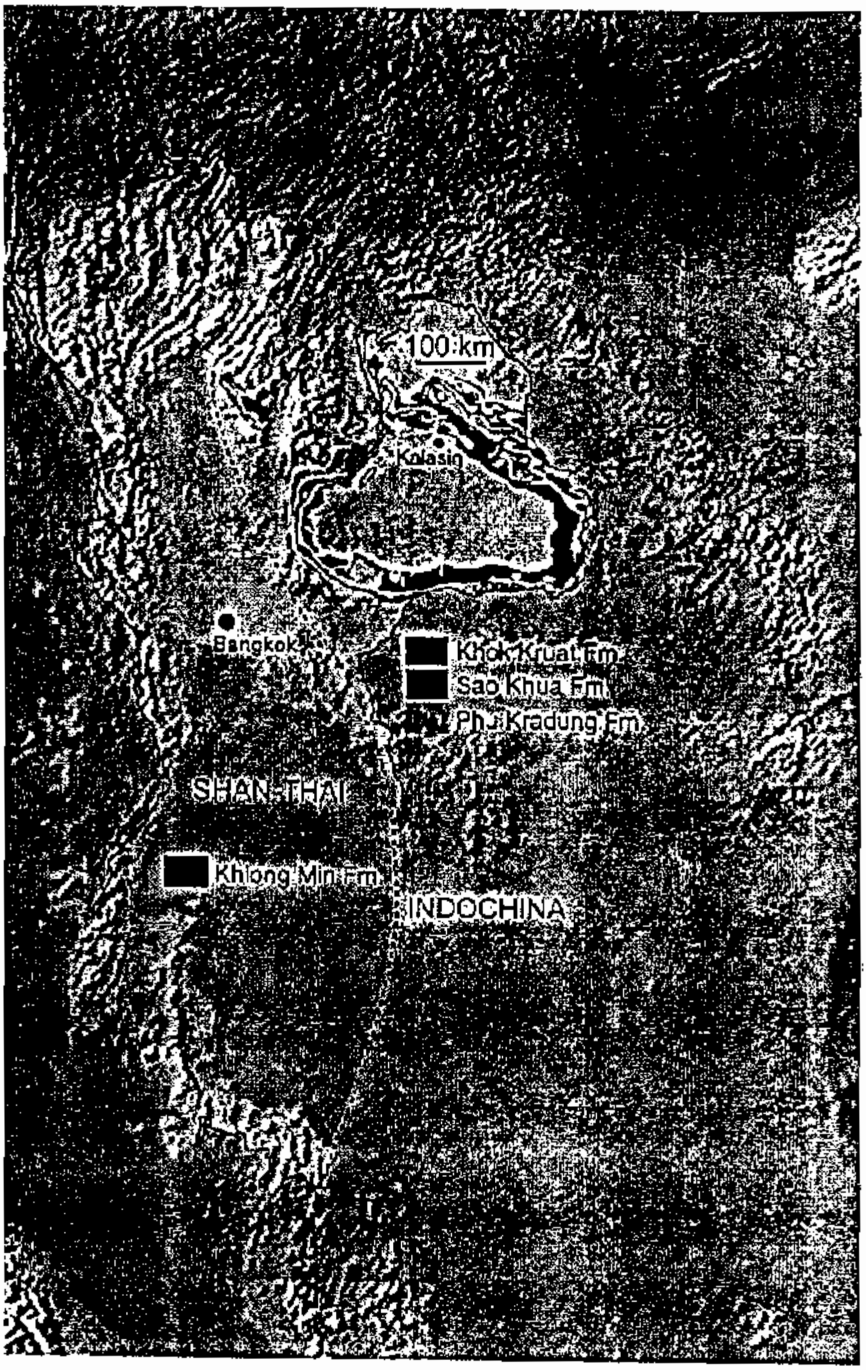

Fig. 1. Map of SE Asia, showing location of the geological formations yielding fossils described in the text.

The Khorat Plateau in NE Thailand is composed of non-marine sediments deposited during the Mesozoic. A recent study (Carter & Bristow 2003) restricted the Khorat Group to five formations: the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat Formations, in ascending order. The main lithologies of the rocks are reddish brown to light grey sandstones, conglomeratic sandstones, siltstones, claystones and conglomerates. The rocks are interpreted as having been deposited

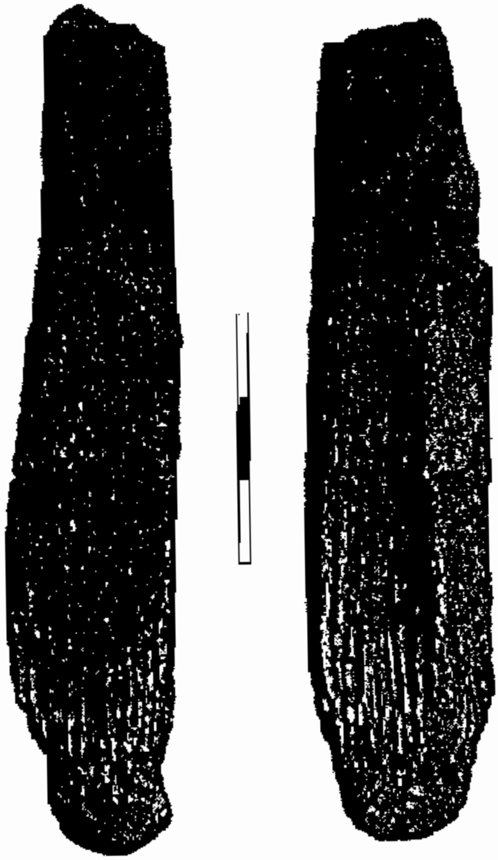

Fig. 2. Isolated spine of an indeterminate actinopterygian (TF 8022), Chong Chat, Phu Kradung Formation. Scale bar, 15 mm.

by meandering and braided rivers in semi-arid conditions (Meesook 2000). In the Khorat Plateau, three of the five formations have yielded vertebrate body fossils. The Phu Kradung Formation provided no conclusive fossils for dating, but as it is conformably overlain by the Early Cretaceous Phra Wihan Formation, which contains palynomorphs at its base, the Phu Kradung Formation is regarded as Late Jurassic or Early Cretaceous in age (Racey *et al.* 1996). Dinosaur remains from the Phu Kradung Formation favour a Late Jurassic age (Buffetaut & Suteethorn 2007). The topmost formation of the Khorat Group, the Khok Kruat Formation, is Aptian in age based on palynomorphs (Racey *et al.* 1996) and vertebrates (Cappetta *et al.* 1990). The Sao Khua Formation overlies the Phra Wihan Formation and is separated from the Khok Kruat Formation by the Phu Phan Formation. Its age is thus constrained to the Early Cretaceous (probably Hauterivian to Barremian).

Institutional abbreviations

MHNG: collection of the Natural History Museum of Geneva, Switzerland. TF: collection of the Sirindhorn Museum, Sahat Sakhan, Kalasin Province. SHM: collection of the Srisuk's House Museum, Khao Yoi, Petchaburi Province.

