วิวัฒนาการและบรรพนิเวศวิทยาของจระเข้ในมหายุคมีโซโซอิก บริเวณที่ราบสูงโคราช ประเทศไทย

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EVOLUTION AND PALAEOECOLOGY OF CROCODILES IN THE MESOZOIC OF KHORAT PLATEAU, THAILAND

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คมศร เลาห์ประเสริฐ: วิวัฒนาการและบรรพนิเวศวิทยาของจระเข้ในมหายุคมีโซโซอิกบริเวณที่ราบสูงโคราช ประเทศไทย (EVOLUTION AND PALAEOECOLOGY OF CROCODILES IN THE MESOZOIC OF KHORAT PLATEAU, THAILAND) อ. ที่ปรึกษา: ผศ. ดร. กำธร ธีรคุปต์, อ. ที่ปรึกษาร่วม: ASSOC. PROF. Gilles Cuny, Ph. D., จำนวน 239 หน้า ISBN 974-14-3900-8.

จากการศึกษาพบจระเข้มหายุคมีโซโซอิกบริเวณที่ราบสูงโคราช 9 ชนิด 6 สกุล จาก 3 วงศ์ จระเข้สกุล *Theriosuchus* จากหมวดหินภูกระดึงและกลุ่ม Teleosaurid, cf. *Peipehsuchus* ได้ถูกพบเป็นครั้งแรก *Siamosuchus phuphokensis* จากหมวดหินเสาขัวและ *Khoratosuchus jintasakulii* จากหมวดหินโคกกรวด ได้ถูกตั้งขึ้นเป็นจระเข้ชนิดและสกุลใหม่ของโลก ขณะที่ *Theriosuchus* sp. A จากหมวดหินเสาขัว "*Goniopholis*" sp. A และ "*G.*" sp. B จากหมวดหินโคกกรวด มีลักษณะเฉพาะซึ่งเพียงพอสำหรับการตั้งขึ้นเป็นชนิดใหม่ได้ แต่ต้องได้รับการเตรียมตัวอย่างเพิ่มก่อน "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980 และ "*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983 ได้ถูกจัดอยู่ในสกุลที่ไม่แน่นอน เนื่องจากลักษณะที่ใช้จำแนกไม่เพียงพอ

การค้นพบกระโหลกจระเข้สกุล *Theriosuchus* ในหมวดหินภูกระดึงชี้ให้เห็นว่า จระเข้ขนาดเล็กในวงศ์ Atoposauridae นี้มีการกระจายอย่างกว้างขวางทั้งในยุโรป จีนและเอเชียตะวันออกเฉียงใต้ นอกจากนี้ยังชี้ให้เห็นว่ายุโรปและเอเชียตะวันออกเฉียงใต้เชื่อมต่อกันแล้วในช่วงจูแรสซิกตอนปลาย แต่ช่วงเวลาของการเชื่อมต่อระหว่างทวีปนั้นยังไม่ทราบแน่ชัด สำหรับจระเข้สกุล "*Sunosuchus*" และ cf. *Peipehsuchus* ยังไม่สามารถสรุปความสัมพันธ์ทางสายวิวัฒนาการได้ เนื่องจากจระเข้สกุล "*Sunosuchus*" ขาดซากดึกดำบรรพ์ของกระดูกกรามบนที่สมบูรณ์ ส่วน cf. *Peipehsuchus* นั้นได้รับการอธิบายบนพื้นฐานของฟันเท่านั้น ดังนั้นจระเข้ทั้งสองสกุลจึงไม่สามารถนำมาอธิบายความสัมพันธ์ของสิ่งมีชีวิตในระหว่างเอเชียตะวันออกเฉียงใต้และจีนได้

การไม่ปรากฏของจระเข้จะงอยปากยาวในหมวดหินเสาขัว อาจจะมีสาเหตุมาจากการเปลี่ยนแปลงของสภาพแวดล้อมที่ชุ่มชื้นในยุคจูแรสซิกตอนปลายมาเป็นสภาพแวดล้อมที่แห้งแล้งในยุคครีเตเชียสตอนต้น วิถีชีวิตเชิงนิเวศของจระเข้จะงอยปากยาวน่าจะถูกครอบครองและแทนที่โดย *Siamosaurus suteethorni* ไดโนเสาร์กินปลาซึ่งเริ่มปรากฏในหมวดหินเสาขัว สมมติฐานนี้สนับสนุนด้วยโครงสร้างจุลภาคของชั้นเคลือบฟันที่คล้าย กันในไดโนเสาร์กินปลาและจระเข้ในมหายุคมีโซโซอิก ซากดึกดำบรรพ์ของจระเข้จะงอยปากกว้างและสั้นยังคงมีความหลากหลายอยู่ในหมวดหินนี้ อาจเป็นเพราะมีอาหารที่หลากหลาย

การค้นพบจระเข้สกุล "*Goniopholis*" ของไทยในหมวดหินโคกกรวดด้วยนั้น แสดงว่าจระเข้กลุ่มนี้ปรากฏอยู่ในที่ราบสูงโคราชตลอดช่วงครีเตเชียสตอนต้น แต่ความสัมพันธ์ทางสายวิวัฒนาการยังไม่ชัดเจน *Khoratosuchus jintasakulii* ถูกตั้งขึ้นในหมวดหินนี้ เป็นจระเข้ซึ่งมีรูปแบบวิวัฒนาการมากที่สุดในมหายุคมีโซโซอิกของไทยกลุ่ม neosuchian, โดยอ้างจากตำแหน่งของ internal choanae ซึ่งถูกล้อมโดยกระดูกท้ายเพดานปากเป็นส่วนใหญ่

สาขาวิชา......วิทยาศาสตร์ชีวภาพ........ **ลายมือชื่อนิสิต**..
ปีการศึกษา......2549.......................... **ลายมือชื่ออาจารย์ที่ปรึกษา**.....กำธร ธีรคุปต์.....
ลายมือชื่ออาจารย์ที่ปรึกษาร่วม..............................

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The Khorat Plateau has yielded so far nine species in six genera of Mesozoic crocodilians, which belong to three different families. *Theriosuchus* from the Phu Kradung and Sao Khua Formations, and a Teleosaurid, cf. *Peipehsuchus* from the Phu Kradung Formation, were recognized as new records in the Khorat Plateau. *Siamosuchus phuphokensis* from the Sao Khua Formation and *Khoratosuchus jintasakulii* from the Khok Kruat Formation were erected as new genera and species, whereas *Theriosuchus* sp. A from the Sao Khua Formation, "*Goniopholis*" sp. A and "*Goniopholis*" sp. B both from the Khok Kruat Formation possess unique characters, which are sufficient to recognize these taxa as new species, but they are in need of more preparation before they can be properly described. "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980 and "*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983 were considered as uncertain genera, based on insufficient diagnostic characters.

The discovery of a *Theriosuchus* skull from the Phu Kradung Formation indicates that the distribution of this dwarf Atoposauridae was widespread from Europe through China and Southeast Asia and also suggests that Europe and Southeast Asia has already been connected at that time, but the exact time of the connection between these continents is not exactly known. For "*Sunosuchus*" and cf. *Peipehsuchus*, the phylogenetic positions of these taxa are still unresolved, because the former lacks the complete upper jaw, while the latter was described on the basis of isolated teeth only. These two taxa thus cannot be used to decipher the relationship of the faunas between Southeast Asia and China.

The disappearance of long-snouted piscivorous crocodilians in the Sao Khua Formation may be caused by a palaeoclimate change from humid environment in the Late Jurassic to semi-arid environment in the Early Cretaceous. Ecological niche of the long-snouted crocodilians seems to be replaced by a fish-eating dinosaur *Siamosaurus suteethorni*, which is unknown before the deposition of the Sao Khua Formation. This hypothesis is supported by the similarity of the enamel microstructure of *S. suteethorni* and the Mesozoic crocodilians. The broad, short-snouted crocodilians were still diverse in this formation, probably because of their more diverse diet.

The Thai "*Goniopholis*" from the Khok Kruat Formation shows the existence of this form throughout the Early Cretaceous Khorat Plateau, but its phylogenetic affinity is still ambiguous. *K. jintasakulii*, also described from this formation, is the most advanced elongate-snouted Thai neosuchian, based on the position of the internal choanae, which is almost enclosed by the pterygoid.

Field of study....Biological Sciences....Student's signature Komsorn
Academic year..2006........................Advisor's signature K. Thirakhupt
Co-advisor's signature....................................

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CHAPTER I

INTRODUCTION

The history of vertebrates spans more than 500 million years, from the appearance in the Cambrian Seas to the present rich and varied faunas. The history of vertebrate life is recorded in a succession of fossils that documents their skeletal anatomy, distribution, and evolutionary changes. Fossil record is the best available evidence for determining the major processes of evolution: the origin of new structures, physiological processes, and adaptive strategies. It is also very useful for palaeontologists to determine the interrelationships of the modern species and understand the pattern of vertebrate evolution.

Fossils of fresh water crocodyliforms are rare because throughout geological history, areas of fresh water were less extensive and served as basins of deposition for shorter periods of time (Carroll, 1997). Not all animals had an equal chance of fossilization. Animals that live in or near the water have usually a great chance of being quickly buried and preserved than animals that live in strictly terrestrial environments. These conditions show that crocodilian could be an appropriate animal, which is preserved as a fossil.

Crocodilians have undergone at least three major episodes of adaptive radiation (Carroll, 1988). They were more diverse and abundant during the Jurassic and Cretaceous than they are now. Most crocodilians had extensive armour of bony plates (Zug *et al.*, 2001). Therefore, crocodilian remains are rather well preserved and suitable for the fossiliferous process. However, they have not received the full attention they deserve in the past. These fossils are very often scattered in many different institutions, which makes their study rather difficult (Clark, 1994). In addition, the fossil record is generally incomplete. Many fossils were destroyed by external geological processes and sometimes by internal geological processes.

During the past twenty-five years, the Thai-French expedition, led by Dr. Varavudh Suteethorn (Department of Mineral Resources, Bangkok) and Prof. Eric Buffetaut (Centre Nationnal de la Recherche Scientifique, Paris), has focused on the Mesozoic non-marine fossil vertebrates from Thailand, ranging in age from Late Triassic to late Early Cretaceous. Particularly, the Phu Kradung, Sao Khua and Khok Kruat Formations show extensive outcrops on the Khorat Plateau. These outcrops have yielded many fossils, including dinosaurs, crocodiles, turtles, bony fishes and sharks, and it is very useful to study their significance in terms of biostratigraphy and palaeogeography. The fossil exploration proceeds with regular excavations every year on new and previously known localities. All specimens are housed at the Sahatsakhan Dinosaur Research Centre (SDRC), Kalasin Province and at the Department of Mineral Resources. Undoubtedly, it turns out that the northeastern Thailand is among the few regions of the world where such a terrestrial fossil record of the development of vertebrate life from the Late Triassic through the Cretaceous has been preserved within a relatively limited area in a reasonably continuous sequence of continental rocks (Buffetaut and Ingavat, 1985).

From the recently collected vertebrate specimens kept at the Sahatsakhan Dinosaur Research Centre and at the Department of Mineral Resources, it has now become possible to reconstruct the interrelationship between crocodilians and the other vertebrate faunas in the communities of the Phu Kradung, Sao Khua and Khok

Kruat Formations over a time span of more than 40 million years. In addition, the study of the evolution and palaeoecology of fossil crocodilians is also important to understand how the geological processes have shaped our environment, how past and present biodiversities are evolving and what makes the origination and extinction of species.

The main aim of the project will be to identify more precisely the crocodilians from the Phu Kradung, Sao Khua and Khok Kruat Formations, to study their adaptations, and to understand their role in the ecosystems, in order to reconstruct the evolutionary history of crocodilians in Southeast Asia during the Jurassic and Cretaceous.

Objectives

1. To establish a list of the Mesozoic crocodyliforms from the Khorat Plateau and to study their taxonomy.
2. To differentiate the crocodyliform and fish-eating dinosaur teeth for understanding the palaeoecology of crocodyliforms and their interaction with the fish-eating dinosaur during the Early Cretaceous.
3. To determine the evolution, palaeoenvironmental and palaeobiogeographical frameworks of the crocodyliform from the Phu Kradung, Sao Khua and Khok Kruat Formation.

Anticipated Benefit

The information obtained will provide the understanding of the fossil patrimony of Thailand and will be useful for the conservation management as well as the development of tourist trails in the northeastern Thailand.

CHAPTER II

LITERATURE REVIEW

Fossil records

Fossils are the remains or indication of past life. They are generally the hard parts of animals that have been petrified, transformed from shell or bone into stone. The processes of fossilization limit the type of information we can gain from extinct organisms. The bodies of most animals are consumed or scattered by predators and scavengers soon after death, and their bones are broken up and decomposed. Perhaps no more than one in a million is so quickly buried that they may become fossilized. The flesh almost invariably decays, but the bones may be infiltrated by water carrying sediments and soluble minerals that fill up the large cavities and precipitate in smaller channels once occupied by cells and blood vessels. In most vertebrate fossils, mineral components of the bone retain their integrity, so that histological details and chemical composition are little altered even after hundreds of million of years. A fossil bone is still bone, but it contains a hard and heavy infilling of other minerals as well. Although the fossil record has the potential for documenting the rate and pattern of evolution, its irregularities have made these data difficult to interpret (Carroll, 1997).

The fossil record is usually far from being complete and represents only a small sample of past life. Therefore, any study of fossils or use of palaeontological data must be based on a clear understanding of the strengths and weaknesses of the records (Raup and Stanley, 1971). Fossils discovered in Darwin's time clearly showed major changes in Earth's biota during geological history, but the fossil records was not sufficiently well known to trace the evolution of any of the living species. Despite more than a hundred years of intense collecting efforts since the time of Darwin's death, the fossil record still does not yield the picture of infinitely numerous transitional links that he expected. In contrast, a very different pattern of the distribution of fossil organisms has been established by palaeontologists (Carroll, 1998).

Taxonomy of crocodyliforms

Among the new groups of reptiles that flourished in Jurassic and Cretaceous times were the crocodilians, which are the largest of modern reptiles (Colbert *et al.*, 2001). They show heavily armored, elongated bodies with long snouts and powerful tails and limbs. The neck, trunk and tail are armored dorsally and sometimes ventrally by bony plates (osteoderms) that are covered with thick keratinous skin (Zug *et al.*, 2001). The teeth of crocodilians are, like mammalian teeth, so-called **thecodont**, which means they are set into sockets to which they are attached by ligaments. They are also excellent swimmers and can move surprisingly fast on land, where they generally are semierectgait (Pough *et al.*, 2001; Zug *et al.*, 2001).

The taxonomic groups of archosaurs have been defined on the basis of overall similarity of their cladistic relationships (Clark, 1986). The Archosauria is determined to the descendents of the common ancestor of birds and crocodilians. The archosaurs, which are more closely related to crocodilians than to birds, are attributed into a group named Suchia (Krebs, 1974). A major group within the Suchia is the Crocodylomorpha (Walker, 1970). It has now been recognized as a group that includes living crocodilians and a broad diversity of fossil forms, all of which share several specializations of the forelimb and shoulder girdle. The Crocodylomorpha consists of sphenosuchians, protosuchians, mesosuchians, and eusuchians. The three latter taxa had been called Crocodylia. However, these taxa are up to now revised and given a name in the order Crocodyliformes (Hay, 1930) by Clark in 1986 whereas the order Crocodylia is defined to the descendents of the common ancestor of the living crocodilians (gravialids, crocodylids, and alligatorids) (Clark, 1984; Brochu, 2000, 2001, 2003). A strictly phyletic classification of crocodilians was firstly attempted by Whetstone and Whybrow in 1983. At that time, they erected name for the group composed of mesosuchians and eusuchians as the Mesoeucrocodylia. Recently, the works of Gasparini (e.g., 1971), Buffetaut (1982), Clark (1986), Ortega et al. (2000), and Wu et al. (2001b) plus the morphology of fossil crocodyliforms, which has become increasingly well known, have especially helped clarifying many problems in the taxonomy of mesoeucrocodylians. In 1988, Benton and Clark erected a new taxon, the Neosuchia, for eusuchians and those mesoeucrocodylians that are most closely related to eusuchians. These include the Atoposauridae, Goniopholididae, Pholidausaridae, Dyrosauridae, *Bernissartia*, *Shamosuchus*, and eusuchians. For the Eusuchia, it is currently defined in reference to the last common ancestor of *Hylaeochampsa* and Crocodylia and all of its descendents (Brochu, 2003).

The first true crocodilian-like form, such as *Protosuchus* and *Orthosuchus*, appeared since the Early Jurassic (Colbert and Mook, 1951; Benton, 1997). At that time, they were small quadrupedal crocodilians, being about 1 m in total length, and possessed their hindlimbs longer than forelimbs.

Table 2-1 Classification of crocodyliforms

Traditional classification [a]	Classification derived from preferred phylogeny [b]	Classification derived from the strict consensus of the most parsimonious-cladogram [c]
Order Crocodylia	Crocodyliformes	Crocodyliformes
Suborder Sphenosuchia	Protosuchidae	*Eopneumatosuchus*
Pseudhesperosuchus	*Protosuchus*	*Gobiosuchus*
Saltoposuchus	*Hemiprotosuchus*	
Sphenosuchus	Kayenta *Edentosuchus*-like form	*Orthosuchus*
Dibothrosuchus	Unnamed taxon	Protosuchidae
Suborder Protosuchia	*Orthosuchus*	Kayenta *Edentosuchus*-like form
Protosuchus	Unnamed taxon	Protosuchinae
Hemiprotosuchus	*Gobiosuchus*	*Protosuchus*
Orthosuchus	Mesoeucrocodylia	*Hemiprotosuchus*
Eopneumatosuchus	Thalattosuchia	Mesoeucrocodylia
Gobiosuchus	*Pelagosaurus*	Fruita form
Suborder Mesosuchia	Unnamed taxon	Unnamed taxon
Infraorder Notosuchia	Teleosauridae	*Notosuchus*
Notosuchus	Metriorhynchidae	*Baurusuchus*
Araripesuchus	Metasuchia	Unnamed taxon
Libycosuchus	Fruita form	*Libycosuchus*
Infraorder Sebecosuchia	Unnamed taxon	Unnamed taxon
Baurusuchus	*Notosuchus*	*Sebecus*
Sebecus	Unnamed taxon	Unnamed taxon
Infraorder Thalattosuchia	*Baurusuchus*	*Araripesuchus*
Teleosauridae	*Libycosuchus*	Neosuchia (revised content)
Metriorhynchidae	Unnamed taxon	Atoposauridae
Pelagosaurus	*Araripesuchus*	*Alligatorium*
Infraorder Metamesosuchia	Unnamed taxon	*Theriosuchus*
Atoposauridae	*Sebecus*	Unnamed taxon
Alligatorium	Neosuchia	*Goniopholis*
Theriosuchus	Atoposauridae	*Bernissartia*
Goniopholididae	*Alligatorium*	Unnamed taxon
Goniopholis	*Theriosuchus*	*Eutretauranosuchus*
Eutretauranosuchus	Unnamed taxon	Unnamed taxon
Pholidosauridae	Pholidosauridae	Dyrosauridae
Pholidosaurus	Goniopholididae	*Sokotosuchus*
Bernissartidae	Dyrosauridae	*Dyrosaurus*
Bernissartia	Unnamed taxon	Unnamed taxon
Infraorder Tethysuchia	*Bernissartia*	*Pholidosaurus*
Sokotosuchus	Eusuchia	Thalattosuchia
Dyrosaurus	*Hylaeochampsa*	*Pelagosaurus*
Suborder Eusuchia	Crocodylia	Unnamed taxon
Hylaeochampsa	*Leidyosuchus*	Metriorhynchidae
Crocodylidae	Crocodylidae	Teleosauridae
Leidyosuchus	Alligatoridae	Eusuchia
Alligatoridae	*Gavialis*	*Leidyosuchus*
Gavialidae		Crocodylidae
		Alligatoridae
		Gavialidae

[a] Based on Buffetaut (1982).
[b] Benton and Clark (1988).
[c] Clark (1994).

Fossil mesosuchian crocodilians were recognized more than 150 genera during the Jurassic and Cretaceous (Benton, 2000). It contains a great various sizes and forms, ranging from tiny and almost mammal-like in habits, such as *Theriosuchus* spp. and *Araripesuchus* spp. (Fig.8 in Ortega et al., 2000), to the largest long-snouted crocodilian, *Sarsosuchus* spp. (Buffetaut and Taquet, 1977). For the Eusuchia, it originally appeared in the Late Cretaceous with their forms very like living crocodilians (Benton, 2000; Brochu, 2003). Numerous other eusuchian families are known only from fossil records. Up to now, modern crocodilians can be divided into three families, i.e., Crocodylidae, Alligatoridae, and Gavialidae (Carroll, 1997). The traditional and phylogenetic classification of the crocodyliforms is shown in table 2-1.

NEOSUCHIAN CROCODILIANS

Neosuchians can be diagnosed by numerous characters of cranial: a rostral section that is wider than deep, the absence of a foramen at the premaxillomaxillary suture in lateral view, a lateral descending process of the lacrimal that is laminar, a straight jugal whose lateral surface is not visible in ventral view, and a cranial projection of the surangular that is forked in lateral view (Ortega et al. 2000). The following paragraphs are the reviews of general information of some widespread neosuchian crocodilians in China and Thailand, i.e., the Atoposauridae, Goniopholididae, Pholidosauridae and Teleosauridae.

Family Atoposauridae

The most frequent features used in the taxonomy of the Atoposauridae are: body size (rather small); short rostral length; paired external nares; relatively small supratemporal fenestrae; slenderness of the limbs and the peculiar limb ratios;

absence or reduction of the dermal armour; enlarged anterior maxillary teeth; external mandibular fenestrae absent; antorbital fenestrae reduced or absent; squamosal not descendant; and dental hypertrophy absent (Nopcsa, 1928; Mook, 1934: Kalin, 1955; Kuhn, 1968; Steel, 1973; Clark, 1985, 1986; Buscalioni and Sanz, 1988).

The first atoposaurid was found in the Jurassic lithographic limestones of Bugey (Cerin, France). The familiar denomination (Atoposauridae), clustering the genus *Atoposaurus, Alligatorellus* and *Alligatorium,* was proposed by Gervais (1871), and Zittel (1890) placed the family within the Crocodylia. The first accurate description was given by Lortet (1892). Nearly a century later, in 1971, three new specimens from the Solnhofen Formation were reported by Wellnhofer (1971), and Clark (1985) reviewed the relationships of the Atoposauridae.