Systematic palaeontology

Osteichthyes Huxley
Actinopterygii Cope
Indeterminate

Phu Kradung Formation

An isolated spine from the locality of Chong Chat in the Phu Kradung Formation shows a spherical articular proximal head and parallel ridges running along its base (TF 8022, Fig. 2). Three main edges make the spine triangular in section, with one border of the triangle concave in shape. There is a trace of enamel on the surface and no axis of symmetry, indicating that it may correspond to a spine bordering a paired fin. The spherical articular head differs from the spines of chondrichthyes and the specimen is provisionally referred to an indeterminate actinopterygian.

'Palaeonisciformes' Hay
cf. *Ptycholepis* Agassiz

Phu Kradung Formation

Pieces of an articulated fish from the locality of Khok Sanam were discovered in July 1997. The specimen comprises several slabs of fine sandstone, with the most complete part consisting of a fragment of a squamation (TF 8023, Fig. 3a) plus five pieces with a few articulated scales. Most of the scales have gone, leaving only dark imprints in the sediment. A few scales, however, are still preserved and show a typical ganoin covering. Thirteen rows of scales are preserved. Scales of the first 11 rows are curved, slightly sigmoidal, and elongated in shape. The short posterior border of each scale is fringed as the result of two or three grooves in the ganoin covering (visible as ridges on the imprints) extending along the posterior half of the scales. The ventralmost two pieces of scales of the fifth row display a peculiar ornamentation with curved and reticulated grooves. They are regarded here as fragments of a cloacal scale. The twelfth row is composed of very shallow and elongated scales, with a groove running along their whole length, and a tapering and slightly curved posterior extremity. This row is separated from the more anterior scales by a

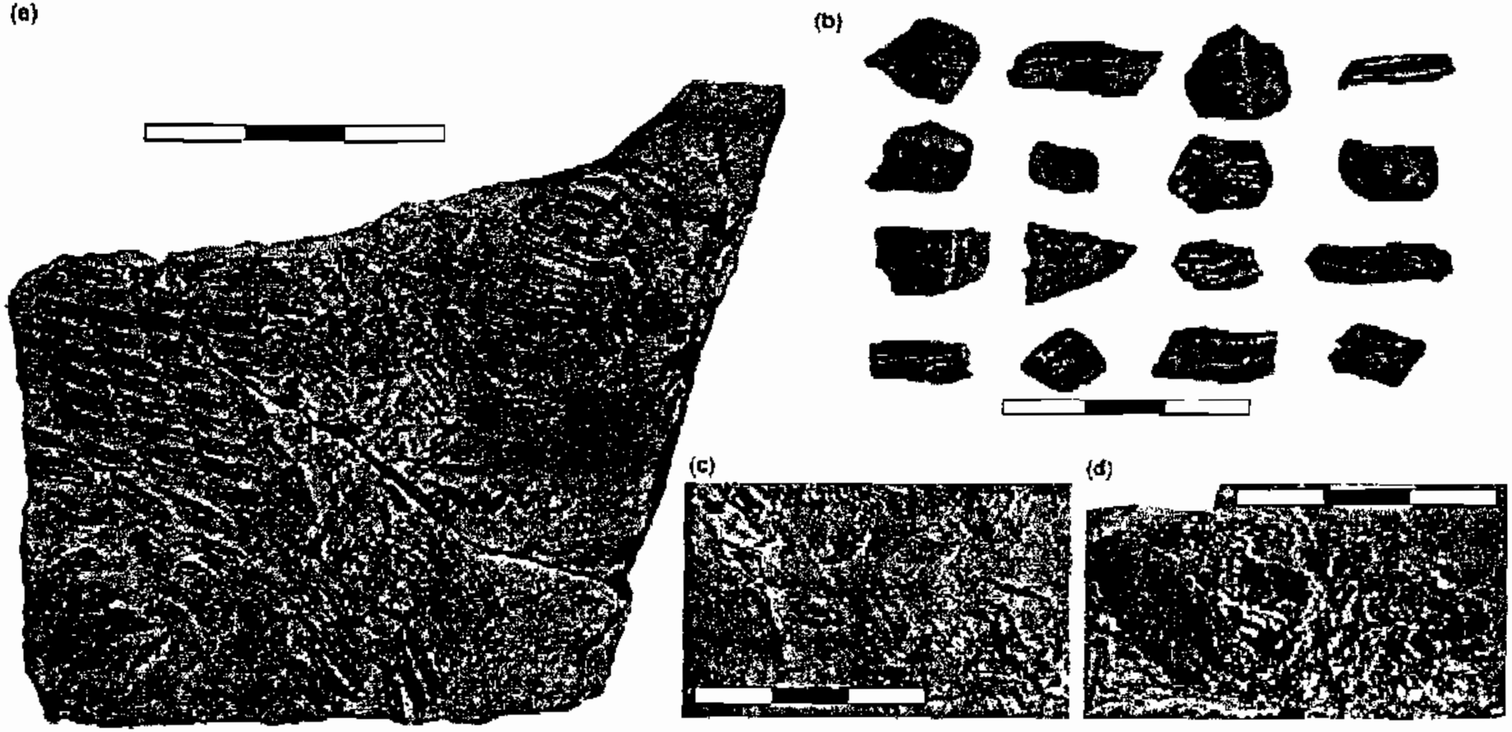

Fig. 3. Cf *Ptycholepis*, Khok Sanam, Phu Kradung Formation. (a) Portion of an articulated specimen (TF 8023). Scale bar: 30 mm. (b - d) Portion of an articulated specimen and isolated elements from a single specimen (TF 8024). (b) Collection of isolated scales. Scale bar: 15 mm. (c) Disarticulated scales on a slab. Scale bar: 30 mm. (d) Fragment of the skull. Scale bar: 30 mm.

gap, but this is probably due to a taphonomic process. The scales of the last row have long axes at an angle of about 35° to the axes of the other scales. Although poorly preserved, the general shape appears fan-like, with a tapering proximal end, and a surface ornamented with smooth grooves. Because of their orientation and morphology, they are regarded as lepidotrichs.

Another semi-articulated specimen discovered in February 2004 may be referred to the same taxon (TF 8024, Fig. 3b–d). The morphology of the scales is variable (Fig. 3b). Elongated scales with longitudinal ridges ending posteriorly as spines are preserved on pieces of sandstone. Fragments of bones ornamented with tubercles are present, but most of them are not identifiable. Isolated scales show that the basal bony plates are proportionally thick, generally with a budge in a non-central position. A fragment of the skull visible in internal view is present, but the bones are too fractured to allow identification (Fig. 3d).