Clark (1985, 1986) mentioned *Alligatorellus* and *Atoposaurus* as synonyms of *Alligatorium* (single valid species *A. meyeri).* He proposed that this family consists of only two genera, *Alligatorium* and *Theriosuchus*. In 1988, Buscalioni and Sanz disagreed with the work of Clark on the validity of the genus *Alligatorellus*. They consequently considered *Alligatorellus* as a valid genus based on the following characters: absence of postero-lateral lobule of squamosal; both frontal take part in supratemporal fossae; ventral surface of angular descends with respect to that of *Alligatorium* or *Theriosuchus*; relatively slender peculiar scapular shape, with an uncurved anterior border; and longer acromial region than that of *Alligatorium* and *Montsecosuchus*.

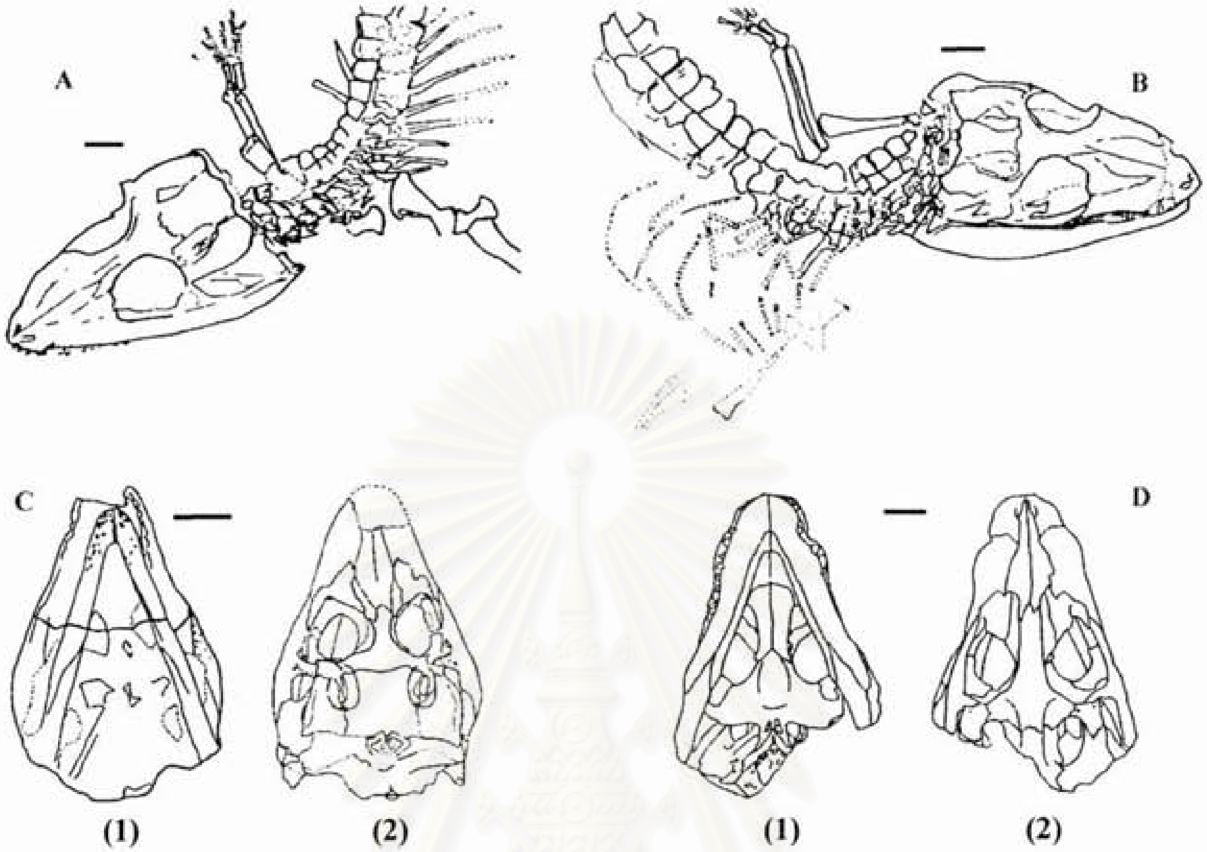


Fig. 2-1 *Alligatorellus beaumonti*, (MNL-15639), cranial and postcranial skeletons in A: dorsal view. Scale bar represents 5 mm. B: *Alligatorium meyeri*, (MHNL 15642/46), cranial and postcranial skeletons in dorsal view. C: *Montsecosuchus deperet*, (MGB-512), a nearly complete skull of holotype, in ventral (1) and dorsal views (2). D: *Theriosuchus pusillus*, (BMNH 48330), a nearly complete skull, in ventral (1) and dorsal views (2). B-D, Scale bars represent 1 cm. A and B: from Buscalioni and Sanz (1988), C: from Clark (1994), D: from Buscalioni and Sanz (1990a).

Montsecosuchus was redescribed from *Alligatorium depereti* by Buscalioni and Sanz in 1990, based on the following diagnostic features: cranial length less than half of the presacral length (cranial/ presacral length ratio = 0.27); ungrooved parietosquamosal suture; retroarticular process caudally project and dorsally recurved; and domed occiput and relatively short zeugopod. Therefore, there are only four valid genera in this family (Fig. 2-1), i.e., *Theriosuchus pusillus* Owen, 1878; *Alligatorium meyeri* Jourdan, 1862; *Alligatorellus beaumonti* Gervais, 1871; and *Montsecosuchus depereti* (Vidal, 1915), based on a revision of the phylogenetic relationship by Clark (1986), Benton and Clark (1988), and Buscalioni and Sanz (1988).

At the present stage, there is only *Theriosuchus* that was described more than one species. Three valid species of this genus are known, i.e., *T. pusillus* Owen, 1878; *T. ibericus* Brinkmann, 1992; and *T. guimarotae* Schwarz and Salisbury, 2005. The genus *Theriosuchus* can be diagnosed based on the following combination of diagnostic characters: brevirostrine skull, with the maxillary rostrum forming between 40% and 45% of the total length of the skull; small antorbital fenestra; slit-like, horizontally oriented and rostrally positioned external nares, separated from each other by the rostral-most extent of the nasals; shallow sulcus on the dorsal surface of the maxillary rostrum, immediately caudal to the junction between the maxilla, premaxilla and nasal; proportionately long jugal; medial base of the postorbital process formed by the ectopterygoid median crest on the frontal and the parietal in later ontogenetic stages; frontal and parietal partially unfused in early ontogenetic stages; dorsal margin of the supratemporal foramen smaller than the orbit throughout ontogeny; lateral margin of squamosal bevelled ventrally; proportionately narrow quadrate with a concave mandibular articular surface; secondary choanae bounded by the palatines rostrally and separated by a median septum of the pterygoid; mandibular symphysis does not extend caudally beyond a point level with the sixth dentary tooth;

ilium with short praeacetabular process and long postacetabular process (Schwarz and Salisbury, 2005).

The stratigraphic range of the Atoposauridae is from the Late Jurassic (Kimmeridgean) to Early Cretaceous (Berriasian). The remains of *Theriosuchus* are restricted to European fossil localities, i.e., France, Germany, England, Portugal, and Spain with the exception of finds in the Early Cretaceous of the Ordos Basin of Inner Mongolia (Clark, 1986; Wu et al., 1996b; Schwarz and Salisbury, 2005).

Family Goniopholididae

The family Goniopholididae consists of five valid genera, i.e., *Goniopholis* Owen, 1841; *Sunosuchus* Young, 1948; *Vectisuchus* Buffetaut and Hutt, 1980; *Eutretauranosuchus* Mook, 1967; and *Calsoyasuchus* Tykoski et al., 2002. The member of this family always show amphibious; a slightly brevirostrine skull with the lateral margins of the rostrum festooned both vertically and laterally; a notch at the suture between premaxilla and maxilla; and maxillary depression on the posterolateral surface of the maxilla. This family has been reported from the Early Jurassic to Early Cretaceous and is widespread throughout the northern hemisphere, from eastern North America, Europe (England, France, Germany, Belgium, Portugal, Russia), and Asia, including Thailand (Buffetaut and Ingavat, 1980, 1983, 1984; Efimov, 1988; Maisch, et al., 2003; Mook, 1967; Salisbury et al., 1999; Schwarz, 2002; Tykoski et al., 2002; Wu et al., 1996a).

Goniopholis Owen, 1841

The genus *Goniopholis* consists of amphibious, medium-sized, platyrostral and slightly brevirostrine neosuchians, which are presumed to have a very similar in their habit to the recent brevi- and mesorostrine crocodilians (Buffetaut 1982). Recently, *Goniopholis* has been considered as the sister group of a clade consisting of Bernissartia, Las Hoyas Neosuchia and Eusuchia (Ortega et al. 2000). *Goniopholis* has been reported in abundance from the middle and late Mesozoic of the Laurasian continent, mainly from eastern North America (Mook 1925), Europe and South East Asia (Buffetaut 1983).

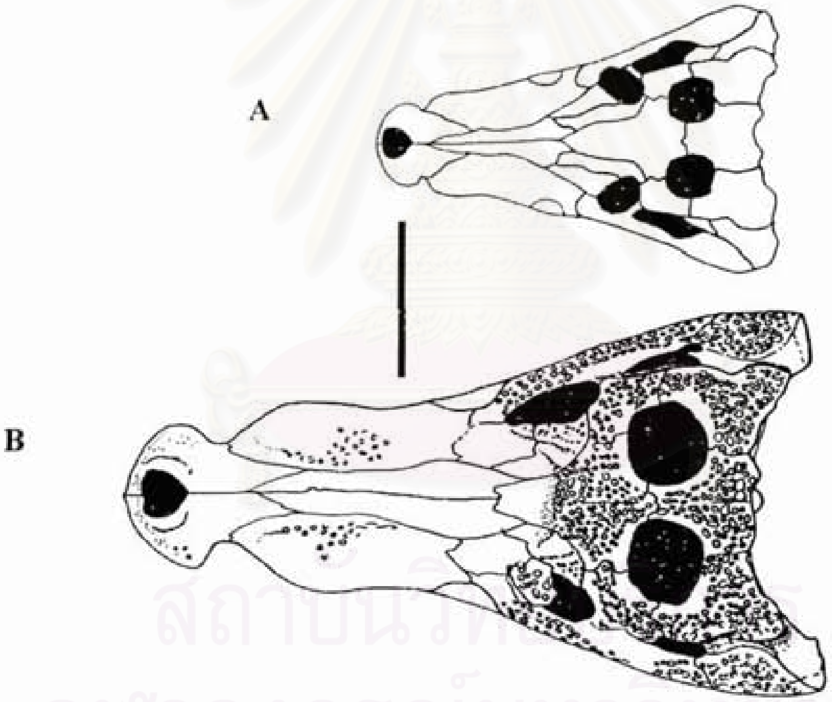


Fig. 2-2 Reconstruction of *Goniopholis baryglyphaeus* skull, (IPFUB Gui Croc 1) in A: dorsal view. B: reconstruction of *G. simus* skull, (IPB R359) in dorsal view. Scale bar represents 10 cm. A: from Schwarz (2002), B: from Salisbury et al. (1999).

Its fossil remains are very common in deposits that are accumulated in freshwater environment with periodic brackish influence in the Upper Jurassic and the

Cretaceous (Schwarz, 2002). The assignment of all Laurasian *Goniopholis* remains to the genus *Goniopholis* is still questioned (see Salisbury et al. 1999 for a recent revision). Moreover, the North American broad-snouted goniopholidid remains, such as *Goniopholis lucasii*, are still required of revision, because their taxonomic status within the Goniopholididae is not well defined. The Southeast Asian specimen is very fragmentary (Buffetaut and Ingavat, 1983).

Schwarz (2002) re-examined taxonomic status of the European *Goniopholis* material and suggested that they are mostly uncertain except *G. simus*. Salisbury (1999) also considered the skulls that were assigned to *G. crassidens* Owen, 1841 as the same taxon as *G. simus* Owen, 1878. *G. crassidens* is, therefore, only based on features of the postcranial skeleton. *G. tenuidens* Owen, 1879 is, owing to its very fragmentary material, a *nomen dubium* (Salisbury 1999). *G. simus* is confirmed as a valid taxon but *G. pugnax* (Koken, 1887) and *G. minor* (Koken, 1887) were considered to be *nomina dubia* by Salisbury et al., (1999). The two skeletons from Bernissart/Belgium referred to *G. simus* by Dollo (1883) were considered to belong to a different taxon instead (Salisbury et al., 1999). The Guimarota *Goniopholis*, *G. baryglyphaeus,* was described by Schwarz (2002) on the basis of some cranial features. The European *Goniopholis*, therefore, remain only three valid species, i.e., *G. crassidens*, *G. simus*, and *G. baryglyphaeus* (Fig. 2-2).

Sunosuchus Young, 1948

Wu et al. (1996a) mentioned seven diagnostic characters for the genus *Sunosuchus*. These include: (1) narrow and elongate snout; (2) small skull table; (3) frontal partially ridged along the midline; (4) anterior location of palatal fenestrae; (5)

oblique dorsal surface of retroarticular process; (6) wide posterior pits on frontal; and (7) long mandible symphysis with a short contribution from the splenial.

The genus *Sunosuchus* is known from a wide geographic range of localities in Central and Eastern Asia. The type species, *Sunosuchus miaoi* Young, 1948, was described from the Late Jurassic Xiangtang Formation of Gansu Province, northern China (Young, 1948; Buffeteaut, 1986), on the basis of a well preserved skull and mandible and some postcranial elements. Three additional species were subsequently described from other localities. The Southeast Asia long-snouted goniopholidid, *Sunosuchus thailandicus* Buffetaut and Ingavat, 1980 was describes based on an almost complete mandible of a very large animal from the Phu Kradung Formation of the Khorat Plateau in North-Eastern Thailand (Buffetaut and Ingavat, 1980, 1984). The Phu Kradung Formation was long considered to be Late, or at most Middle Jurassic in age, but recent investigations rather suggest a Late Jurassic or even Early Cretaceous age (Racey et al., 1994, 1996). *Sunosuchus shartegensis* Efimov, 1988 is based on incomplete cranial material from the Upper Jurassic of Shar Teg in Outer Mongolia (Efimov, 1988a, b). This species is only briefly described and poorly illustrated. *Sunosuchus junggarensis* Wu, Brinkman and Russell, 1996 was described in detail on the basis of numerous skeletal elements, including a complete skull, from the Late Jurassic (Oxfordian) Shishugou Formation of Pingfengshan in the Eastern Junggar Basin. It is the best known representative of the genus.

Almost all of the *Sunosuchus* materials, except *S. thailandicus*, were discovered from Central, East, and Southeast Asia, ranging from the Middle to Late Jurassic in age (Averianov, 2000; Maisch et al., 2003).

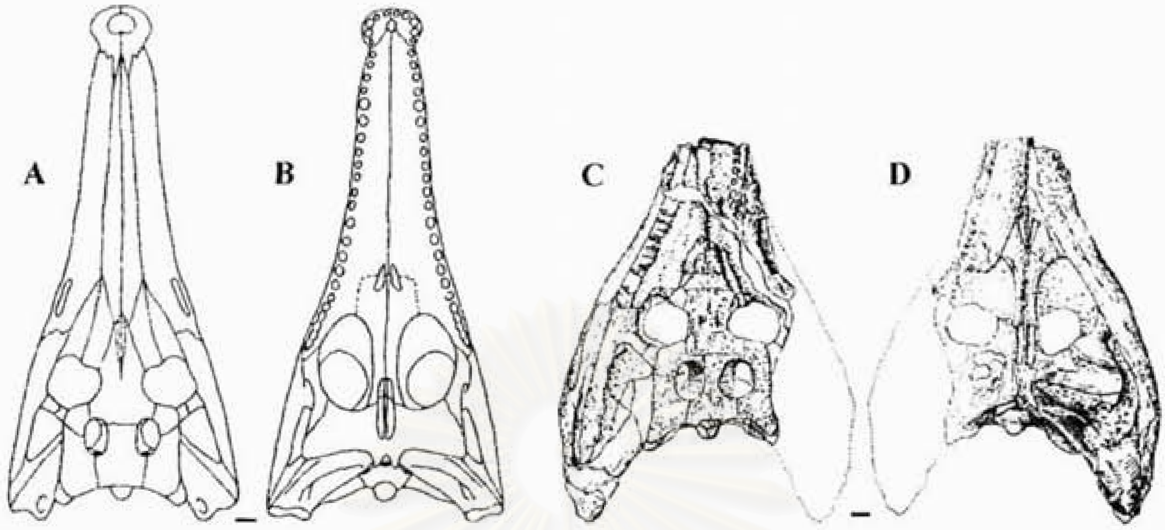


Fig. 2-3 Reconstruction of *Sunosuchus junggarensis*, (V 10606) in A: dorsal view, and B: ventral view. C: *Sunosuchus miaoi*, (V 500) in dorsal view and D: in ventral view. Scale bars represent 1 cm. A and B: from Wu et al. (1996a), C and D: from Young (1948).

Vectisuchus Buffetaut and Hutt, 1980

Vectisuchus leptognathus, a small-sized goniopholidid was found in the Wealden beds of the Isle of Wight, Great Britain, and described by Buffetaut and Hutt (1980). The locality is considered as the earliest Cretaceous (Neocomian) in age. The shape and relatively size of the supratemporal fossae, the development of the pterygoids, the ornamentation of the bones, and the condition of the internal choanae of this genus resemble that of previously known the European *Goniopholis* and some related North American forms of late Jurassic and early Cretaceous. However, the slender and somewhat elongate snout as well as the long mandibular symphysis extending back to the level of the eleventh tooth is quite unlike the other short-snouted goniopholidids, in which the symphysis reaches the level of the seventh tooth.

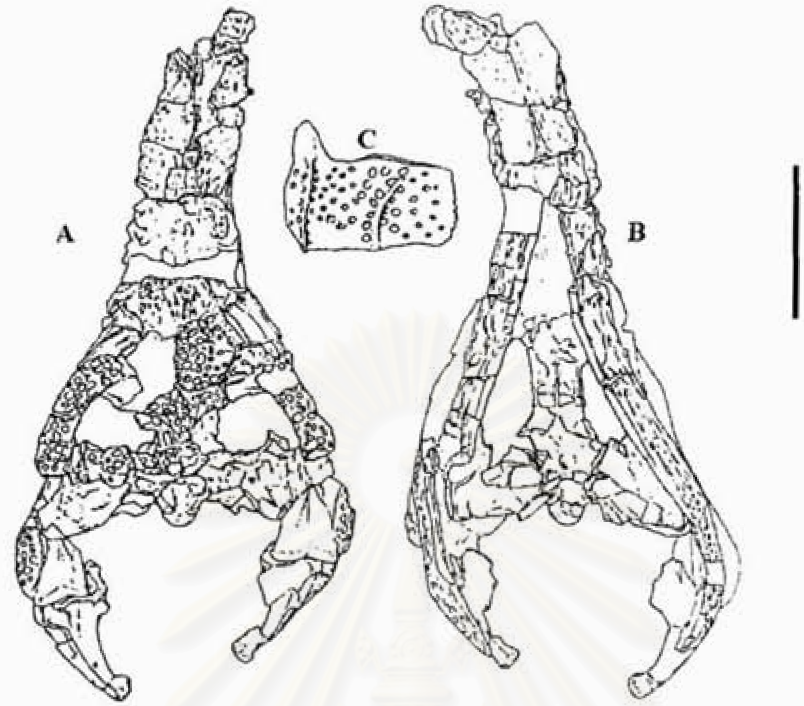


Fig. 2-4 *Vectisuchus leptognathus*, (Nr. 50984, holotype) in A: dorsal view and B: ventral view. C: scute from the middle part of the dorsal armour in dorsal view, showing ridges and anterolateral process. Scale bar represents 5 cm. A-C: from Buffetaut and Hutt, (1980).

Vectisuchus was distinguished from the other genera of Goniopholididae based on the following characters: slender, moderately elongate snout sharply demarcated from the posterior part of the skull; postorbital pillar somewhat displaced inwards and sloping backwards; well-developed pterygoid wings; internal choanae limited anteriorly by the palatines, but situated mostly in the pterygoids; mandibular symphysis relatively long, with the splenials taking part in it; mandibular slightly expanded anteriorly, with third and fourth alveoli large and contiguous; dorsal scutes bearing an anterolateral process and two longitudinal ridges (Buffetaut and Hutt, 1980).

Although *Vectisuchus* is reminiscent of the Pholidosauridae, its snout is much shorter than in any pholidosaurid and the supratemporal fossae are smaller. Buffetaut and Hutt (1980) suggest to classify *Vectisuchus* as an incipiently Longirostrine goniopholidid, with some peculiar specializations such as forwards-facing orbits. The transition from short-snouted to long-snouted forms is an evolutionary event that has occurred repeatedly during the history of the Crocodylia (Langston, 1973), but intermediate conditions such as the exhibited by this genus are seldom encountered in the fossil record (Buffetaut and Hutt, 1980).

***Eutretauranosuchus* Mook, 1967**

A North America non broad-snouted goniopholidid, *Eutretauranosuchus delfsi*, from the Upper Jurassic Morrison Formation, USA, was described by Mook (1967) on the basis of well-preserved skull, jaw, most of the precaudal and a few caudal vertebrae, a few limb bones, and some scutes. Recently, the holotype (CMNH 8028) is housed in the collection of Cleveland Museum of Natural History. Mook (1967) justified *E. delfsi* as a new genus of the Goniopholididae based on the following diagnostic characters: very large, long and slender internal narial aperture; and a pair of anterior palatal opening. *E. delfsi* possesses moderately long skull. There is a pronounced depression ("maxillary depression") at the base of the snout. The postorbital bar is clearly subdermal. The prefrontal bone extends farther forward than the frontal. The nasal does not enter forward to the level of the eleventh maxillary tooth. The frontoparietal suture is located rather far back, allowing a considerable participation of the frontal in the anterior borders of the supratemporal fenestrae. The interfenestral bar is relatively broad and flat, and its edges are slightly uprolled. The internal choana is usually long and slender. Its length is several times longer than its breadth, and its general size is relatively much longer than other crocodilians. Anterior to the internal choana, there is another opening, which is similar in shape to the internal choana, but smaller. It is divided by two slender bones, which appear to be processes of the palatines.

The lower jaw is long, slender and usually low anteriorly. The symphysis includes eight mandibular teeth on each side. The splenial bones enter the symphysis. They extend forward to the level of the seventh mandibular teeth. Twenty-four alveoli are present in each ramus. Of these numbers the third and fourth alveoli are slightly larger than the rest, which are subequal in size. The first eighteen alveoli have separate walls, nineteen to twenty-four merge together. The external mandibular fenestrae are small and oblique in position. They are much longer than high. The anterior internal fenestra is moderately large and the posterior one is small.

Calsoyasuchus **Tykoski et al., 2002**

Calsoyasuchus valliceps was discovered from the Early Jurassic Kayenta Formation (Sinemurian-Pliensbachian) of the Navajo Nation, United State of America. High-resolution X-ray CT analysis reveals that its long snout houses an extensive system of pneumatic paranasal cavities. This genus was described by Tykoski et al., (2002), based on the following diagnostic characters: lacrimal–nasal contact occurs only along anterior edge of lacrimal; frontal does not reach supratemporal fenestra; teeth that are finely serrated; snout bowed downward and back upward so the tip of the rostrum is as high or more dorsally placed than skull table (when skull table is held horizontal); an internarial process rises from narial naris; the medial edges of the maxillary palatal processes curve ventrally, forming

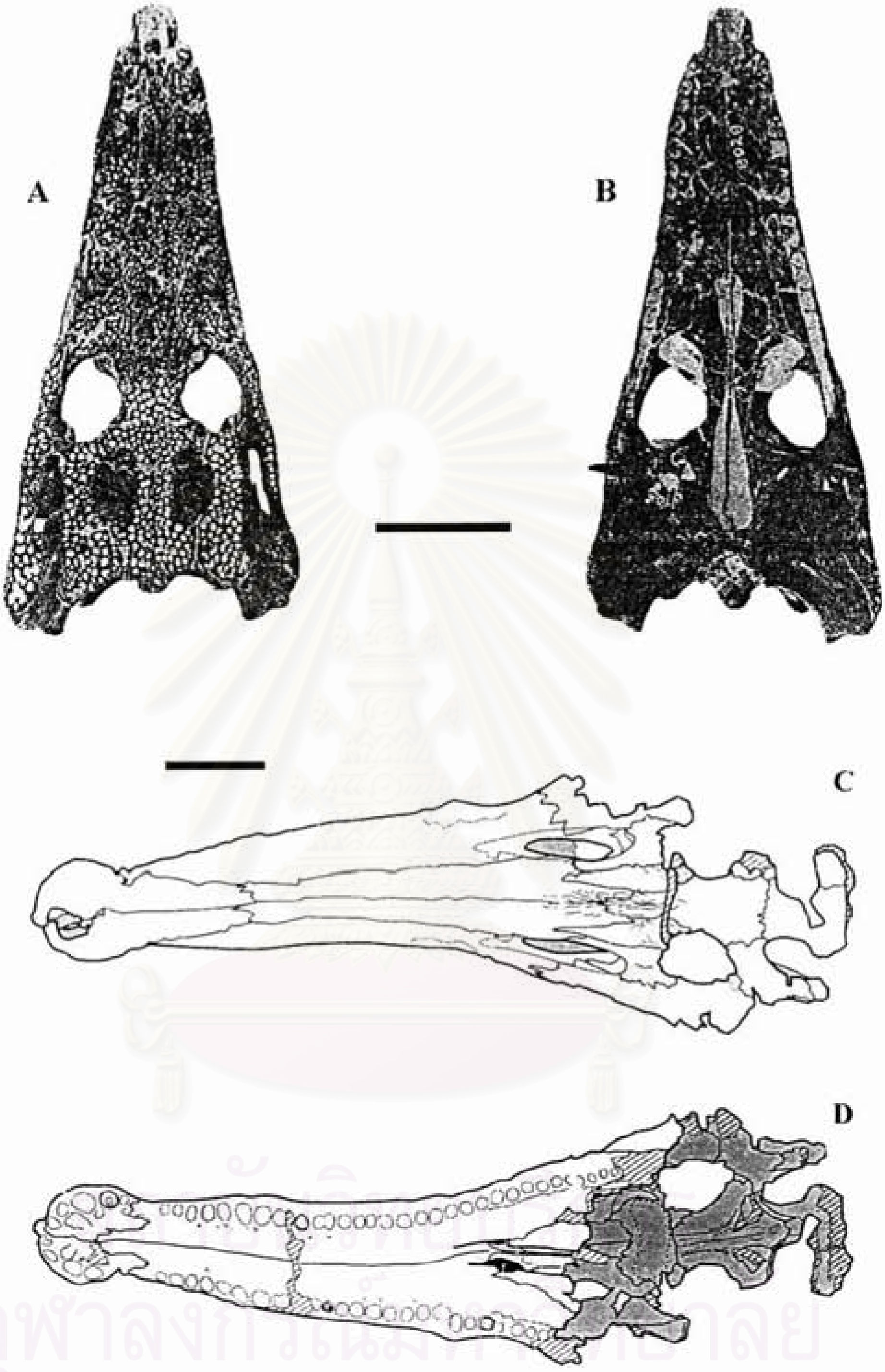


Fig. 2-5 *Eutretauranosuchus delfsi*, (CMNH 8028) a nearly complete cranium in dorsal view A: and B: in ventral view. C: drawing of *Calsoyasuchus valliceps*, (TMM 43631-1) a nearly complete cranium in dorsal view and D: in ventral view. Scale bars represent 5 cm. A and B: from Mook (1967), C and D: from Tykoski et al. (2002).

median ridge that descends below anterior alveolar border; medial maxillary floor to partially divide external accessory cavities very elongate; posterior end of maxilla divergent laterally, medially exposing the jugal anteroventral to the orbit; a deep pocket in medial surface of lacrimal anterior to the orbit; a deep and narrow median valley on posterior part of nasals and anterior third of frontal; lateral part of pterygoid anterior process with inverted ''U'' cross-section posterior to primary choana.

Preliminary phylogenetic analysis of Tykoski et al., (2002) indicates that the new species is the oldest known member of a monophyletic Goniopholididae, and within this lineage, it seems to be the sister taxon of *Eutretauranosuchus*, from the Late Jurassic Morrison formation of Colorado.

Family Pholidosauridae

The phylogenetic relationship of the Pholidosauridae is still ambiguous. This family seriously requires revision, because their taxonomic status is not well defined. According to the previous works of Meyer (1841), Owen (1841, 1878), Mook (1942), Young (1948), Romer (1966), Sereno et al. (2001), and Wu et al. (2001b), Pholidosauridae has been mentioned that it consisted of the genus *Crocodilaemus* and *Petrosuchus* Owen, 1878 from the Upper Jurassic Europe (Fig. 2-6), *Pholidosaurus* Meyer, 1841 from the Upper Jurassic to Lower Cretaceous Europe, *Suchosaurus* Owen, 1841 from the Lower Cretaceous Europe, *Sarcosuchus* De Broin and Taquet, 1966 from the late Lower Cretaceous Africa and South America, and *Anglosuchus* Mook, 1942 from the Jurassic North America. Formerly, *Terminonaris* Osborn, 1904 had been included into the family Pholidosauridae. A phylogenetic analysis of Wu et al. (2001b) suggested that *Terminonaris* was not a pholidosaurid but is, instead, closely related to *Dyrosaurus*. This analysis continues to support the hypothesis that long-snouted crocodyliforms of the traditional ''mesosuchian grade'' form a clade. From this reason, *Sarcosuchus* may probably be excluded from the Pholidosauridae, based on a phylogenetic analysis of Sereno et al. (Fig. 4C in 2001).

The family Pholidosauridae can usually be diagnosed by the following characters: small supratemporal fenestrae, subcircular in outline, moderately and subequally space from the external and posterior borders of the superior cranial surface, from the orbits and from each other; frontal bone participating in the borders of the supratemporal fenestrae; frontal and prefrontal bones extending forward to approximately the same level; small, sharp and pointed teeth, and slightly curved crowns; well-defined vertical ridge enamel without carina (Andrews, 1913; Owen, 1841, 1878; Mook, 1942).

Teleosauridae

Teleosauridae is marine crocodilian. It is defined here to identify a clade of long-snouted forms excluding metriorhynchosaurids and other long-snouted crocodyliforms. Although sometimes excluded from Thalattosuchia (Steel 1973), Teleosauridae is probably most closely related to metriorhynchosaurid and thalattoscuhians (Clark 1994). *Peipehsuchus* Young, 1948 from the late Lower Jurassic (Fig. 2-7), has been suggested as a teleosaurid by various authors (Buffetaut pers. comm) and confirmed by the discovery of a complete skull by Li (1993).

It can be identified based on the following characters (Mook, 1934): elongate and slender snout; subrectangular supratemporal fenestrae, much larger than orbits; frontal participates in borders of supratemporal fenestrae; maxillaries meet on midline superiorly, excluding nasals from contact with premaxillaries or from entering external aperture; platycoelous vertebrae; fore limbs much smaller than hind limbs; complete dermal armor. This family ranges in age from the early Jurassic to middle Cretaceous of Europe and North America.

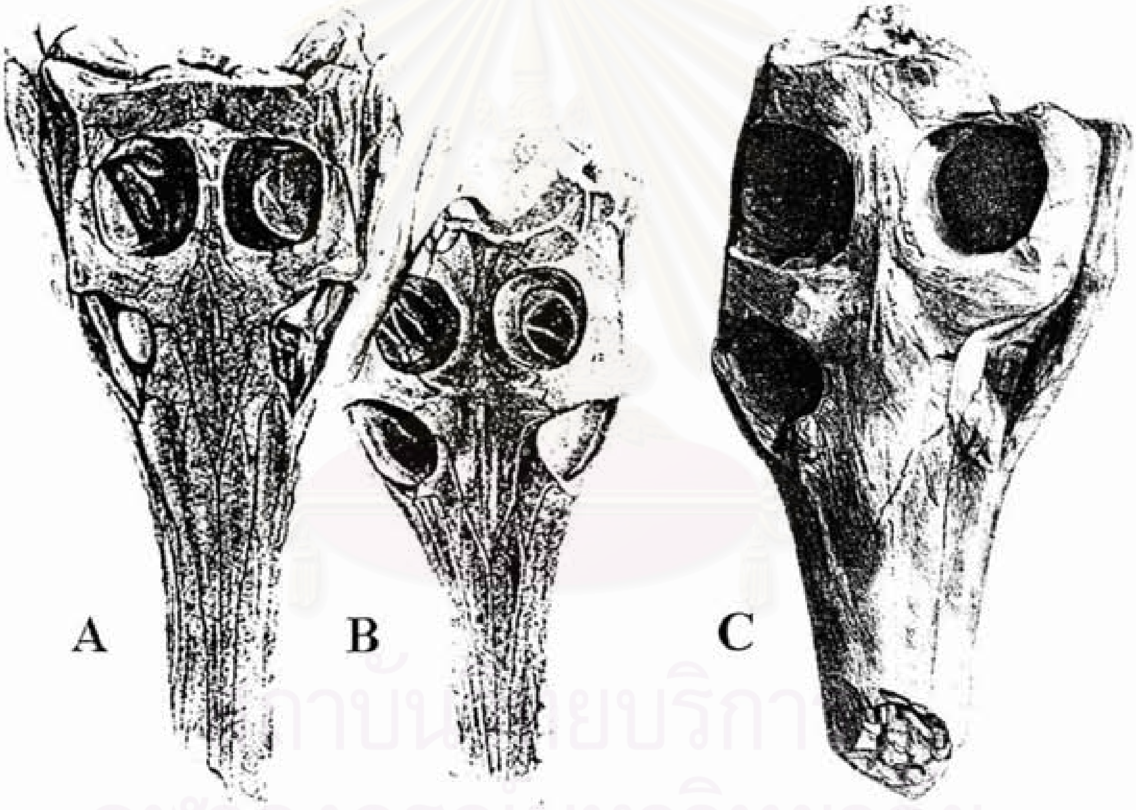


Fig. 2-6 Dorsal view of the Pholidosauridae skulls in A: *Anglosuchus geoffroyi* (Owen), and B: *A. laticeps* (Owen). These are referred by Mook (1942). C: *Petrosuchus levidens* Owen, 1878, (BMNH 3414). A and B from Mook (1942), C: from Owen (1878). No scale bar.

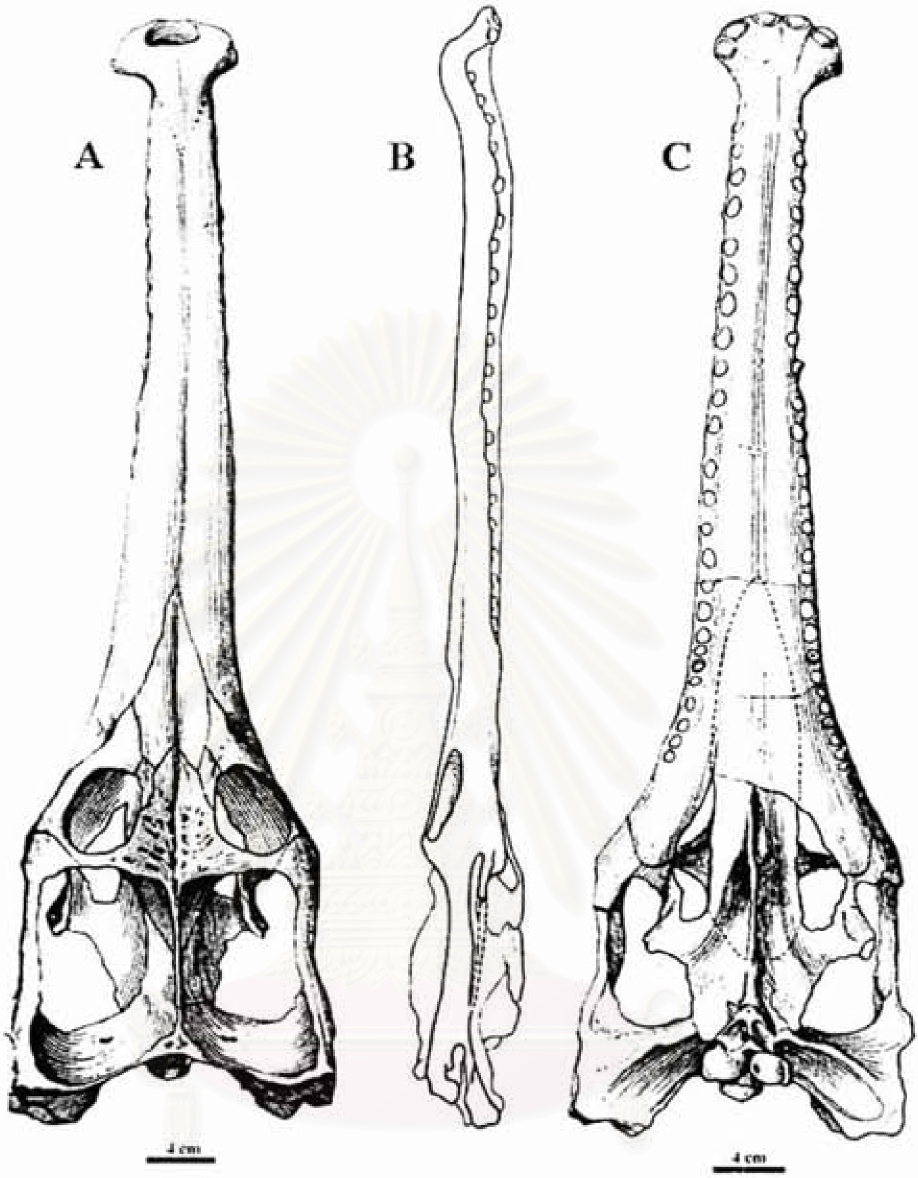


Fig. 2-7 A skull of *Peipehsuchus teleorhinus* in A: dorsal view, B: lateral view, and C: ventral view. A to C from Li (1993).

Fossil crocodilians in Thailand

Almost thirty years ago, the Thai-French expedition, led by Dr. Varavudh Suteethorn (Department of Mineral Resources, Bangkok) and Prof. Eric Buffetaut (Centre Nationnal de la Recherche Scientifique, Paris), has focused on the Mesozoic non-marine fossil vertebrates from Thailand, ranging in age from Late Triassic to late

Early Cretaceous. The Mesozoic crocodilians of Thailand have been studied since the early 1980s. Buffetaut and Ingavat (1980) found a crocodile jaw fragment from the Jurassic of Thailand (Phu Kradung Formation) at km 80 + 800 on the highway between Amphoe Nong Bua Lum Phu and Udon Thani Province. It is referred to a new species of the genus *Sunosuchus* Young, 1948, i.e., *S. thailandicus*, and the first Mesozoic crocodyliform known in Thailand (Buffetaut and Ingavat, 1980). The genus *Sunosuchus*, which is interpreted here as belonging to the family Goniopholididae (Mesosuchia), was previously known only from the continental Jurassic of North-Central China. The occurrence of this freshwater crocodilian in the Khorat Group of Thailand provides evidence that, whatever its previous palaeogeographical history might have been, by Jurassic times Southeast Asia is a part of Laurasia.

Buffetaut and Ingavat (1984) described a nearly complete lower jaw of the longirostrine mesosuchian crocodilian, *Sunosuchus thailandicus* Buffetaut and Ingavat (1980), from the Phu Kradung Formation (early Jurassic) of Northeastern Thailand, and the affinities of the genus were again discussed. The jaw is large and robust, with a long symphysis, and each dentary contains about thirty teeth. Despite the unusual elongated mandibular symphysis, the genus is referred to the Goniopholididae rather than to the Pholidosauridae, on the basis of the skull characters present in the Chinese species *S. miaoi* Young (1948). *Sunosuchus*, however, is in some respects morphologically intermediate between the Goniopholididae and the Pholidosauridae.

In 1983, Buffetaut and Ingavat discovered a new species of *Goniopholis* (Order Crocodylia, Suborder Mesosuchia, and Family Goniopholididae), which they described as *Goniopholis phuwiangensis* on the basis of a dentary from the Sao Khua Formation found at Phu Wiang, in Northeastern Thailand. It is closely related to forms from the Upper Jurassic of North America and Europe and the Lower Cretaceous of Europe, and suggesting a Late Jurassic to Early Cretaceous age for the Sao Khua Formation. The age of the Sao Khua Formation has been since then confirmed as Early Cretaceous. So far, numerous remains of crocodilians found in the last 15 years from the Phu Kradung, Sao Khua, and Khok Kruat Formations have not yet been studied in details. Only these two taxa (*Sunosuchus thailandicus* and *Goniopholis phuwiangensis*) of the Thai Mesozoic crocodilians have been studied and described. All materials are kept in the collection of the Sahatsakhan Dinosaur Research Centre, Kalasin province, and at the Department of Mineral Resources in Bangkok.

Khorat Plateau

Thailand consists of two continental blocks or microcontinents, i.e., Indochina block in the eastern part and "Shan-Thai" or "Sibumasu" block in the western part (Buffetaut and Suteethorn, 1998). Most of the non-marine Mesozoic rocks are in the Indochina block, which exposed a highland called "Khorat Plateau" or "Isan". The average elevation of the Khorat plateau basin is 200 m and covers an area of about 180,000 km^2 in eastern Thailand. The saucer-shaped plateau is tilted towards the South-East, and is drained by the Mun and Chi Rivers, tributaries to the Mekong River, which is also the boundary of the area. It is separated from Central Thailand by the Phetchabun Mountain Range and in the south from Cambodia by the Dongrek Mountain Range (Meesook, 2000; Department of Mineral Resources, 2001).

A set of sandstones, siltstones, mudstones and freshwater limestones that deposited during the Mesozoic Era in the Khorat Plateau is classified as the Khorat Group. Its covered area also extends into Laos, Cambodia, Vietnam and Southwestern China (Racey *et al.,* 1994, 1996; Meesuk, 2000; Department of Mineral Resources, 2001; Carter and Bristow, 2003). In Thailand, the Khorat Group is exposed in the northeastern and southern parts of Thailand. The sediments of these areas range in age from the Late Jurassic (Phu Kradung Formation) to the Albian-Aptian (Khok Kruat Formation), and its total thickness is nearly 3200 m. More recently these deposits were presumed that appeared since the Triassic collision event between the Shan-Tai (=Sibumasu) terrane and the Indochina blocks, which is Indosinian Orogeny (Hahn, 1967; Bunopas and Vella, 1978; Hutchison, 1989). Almost all the Khorat Group sediments were transported by large braided river systems that flowed from the present day N to NE. Changes in fluvial character, which forms the basis for the lithostratigraphic subdivision of the Khorat Group, are probably the results of a combination of climate change, tectonics or redirection of fluvial drainage systems but not a major change in source (Carter and Bristow, 2003).