Scales with similar morphology have been discovered in the locality of Wang Din So, near Phitsanulok, in the Phu Kradung Formation (P. Srisuk, pers. comm.). Thick elongated ganoid scales with longitudinal ridges or grooves are not common among Holostei, but they occur in more basal actinopterygians. *Ptycholepis*, in particular, has scales with such ornamentation (Bürgin 1992). A specimen of *P. bollensis* from the Early Jurassic of Holzmaden, housed in the Geneva Natural History Museum (MHNG V. 1600), shows that scales located in the posterior part of the body, near the dorsal and ventral borders of the body, are very shallow and elongated, and slightly sigmoid in shape. The cloacal scale, moreover, is proportionally larger and shows patterns of ganoid ridges reminiscent of some of the larger scales in the Thai specimen, although the pattern is symmetrical and more regular in the German species. If the specimens from Khok Sanam are correctly interpreted, an important difference from *Ptycholepis bollensis* and the Triassic species of *Ptycholepis*, as far as this part of the body is known (Bürgin 1992), is the longer anal fin in the Thai species. Although other basal actinopterygians display ganoid scales with strong ornamentation, *Colobodus* (Mutter 2004) or *Ameghinichthys antarcticus* from the Tithonian of the Antarctic Peninsula (Arratia *et al.* 2004) for instance, they are never as shallow as in *Ptycholepis*. Consequently, we refer that material provisionally to cf. *Ptycholepis*. *Ptycholepis* is a genus known from the middle Triassic to the late Early Jurassic (Bürgin 1992). If it belongs to that genus, the Thai taxon is probably the youngest one known so far. Other 'palaeonisciforms' are known in the Late Jurassic and in the Early Cretaceous, such as several species of *Coccolepis* and some related genera (Hilton *et al.* 2004), but these are very different from the specimens described here. The occurrence of cf. *Ptycholepis* in the Phu Kradung Formation supports an 'old' age for that formation, Late Jurassic rather than Early Cretaceous, in accordance with dinosaur remains (Buffetaut & Suteethorn 2007). However, we should keep in mind that (1) the assignation of that material to cf. *Ptycholepis* is tentative, pending the discovery of more complete material, and (2) if the identification is confirmed, the occurrence of *Ptycholepis* in the Early Cretaceous is not impossible in freshwater environments, where basal fish taxa appear to persist longer. A 'palaeonisciform' has been reported from the Late Jurassic Long Binh Formation in Vietnam (Filleul & Vu Khuc 2001), but its state of preservation does not allow comparisons with material from Khok Sanam.

Holostei *sensu* Grande 2005
Semionotiformes *sensu* Olsen & McCune 1991
'Semionotidae' *incertae sedis*

Pending a better diagnosis of the taxa described here, we refer here to the poorly defined and possibly not monophyletic family 'Semionotidae' (or 'semionotids') all the fish remains that share with *Semionotus*, *Lepidotes* and relatives similar gross morphology of scales and, for some of them, dentition. Ganoid scales (i.e. scales with a bony plate covered by ganoin) occur in other taxa than 'Semionotidae'. We observed the general morphology of ganoid scales from taxa belonging to several clades of basal actinopterygians (Fig. 4). Different morphologies can be recognized in scales located in the lateral abdominal area among these clades (scales located near the dorsal and ventral margins, as well as scales from the caudal area have less characteristic shape). Most taxa have one or two pegs located on the dorsal margin of the scales (basal teleosts, aspidorhynchiformes, *Dapedium*, macrosemiids, ionoscopiforms) or have no pegs at all (ginglymodi, amiiforms) (personal observations). 'Semionotidae' (*Lepidotes*, *Semionotus* and some closely related genera) are the only taxa we checked that have pegs at both the dorsal and ventral edges of the anterior margin of the scales (Fig. 4, arrows). This feature has been observed in several species referred to the genus *Lepidotes* housed in the Natural History Museum in London (i.e. *L. latifrons*, *L. elvensis*, *L. minor* and *L. semiserratus*). Although a broader survey will be necessary to assess the distribution of this feature, we hypothesize here that the presence of two pegs on the anterior margin of ganoid scales is an apomorphy shared by *Lepidotes*, *Semionotus* and probably some closely related taxa. This character allows assignment of isolated scales to 'Semionotidae'

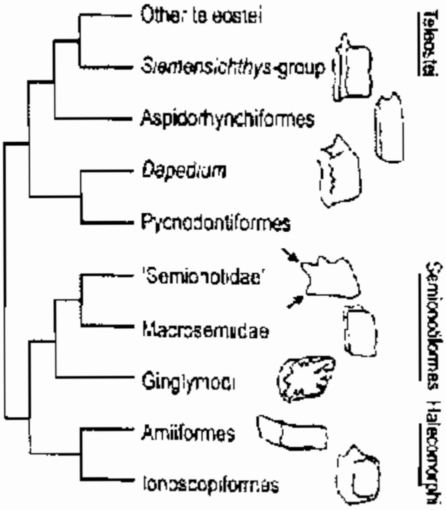

Fig. 4. Schematic outlines of scales from the abdominal flanks of various basal actinopterygians mapped on a composite phylogeny. 'Semionotidae' (*Lepidotes*, *Semionotus* and some closely related genera) are the only ones to bear pegs at the dorsal and ventral edges of the anterior margin of the scales (arrows). *Siemensichthys* group: *Siemensichthys macrocephalus*, redrawn from Arratia (2000, fig. 10); Aspidorhynchiformes: *Belonostomus genevensis*, MHNG V. 1672; *Dapedium*: *Dapedium* sp., MHNG V. 1589; 'Semionotidae': *Lepidotes mantelli*, redrawn from Woodward (1916, plate VII, fig. 5); Macrosemiidae: *Notagogus denticulatus*, redrawn from Schultze (1996, fig. 5); Ginglymodi: *Atractosteus africanus*, redrawn from Cavin *et al.* (1996, plate I, fig. 4); Amiiformes: *Sinamia zdanskyi*, redrawn from Schultze (1996, fig. 5); Ionoscopiformes: *Oligopleurus* sp. (regarded tentatively as an ionoscopiformes here), MHNG V. 1797.

Khlong Min Formation

The locality of Mab Ching in peninsular Thailand, on the Shan-Thai block, yielded smooth ganoid scales and some skull fragments assigned to a 'semionotid' fish. Some scales are large, more than 2.5 cm in length, and correspond to individuals that were over 1 m in length. A small isolated tooth, with a bulbous crown and a conical cap of acrodine, is referred with caution to that taxon (Fig. 5). No button-shaped tooth has been reported from the Khlong Min Formation so far.

Phu Kradung Formation

The Phu Kradung Formation yielded a rich 'semionotid' fauna. Two species, *Lepidotes buddhabutrensis* Cavin *et al.* 2003 and *Isanichthys palustris* Cavin & Suteethorn 2006, have been described from the Phu Nam Jun locality on the basis of articulated specimens, and will not be mentioned here, except for purposes of comparison. Scales of both taxa were sampled on articulated specimens and are shown in Figure 5. It is noteworthy that *L. buddhabutrensis* has been referred with caution to the genus *Lepidotes*, but a study in progress shows that it is not closely related to the type species, *L. elvensis* (de Blainville 1818), and it will probably be assigned to a new genus. Two other localities of the Phu Kradung Formation yield abundant 'semionotid' remains: Khok Sanam and Chong Chat. Apart from numerous isolated thick and smooth ganoid scales and some skull bones (among them a probable extrascapula), the locality of Khok Sanam yielded five fragment of a single *Lepidotes*-like individual. Each piece shows large diamond-shaped ganoid scales. The almost complete left opercle is preserved (TF 8025, Fig. 6a). The bone is 1.7 times deeper than long and its surface is marked with faint grooves diverging from the centre of ossification. The articular facet is large, it protrudes slightly from the anterior margin, and its external side is marked by a thickening of the bone. The dorsal margin of the bone is straight and horizontal. The posterior margin is regularly curved and the bone tapers to a point ventrally. The anterior margin is slightly convex. An area along the anterior border of the bone forms a plane, which marks an angle with the main body of the bone; this surface was probably covered by the preopercle. The shape of the opercle of this *Lepidotes*-like fish differs from that of *L. buddhabutrensis*, which is almost square in shape and has no ventral tapering (Fig. 6b). The individual from Khok Sanam shows a fragment of an elongated bone, slightly shifted, with a 'L' section reminiscent of the cleithrum. Another piece contains the left cleithrum still embedded in matrix with scales and fragments of bones. The identification of these fragmentary specimens is tentative. Isolated scales from Khok Sanam, with similar gross morphology to scales attached to the opercle, show the bases of two broken anterior pegs, which are anteriorly directed (Fig. 5). Although most 'semionotids' have an opercle with a straight and long horizontal ventral margin, there are 'semionotids', such as *L. lennieri* (Wenz 1967), with an opercle with a ventral tapering extremity. The shape of the opercle of the specimen from Khok Sanam differs from that of *L. buddhabutrensis*, which is almost square in shape and has no ventral tapering (Fig. 6b).

Chong Chat yielded numerous isolated 'semionotid' material and a sub-complete specimen (TF 8026), which is currently under description. It is now unclear if this specimen belongs to *L. buddhabutrensis*. It can be distinguished from *I. palustris* by its deeper body, with at least 30 rows

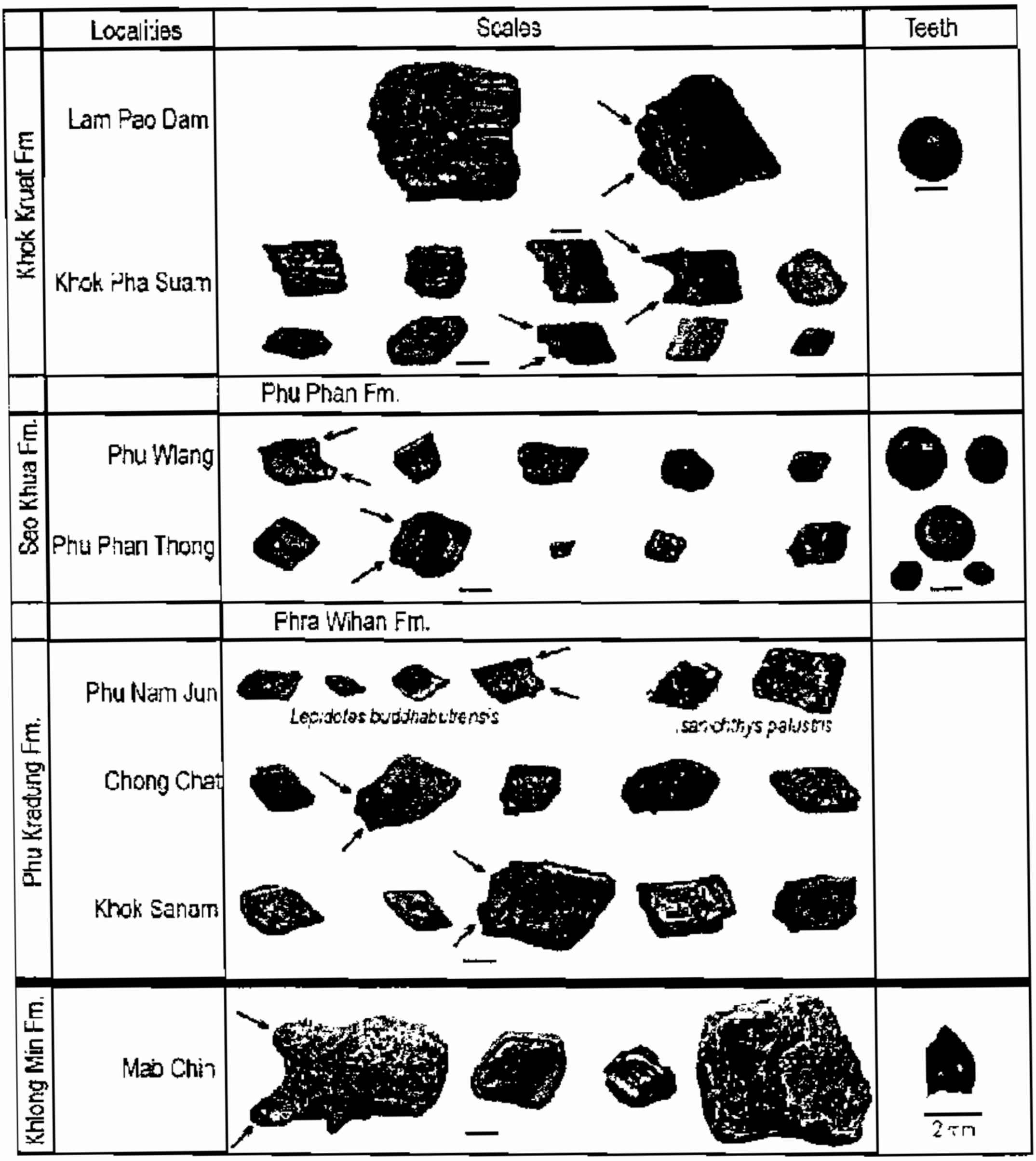

Fig. 5. Diversity of 'semionotid' remains in the Jurassic and Cretaceous of Thailand. Only a selection of localities and specimens is shown. The succession between localities within each formation does not correspond to the stratigraphic succession. The two lines of scales for Khok Pha Suam correspond to the two recognized taxa known in that locality (scales with ridges and smooth scales). Arrows show both anterior pegs. All specimens are at the same scale, unless otherwise specified (scale bars: 5 mm).

of scales along a vertical series in the middle of the body, whereas *I. palustris* has only 20, among other characters.

Dan Luang, Phu Dan Kaeng, Lam Payang (Phu Klang) and Wan Din So are other localities of the Phu Kradung Formation yielding smooth ganoid *Lepidotes*-like scales. It is worth pointing out that no button-shaped crushing teeth are known from the Phu Kradung Formation so far.

Sao Khua Formation

The localities of Phu Wiang, Phu Phan Thong, Phu Mai Paw in the Sao Khua Formation have yielded

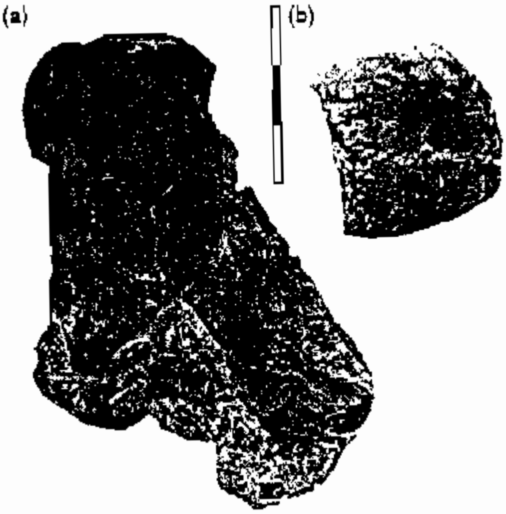

Fig. 6. (a) Left opercle and fragment of squamation of a 'semionotid' fish (TF 8025), Khok Sanam, Phu Kradung Formation. (b) Left opercle of *Lepidotes buddhabutrensis*, Phu Nam Jun, Phu Kradung Formation, K12-2 (holotype). Scale bar: 30 mm.

smooth ganoid scales and button-shaped crushing teeth referable to 'semionotids' (Fig. 5). The localities of Phu Kum Khao (K4) and Phu Phok, in the Sao Khua Formation, have both yielded a single button-shaped tooth referable to a 'semionotid' (the Phu Phok material includes numerous ganoid scales, but most of them probably belong to sinamiids; see below). Cuny *et al.* (2006) reported button-shaped and hook-shaped pharyngeal teeth in the Phu Phan Thong locality that are referable to *Lepidotes*. The button-shaped teeth are rounded or ovoid, with a smooth surface and sometimes a small pit at their apex (Fig. 5). We are not able to distinguish several taxa among the available 'semionotid' remains from the Sao Khua Formation at present.