Mesozoic sediments in the Khorat Plateau was originally studied and called "Khorat Series" by Brown et al. (1953), which included all Mesozoic sedimentary rocks in Thailand. In 1963, the named "Khorat Group" was erected by Ward and Bunnag (1964). They divided the Khorat Group, from base to top, into seven formations, i.e., the Nam Pong, Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, Khok Kruat, and one unnamed Formations. Currently, the Khorat Group is considered as a set of five formations based on an effectiveness of detrital zircon thermochronology (Carter and Bristow, 2003), which consists of the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, and Khok Kruat Formations. They yield a number of the late Jurassic to early Cretaceous non-marine fossil vertebrates such as dinosaurs, crocodiles, turtles, bony fishes and sharks, especially Phu Kradung, Sao Khua, and Khok Kruat Formations (Buffetaut & Ingavat, 1983; Buffetaut, 1985; Buffetaut and Suteethorn, 1998, 1999; Cuny, 2003; Lionel, 2002; Tong et al., 2003). Brief lithological description of each formation is cited from Ward and Bunnag (1964), Mouret et al. (1993), Sattayarak (1997), Department of Mineral Resources (2001), and Meesook (2000) as follow:

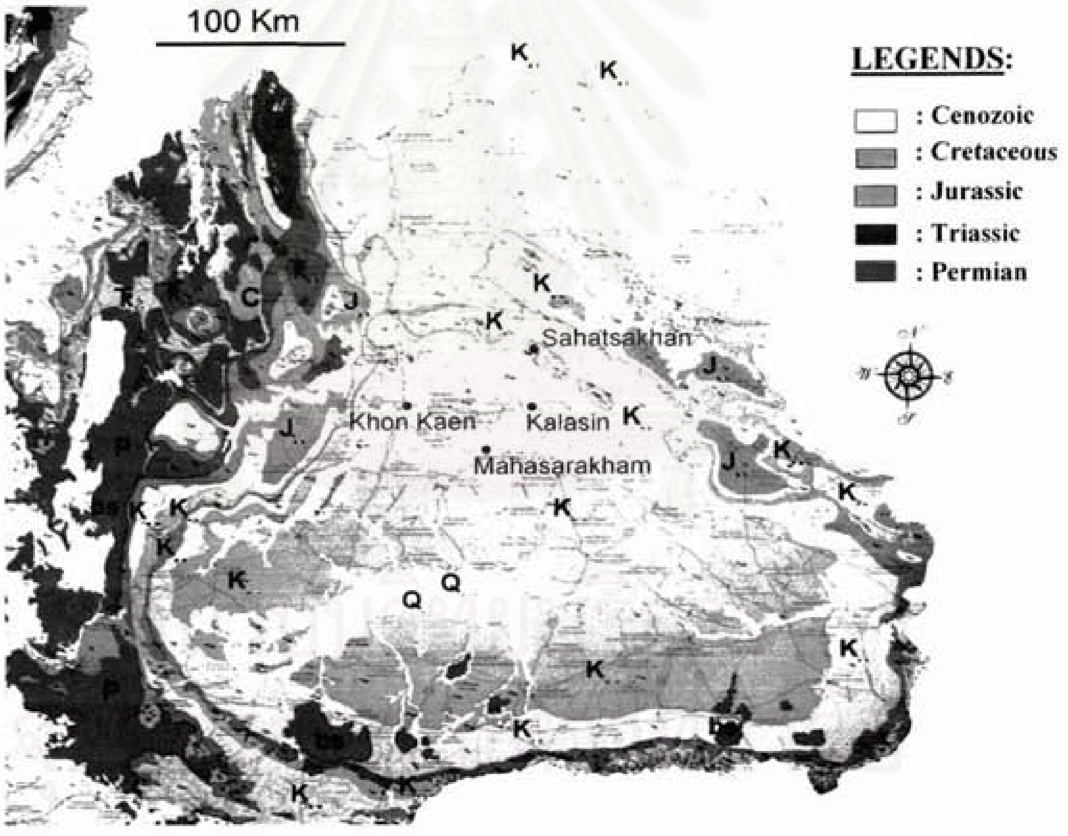


Fig. 2-8 Geological map of the northeastern Thailand (DMR, 1999). Abbreviation: bs, basalt; C, Carboniferous; J, Jurassic; K, Cretaceous; P, Permian; Q, Quaternary; TR Triassic

Phu Kradung Formation

The Phu Kradung Formation is the lowest formation of the Khorat Group. According to age constraints provided by the overlying formations, the Phu Kradung Formation may be regarded as Late Jurassic or basal Cretaceous in age. This formation is about 1,001 m thick at the type section. It mainly consists of maroon micaceous siltstone, mudstone, sandstone and conglomerate. Sandstone is less calcareous and micaceous than siltstone. Lenses of fine-clast conglomerate with calcareous cement are often associated with sandstone through the unit. Clasts can be limestone, siltstone, granite, volcanics and caliche. In many places, conglomerate with clasts of mainly limestone occurs at the base of the unit. Sandstone can be either green or gray on color. The sediments of the Phu Kradung Formation were deposited in continental environments, varying from meandering river to lacustrine environments. Repetitive cycle of meandering channel and floodplain deposits can be clearly seen in various outcrops together with local pedogenesis on the top of these floodplain sequences. The palaeoclimatology of this formation is interpreted as semi-arid condition.

The Phu Kradung Formation contains diverse vertebrate assemblages, although most of the fossils are preserved as isolated elements. Among dinosaurs, remains of theropods, sauropods, ornithopods and stegosaurs have been recovered. Non-dinosaurian tetrapods comprise crocodiles, turtles and temnospondyls (Lionel, 2002; Buffetaut et al., 2003). These biotas are usually found in channel conglomerates and floodplain sandstones and siltstones of meandering river deposits. Wood is more abundant than in the Sao Khua and Khok Kruat Formations (Meesook, 2000).

Phra Wihan Formation

This formation is broadly distributed along the western, eastern, and southern parts of the Khorat Plateau. It also occurs in the northern and middle parts of the Phu Phan Range along the NW-SE trending anticlinal axes, which run from the north through the middle parts, and less extensive in the southern portion. The unit consists of pale-gray and white sandstone (subarkose to quartz arenite), subordinate intercalated maroon and reddish-brown siltstone, mudstone, and conglomerate. Cross lamination and fine-pebble prientation, particularly in sandstone beds, can be observed. Small amounts of calcareous cement and mica content exist in sandstone and less mica in siltstone. The sedimentary deposition of this formation indicates that the physical environments have changed from the meandering river system to mainly braided river system due to the changes from semi-arid to slightly humid climate, demonstrating by the presence of some plant remains in mudstones and the uplifting in surrounding areas of the plateau (Meesook, 2000). Only dinosaur tracks have been recorded on the sandstone beds and some palynomorphs in mudstones.

Sao Khua Formation

The Sao Khua Formation can be observed throughout the western, eastern, and southern parts of the plateau and most parts of the Phu Phan Range along the NW-SE trending anticlinal axes. This formation contains various cycles of reddish brown mudstone, siltstone, and fine- to medium-grained sandstone. Sandstone tends to be light gray and gray in color. Calcareous cement and mica content, lenses of fine-clast conglomerate (including cross lamination/ bedding) appear in some sandstone beds.

Calcretes and silcretes are generally thicker and more predominant than in the Phu Kradung and Khok Kruat Formations.

During this time, the deposition of sediments suggests that the prevailing braided river system has changed to meandering river together with the changes from slightly humid to semi-arid palaeoclimate. The palaeoclimate during this time was more semi-arid than that of the Late Triassic –Jurassic, which contained many calcrete horizons and some bedded and nodule silcrete layers. Repetitive cycle of meandering channel and floodplain deposits can also be clearly seen in various outcrops with local pedogenesis on the top of these floodplain sequences and more conspicuous than from the Jurassic (Meesook, 2000). This formation represents a depositional environment, which consists of a very extensive floodplain with low energy meandering rivers. This environment explains the partially articulated status of the fossil under study. Other vertebrate remains were also discovered from this bed, include: *Siamosaurus suteethorni* teeth, theropod dinosaur eggs (Buffetaut et al., 2003a; 2005), a pterodactyloid pterosaur tooth (Buffetaut et al., 2003b), many *Lepidotes* sp. scales, centrums, jaws, and a number of isolated teeth of indeterminate fishes; *Heteroptychodus steinmanni* teeth (Cuny et al., 2003) and shell fragments of 2 undescribed taxa of turtles (Claude, pers. comm.).

Phu Phan Formation

The Phu Phan rocks are well exposed in most parts of the Phu Phan Range along the NW-SE trending anticlinal axes, particularly along the Mae Khong River banks. The rocks are formed as escarpment slopes, which delineate the outer rims of the range. The formation mainly contains resistant sandstone and commonly crops out on the top of mesas and hills. It consists of yellowish gray, greenish gray, and pinkish gray sandstones, conglomeratic sandstone to conglomerate, and rare reddish brown siltstone and shale. Cross bedding, both planar and trough, are ordinary.

After prolonged meandering river system of the Sao Khua Formation, large amount of sands and gravels from the northeastern part of the plateau were also laid down in the Khorat Basin by high-energy braided river in this formation. Because of high–energy current, invertebrate and vertebrate remains, preserved in the siltstones and claystones of the Sao Khua Formation, were removed and re-deposited at the base of the Phu Phan conglomeratic sandstones. The palaeoclimate during this time was humid. Only dinosaur tracks have been recorded on the sandstone beds.

Khok Kruat Formation

The Khok Kruat Formation is separated from the overlying Mahasarakham Formation, due to the appearance of unconformity. Therefore this formation is considered as the top of the Khorat Group. It has a wide distribution in the central low-lying areas of the plateau and the outer parts of the Phu Phan Range, bounded along the outer rims of the Phu Phan Formation, with apparently conformable contacts. It is about 430-700 m thick and consists of reddish brown maroon sandstone, siltstone, mudstone, and conglomerate with calcrete nodules and caliche in the upper part of the mudstone. Clasts in bluish gray conglomerate are more caliche and red siltstone.

The palaeoclimate had changed from humid to semi-arid in this formation. The cyclic depositions of the Khok Kruat Formation were channel sandstones and floodplain sequences. The Khok Kruat Formation is currently dated as the late Early Cretaceous (Aptian-Albian) by the occurrence of freshwater hybodont shark, *Thaiodus ruchae,* which is also known from the Aptian-Albian Takena Formation of the Lhasa block of Tibet (Cappetta, *et al.*, 1990) and by the palynomorphs suggesting an Aptian age (Sattayarak, *et al.*, 1991, Racey *et al.*, 1994, 1996). Besides crocodile, this formation has also yielded remains of various vertebrate faunas, including hybodont sharks (Cuny *et al.*, 2003, 2006), semionotiform fishes, turtle (Tong *et al.*, 2005), diverse dinosaurs and pterosaurs (Buffetaut *et al.* 2003a, b).

CHAPTER III

MATERIALS AND METHODS

A. Study site: The Khorat Plateau

Because the vertebrate fossilization in the Phra Wihan and Phu Phan Formations reveal only the dinosaur footprints (Fig. 3-1), therefore the author has decided to study only the rest three formations of the Khorat Plateau, i.e., the late Jurassic Phu Kradung Formation, the early Cretaceous Sao Khua Formation and the Aptian-Albian Khok Kruat Formation. These three formations show extensive outcrops on the Khorat Plateau and also have yielded many vertebrate fossils such as crocodiles, turtles, dinosaurs, fishes and sharks (Buffetaut and Suteethorn, 1998; Cuny, 2003; Cavin, 2002; Tong, 2003, 2005).

Nine assemblages were excavated during 2002 to 2005. For the Phu Kradung Formation, Chong Chat (Nongbualumpoo province), Dan Kerng and Dan Luang (Mukdahan province) were study sites. PW 1A (Khon Kaen province), Khok Kong (Kalasin province), and Phu Phok (Sakon Nakhon province) represent the Sao Khua Formation whereas Ban Samran (Khon Kaen province), Khok Pha Suam (Ubon Ratchathani province), and Ban Saphan Hin (Nakhon Ratchasima province) represent the youngest Khok Kruat Formation. All localities are shown in Fig. 3-2.

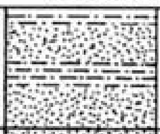
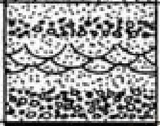
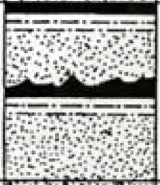
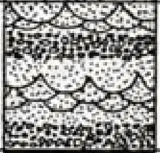
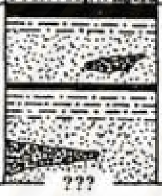
Group	Formation	Lithologic column	Description	Thickness (m)	Age
UNCONFORMITY					
KHORAT	Khok Kruat		Sequences of reddish-brown sandstone and siltstone with fossils of vertebrates	430-700	Early Crertaceous
	Phu Phan		Sequences of grayish-white, sandstone and conglomeratic sandstone with plant remains	80-140	Early Cretaceous
	Sao Khua		Sequences of reddish-brown sandstone and siltstone and claystone; fossils of vertebrates, bivalves and palynomorphs	200-720	Early Cretaceous
	Phra Wihan		A sequence of whitish-gray sandstone and conglomeratic sandstone; fossils of dinosaur tracks and palynomorphs	50-140	Early Cretaceous
	Phu Kradung		Sequences of maroon claystone, siltstone, sandstone and occasional conglomerate; fossils of vertebrates, bivalves and palynomorphs	800-1,100	Jurassic
UNCONFORMITY					

Fig. 3-1 Lithological column of the Mesozoic Khorat Group in Thailand (modified from Meesook, 2000; Carter and Bristow, 2003)

B. Methodology:

1) Taxonomic status of Thai Mesozoic crocodyliforms

1.1 Field work

Nine assemblages of these three formations (Phu Kradung, Sao Khua and Khok Kruat Formations) were surveyed and excavated every year, during 2002 until 2005. These studied localities are shown in Fig. 3-2.

The excavation was started by digging through the overburden to reach the fossiliferous layer and followed by searching for the macrofossils, such as bones, vertebrae or skulls of fossil crocodilians. The following data about the sediments in each site were also recorded:

- Geographic Position
- Lithologic characters, sequences and relationship such as mixing or graduation.
- Textural feature such as grain size, distribution, sorting, roundness and color.
- The occurrences in the section or exposures.

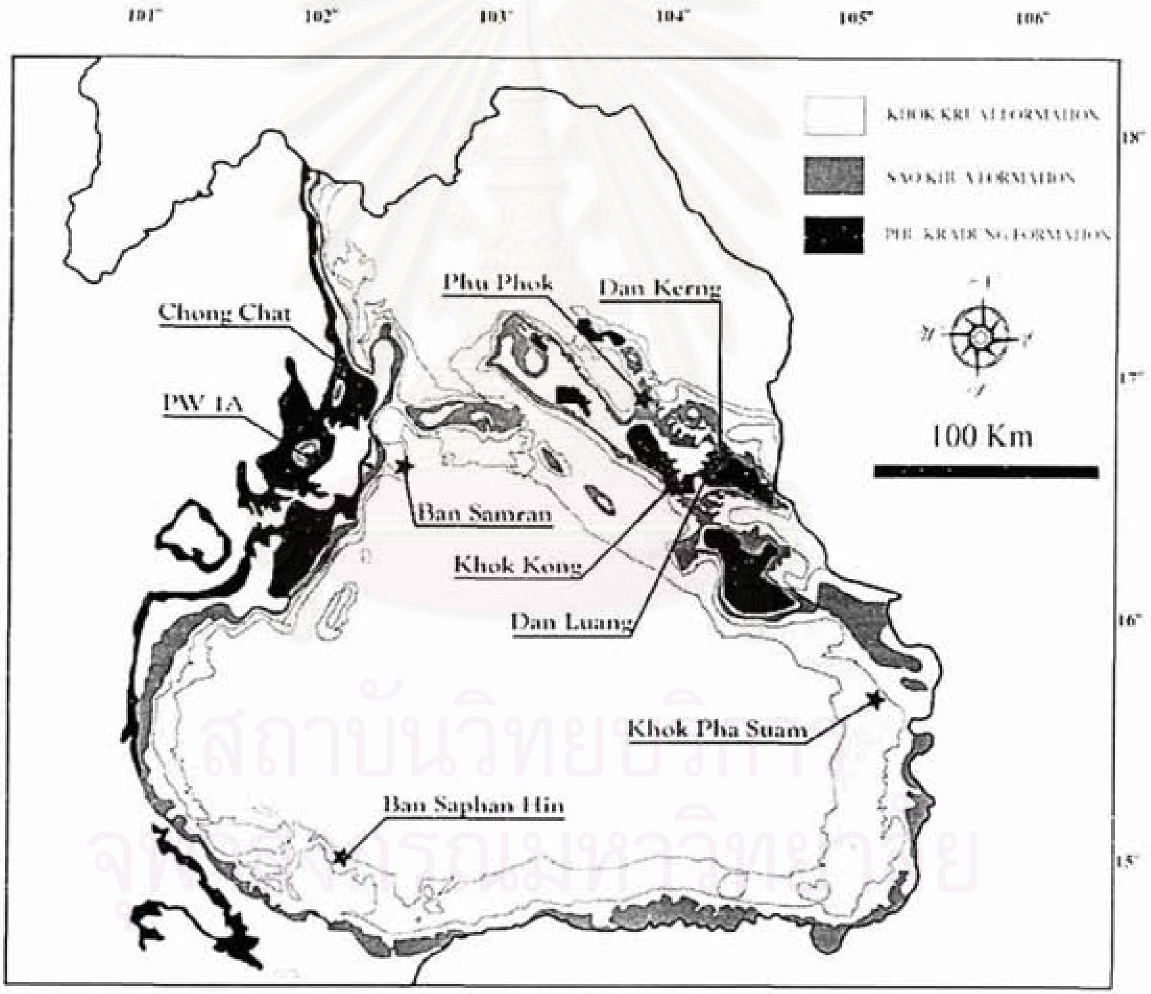


Fig. 3-2 Geological map of the Khorat Plateau showing nine studied assemblages from three formations.

1.2 Laboratorial work

Two holotypes of fossil crocodiles described by the Thai-French Team, *Sunosuchus thailandicus* Buffetaut and Ingavat, 1980 and *Goniopholis phuwiangensis* Buffetaut and Ingavat, 1983, were revised and their taxonomic status was re-examined.

Moreover, undescribed specimens, which are housed in the collection of the museum of the Sahatsakhan Dinosaur Research Centre, Kalasin province, and the Museum of Petrified Wood and Mineral Resources, Nakhon Ratchasima province, were prepared and studied for the first time as shown in Table 3-1

These fossil records were studied on their anatomies. This methodology was carried out at the Sahatsakhan Dinosaur Research Centre, Kalasin Province. The specimens were also compared with well-known specimens to assess their taxonomic identification at the lowest possible level, from the following European Museums:

1) The Natural History Museum, London, United Kingdomn (BMNH)
2) Geoscience Centre of the University of Göttingen, Germany (GZG)
3) Institut für Palaontologie der Universität Bonn, Germany (IPB)
4) Institut für Palaontologie der Freien Universität Berlin, Germany (IPFUB)
5) Museum für Naturkunde Berlin, Germany (MNB)
6) Institut und Museum für Geologie und Palaontologie, Tübingen, Germany (GPIT)
7) Institut Royal des Sciences Naturelles de Belgique, Belgium (IRSNB)

8) The Paleontology Institute of the Russian Academy of Sciences, Russian Federation (PIN)

Table 3-1 The undescribed crocodilian specimens of this study. Abbrivation: Fm., Formation; Spec. No., specimen number.

Fm.	Spec. No.	Localities	Material
Khok Kruat	NRRU–A 1803	Ban Saphan Hin Nakhon Ratchasima province	part of cranium
	NRRU–A 1216	Ban Saphan Hin Nakhon Ratchasima province	part of the right jugal
	NRRU–A 1791	Ban Saphan Hin Nakhon Ratchasima province	part of the left dentary
	KPS–1	Khok Pha Suam Ubon Ratchathani province	part of the left mandible
Sao Khua	PWC–2/1 to 2/6	Phu Wiang Khon Kaen province	incomplete skull and postcranial skeletons
	PPC–1/1 to 1/88	Phu Phok Sakon Nakhon province	fragmented cranium and post cranial skeletons
	PPC–2	Phu Phok Sakon Nakhon province	nearly complete rostrum and dentaries
Phu Kradung	CCC–1	Chong Chat Nong Bua Lam Phu province	part of the left dentary
	DKC–1	Dan Kerng Mukdahan province	middle part of the left dentary
	DLC–1	Dan Luang Mukdahan province	caudodorsal part of the right surangular

All Mesozoic non-marine vertebrate fossils of the Phu Kradung, Sao Khua and Khok Kruat Formations were also studied on their taxonomic status. Subsequently, the re-identified specimens were numbered. All specimens are kept in the collection of the museum of the Sahatsakhan Dinosaur Research Centre.

Tooth specimens were collected from three formations of the Khorat Group, i.e., the Phu Kradung, Sao Khua and Khok Kruat Formations (Fig.3-1), and were investigated under stereomicroscope to categorize morphotype differences on the basis of shapes (size and curvature) of the crowns, ridge ornamentations, and the presence of serrations.

Skull Anatomical Abbreviations —**bo**: basioccipital, **bsph**: basisphenoid, **cap**: capitulum, **cau**: caudal, **cond occ**: occipital condyle, **cq**: cranioquadrate canal, **cr B**: quadrate crest B, **cr C**: quadrate crest C, **cr int**: interorbital crest, **cra**: cranial, **cra pro**: craniolateral process, **eu**: eustachian foramen, **For m**: foramen magnum, **For pot**: posttemporal foramen, **For sqot**: squamosotoccipital foramen, **fst**: supratemporal fenestra, **fti**: infratemporal fenestra, **hy**: hypapophysis, **j**: jugal, **l**: lacrimal, **m 1- m 18**: maxillary alveoli 1 to 18, **max**: maxilla, **mdep**: maxillary depression, **na**: nasal, **ne**: external naris, **no**: notch at the suture between premaxilla and maxilla, **Or**: orbit, **ot**: otoccipital, **p**: parietal, **pmx**: premaxilla, **pm 1- pm 5**: premaxillary alveoli 1 to 5, **prezy**: prezygapophysis, **po**: postorbital, **po bar**: postorbital bar, **postzy**: postzygapophysis, **q**: quadrate, **qj**: quadratojugal, **r**: ridge, **so**: supraoccipital, **sq**: squamosal, **tub**: tuberculum.

1.3 Screen-washing of sediments to recover microvertebrate fossils

Another method for seeking new specimens from the study sites is screen-washing. This method aims at recovering vertebrate microremains, which are usually hardly noticeable by the naked eye. Sediments from each locality, about 50-100 kilograms, were taken back to the Sahatsakhan Dinosaur Research Centre for screen-washing. The wet sieving method (Mckenna *et al.*, 1994) has been applied to separate microfossils from sands and gravels. Water and a pair of screens are used to separate fossils from the surrounding mudrock. A coarse upper screen stops large bone and plant fragments, while a very fine lower screen about 0.5 and 1.7 mm mesh-sized sieves (Cuny et al., 2003) were used for the small specimens.

1.4 Enamel microstructure

The cross section of crocodilian and dinosaur teeth were embedded in resin (Araldite GY 251: Hardener HY 956) to facilitate sectioning. Sections were cut with a diamond studded rock saw with a very thin blade to minimize the loss of material. The face of the sections were ground smooth with 1000 grit to remove scratches and grooves left by the saw blade. Etching was performed with 2N HCl for 3 to 5 seconds. Then the samples were cleaned in water for 30 seconds to remove grit particles and loose crystallites. In order to recognize histological characters permitting to differentiate crocodile teeth from those of the dinosaur *Siamosaurus,* which are very much crocodile-like from a morphological point of view, the samples were sputtercoated with gold at low current strength (15 mA) and investigated under the JEOL scanning electron microscope (model JSM 6460 LV with acceleration voltage 0.1-30kV).

2) Evolution and Palaeoecology

2.1 Sedimentary structure and lithology of nine assemblages

In each studied site, textural feature such as grain size, distribution, sorting, roundness and color of the sediments in each assemblage were investigated. In addition, lithologic characters, sequences and relationship, such as mixing or graduation as well as the occurrences in the section, were recorded. This information would be used to explain the palaeoenvironment of the late Jurassic Phu Kradung Formation to early Cretaceous Sao Khua and Khok Kruat Formations.

2.2 Evolution of the Thai Mesozoic crocodyliforms

Fossil crocodilians from the Phu Kradung, Sao Khua and Khok Kruat Formations as well as the European Mesozoic crocodilians were compared each other and their morphological differences were observed. Other components of the fauna and the environment from that time were analyzed and interpreted to reconstruct their evolution.