Khok Kruat Formation

The Khok Pha Suam locality has yielded the most abundant 'semionotid' material from the Khok Kruat Formation. Thousands of isolated scales have been collected. They can easily be separated into two sets (Fig. 5). One set is represented by smooth ganoid scales, with the lateral face showing a narrow band without ganoin that was covered by the anterior scale. The other set consists of slightly larger scales on average, and the ganoid surface is ornamented with parallel or slightly diverging grooves that sometimes mark the posterior edge of the ganoin with a denticulate pattern. These scales are deeper on average than those from the other set, they have better-marked edges, and the anterior ganoin-free area that was covered by the preceding scale is proportionally larger. In well-preserved scales, the anterior margin bears dorsally and ventrally a pair of well-developed pegs. As the morphology of the scales of the two sets is clearly distinguishable, and as no scale with intermediate morphology between the two sets has been found, we regard them as belonging to two different taxa. Dorsal ridge scales are abundant at Khok Pha Suam and show a great variety of shape. These scales have been used to distinguish species, or populations, among semionotid assemblages of the Late Triassic of the USA (McCune 1987). However, this diagnostic feature cannot be used on the Khok Pha Suam material, as articulated specimens are not available. Although we cannot completely rule out the possibility that the scales of Khok Pha Suam do not belong to a 'semionotid', their general morphology, with a pair of well-developed anterior pegs, is in favour of an assignment to 'semionotids'.

No button-shaped crushing teeth are known from Khok Pha Suam at present. This is probably not a sampling artefact, as these teeth are extremely resistant and the collecting effort was considerable at this site.

In the locality of Lam Pao Dam a large *Lepidotes*-like fish is known from button-shaped crushing teeth and thick ganoid scales. The latter show traces of two anterior pegs, and their surface is ornamented with parallel rows of small pits (Fig. 5). An indeterminate piece of bone from the skull shows a rather similar ornamentation, indicating that this pattern probably covered the whole body. This pattern is unique among 'semionotids' from Thailand and probably corresponds to a particular taxon.

Isolated 'semionotid' remains constitute a large component of the fossil vertebrates from Jurassic and Cretaceous localities of Thailand. Figure 5 provides an overview of the main types of scales and teeth in the succession of formations. Although few taxa are sufficiently known to be diagnosed, seven forms can be distinguished on the basis of the scales–teeth associations found among the assemblages: a large semionotiform in the Khlong Min Formation, two or three taxa in the Phu Kradung Formation (two in Phu Nam Jun, *L. buddhabutrensis* and *Isanichthys*, and possibly one in Chong Chat represented by a sub-complete specimen), one with crushing teeth in the Sao Khua Formation, three in the Khok Kruat Formation (two forms without crushing teeth in Khok Pha Suam distinguishable on the basis of the scale morphology, and a large one with crushing teeth in Lam Pao Dam). A histological study of the micro-ornamentation of the surface of the ganoin conducted by one of us (U.D.) should allow the testing of this diversity by using another approach.

Halecomorphi *sensu* Grande & Bemis 1998
Caturidae Owen
cf. *Caturus* Agassiz

Sao Khua Formation

Cuny *et al.* (2006) reported from the Phu Phan Thong locality pointed teeth with two well-developed carinae, which may belong to cf. *Caturus*.

Sinamiidae Berg

Sao Khua Formation

The first sinamiid from SE Asia, *Siamamia naga* Cavin *et al.* (2007*b*), was reported in the locality of Phu Phok. Since then, remains of sinamiids have been recognized in the collection of the Sirindhorn Museum, coming from several other localities in the Sao Khua Formation. An isolated basioccipital similar in structure to the basioccipital from *Siamamia naga* is known from the locality of Phu Mai Paw (TF 8027, Fig. 7b). It shares with *S. naga* lateral sides of the ossification deeply excavated, an anterior process that was embedded in the cartilage flooring the brain cavity, a V-shaped concavity and paired unfinished areas that were capped with cartilage on the dorsal side of the bone. However, differences from *S. naga* are observed, especially in the proportions of the ossification, which is shorter, wider and flatter in the Phu Mai Paw material. The isolated ganoid scales from Phu Mai Paw may be referred to the sinamiid because of an almost complete covering of the dorsal surface by a thin layer of ganoin (there was probably no overlapping between scales) and because of the absence of peg and socket structure.

A small articulated sinamiid specimen comprising the head and about half of the squamation was discovered in Phu Phok (TF 8028, Fig. 8). The skull, nearly 25 mm in length, is preserved in three dimensions and weakly distorted, but the ossifications are fractured, making the recognition of sutures difficult. The parietal appears to be unpaired, which is an autapomorphy of the sinamiids. The recognizable skull bone pattern agrees with the sinamiid pattern in the shape of the frontal, dermopterotic and preopercle, and the shape of the teeth. The scales are also reminiscent of sinamiid scales in their complete and thin ganoin covering. There are, however, significant differences from other sinamiids, in particular from *Siamamia naga*. The main difference is the lower jaw, which appears to be short and very deep, with a short anterior

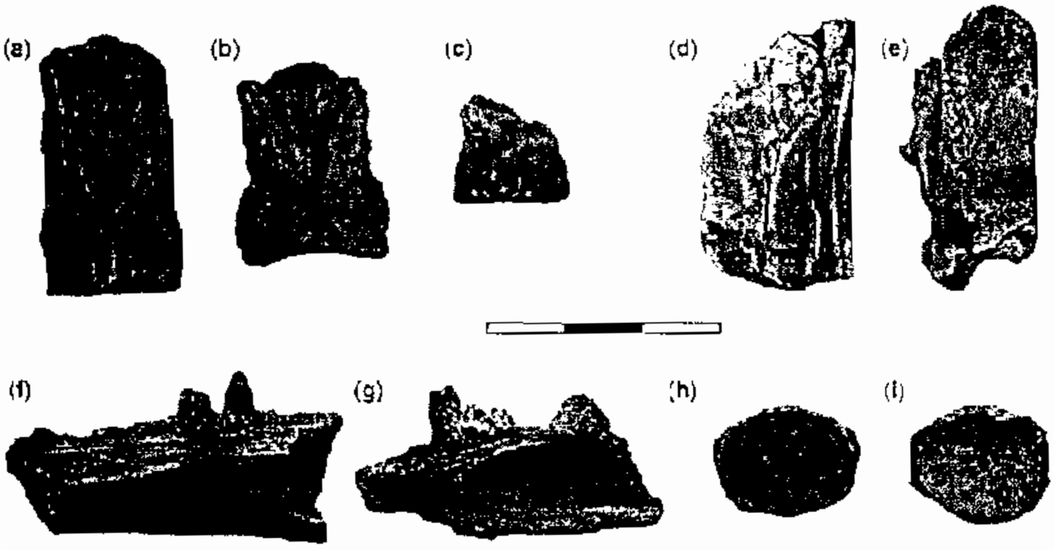

Fig. 7. Sinamiidae. (a–c) Basioccipitals in dorsal views. (a) *Siamamia naga* (TF 8008), Phu Phok, Sao Khua Formation; (b) sinamiid indet. (TF 8027), Phu Mai Paw, Sao Khua Formation; (c) sinamiid indet. (TF 8030), Khok Pha Suam, Khok Kruat Formation. (d, e) Left dermopterotics. (d) *Siamamia naga* (TF 8005), Phu Phok, Sao Khua Formation; (e) sinamiid indet. (TF 8032), Khok Pha Suam, Khok Kruat Formation; (f, g) Right dentaries. (f) *Siamamia naga*, Phu Phok, Sao Khua Formation. (g) sinamiid indet. (TF 8031), Khok Pha Suam, Khok Kruat Formation. (h, i) Centra. (h) *Siamamia naga* (TF 8015), Phu Phok, Sao Khua Formation; (i) sinamiid indet. (TF 8029), Khok Pha Suam, Khok Kruat Formation. Scale bar: 15 mm.

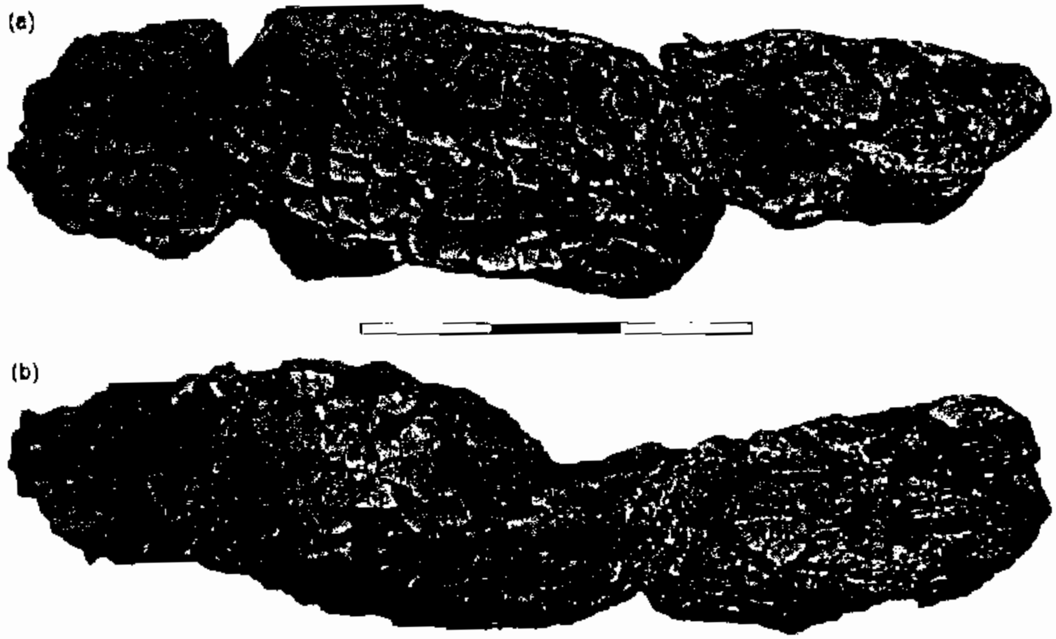

Fig. 8. Subcomplete individual of an indeterminate Sinamiidae (TF 8028), Phu Phok, Sao Khua Formation. (a) lateral view; (b) dorsal view. Scale bar: 30 mm.

toothed area (seven cylindrical teeth with a sharp apex are visible on the right hemi-mandible), followed posteriorly by a deep coronoid process. The ventral margin of the lower jaw is gently curved and the articulation with the quadrate is probably anterior to the orbit. This specimen, which probably belongs to a new taxon, is currently under description.

Khok Kruat Formation

Five centra, a posterior fragment of a basioccipital, fragments of jaws, a piece of a left dermopterotic and scales from the locality of Khok Pha Suam can be assigned with confidence to a sinamiid fish. The centra are ovoid in shape, short, with lateral faces ornamented with small grooves in small individuals and almost smooth in large ones. One small centrum is pierced by a small hole for the notochord (TF 8029, Fig. 7i). The fragment of basioccipital (TF 8030) has the lateral sides deeply excavated with a foramen in the bottom, and paired unfinished areas that were capped with cartilage dorsally. The shape in ventral view, with diverging ridges, is more reminiscent of the sinamiid from Phu Mai Paw than of *S. naga* from Phu Phok (compare Fig. 7a, b and c). Pieces of jaws comprise two fragments of dentaries, a fragment of a premaxilla and two fragments referred with caution to maxillae. The largest fragment of dentary is a right one still bearing three broken teeth (TF 8031, Fig. 7g). The teeth are slightly anteroposteriorly compressed, with a cylindrical shaft that slightly curved inward at the top. In internal view a large V-shaped concavity for the Meckel cartilage is present. The ventral margin of the bone marks a thinning just anterior to the anterior extremity of the concavity, indicating that the symphyseal region was probably shallower than the posterior region of the mandible. The other fragment shows laterally five elongated openings for the mandibular sensory canal and dorsally the sockets for seven compressed teeth. The general shape of these ossifications is reminiscent of *S. naga* (in the shape of teeth, and the opening for the sensory canal) but in the Khok Pha Suam specimen the lower jaw looks shallower at the symphysis, and was probably shorter in length. A fragment of a premaxilla, probably the posterior part of a left one, is present. The sockets for three large teeth, slightly compressed anteroposteriorly, are visible. There are no marked differences from that part of the premaxilla in *S. naga*. The two small fragments referred to maxillae bear deep sockets for the teeth. One has empty sockets, subrectangular in shape, and the other still has some small pointed teeth covered laterally by a bony lamella. The former specimen is reminiscent of *S. naga*, whereas the latter is only tentatively referred to a sinamiid here. The left dermopterotic (TF 8032) is reminiscent of that of *S. naga* with its flat dorsal face (skull roof) and a ventral lamina. However, this lamina is more developed than in the Phu Phok species and the ornamentation on the dorsal face is coarser (compare Fig. 7d and e).

As described above, the sinamiid remains from Khok Pha Suam show differences from *S. naga* from the Sao Khua Formation of Phu Phok, and this sinamiid probably belongs to another taxon. However, more diagnostic material is required to coin a new name.