2.3 Palaeoecology of the Thai Mesozoic crocodyliforms

All information from field works and laboratorial works were integrated. The interactions and relationships between the fossil crocodiles and the other components of the faunas were analyzed and used to infer working hypothesis. Finally, all data will be gathered to reconstruct the paleoecology such as relationships between species, palaeobiogeographical framework and palaeoenvironmental framework. This study is based on the uniformitarianism, the interpretation of the inanimate past by reference to the natural geological processes going on today and by comparison with present life, and the interpretation of the past in the light of the present (Ager, 1963).

CHAPTER IV

SYSTEMATIC PALAEONTOLOGY OF THE MESOZOIC CROCODYLIFORMS FROM THAILAND

The following overview of the Mesozoic crocodiles from the Khorat Group is based on specimens, which are housed in the collection of the Sahatsakhan Dinosaur Research Center, Kalasin Province as well as type specimens on reports from Buffetaut and Ingavat (1980, 1983 and 1984). These specimens occur only in three formations of the Khorat Group, namely the Phu Kradung, Sao Khua and Khok Kruat Formations. Therefore, this summary will be presented in stratigraphic order, running from the oldest to youngest formations.

PART I—THE PHU KRADUNG FORMATION

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Benton and Clark, 1988

FAMILY ?GONIOPHOLIDIDAE Eastman, 1902

***"Sunosuchus" thailandicus* Buffetaut and Ingavat, 1980**

(Fig. 4-1 to 4-3)

Specimen— TF 1370 (Fig. 4-1A), a nearly complete lower jaw, from Muang District, Nong Bua Lum Phu Province and KP 11, 12, 15, 18 (Fig. 4-1B), parts of a lower jaw, from Khum Phok District, Mukdahan Province.

Description— The total length of TF 1370 is 1140 mm whereas the maximum width of the specimen is 65 mm (at the level of the surangular). The specimen is a large and robust jaw with a long symphysis, 475 mm in length. There are thirty dentary alveoli in each ramus. Teeth, which are preserved *in situ*, show only the base of their crown. The cranial end of TF 1370 is fan-shaped. The flared part corresponds to the large third and the fourth dentary alveoli. The retroarticular process of the specimen bends slightly caudodorsally. The original description of TF 1370 was published by Buffetaut and Ingavat in 1980 and 1984.

Dentary fragments (KP 11, 12, 15, and 18) from a single individual, of which some pieces can be fitted together, have been found in Khum Phok, Mukdahan Province. Dorsally, the cranial end of the dentaries is transversally expanded, fan-shaped, and shows a strong angulation at the level of the fourth dentary alveolus. The diameters of the third and the fourth dentary alveoli indicate the largest teeth on the preserved specimen. In ventral view, the ornamentation of the Khum Phok specimen is heavily sculptured with grooves and pits. Its maximum width at the level of the fourth dentary alveoli is 175 mm, which is larger than TF 1370 showing only 160 mm.

Discussion—The type species of the genus *Sunosuchus*, *S. miaoi* Young 1948, a crocodile from the Late Jurassic Xiangtang Formation of Gansu Province, northern China is described on the basis of a skull without the cranial rostrum. The type species shows maxillary depressions and a pair of anterior palatal opening (Buffetaut, 1986; Buffetaut and Ingavat 1980, 1984; Maisch et al., 2003; Witmer, 1995; Young, 1948).

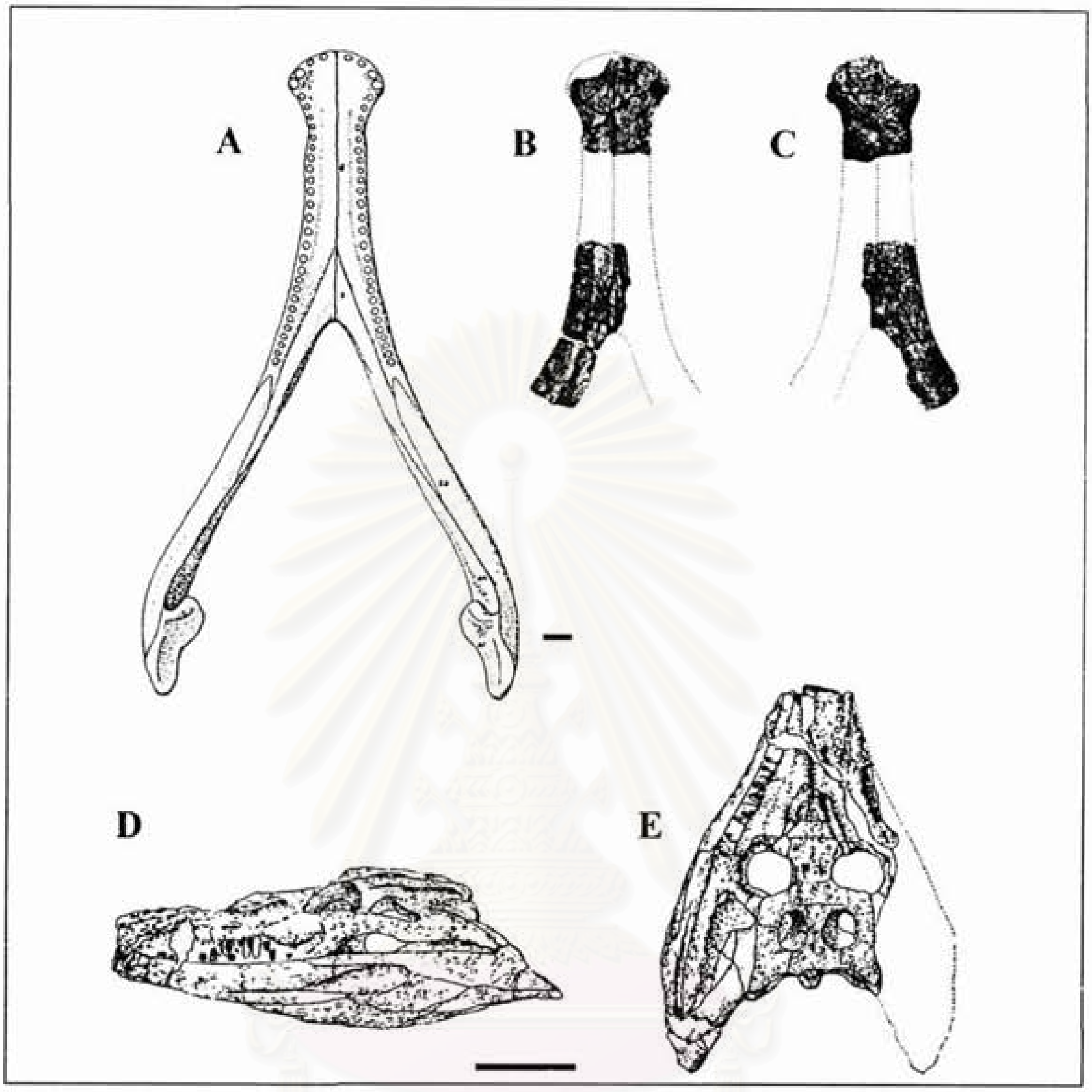


Fig. 4-1 "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980, TF 1370, holotype lower jaw in A: dorsal view. B: parts of dentaries from Khum Phok (K 11, 12, 15 and 18) in dorsal view and C: ventral view. D: *Sunosuchus miaoi* Young, 1948, V 500, holotype partial cranium, in lateral view and E: dorsal view. All scale bars represent 5 cm. A: from Buffetaut and Ingavat (1980), D and E: from Young (1948).

Comparison between *S. miaoi* and TF 1370 were relatively difficult, because *S. miaoi* is lacking the anterior part of the mandible whereas TF 1370 is known only from the lower jaw. However, Buffetaut and Ingavat (1980) included TF 1370 in the genus *Sunosuchus* based on the similarities of the mandibular rami between the Thai specimen and *S. miaoi*, particularly the caudal portion such as the external mandibular fenestra, and the character of the teeth. At that time, they also erected TF 1370 as a new species, *Sunosuchus thailandicus*, based on the differences of its size, which were larger than that of *S. miaoi*.

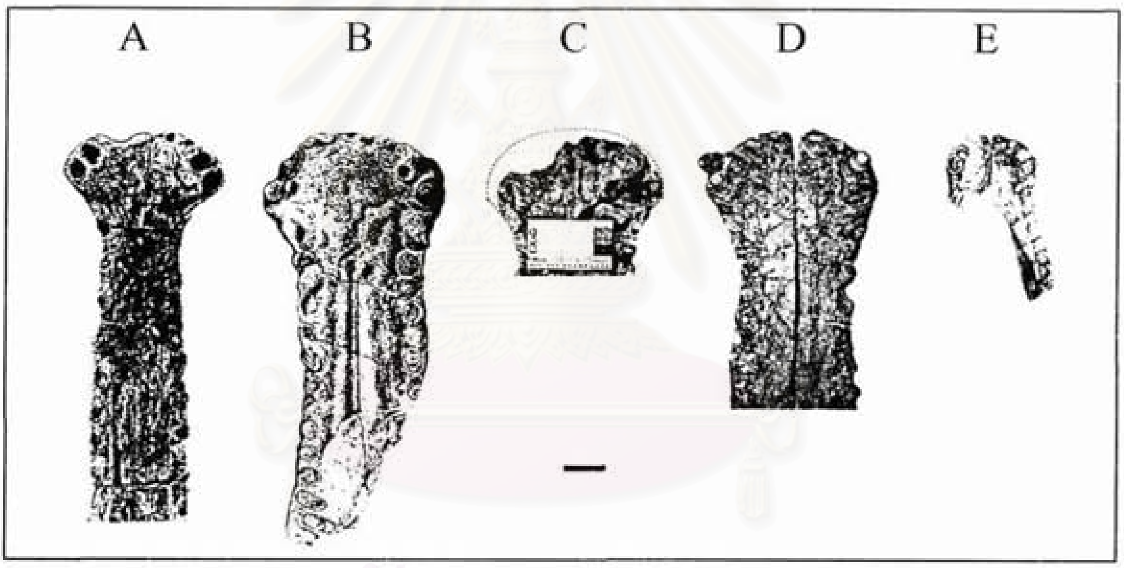


Fig. 4-2 The angulation of the tooth row on the pholidosaurids and goniopholidids dentaries in dorsal view. A: *Sarcosuchus imperator* reference by Buffetaut and Taquet (1977), B: *Sarcosuchus hartti* (No. R 3423), C: Khum Phok specimen (K 15 and 18), D: "*Sunosuchus*" *thailandicus* (TF 1370), and E: *Goniopholis crassidens* (BMNH 1807). Scale bar represents 5 cm. A and B: from Buffetaut and Taquet (1977), E: from Owen (1879).

A recent phylogenetic analysis (Lauprasert et al., submitted) suggests that *Sunosuchus* and the other non broad-snouted Goniopholididae (*Calsoyasuchus* and *Eutretauranosuchus*) share unique characters as follows: maxillary depressions on the caudolateral surface of the maxillae and a pair of anterior palatal opening. However, the attribution of TF 1370 to the genus *Sunosuchus* does not involve these characters, but is based on the shape of the external mandibular fenestra, ornamentation on the jaw surface and tooth morphology, of which only the base of the crowns are preserved. From my point of view, these are not sufficient characters to identify the genus or the family of TF 1370.

A number of differences between TF 1370 and the type species, *Sunosuchus miaoi*, are recognized in this study. The retroarticular process of TF 1370 bends slightly caudodorsally, whereas that of *Sunosuchus miaoi* is orientated caudoventrally. The external mandibular fenestra of TF 1370 is also larger than that of *S. miaoi*. In addition, tooth morphology is not a diagnostic character of the genus *Sunosuchus* because a similar morphology, such as the stout, conical tooth with two well-developed smooth carinae on opposite sides, is also found in other goniopholidids. In 1996, Wu, Brinkman and Russell defined another *Sunosuchus* species, *Sunosuchus junggarensis*, from the late Jurassic (Oxfordian) Shishugou Formation in the Eastern Junggar Basin (Maisch et al., 2003), which possesses the best known skull for the genus *Sunosuchus*. The skull of *S. junggarensis* is consequently practical to reconstruct the missing portions of *Sunosuchus miaoi*.

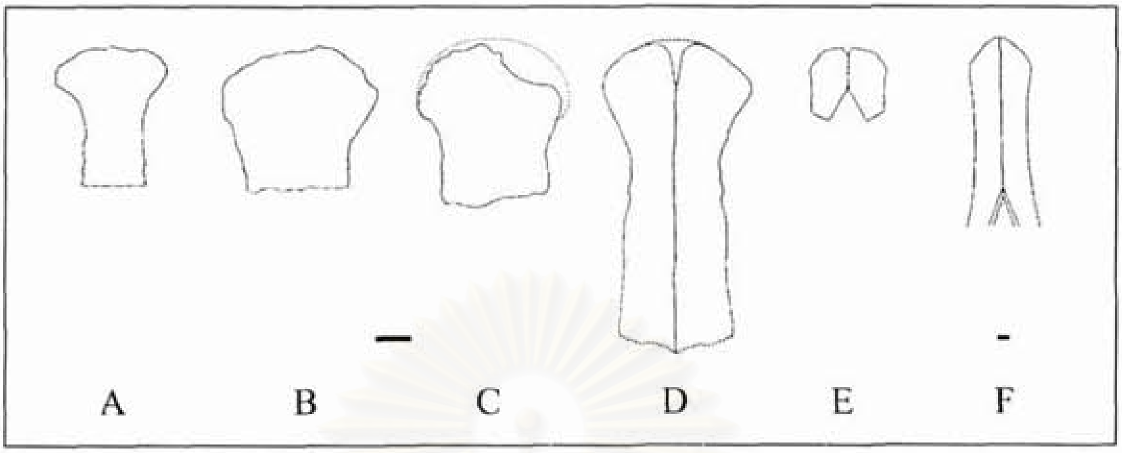


Fig. 4-3 Comparisons among dentary outlines of the pholidosaurids and goniopholidids in ventral view. A: *Sarcosuchus imperator*, B: *Sarcosuchus hartti* (No. R 3423), C: Khum Phok specimen (K 15 and 18), D: "*Sunosuchus*" *thailandicus* (TF 1370), E: *Goniopholis crassidens* (BMNH 1807), and F: *Sunosuchus junggarensis* (IVPP V 10606), holotype. Scale bars represent 5 cm in A to E and 1 cm in F. A, B: from Buffetaut and Taquet (1977), E: from Owen (1879), and F: from Wu et al., 1996a.

Comparisons between TF1370 and the other goniopholidids, including *Sunosuchus junggarensis*, show several different characters as follow. The mandibular symphysis of TF 1370 is longer than any of the known goniopholidids. The dentary symphysis of TF 1370 reaches the level of the seventeenth and the eighteenth dentary alveoli and extends to the level of the twenty-fourth and the twenty-fifth dentary alveoli when the splenial symphysis is included. The mandibular symphysis usually reaches the level of the sixth dentary alveolus in *Goniopholis* (a broad-snouted goniopholidid from Europe) whereas it reaches the level of the seventh dentary alveolus in *Eutretauranosuchus delfsi* (a slender-snouted goniopholidid from the Morrison Formation), the fourteenth and the fifteenth dentary alveoli in *Sunosuchus junggarensis* (IVPP V 10606), and the eleventh dentary alveoli in *Vectisuchus leptognathus*, a relative non broad-snouted goniopholidid from the Wealden of England (Buffetaut and Hutt, 1981). However, this character is not preserved in *Calsoyasuchus*, a primitive long-snouted goniopholidid from the Lower Jurassic, Kayenta Formation. Wu et al., (1996a) has been mentioned that the genus *Sunosuchus* possesses a short splenial symphysis. This feature has been used as a diagnostic character of *Sunosuchus* by Averianov (2000). Moreover, *Eutretauranosuchus* and *Goniopholis* also possess the length of the splenial symphysis only 1-2 dentary alveoli. On the contrary, the splenial symphysis length of TF 1370 is about seven dentary alveoli, which is evidently longer than that of the other goniopholidids.

A re-examination of *G. crassidens* (BMNH 1807), *G. simus* (BMNH 41098 and IPB R359), *G. baryglyphaeus* (IPFUB Gui Croc 1), *Eutretauranosuchus delfsi* and *Sunosuchus junggarensis* shows that the cranial ends of these goniopholidids are not expanded as widely as in TF 1370. On the contrary, they present a distinct angulation of the tooth row at the level of the second and the third dentary alveoli (see more descriptions in Buffetaut and Ingavat, 1983; Wu et al., 1996a).

Buffetaut and Ingavat (1984) suggested that TF 1370 was relatively related to the family Pholidosauridae, especially the giant crocodile *Sarcosuchus*, from the lower Cretaceous of Niger and Brazil (Buffetaut and Taquet 1977; Sereno et al., 2001). This study also agrees with their suggestion on the basis of a number of characters, which are similar between TF 1370, the Khum Phok specimens and the

Pholidosauridae. These include the presence of the long mandibular symphysis. *Sarcosuchus imperator* possesses a dentary symphysis reaching the level of the twentieth dentary alveolus (Sereno et al., 2001) and reaches at least the level of the twenty-third dentary alveolus for the mandibular symphysis (Buffetaut and Ingavat, 1984). The distal expansions of TF 1370 and the Khum Phok specimens correspond to the large third and fourth alveoli. This is a character of *Sarcosuchus* and its sister taxon *Terminonaris*, a smaller North American genus (Sereno et al., 2001). The retroarticular process of TF 1370 curves caudodorsally and runs in the same direction to some pholidosaurids such as *Sarcosuchus imperator* and *Terminonaris robusta* (Wu et al., 2001b). The external mandibular fenestrae are visible in TF 1370, as well as in *Sarcosuchus imperator* and *Terminonaris robusta*, although they are different in size. TF 1370 cannot be included in the genus *Terminonaris*, because the general shape and the proportion of the dentaries width of *Terminonaris* are distinctly smaller than those of TF 1370. In addition, the North American *Terminonaris* specimens have all been found in marine deposits (Wu et al., 2001b) whereas TF 1370 was found in non-marine sediment.

This reassessment shows that the taxonomic status of TF 1370 is now rather ambiguous, due to the lack of diagnostic characters of the long snouted goniopholidid, as mentioned above. The result of this study indicates that TF 1370 probably does not belong to the genus *Sunosuchus* or even the family Goniopholididae. Moreover, this study also found a number of characters in common between the Thai long-snouted crocodilians and the pholidosaurids, i.e., possession of a long mandibular symphysis (longer than the other goniopholids); without a strong angulation between the 2nd and 3rd alveoli; cranial end of the dentary transversely wide and the retroarticular process oriented caudodorsally. For the above reasons, TF 1370 and the Khum Phok specimens can only be determined as a long-snouted crocodilian, which could belong either to the family Goniopholididae or Pholidosauridae on the basis of the ornamentation on the jaw surface and tooth morphology. However, the phylogenetic relationships of the family Pholidosauridae, particularly the genus *Sarcosuchus* and *Pholidosaurus*, are up to now unclear and require revision. Until a complete upper jaw or a skull of the Thai long-snouted crocodilian is discovered, it seems suitable to consider TF 1370 and the Khum Phok specimens as belonging to an uncertain family and genus for the time being, retaining the specific name of Buffetaut and Ingavat (1980) as "*Sunosuchus*" *thailandicus*. In order to make a justified taxonomic decision, more material is necessary. Further discovery of a complete skull might solve the affinities of TF 1370 and the Khum Phok specimens, which probably were the largest goniopholid of the world or the first pholidosaurid of Thailand.

GONIOPHOLIDIDAE Cope, 1875 or PHOLIDOSAURIDAE Eastman, 1902

(Fig. 4-4 and 4-5)

Specimen— DKC-1 (Fig. 4-4), a middle part of the left dentary and DLC-1 (Fig. 4-5), and a caudodorsal part of the right surangular. The specimens were collected from Kham Cha-I District, Mukdahan Province.

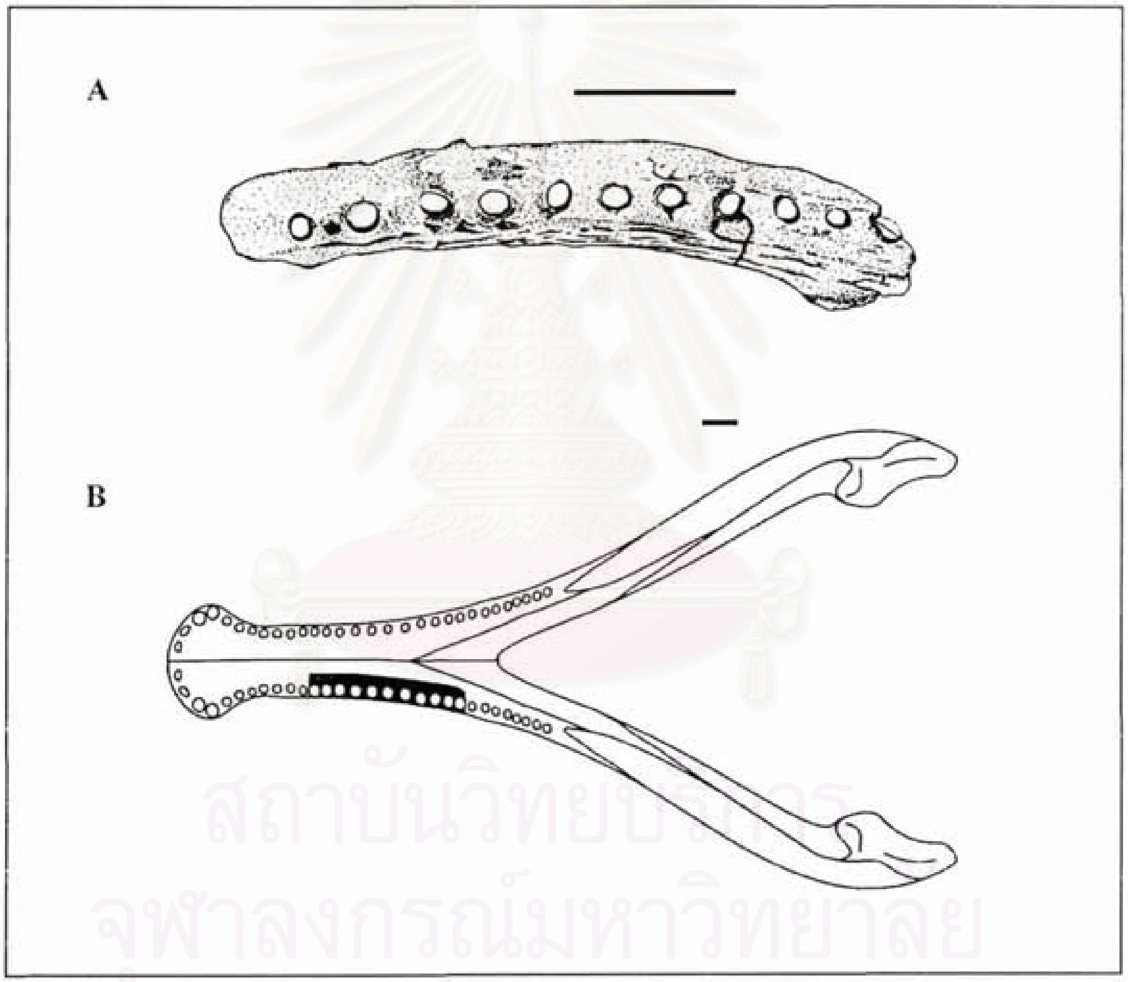


Fig. 4-4 Partial left dentary (DKC-1) from Kham Cha-I District, Mukdahan Province in A: dorsal view. B: Approximate position of the specimen on the lower jaw of a long-snouted crocodilian, "*Sunosuchus*" *thailandicus*, in dorsal view. All scale bars represent 5 cm.

Description of the dentary— In dorsal view, DKC-1 is slightly curved and is 220 mm in length. Its cranial and caudal margins are broken. Eleven dentary alveoli can be counted on the specimen. The dentary alveoli are circular in shape and separated by rather equal septums, about 7–9 mm long each. Their diameter is also equal in size at about 6–7 mm. From the third to the eleventh dentary alveoli, the tooth row slightly leans lingually. Medial to the tooth row, the dentary floor is partly preserved and is about 15–22 mm in width, but does not reach the mandibular symphysis. The ventral parts of the specimen are also broken. The lateral surface of DKC-1 is preserved for about 25 mm of its height. Its surface is heavily sculptured with long parallel grooves.

Discussion—DKC-1 shows a regular width of the dentary floor along the specimen. This character indicates that the specimen is a long-snouted crocodilian. The presence of equal alveolus size and the labiolingual curvature of the tooth row in DKC-1 shows that it should be situated at the middle part of the left dentary, more probably at the level of the twelve or the thirteen to the twenty-second or the twenty-third dentary alveoli (Fig. 4-4B). The heavily sculptured ornamentation of DKC-1 is seen in the family Goniopholididae and Pholidosauridae. With these evidences, the specimen can be identified just to the family level. It can be either a long-snouted goniopholidid or pholidosaurid. In order to make a decision on the taxonomic status at generic and specific levels for DKC-1, more complete material is required.

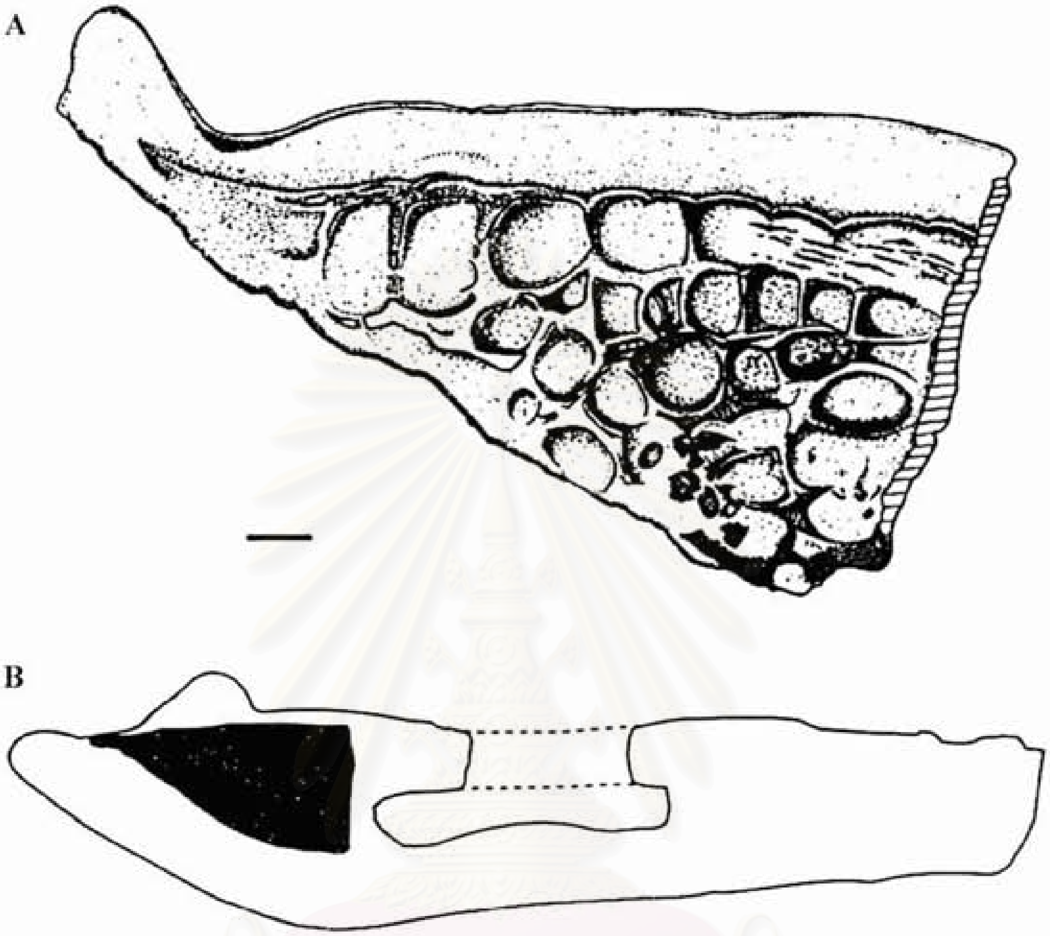


Fig. 4-5 Part of the right surangular (DLC-1) from Kham Cha-I District, Mukdahan Province in A: lateral view. B: Approximate position of the specimen on the lower jaw of a long-snouted crocodilian, "*Sunosuchus*" *thailandicus*, in lateral view. All scale bars represent 5 cm.

Description of the surangular— DLC-1 is the caudodorsal part of the right surangular. It is 162 mm long, 80 mm high and 15 mm wide. The latter measurement indicates that the specimen is lateromedially compressed. The dorsal surface of the specimen is distorted whereas its labial and lingual margins are merged together as a thick ridge in the cranial part and then become a groove in the caudal part. In lateral view, the ornamentation of DLC-1 is heavily sculptured and varies in shape, with oval, quadrate, and rounded pits about 10–20 mm wide and about 2–5 mm deep. Its ventral margin is broken away while the dorsal part shows a broad smooth surface along its margin, about 15 mm high. The caudal part of the specimen is upward and leans lingually. In medial view, the surface is rather flat and smooth, having been worn away. In ventral view, the cranial part is straight whereas the caudal part of DLC-1 is curved lateromedially.

Discussion— Although the caudal part is compressed, the curvature on the most caudal portion of DLC-1, which sends a process caudodorsally to contact the articular, can be observed. This feature indicates that the specimen is the caudodorsal part of the surangular. The sculptured ornamentation of DLC-1on the lateral surface and its general size are very similar to that of "*Sunosuchus*" *thailandicus*. At the present stage, the ornamentation and general size are inadequate characters to justify a generic and specific attribution. However, the ornamentation, which is heavily sculptured and varies in shape, is known in both the goniopholidid and pholidosaurid crocodilians. Therefore, DLC-1 could belong either to the family Goniopholididae or Pholidosauridae.

Family ATOPOSAURIDAE Gervais, 1971.

Genus *Theriosuchus* Owen, 1878.

Cf. *Theriosuchus* sp.

(Fig. 4-6)

Specimen— CCC-1 (Fig. 4-6A–D), a part of the left dentary from Chong Chat, Nong Bua Lum Phu Province.

Description—This specimen is 28 mm long without the cranial and caudal extremities. In dorsal view, eight dentary alveoli can be counted on the specimen. The mesial margin of the first dentary alveolus is lacking, exposing a replacement tooth. The other teeth are preserved in their alveoli, but the tips are broken. The first to the third dentary alveoli are located adjacent to the labial margin while the fourth to the seventh dentary alveoli gradually bend lingually and reach the lingual margin at the level of the eighth dentary alveolus. The teeth are slightly compressed labiolingually in cross-section.

Study with a Scanning Electron Microscope reveals the morphology of the replacement tooth in the first dentary alveolus. It is remarkably slender in shape and pointed at the apex. Its surface is covered by very thin and sharp ridges only at the base and tip of the crown (Fig. 4-6B). They are oriented basoapically, but they are absent in the middle part of the crown. The teeth in the second to the fourth dentary alveoli are preserved in their sockets. They are circular in cress-section with the diameter about 1 mm mesiodistally. The teeth in the fifth to the eighth dentary alveoli are larger than the teeth in the cranial portion. They are oval in cross-section, about 2–

3 mm mesiodistally, and slightly curved lingually. Except for the replacement tooth, the teeth are missing their tips. The tooth in the sixth dentary alveolus is the best preserved one and shows a lanceolate shape. It is wide and slightly swollen basally whereas its apical part is tapered. A well developed crenulated carinae (Pol and Apesteguia, 2005), which run basoapically (Fig. 4-6D), can be recognized at the mesial and distal edges of the tooth. The enamel on the surfaces of the tooth crown is covered with distinct, irregular ridges.

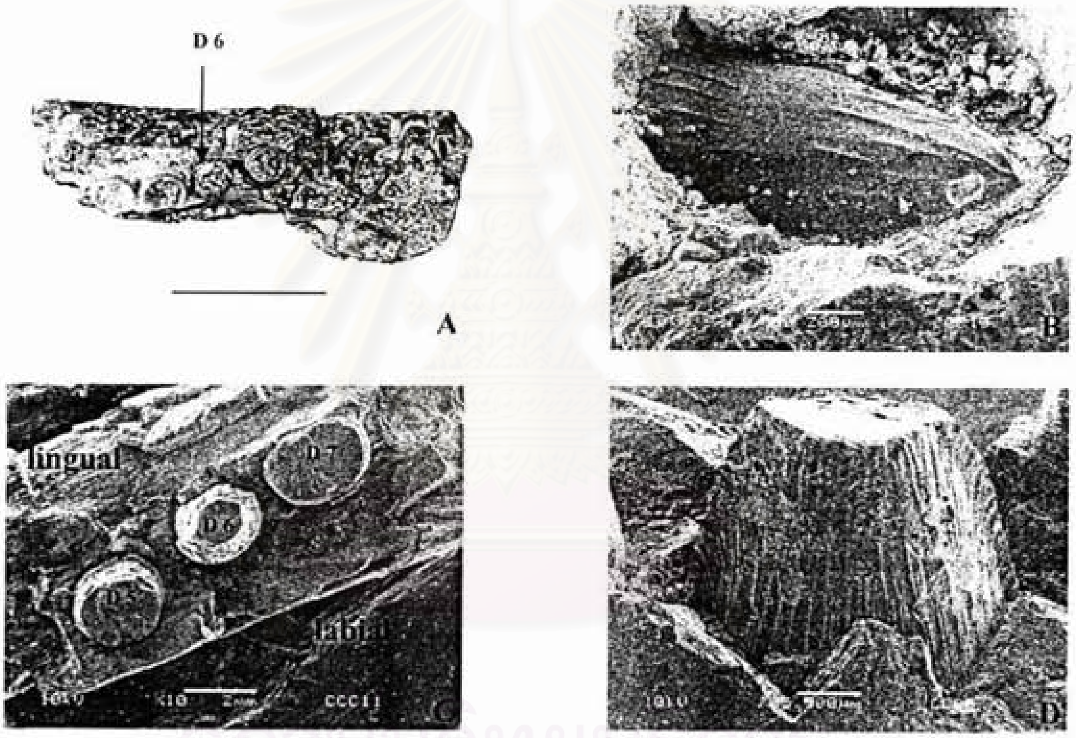


Fig. 4-6 Part of left dentary (CCC-1) from Chong Chat, Nong Bua Lum Phu Province in A: dorsal view, scale bar represents 10 mm. B: a replacement tooth of the first alveolar in dorsal view. C: the fifth to seventh dentary teeth in dorsal view. D: the sixth dentary tooth in lingual view. Abbreviation: D, dentary tooth

The first to the fifth dentary alveoli are separated from each other by a thin interalveolar septum whereas the dentary alveoli, from the sixth to the caudal-most portion, are united in a single groove. Medial to the tooth row, the specimen presents part of the dentary floor cranially. It is about 7 mm wide and tapered distally, reaching the tooth row at the level of the fifth dentary alveolus.

In lateral view, its dorsal margin is increased in height caudally and reaches its maximum at the level of the fifth dentary alveolus. The lateral surface of the specimen is heavily sculptured and forms longitudinally directed grooves. Its ornamentation also extends to the ventral surface of the specimen. In ventral view, the cranial part of the specimen is relatively flat while the caudal part is rather convex. In medial aspect, the mandibular symphysis can be seen from the level of the first to the third preserved dentary alveoli, but its surface is rather crushed and obscured. The splenial bone is partly preserved and increases in height from its rostral to caudal extremities. The splenial facet, integrated into the mandibular symphysis, is visible along the lingual margin of the dentary floor.

Discussion—The specimen from Chong Chat is, at first sight, reminiscent of a juvenile crocodilian. However, there are a number of osteological characters that clearly identify CCC-1 as an adult individual. These features consist of the possession of a dense sculpturing on the bone surface and well-developed rugosity of the dermal bone (Joffe, 1967; Schwarz and Salisbury, 2005). The specimen shows interalveolar septums cranially and a single groove caudally. This character is reminiscent of the genera *Theriosuchus* and *Araripesuchus* (Owen, 1879; Buscalioni and Sanz, 1988; Pol and Apesteguia, 2005; Schwarz and Salisbury, 2005). However, CCC-1 can be distinguished from the genus *Araripesuchus* by the presence of serration on the mesial and distal margins of the teeth, and a short and narrow alveolar groove (Ortega et al., 2000; Pol and Apesteguia, 2005). The pseudocaniniform teeth are usually situated in the sockets, where are separated by the interalveolar septum. While the lanceolate-shaped teeth, low-crowned teeth, and strongly labiolingually flattened teeth are place in a single groove (Schwarz and Salisbury, 2005). The presence of both interalveolar septums and a single groove and the difference of their cross-section (at the base of the crown) indicate that the dentition of CCC-1 is heterodontous crocodilian, which consists of pseudocaniniform and lanceolate–shaped teeth. Tooth morphology of the sixth alveolus, lanceolate–shaped, is a good diagnostic character to include CCC-1 in the genus *Theriosuchus* (Brinkmann, 1992; Buscalioni and Sanz, 1988; Wu et al., 1996b; Schwarz and Salisbury, 2005).

Theriosuchus pusillus and *T. ibericus* possess four tooth morphotypes. These include pseudocaniniform, lanceolate-shaped, low-crowned, and strongly labiolingually flattened teeth (Brinkman, 1992) whereas *T. guimarotae* show only two morphotypes, i.e., pseudocaniniform tooth and lanceolate–shaped tooth (Schwarz and Salisbury, 2005). Although CCC-1 shows its tooth morphotype similar to *T. guimarotae*, it cannot be compared with each other because the specimen from Chong Chat lacks the cranial and caudal teeth. The presence of strong crenulation on the mesial and distal carinae distinguishes CCC-1 from *T. guimarotae*, which possesses weak and faint carinae (Schwarz and Salisbury, 2005).

Based on two synapomorphic traits as follow: a small body size (Buscalioni and Sanz, 1988), and a typical dentition (Schwarz and Salisbury, 2005), the Chong Chat specimen is conferred to the genus *Theriosuchus*, Family Atoposauridae for the time being. Additional material is definitely required to insist its taxonomic status and understand the affinity of the Thai dwarf neosuchian crocodilian from the Phu Kradung Formation.

PART II—THE SAO KHUA FORMATION

Early Cretaceous (Ante-Aptian),

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Benton and Clark, 1988

FAMILY GONIOPHOLIDIDAE Cope, 1875

SIAMOSUCHUS, Lauprasert *et al.*, submitted

Siamosuchus phuphokensis, Lauprasert *et al.*, submitted

(Fig. 4-7)

Specimen— Holotype: PPC 1/1, anterior portion of a rostrum including premaxillae, external nares, part of maxillae and nasals; **Type series:** PPC 1/2–88, parts of maxillae, nasals, left lacrimal, frontal; part of left postorbital; part of left jugal; part of posterior cranial table; postcranial skeletons represented by isolated vertebrae, femur, tibia-fibula, humerus, radius-ulna, pelvic girdles, and dorsal and ventral osteoderms. All specimens were collected from Phu Phok, Tambon Kok Prasil, Phu Phan District, Sakon Nakhon Province.

Description and Discussion— see in Lauprasert et al. (submitted) in appendix III.

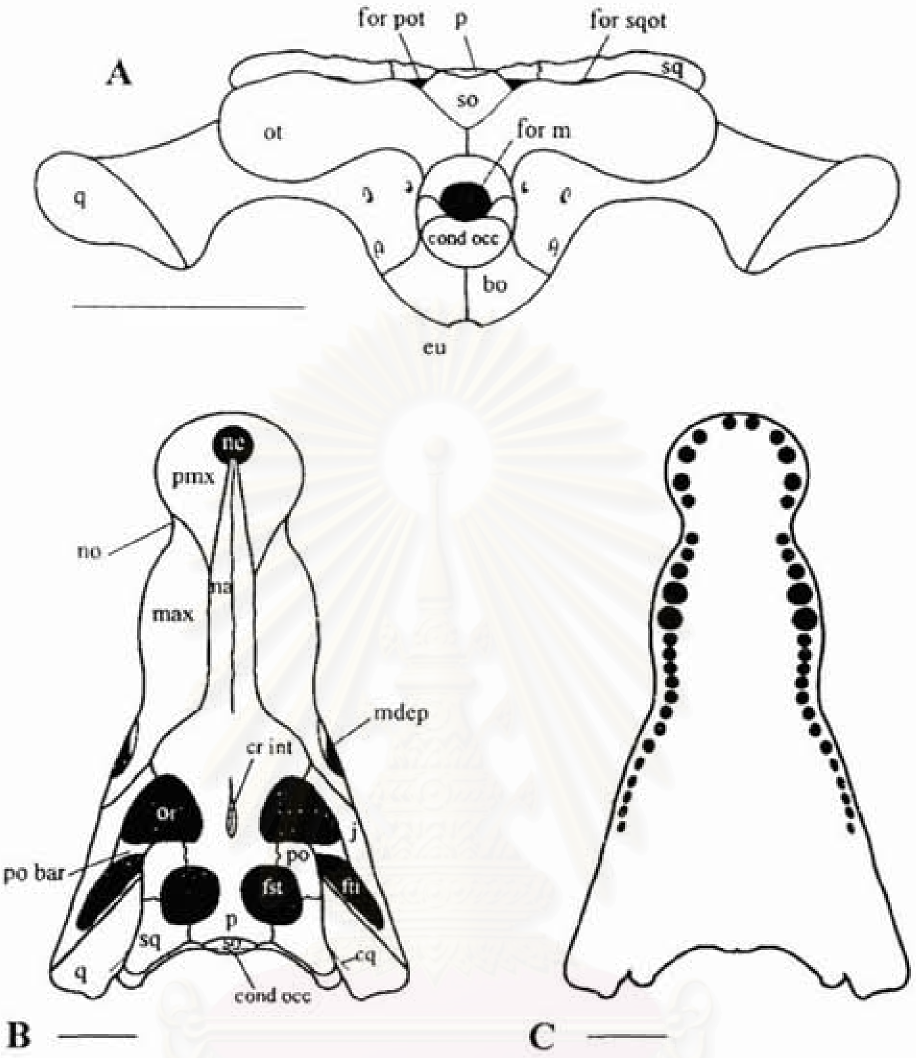


Fig. 4-7 Reconstruction of the skull of *Siamosuchus phuphokensis*, gen. et sp. nov., Lauprasert et al, submitted, in A: occipital view, B: dorsal view, and C: palatal view. Abbreviations: (see in chapter III). All scale bars represent 5 cm.

FAMILY GONIOPHOLIDIDAE Cope, 1875

"*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983

(Fig. 4-8)

Specimen— TF 1478 (Fig. 4-8A), a part of the left dentary, from Phu Wiang District, Khon Kaen Province.

Description—The specimen is 118 mm in length whereas its maximum width is 33.5 mm. The anterior and posterior extremities of this specimen are not preserved. Ten dentary alveoli, from the second alveolus to the eleventh alveolus, can be counted on the specimen. In dorsal view, the lateral margin of TF 1478 shows two convexities. The first convexity is located along the third and the fourth dentary alveoli, whereas the second one starts at the ninth dentary alveolus. The mesiodistal diameters of the third and the fourth dentary alveoli indicate that they are larger than the other teeth. Both of them are contiguous whereas the fifth to the eleventh dentary alveoli are separated by unequal interalveolar septum. In medial view, the Meckelian groove is found along the level of the fourth and the fifth dentary alveoli. Numerous striations, radiating from the Meckelian groove, are clearly visible. The posterior end of the dentary symphysis can be recognized at the level of the seventh dentary alveolus. It is not possible to determine the length of the splenial symphysis because the splenial is not preserved, but the continuity between the symphyseal surface and the sutural surface for the splenial indicates that the splenials of TF 1478 are involved in the mandibular symphysis. In lateral view, TF 1478 shows two curves, which correspond to the convexities of the dorsal view. The first is convex around the level of the third and the fourth dentary alveoli and the other convexity is placed around the level of the ninth and the eleventh. The original description of TF 1478 was published by Buffetaut and Ingavat in 1983.