Pycnodontiformes Berg
cf. *Gyrodus* Agassiz

Khlong Min Formation

A small prearticular pycnodont dentition, preserved on a slab of sandstone, is reported from the locality of Mab Ching (TF 8033, Fig. 9a and b). The specimen, 9 mm in length, bears three main rows of teeth. The lateral-most row comprises nine large ovoid teeth decreasing in size anteriorly. The two large posterior-most teeth bear two rows of faint tubercles, whereas the anterior teeth are smooth. The medial row consists of 12 transversally elongated

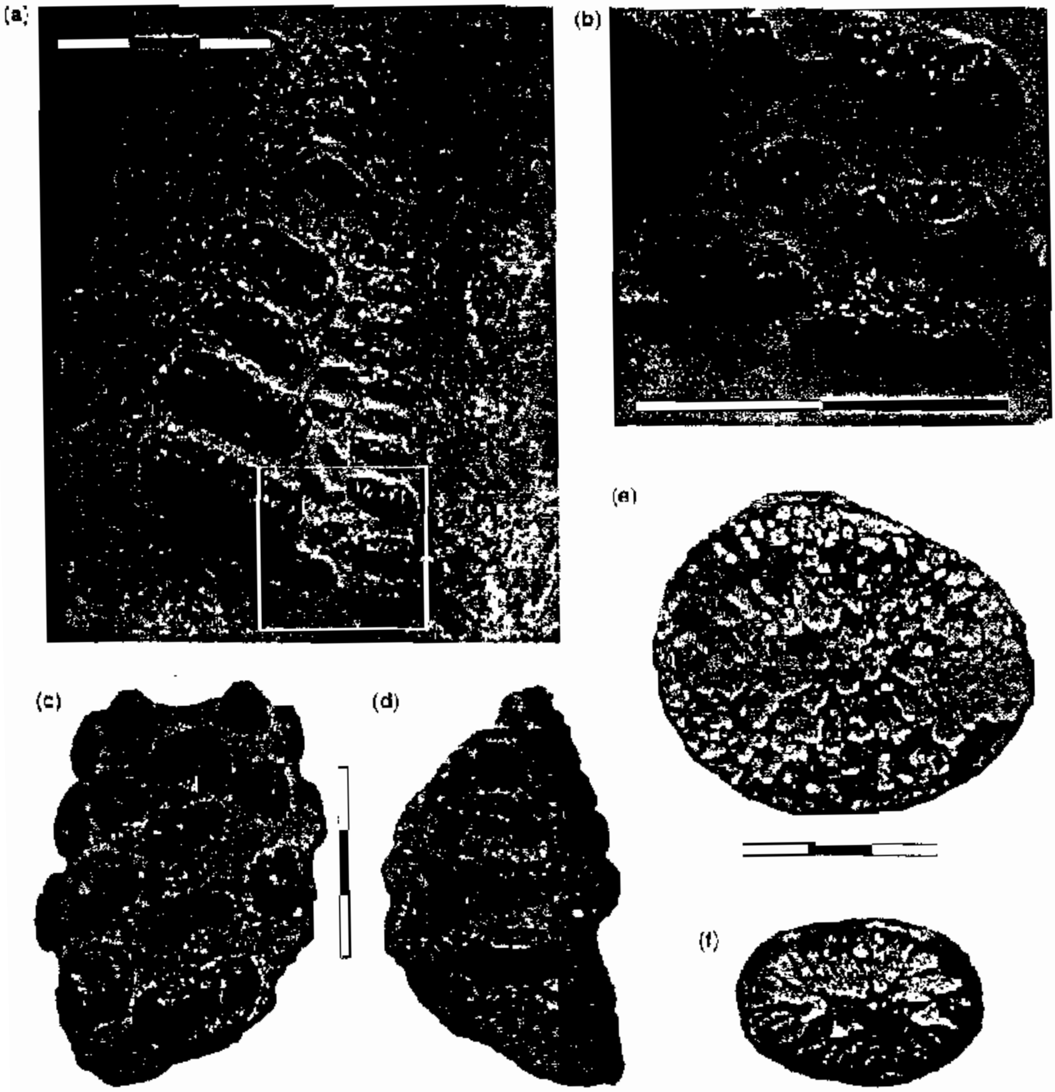

Fig. 9. Pycnodontiformes. (a–b) Left prearticular dentition of cf. *Gyrodus* (TF 8033), Mab Ching, Khlong Min Formation. (a) Complete dentition, scale bar: 3 mm; (b) close up view of the outlined area in (a), scale bar: 2 mm. (c–f) Vomers ((c) TF 8034; (d) TF 8035) and isolated teeth ((e) TF 8036; (f) TF 8037) of cf. *Anomoeodus*, Phu Phan Thong, Sao Khua Formation. (c–f) Scale bars: 3 mm.

Table 1. *Jurassic and Cretaceous bony fish taxa from Thailand*

	Actino. indet.	cf. *Ptycholepis*	Semio. indet 1	*L. buddhabutrensis*	*L. palustris*	Semio. indet. 2 (button teeth)	Semio. indet. 3 (smooth scales)
Khok Kruat Fm							×
Sao Khua Fm						×	
Phu Kradung Fm	×	×		×	×		
Khlong Min Fm			×				

teeth (one or two supplementary teeth may have been present anteriorly). Their contour is irregular in shape, because of the large cusps on the occlusal face. On the posterior-most tooth five cusps similar in size are transversally aligned, forming crenulations (Fig. 9b), and on the more anterior teeth the internal-most cusp increases in size. The anterior teeth are smooth. The intermediate row, between the lateral and the medial rows, is formed by at least 12 teeth, which are irregular in size and shape. The posterior teeth have one to three cusps, and the anterior teeth are smooth. At the anterior tip of the dentition the bases of two small rounded teeth are visible, lateral to the lateral row of large teeth. It is unclear whether they are supplementary teeth or are part of a fourth row that could have developed during growth (the specimen is probably a juvenile individual).

Crenulations on vomerine and prearticular teeth are present in the pycnodonts *Gyrodus*, *Mesturus*, *Micropycnodon* and *Tepexichthys*, as described by Poyato-Ariza & Wenz (2002). According to those workers, *Mesturus* has only subcircular prearticular teeth, whereas the other three genera have oval prearticular teeth; three rows are present in *Tepexichthys* on the prearticular, four rows are present in *Micropycnodon* and *Gyrodus*, and more than four rows are present in *Mesturus*, although two are irregular; *Gyrodus* and *Tepexichthys* have nine teeth on the main prearticular row, as in the described specimen. According to these characters, defined on articulated specimens, the dentition from Mab Ching should be referred to *Tepexichthys*, a genus described in the Albian of Mexico. However, if we regard the two lateral teeth on the prearticular as evidence of a fourth row, the specimen can be referred to *Gyrodus*, a genus known in the Late Jurassic of Europe and Chile. We retain here the latter identification, but this should be regarded with caution, as is usual for identification of isolated dentitions.

cf. *Anomoeodus* Forir

Sao Khua Formation

Pycnodont remains have been recently discovered in the locality of Phu Phan Thong (Cuny *et al.* 2006, P. Srisuk, pers. comm.). They consist of two small incomplete vomerine dentitions, plus some isolated teeth. The vomerine dentitions (TF 8034 and TF 8035, Fig. 9c and d, respectively) have a median row of ovoid teeth, slightly curved with the concave margin facing anteriorly. A ridge runs along the transversal axis, delimiting anteriorly a groove. On the largest teeth, some cusplets are present along the anterior margin of that depression. Lateral to the median row is a paired row of teeth, squarish in shape on one specimen and ovoid in shape on the other (the latter specimen probably corresponds to a more anterior portion of the vomer dentition than the former). A concavity, with irregular margin on the largest teeth, is present on the squarish teeth. A paired lateral row of ovoid teeth is present on both specimens. Isolated teeth, from the same locality, are referred to cf. *Anomoeodus* (TF 8036 and TF 8037, Fig. 9e and f, respectively). The unworn teeth are circular or ovoid, with a central rounded cusp and radiating merging ridges. Some of these teeth are larger than teeth on the vomers, indicating the occurrence of rather large pycnodont fishes. P. Srisuk (pers. comm.) referred isolated teeth from Phu Phan Thong similar in shape to the above-described teeth to *Gyrodus* sp.