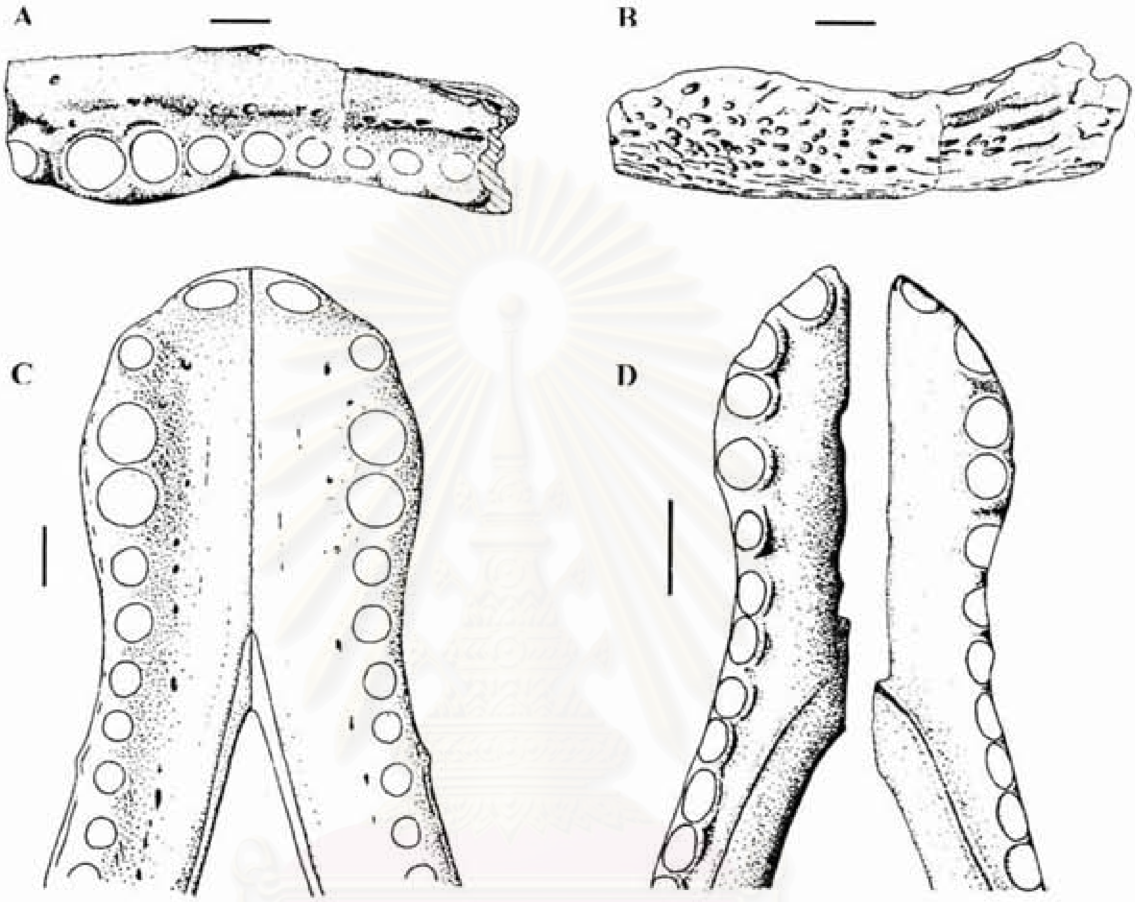


Fig. 4-8 "*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983, TF 1478, holotype a part of the left dentary in A: dorsal view and B: lateral view. C: Reconstruction of the anterior dentary of "*Goniopholis*" *phuwiangensis*. D: *Eutretauranosuchus delfsi* Mook, 1967, CMNH 8028, a lower jaw in dorsal view. All scale bars represent 5 cm. C: from Buffetaut and Ingavat (1983), D: drawing from Mook (1967).

Discussion: The enlarged and contiguous third and fourth dentary alveoli are a diagnostic character of the family Goniopholididae and Pholidosauridae (Buffetaut and Ingavat, 1983). However, the latter family is known only from long-snouted crocodilians. The presence of a short dentary symphysis indicates that the Phu Wiang specimen belongs to a short-snouted crocodilian. Therefore, TF 1478 definitely belongs to the family Goniopholididae.

Buffetaut and Ingavat (1983) described TF 1478 as the genus *Goniopholis*, based on the following diagnostic characters: (1) dentary symphysis reaching the sixth dentary alveoli; (2) anterior portion of the lower tooth row without marked angulation (see Buffetaut and Ingavat, 1983 for details); (3) lateral edge of the third and fourth dentary alveoli without strong outward protrusion, and (4) strongly undulated alveolar margins in lateral view. Obviously, the attribution to the genus *Goniopholis*, at that time, was mainly based on the characters of the tooth row and the symphysis region (Buffetaut and Ingavat, 1983), because complete skulls were lacking. Nevertheless, this study has demonstrated that the first to third "diagnostic" characters, as mentioned above, are not found in the European *Goniopholis*.

A recent phylogenetic analysis (Lauprasert et al., submitted) suggests that *Goniopholis simus* Owen, 1878, and *G. baryglyphaeus* Schwarz, 2002 form a clade, which shows a combination of skull characters. Although the type species of the genus *Goniopholis*, *G. crassidens* Owen, 1841, is not included in the phylogenetic analysis, due to its lack of several characters, its dentary shows a marked angulation at the level of the third alveolus (Fig. 4-2E). Additionally, its dentary symphysis ends at the level of the sixth alveolus. These two features also appear in the other European *Goniopholis*, *G. simus* (Fig. 10C in Salisbury et al., 1999) and *G. baryglyphaeus* (Fig. 3C in Schwarz, 2002).

In TF 1478, the dentary symphysis reaches the level of the seventh alveolus and the lateral margin does not possess a marked angulation. This feature resembles that of the North American goniopholidid, *Eutretauranosuchus delfsi*, whose symphysis ends at the level of the seventh alveolus and at the level of the eighth tooth when the splenial symphysis is included. Furthermore, there is no marked angulation on the dentary in the North American slender-snouted goniopholidid. The genus *Goniopholis* can be distinguished from *Eutretauranosuchus* by the absence of a pair of the anterior palatal opening. However, this feature is not preserved in TF 1478. The Phu Wiang specimen is however precluded from the reference to the genus *Eutretauranosuchus* based on a convexity at the tenth and eleventh dentary alveoli, which is also stronger than that of *E. delfsi* (Buffetaut and Ingavat, 1983). In addition, this study observed that the third and the fourth dentary alveoli of TF 1478 are more contiguous than that of *Eutretauranosuchus*.

A short-snouted goniopholidid, *Siamosuchus*, from the Sao Khua Formation of northeastern Thailand has been erected as a new genus, based on the diagnostic characters of the nearly complete upper jaw and some postcranial skeletons (Lauprasert et al., submitted). Comparison between *Siamosuchus phuphokensis* and TF 1478, however, is not possible because there show no elements in common. Therefore, the phylogenetic position of TF 1478 is ambiguous.

The best attitude at the present stage for the short-snouted goniopholidid from Phu Wiang, TF 1478 is to consider it as a new species based on some differences on the dentary as discussed earlier. Because the relationships between the European, North American, and Thai species of *Goniopholis* are still extremely obscure, the author has a preference to attribute TF 1478 as belonging to an uncertain genus "*Goniopholis*" and retains the specific name of Buffetaut and Ingavat (1983) as "*Goniopholis*" *phuwiangensis*. Additional material, consequently, is required in order to make a justified generic attribution and is very necessary for understanding the affinity between "*Goniopholis*" *phuwiangensis* and the other goniopholidids, especially *Siamosuchus phuphokensis*, a crocodyliform discovered from the same formation.

Family ATOPOSAURIDAE Gervais, 1871

Genus *Theriosuchus* Owen, 1878

Theriosuchus cf. *pusillus* Owen, 1879

(Fig. 4-9)

Specimen— PPC-2 (Fig. 4-9), a nearly complete rostrum and dentaries from Phu Phok, Tambon Kok Prasil, Phu Phan District, Sakon Nakhon Province.

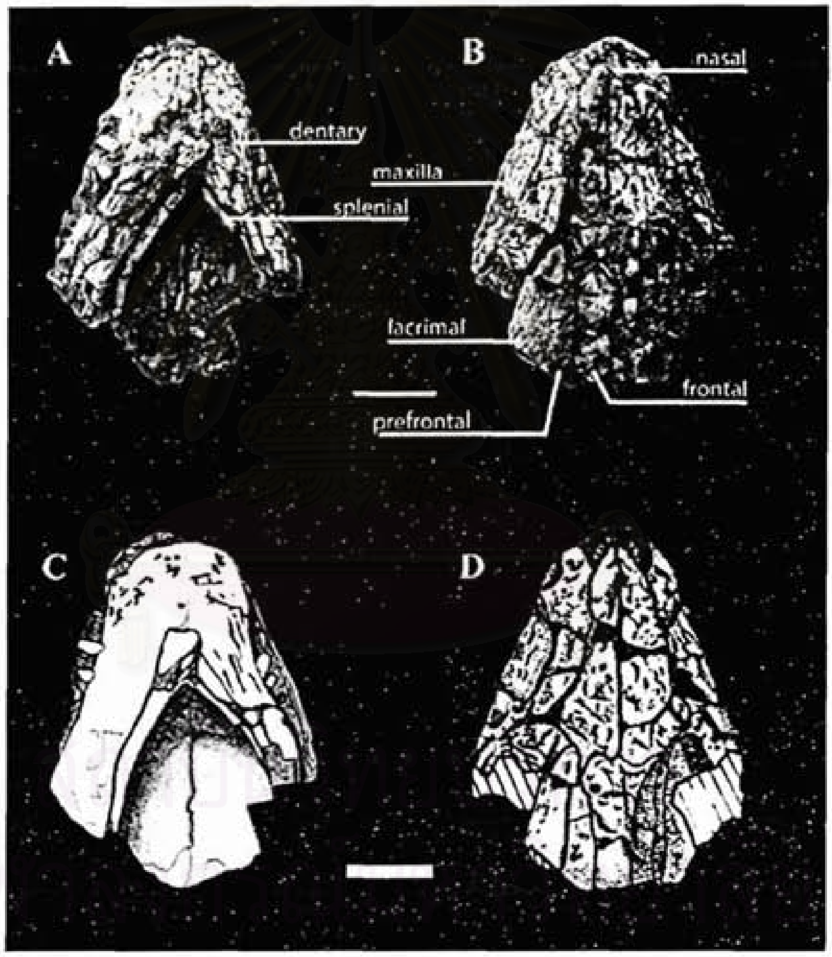


Fig. 4-9 Photographs of *Theriosuchus* cf. *pusillus*, PPC-2, an incomplete skull from Phu Phok, Sakon Nakhon Province in A: ventral view, B: dorsal view. C and D: Drawing of PPC-2 in ventral and dorsal views, respectively. Scale bar represents 1 cm.

Description:

Skull and proportion: PPC-2 is 32 mm long, lacking its posterior extremity. The dorsal surface of the specimen is slightly concave at the middle of the cranium. The skull extends posterolaterally in anteroposterior direction (Fig. 4-9B and D). Its surface is crushed, particularly the posterolateral portion of the right side. The specimen consists of a rostrum portion of the skull showing: the premaxillae, maxillae, nasals, partial lacrimals, partial prefrontal, partial frontal, partial dentaries, partial splenials, and some teeth.

Upper jaw: In dorsal view, the premaxilla is rounded anteriorly and laterally. Its posterolateral margin shows a constriction at the premaxillomaxillary suture, which is located between the fifth premaxillary and the first maxillary teeth. The maximum width of the premaxilla is equal to its maximum length. The premaxillary bar of the specimen is very narrow, about 1 mm. In medial view, the premaxillae are concave behind the posterior margin of the premaxillary bar and form the wall of the external nares. The posterior extremities of the premaxillae are separated by the nasal bones, which extend anteriorly and divide the external naris into two parts. The maxillae are relatively sub-vertical in shape. Their posterior extremities are broken. In dorsal view, the premaxillomaxillary suture runs anteromedially. The lateral margin of the maxilla abruptly widens posterolaterally with two concavities. The first concavity is at the level behind the premaxillomaxillary suture and the second is at the level of the sixth and the seventh maxillary teeth. The medial margin of the maxilla is in contact with the lateral margin of the nasal anteriorly whereas its posterior part is bordered by the lacrimal.

The external nares are relatively elliptical and anteroposteriorly compressed. They are located at the most anterior part of the skull. The posterior margins of the external nares are bounded by the nasals, 3 mm wide. The incisive foramen cannot be detected because of matrix covering the inside of the external nare. The nasal tapers anteriorly until it comes in contact with the posterior margin of the premaxillary bar, whereas its posterior part widens gradually and reaches its maximum width at the level in front of the anterior margin of the lacrimal. The nasal becomes narrow again where it meets the lacrimal and prefrontal. However, the shape and suture of the nasal are obscured in the most posterior margin, because the bone surfaces are crushed and enclosed by matrix. The left lacrimal of PPC-2 is partly preserved, lacking the lateral part. It is relatively robust and thick in shape. The dorsal surface of the lacrimal is slightly convex and shows sculptured ornamentation. The anterior portion of the lacrimal is tapered. Its anterior tip separates the maxilla laterally and the prefrontal medially. The position of the prefrontals can be recognized based on the presence of their descending processes, which are in contact with the dorsal surface of the pterygoid. The prefrontal is narrower and shorter than the lacrimal. The anterior part of the prefrontal tapers and slightly curves laterally. At its anterior extremity, the prefrontal meets the nasal and lacrimal. Its medial surface is in contact with the frontal margin along its length. The frontal is poorly preserved and rather obscured, because of the covering of the matrix on its surface. Its posterior part is not preserved. However, the width of the frontal can be determined by a space between the descending processes of the prefrontals, which is slightly wider than the widths of the prefrontal and lacrimal. In lateral view, the rostrum also shows festooned shape, which forms at least two convexities in vertical direction. The first convexity reaches its maximum at the level of the third and the fourth premaxillary teeth while the second one is at the level of the fourth and the fifth maxillary teeth.

In ventral view, some of the teeth of PPC-2 are preserved *in situ* and some are displaced. The displaced teeth are still affixed on the lateral surface of the skull by the matrix. Five premaxillary teeth can be counted, lacking their tips. The third and the fourth premaxillary teeth are almost equal in size, but their mesiodistal diameter indicates that the fourth is the largest premaxillary tooth whereas the fifth is the smallest one. At the premaxillomaxillary suture, a diastema, about 2 mm long, is recognized. The first to the seventh maxillary teeth can be observed on the left maxilla, but the apex of their crowns is preserved only on the fifth and the sixth maxillary teeth. The second and the third maxillary teeth are gradually enlarged whereas the size of the fourth maxillary tooth to the other posterior teeth diminishes. The surface of these tooth crowns is covered with distinct, irregular ridges, running basoapically. The palatal surface of PPC-2 is crushed. Only the palatine process of the maxilla and the anterior part of the palatine process of the palatine are recognized, but the suture between them is ambiguous. The posterior and anteromedial margins of the suborbital fenestrae are not preserved.

Lower jaw: The lower jaw is still attached to the rostrum by the matrix. It is rather shorter and narrower than the upper jaw because all the dentary teeth occlude inside the premaxillary and maxillary tooth rows. In lateral view, the anteroventral margin of the dentary bends anterodorsally while the posteroventral margin of the dentary is straight. The first and the second dentary teeth are separated by a broad interalveolar septum. They are slender in shapes, conical in cross-sections and pointed at the apices. These teeth possess a few faint basoapical ridges on their labial surface. The third and the fourth dentary teeth, opposite to the premaxillomaxillary suture, are larger than the other teeth. Both of them are missing their apices. Only the fourth dentary tooth is visible outside the rostrum at the notch of the premaxillomaxillary suture. The fifth dentary tooth exposes only the base of the crown out of the matrix. The more posterior part of the dentary is covered by the maxillary teeth.

In ventral view, the mandibular symphysis reaches the level of the sixth dentary tooth. Each splenial is crushed, but they are still in connection with the dentary laterally. The splenial is labiolingually compressed in shape and bend anteromedially. The anterior end of the splenial is integrated posteriorly into the mandibular symphysis. Posterior to the mandibular symphysis, each ramus of the mandible diverges at an angle of about 35 degrees with the longitudinal axis of the symphysis. Laterally, the lateral and ventral surfaces of the dentary are sculptured with several pits, which are visible in the anterior part, whereas irregular ridges and grooves are visible in the posterior part.

The dentition of PPC-2 shows a heterodont structure. The conical and slightly lingually curved teeth are called pseudocaniniform teeth. The base of the tooth crown in this morphotype is circular in cross-section and acutely pointed at the apex. PPC-2 shows pseudocaniniform premaxillary teeth and the first to the fifth dentary teeth are also pseudocaniniform. Another morphotype shows strongly labiolingually flattened tooth. The tooth crown of this morphotype is wide and flat at the base, tapering apically to a sharp tip. This morphotype is recognized on the more posterior teeth of the maxillae (the fifth to the seventh maxillary teeth). The anterior teeth of the maxillae (the first to the fourth maxillary teeth) are preserved only as the lower half of their crowns. These teeth are slightly compressed labiolingually, indicating they were probably lanceolate-shaped teeth.

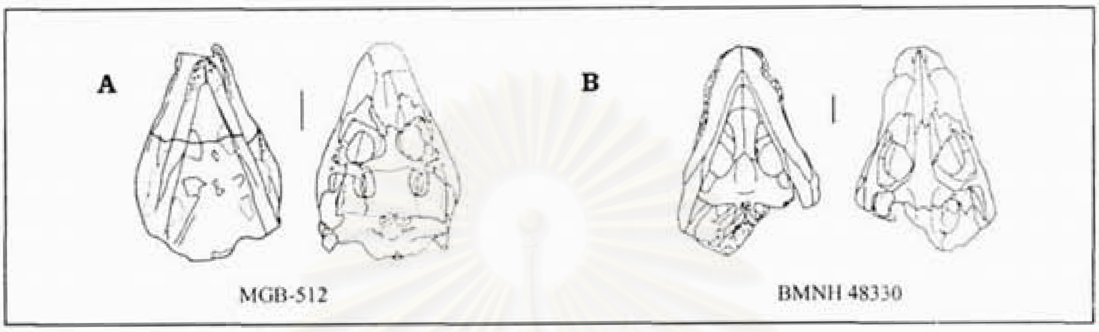


Fig. 4-10 *Montsecosuchus depereti* (Vidal, 1915), nearly complete skull of holotype, MGB-512 in A: ventral and dorsal views. B: *Theriosuchus pusillus* Owen, 1878, nearly complete skull of paratype, BMNH 48330 in ventral and dorsal views. Scale bars represent 1 cm.

Discussion: The posterolateral extension of the maxillae (Fig. 4-9A to C) and short mandibular symphysis of PPC-2 indicate that the specimen is a broad and short-snouted crocodilian. The phylogenetic position of PPC-2 can be included in the family Atoposauridae, based on the following diagnostic characters: a brevirostrine skull (Buffetaut, 1982; Clark, 1986) with the maxillary transversely flattened, symmetrical and pointed at the apex (Clark, 1986); a pair of external nares (Buscalioni and Sanz, 1988). A revision of the phylogenetic relationship of the Atoposauridae by Clark (1986), Benton and Clark (1988), and Buscalioni and Sanz (1988) suggested four valid genera in this family, i.e., *Theriosuchus* Owen, 1878; *Alligatorium* Jourdan, 1862; *Alligatorellus* Gervais, 1871; and *Montsecosuchus* (Vidal, 1915) (Fig. 4-10A). This study considers that PPC-2 is to be included in the genus *Theriosuchus* because it shows some apomorphic traits of this genus, i.e., strong festooned maxillary, anteriorly wide premaxillae, and a diastema at the premaxillomaxillary suture (Buscalioni and Sanz, 1988).

According to Owen (1878, 1879), Joffe (1967), Buffetaut (1982), Clark (1986), Buscalioni and Sanz (1988), Brinkmann (1992), Wu et al., (1996b), and Schwarz and Salisbury (2005), there are three valid species of the genus *Theriosuchus*, i.e., *Theriosuchus pusillus* Owen 1879, *T. ibericus* Brinkmann, 1992, and *T. guimarotae* Schwarz and Salisbury, 2005. However, Schwarz and Salisbury (2005) noted that Brinkmann (1992) established a new species, *T. ibericus*, based only on the procoelous caudal vertebrae, which is an ambiguous character, because the specimens are not well preserved. Although the differences in tooth morphology and internal choanae width were used in the diagnosis, these two features of *T. ibericus* are slightly different from those of *T. pusillus* and seem unlikely to be good characters to justify a new species, because their shapes may result from individual variations. Consequently, the validity of *T. ibericus* is still suspicious (Schwarz and Salisbury, 2005). Therefore, PPC-2 will merely be compared with *T. pusillus* and *T. guimarotae* in this study.

The nasal of PPC-2 becomes abruptly wide at the premaxillomaxillary suture. This character is similar to *T. pusillus* (Fig. 4-10B) whereas it is wider than that in *T. guimarotae* (Fig. 5A in Schwarz and Salisbury, 2005). A transverse contact between the lacrimal and the nasal, which has disappeared in *T. guimarotae*, is found in the Phu Phok *Theriosuchus* and *T. pusillus*. The premaxillomaxillary suture of PPC-2 and *T. pusillus* are slightly oriented anteromedially while that of *T. guimarotae* is oriented posteromedially. Generally, the genus *Theriosuchus* shows four tooth morphotypes (from anterior to posterior), i.e., pseudocaniniform, lanceolate-shaped, low-crowned, and strongly labiolingually flattened teeth (Buscalioni and Sanz, 1988; Schwarz and Salisbury, 2005). In *T. guimarotae*, it possesses only two tooth morphotypes, pseudocaniniform and lanceolate-shaped. Although two tooth morphotypes are recognized in PPC-2, their patterns are clearly different from those of *T. guimarotae*. They are pseudocaniniform (at the anterior part of the premaxillae and the dentary) and strongly labiolingually flattened (at the most posterior part of the maxillae). Moreover, the shape of the first to the fourth maxillary teeth of PPC-2, which are obviously different from the two former morphotypes, looks like lanceolate-shaped tooth. These three tooth morphotypes in PPC-2 are reminiscent of the dentition pattern of *T. pusillus*. Based on the above mentioned differences, the Phu Phok *Theriosuchus* can be separated from *T. guimarotae*.

At the present stage, PPC–2 shows several similarities to *T. pusillus*, particularly the rostrum shape and tooth morphotype. However, the specimen is lacking the posterior portion of the skull and is rather crushed, it is therefore more appropriate to refer to it as *Theriosuchus* cf. *pusillus* for the time being. The discovery of *Theriosuchus* from the Sao Khua Formation reinforces the abundance of this genus outside Europe, after its first record from the Ordos Basin of China (Wu et al., 1996b). It also indicates the evolution of the Atoposaurid lineage from the Late Jurassic to Early Cretaceous in the Khorat Group.

Family ATOPOSAURIDAE Gervais, 1871

Genus *Theriosuchus* Owen, 1878

Theriosuchus sp. A

(Fig. 4-11)

Specimen— PWC-2/1 to 2/76 (Fig. 4-11A to D), an incomplete skull (PWC-2/1 to 2/2) and parts of the postcranial skeleton (PWC-2/3 to 2/6), from Phu Wiang District, Khon Kaen Province.