P. Srisuk (pers. comm.) reported four 'splenial' (prearticular) and one vomerine dentitions from the Sao Khua Formation in a locality situated along the highway between Udon Thani and Nong Bua Lam Phu. The gross morphology of the vomerine dentition (SHM-PT5, referred to *Stemmatodus* sp. by P. Srisuk, pers. comm.) is reminiscent of the vomerine dentitions from Phu Phan Thong. A prearticular dentition (SHM-PT1, referred to *Micropycnodon* sp. by P. Srisuk, pers. comm.) displays four rows of teeth. The main row is composed of elongated and slightly curved ovoid teeth. The lateral-most row shows smaller drop-shaped teeth. Between these rows of elongated teeth occurs a row of small sub-circular teeth, and another row with similar teeth occurs along the medial margin of the bone.

Identification of these isolated fragmentary remains is difficult. If we regard this material as belonging to a single taxon, the shape and

Semio. indet. 4 (ridged scales)	Semio. indet. 5 (button teeth & pits on scales)	cf. *Caturus*	*Siamamia naga*	Sinamiid new species 1	Sinamiid new species 2	cf. *Gyrodus*	cf. *Anomoeodus*	*Ferganoceratodus martini*
×	×				×			
		×	×	×			×	
								×
						×		×

ornamentation of vomerine teeth showing grooves and crenulations, and the arrangement and shape of prearticular teeth are reminiscent of the genus *Anomoeodus* as defined by Kriwet (1999), a genus known in the Early and Late Cretaceous, with doubtful occurrences in the Early Tertiary (Kriwet 1999). Srisuk also referred prearticular dentitions from Phu Phan Thong to *Anomoeodus* sp., and mentioned the occurrence of *Micropycnodon* and *Stemmatodus* in the locality of Phu Noi, Sakon Nakhon, in the Sao Khua Formation (P. Srisuk pers. comm.). We prefer here to retain the occurrence in the Sao Khua Formation of cf. *Anomoeodus* only, pending further discoveries.

Sarcopterygii Romer
Dipnoi Müller
Ferganoceratodus Kaznyshkin & Nessov

Ferganoceratodus martini was described from the Phu Nam Jun locality in the Phu Kradung Formation on the basis of an articulated skull roof and associated jaws (TF 7712, Cavin *et al.* 2007*a*). A taxon close to or similar to *F. martini* has been reported in the Triassic Huai Hin Lat Formation (Martin & Ingavat 1982), as well as in the Middle Jurassic locality of Mab Ching and in Ban Khok Sanam, in the Phu Kradung Formation (Martin *et al.* 1997; Cavin *et al.* 2007*a*) on the basis of isolated tooth plates. An isolated left mandibular tooth plate has been found in 2007 in the locality of Chong Chat, Phu Kradung Formation (TF 3038).

Succession of the Jurassic and Cretaceous fish assemblage in Thailand

Table 1 shows an overview of the bony fish assemblages from the Jurassic and Cretaceous of Thailand. The diversity, with at least 16 taxa, is higher than previously assumed, especially for 'semionotids'. Fishes from the Khlong Min Formation are still poorly known. The bony fish fauna provides little evidence to confirm or invalidate dating of the Mab Ching locality or to test palaeogeographical scenarios for the Middle–Late Jurassic. The occurrence of *Ferganoceratodus* is in agreement, however, with a terrestrial connection between southern Thailand and Central Asia at that time (Buffetaut *et al.* 2006). The Phu Kradung formation contains the most diverse bony fish fauna so far. Two or three 'semionotids' are present (depending on whether the taxon from Chong Chat is a new species or belongs to *L. buddhabutrensis*). At present, we are not able to assess the palaeogeographical affinities of these taxa. Dinosaurs from the Phu Kradung Formation show affinities with those from the Upper Shaximiao Formation of Sichuan and the Shishugou Formation of Xinjiang (Buffetaut *et al.* 2006, Buffetaut & Suteethorn 2007), and further studies should allow us to test whether 'semionotids' from the Phu Kradung Formation also show close relationships with 'semionotids' from the Late Jurassic of West and South China. The possible occurrence of a palaeonisciform in the Phu Kradung Formation is of little palaeogeographical interest until the taxon is better known, but it may indicate a refugium for relicts in SE Asia, as was suggested for the Jehol biota (Luo 1999).

Five bony fish taxa are known in the Sao Khua Formation and two of them represent the oldest occurrences in SE Asia: a 'semionotid' with button-shaped teeth and sinamiids. The osteology of the 'semionotid' with button-shaped teeth is not sufficiently known to assess whether it has affinities with other 'semionotids' with similar teeth or whether this pattern is due to convergence. The sinamiids, however, indicate close relationships with Chinese faunas, but we cannot decide at present whether the Thai taxa are closer to sinamiids from the *Lycoptera* fauna from North China, to sinamiids from the *Mesoclupea* fauna from south China, or to the sinamiids from Korea and Japan described by Yabumoto *et al.* (2006) (Cavin *et al.* 2007*b*). It is worth mentioning that the dinosaur assemblage from the Sao Khua Formation appears rather different from the Early Cretaceous dinosaur assemblage of China (Buffetaut *et al.* 2006). The Khok Kruat bony fish assemblage is different from assemblages of the preceding formations, showing a new diversification of the freshwater 'semionotids'.

Conclusion

The present study shows the potential of bony fish remains for biostratigraphic and palaeogeographical studies, with very distinct faunas in each formation (and probably differences within each formation); however, most of the work remains to be done. For instance, Cuny *et al.* (2006) observed a wide geographical distribution of the hybodont taxa from the Sao Khua Formation, whereas the Khok Kruat shark assemblage appears to be more endemic, although with a wide distribution within a South Asian continental province (Cappetta *et al.* 2006). We cannot test this hypothesis with the bony fish record for the time being. One important issue is to assess whether species from the two main lineages reported here, 'semionotids' and sinamiids, form clades endemic to SE Asia in the Late Jurassic and Early Cretaceous, or are representatives of taxa from surrounding areas (especially mainland Asia) that dispersed at several times towards SE Asia. Phylogenetic analyses based on more complete osteological material, including microstructure of the ornamentation of the ganoin of the scales, are now necessary.

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BIOGRAPHY

BIOGRAPHY

NAME	Miss Uthumporn Deesri
DATE OF BIRTH	September 9, 1980
PLACE OF BIRTH	Nong Khai Province, Thailand
INSTITUTIONS ATTENDED	Mahasarakham University 1999-2002: Bachelor's degree of science in Biology (Zoology), Mahasarakham University 2003-2013: Master and PhD degree in Biology (Palaeontology Program), at the Biology Department, Faculty of Science, Mahasarakham University, Thailand
SCHOLARSHIPS	University Development Committee (UDC) scholarship Mahasarakham University Development Fund (Creative works and paper presentation scholarship) Swiss National Science Foundation grants (200021-113980) King Prajadhipok and Queen Rambhai Barni Memorial Foundation grant
HOME ADDRESS	144 Moo 7, Hun Na Ngam sub-district, Sribunruang District, Nong Bua Lamphu, Thailand

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