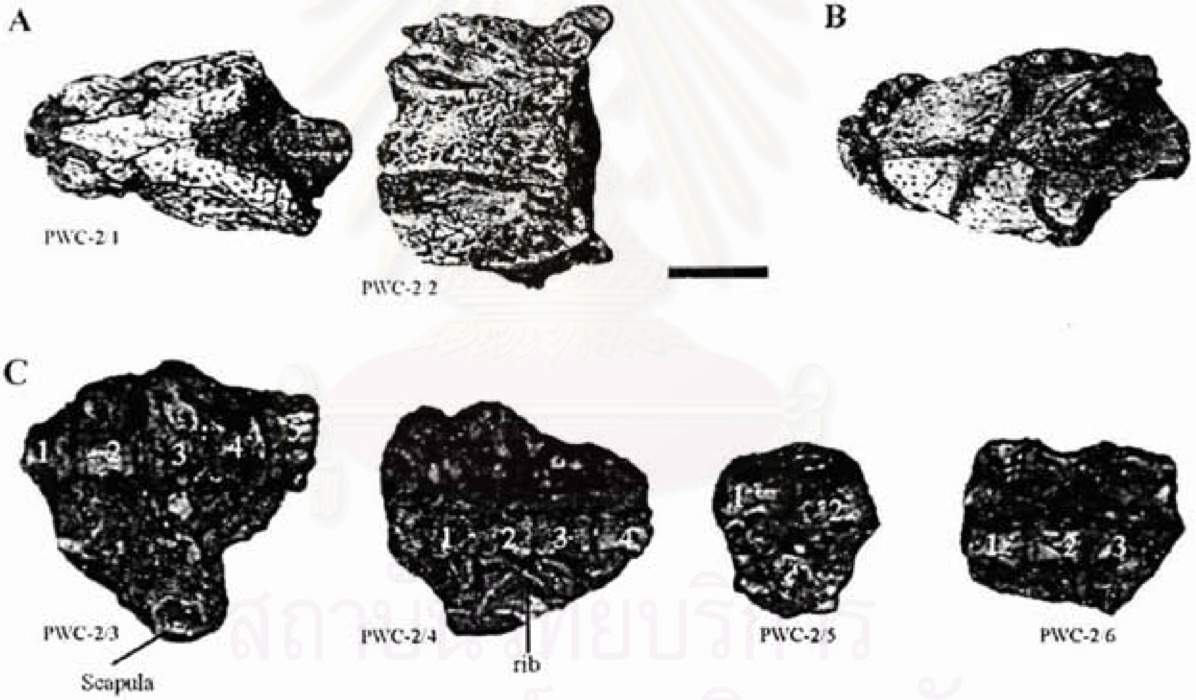


Fig. 4-11 *Theriosuchus* sp. A, PWC-2/1, holotype; a part of the rostrum and an anterior part of the dentary, and PWC-2/2, type series; a nearly complete cranial table in A: dorsal view. B: PWC-2/1, in ventral view. C: PWC-2/3 to 2/6 the vertebrae and osteoderms in ventral view. Scale bar represents 1 cm.

Description—An incomplete skull from Phu wiang consists of a nearly complete rostrum, which articulates with half of the anterior dentaries (PWC-2/1), and a nearly complete cranial table (PWC-2/2). Some vertebrae and osteoderms (PWC-2/3 to 2/6) from a single individual were also found. The reconstruction of the skull length is about 63 mm, of which the rostrum part (length of pre-orbital region) forms about 30 mm or about 50 % of the length of the skull. The cranial specimens show heavily sculptured ornamentation and strong rugosity on the surface.

PWC–2/1:

<u>Upper jaw</u>: In anterior view, each premaxilla curves medially and meets each other at the midline of the skull and form a laminar premaxillary bar, about 1 mm in height. Dorsally, the premaxilla is rounded anteriorly and laterally with the maximum convexity at the level of the fourth premaxillary tooth. This convexity corresponds to the curvature of its vertical plane, which reaches the maximum convexity at the same tooth. The posterior part of the premaxilla is abruptly constricted at the premaxillomaxillary suture. At this contact, a wide diastema, about 3–4 mm long, in the lateral margin is visible.

In ventral view, five premaxillary teeth, which show only the base of the crowns preserved, can be counted. The fourth premaxillary tooth is the largest while the fifth premaxillary one is the smallest. The premaxillomaxillary suture runs slightly anteromedially and ends at the level of the first maxillary tooth. The external nares are situated at the anterior end of the skull.

In lateral view, the dorsal margin of the external nares sharply inclines anteroventrally. Dorsally, although the anterior tips of the nasals are partly preserved, it can be determined that the external nares are completely divided by the anterior processes of the nasal. The external nares have an invert heart-shaped outline, which faces dorsolaterally. The anterior and lateral margins of the external nares extend outward and almost reach those of the premaxillae. The nasal tapers anteriorly and gradually widens posteriorly, having an almost triangular shape. It enters the posterior margin of the premaxilla and reaches its anterior margin. At the level of the premaxillomaxillary suture, the nasal widens abruptly, about two times as broad as it is anteriorly. Its posterolateral margin is slightly concave and runs in a posterolateral direction. The posterior extremity of the nasal is broken away. The maxilla of PWC-2 faces laterodorsally as in the premaxilla. Its anterior extremity is bounded by the premaxilla while its posterior extremity is lacking.

In dorsal view, the maxilla shows a sinusoidal lateral margin, in which the first convexity reaches its maximum curvature at the level of the fourth maxillary tooth. It becomes slightly concave in the region of the seventh to the eighth maxillary teeth. Laterally, the surface of the maxilla shows a festooned shape in a vertical plane, corresponding to its curvature in dorsal view. Parallel to its ventral margin, the maxilla surface is marked by a row of oval vascular foramina, about 2 mm above the ventral margin. A groove also extends into the premaxilla anteroventrally and reaches the level of the posterior end of the external nares. In medial view, the maxilla is in contact with the lateral margin of the nasal. A small oval depression is seen at the posteromedial end of the maxilla. The surface between the row of oval vascular foramina and the oval depression is distinctly convex and rugose. In ventral view, five maxillary alveoli can be seen on the left side. The first and the second ones are circular in shape. The third to the fifth ones show *in situ* teeth fragments. The lingual surface of the third and the fourth maxillary teeth is almost covered by matrix. Therefore, it is difficult to determine the original shape of these teeth. However, the fifth maxillary tooth shows its tip, exposed from the matrix. Its tip tapers apically and is slightly labiolingually compressed.

Lower jaw: The anterior part of the dentary, from the anterior extremity to the seventh dentary tooth, is preserved. It is flattened dorsoventrally and its width is about twice its height. The lateral and ventral surfaces of the dentary exhibits sculptured ornamentation. Their anterior parts possess small pits whereas the posteromedial parts of the symphyseal region possess grooves and ridges.

In lateral view, the dentary raises up from the neighboring alveoli at the level of the third and the fourth dentary teeth. Ventrally, the specimen shows the dentary symphysis, reaching the level of the fifth dentary tooth. The symphysis extends to the sixth dentary tooth when the splenial is included. Posterior to the mandibular symphysis, each ramus of the mandible diverges at an angle of about 25 degrees from the longitudinal axis of the symphysis.

PWC-2/2: The anterior and ventral surface of the specimen are worn and covered by matrix, consequently it is difficult to describe the braincase portion of PWC-2/2. Only the posterior part of its postorbital process is preserved on the left side, and it is in contact with the squamosal by a transversal suture. Its medial wall forms about one-third of the anterolateral margin of the supratemporal fenestra. The rest is formed by the anteromedial margin of the squamosal. The squamosal is a triradiate bone, L-shaped in dorsal view. Medially, it sends a process to contact the parietal and forms half of the posterior wall of the supratemporal fenestra. The lateral margin of the squamosal shows an anteroposterior ridge, which is straight anteriorly and gradually bends posteromedially at the same level than the posterior end of the supratemporal fenestra. This ridge separates the squamosal into two areas, i.e., the sculptured area medially and unsculptured area laterally.

In lateral view, the unsculptured area is beveled ventrally. The parietal of PWC-2/2 forms the posteromedial part of the cranial table. The anterior extremity of the parietal is equal in width to its posterior extremity. The parietal maintains equal width along its length, having a rectangular shape. The lateral margin of the parietal shows a ridge, which is slightly concave medially, forming the entire medial wall of the supratemporal fenestra. This ridge extends posteriorly and reaches the posterior margin of the parietal.

In medial view, the posterior half of the parietal shows a faint midline ridge. Its posteromedial margin, about 5.5 mm in width, is concave anteriorly and corresponds to the exposition of the dorsal surface of the supraoccipital, which excludes the parietal from the posterior margin of the cranial table. The supratemporal fenestra is very narrow and ovoid in shape. Its maximum width is about one-third of its maximum length.

In occipital view, both squamosals decline lateroventrally from the parietal. The occipital surface is rather worn and covered by matrix. However, the occipital condyle and the foramen magnum can be recognized. The occipital condyle faces posteriorly and is bordered dorsally by the foramen magnum, which is sub-circular in shape. Laterally, on the left side, the quadratojugal shows only a part of its dorsolateral surface. Its surface is unsculptured. The anterior margin of the quadratojugal runs dorsomedially inward to the braincase.

PWC-2/3 to PWC-2/6: These specimens are from the postcranial skeletons, i.e., fragments of the scapula, vertebrae and osteoderms. The osteoderms, which are preserved on PWC-2/3, are about 12 mm in average width and 8 mm in average length. The imbrication of these osteoderms is visible. The osteoderms possess a strong anteroposterior keel on their dorsal surface. The keel is located rather laterally and divides the dorsal surface of the osteoderm into two parts, the narrow part laterally and the wide part medially. The surface of the first part declines lateroventrally from that of the latter part at an angle of approximately 35 degrees. The osteoderms of PWC-2/4 and PWC-2/5 are badly preserved. They are covered by matrix and are crushed. PWC-2/6 shows four osteoderms on its dorsal surface, about 8 mm in average width and 7 mm in average length. They are rectangular in shape. These osteoderms are shorter and narrower than those of PWC-2/3. However, they also possess an anteroposterior keel, which is closer to the middle of the osteoderms than that of PWC-2/3. These characters indicate that PWC-2/6 is a part of the tail.

In ventral view, five vertebrae can be counted in PWC-2/3. These vertebrae are about 5–7 mm in average length and 4–5 mm in average width. The length and width of these vertebrae are gradually increased posteriorly. The mesial portions of the scapulas are found in this specimen. They are placed between the second and the third vertebrae. Only the ventral surface of these scapulas emerges from the matrix and run posterolaterally. A fragment of the shaft of the left scapula is also recognized. For the above reasons, the vertebrae, which are located in front of the third vertebra, are cervical vertebrae while the third to the fifth vertebrae are dorsal vertebrae. Four vertebrae of PWC-2/4, about 5 mm in average length and 4 mm in average width, are preserved. This specimen shows several fragments of the thoracic ribs, but they are embedded in the matrix. Three caudal vertebrae are preserved in PWC-2/5, but only two caudal vertebrae can be measured because the last one is broken. These caudal vertebrae are about 7 mm in average length and 4 mm in average width. The shape of these caudal vertebrae is more slender and longer than that of the dorsal vertebrae in PWC-2/3 and PWC-2/4. PWC-2/6 shows two caudal vertebrae, about the same size as in PWC-2/4. All the preserved vertebrae are amphicoelous.

Discussion: The specimen from Phu Wiang shows the following diagnostic characters of the family Atoposauridae: maxillary and dentary teeth transversely flattened, and apically tapering to a point; a small unsculptured area at the posterolateral margin of the squamosal; short rostral length; a pair of external nares (Buffetaut, 1982; Clark, 1986; Benton and Clark, 1988; Buscalioni and Sanz, 1988). This study attributes the Phu Wiang dwarf atoposaurid to the genus *Theriosuchus* based on the following combination of diagnostic characters: a midline ridge on the dorsal surface of the parietal; lateral margin of the squamosal beveled ventrally; maxilla festooned both vertically and laterally; anteriorly wide premaxillae; a diastema at the premaxillomaxillary suture; and mandibular symphysis restricted to the level of the sixth dentary tooth (Buffetaut, 1982; Clark, 1986; Benton and Clark, 1988; Buscalioni and Sanz, 1988; Buscalioni and Sanz, 1990; Wu et al., 1996b; Schwarz and Salisbury, 2005).

When the atoposaurid specimen from Phu Wiang is compared with the other *Theriosuchus*, including PPC-2 from Phu Phok, it can be distinguished from PPC-2 and the European *Theriosuchus*, *Theriosuchus pusillus*, *T. ibericus*, and *T. guimarotae* based on several differences of the skull as follow. In the European *Theriosuchus* and PPC-2, they generally possess slit-like external nares, which are oriented anteriorly and horizontally on the rostrum. In the atoposaurid from Phu Wiang, however, the external nares widen laterally and anteriorly, almost reaching the premaxilla margin. The maxilla of the Phu Wiang specimen is more sub-vertical than that of the other *Theriosuchus*. Its rostrum is rather slender and narrower than that of the other *Theriosuchus*. Its supratemporal fenestra is ovate and narrow in shape whereas that of *T. guimarotae* is almost rectangular in shape. The supratemporal fenestra of *T. pusillus* and *T. ibericus* are relatively rounded and wider than that of the Phu Wiang specimen. The width of the anterior extremity of the European *Theriosuchus* is narrower than that of the posterior extremity. It is generally about one-third of the posterior length. This character is unique in the Phu Wiang *Theriosuchus*, which shows a similar width of the anterior and the posterior extremities. It also maintains the width along the anteroposterior length. This feature is not preserved in PPC-2. Furthermore, the dentary of the Phu Wiang specimen seems more slender than that of the other *Theriosuchus* based on the angulation of the mandibular symphysis, which is approximately 30 degrees whereas it is approximately 40 degrees in *T. guimarotae* (Schwarz and Salisbury, 2005), 60 degrees in PPC–2, and 50 degrees in *T. pusillus* (BMNH 48330). This character is not mentioned for *T. ibericus*.

Moreover, the Phu Wiang *Theriosuchus* shows two synapomorphies with PPC-2, *T. pusillus* and *T. ibericus*. These are the premaxillomaxillary suture of *Theriosuchus* from Phu Wiang, which is slightly anteromedially oriented similar to that of PPC-2, *T. pusillus* and *T. ibericus*. On the contrary, this suture is posteromedially oriented in *T. guimarotae*. The nasals of the Phu Wiang *Theriosuchus*, PPC-2, *T. pusillus* and *T. ibericus* taper anteriorly, abruptly widen posteriorly and are transversely in contact with the lacrimal and prefrontal whereas *T. guimarotae* does not exhibit any of those characters (Fig. 5A in Schwarz and Salisbury, 2005).

This study considers therefore the specimen from Phu Wiang as a new species of the genus *Theriosuchus*, based on the following autapomorphies traits: external nares anteriorly and laterally wide; anterior and posterior extremities of the parietal almost equally wide; narrow angulation of the mandibular symphysis; narrow and slit-like supratemporal fenestrae; and narrow and slender rostrum. The premaxillomaxillary suture and the transversal contact among nasal, lacrimal and prefrontal indicate that the Phu Wiang *Theriosuchus* is phylogenetically closer to PPC–2, *T. pusillus*, and *T. ibericus* than to *T. guimarotae*. Up to now, the genus *Theriosuchus* was known from the Late Jurassic (Kimmeridgian) to the Early Cretaceous (Barremian) of Europe (Clark, 1986; Wu et al., 1996b; Schwarz and Salisbury, 2005). This stratigraphic distribution is similar to that of *Theriosuchus* in the Khorat Group, which is also known from the Late Jurassic (the Phu Kradung Formation) to the Early Cretaceous (the Sao Khua Formation). The validity of this new species increases the diversity of the Mesozoic crocodilian during the Early Cretaceous of Thailand. The publication of this specimen is now under preparation.

PART III —THE KHOK KRUAT FORMATION

Early Cretaceous (Aptian/Albian)

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Benton and Clark, 1988

FAMILY GONIOPHOLIDIDAE Cope, 1875

"Goniopholis" sp. A

(Fig. 4-12)

Specimen— KPS–1 (Fig. 4-12A and B), a nearly complete left mandible, from Khok Pha Suam, Sri Muang Mai District, Ubon Ratchathani Province.

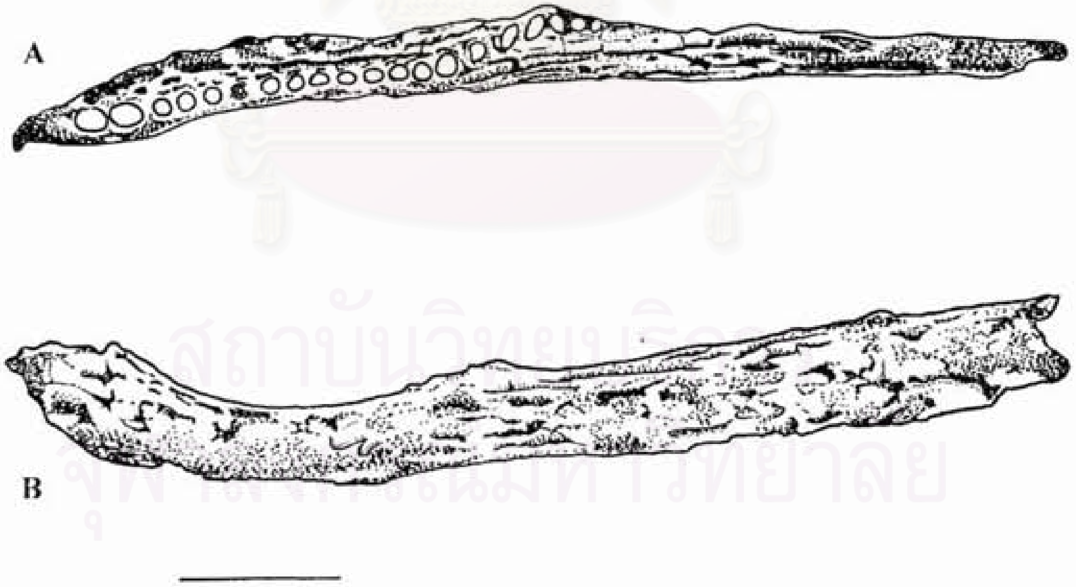


Fig. 4-12 "*Goniopholis*" sp. A, KPS–1, a nearly complete left mandible from Khok Pha Suam, Sri Muang Mai District, Ubon Ratchathani Province in A: dorsal view and B: lateral view. Scale bar represents 5 cm.

Description— KPS-1 is 327 mm in length, consisting of a dentary, splenial, surangular and angular. The anterior extremity to the second alveolus of the specimen is lacking. The dentary is elongated in shape and about 285 mm in length. In dorsal view, twenty-three dentary alveoli, the second to the twenty-fourth ones, can be counted. The mesiodistal diameters of these teeth are shown in table 4-1. The dentary alveoli are separated by equal interalveolar septum of 2 mm long, except between the second and the third, the fourth and the fifth ones, which show slightly wider space, about 5 mm.

Anteriorly, the ventral surface of KPS-1 is strongly convex transversally. Above this convexity, the base of the root of the second dentary tooth is observed *in situ*. It is below the level of the third dentary alveolus. The tooth curves anterodorsally to the dorsal surface of the dentary. It is conical in cross–section and slightly curved lingually.

In dorsal view, the lateral margin of the specimen exhibits three convexities. The first convexity is situated at the level of the fourth dentary alveolus, which suggests that the largest tooth on the dentary was there. The second convexity reaches its maximum at the level of the sixteenth dentary alveolus. The third convexity is located at the level of the anterodorsal extremity of the surangular. The dentary floor is partly preserved at the medial margin of the fourth to the sixth dentary alveoli. It extends laterally for only 10 mm. Because the splenial is crushed and distorted, a part of its medial surface is visible in dorsal view only from the sixth to the seventeenth dentary alveoli. A row of vascular foramina are visible in the medial margin of the tooth row, each about 1-2 mm in diameter. From its posterior end to the twenty-fourth dentary alveolus, the specimen preserved only its dorsolateral margin, which is rather obscured, because of the bone crushing. The sutural contact between the dentary and the surangular cannot be determined in dorsal view.

The medial surface of KPS-1 is poorly preserved, lacking the symphyseal region and Meckelian groove. The upper portion of the splenial is preserved whereas the lower portion is broken. Posteriorly, the eighteenth to the twenty-fourth dentary alveoli are worn but parts of their labial edges remain partially intact. Posterior to the twenty-fourth dentary alveolus, the specimen presents only the lateral part of the mandible, which is worn and obscured. On the contrary, the anterior part of the lateral surface of KPS-1 is rather well preserved and smooth. The dorsal margin of the specimen presents two convexities. The first convexity rises to the level of the third and fourth dentary alveoli. The dorsal margin becomes strongly concave and reaches the maximum concavity at the level of the tenth and eleventh dentary alveoli. The second convexity reaches the maximum curvature at the level of the eighteenth dentary alveolus. These convexities are about twice as high as the maximum of the concavity. After the level of the twenty-fourth dentary alveolus, the dorsal and ventral margins are broken. The lateral surface of this bone is strongly convex at the level of the sixth to seventeenth dentary alveoli and rather flattened posteriorly. A longitudinal row of small pits, parallel with a constant distance about 5 mm from the dorsal margin, are visible. It extends posteriorly from the level of the third to eleventh dentary alveoli.

Posteriorly, the mandibular fenestra is not preserved in this specimen. The lateral surface is cracked due to the crushing of the bone. Accordingly, it is not possible to determine the sutural contact among the dentary and surangular, and angular.

Table 4–1 Dentary alveoli measurements of the Khok Pha Suam specimen (KPC-2)

Alveoli	2nd	3rd	4th	5th-6th	7th-15th	16th-18th	19th-24th
Diameter (mm)	7	8	10	5	6	8	6

Discussion: The number of the dentary teeth and the curvatures of the tooth row indicate that KPS-1 is a short-snouted crocodilian. Moreover, the presence of the enlarged and contiguous third and fourth dentary alveoli reinforces the idea that KPS-1 belongs to the family Goniopholididae. As mentioned in the discussion of "*Goniopholis*" *phuwiangensis* and "*Sunosuchus*" *thailandicus* (see part I and II), it is very difficult to determine the generic level of a goniopholidid from only a part of its lower jaw. At present, KPS–1 could belong to *Goniopholis*, *Eutretauranosuchus*, or *Siamosuchus*, a new genus of broad-snouted goniopholidid from the Sao Khua Formation (Lauprasert et al., submitted). Although *Siamosuchus* was described from the same Formation as KPS-1, it should be excluded from the taxonomic comparison because it shows no elements in common with the Khok Pha Suam specimen.

A recent phylogenetic analysis (Lauprasert et al., submitted) suggest that *Eutretauranosuchus* forms a clade with the other non broad-snouted goniopholidid such as *Sunosuchus* and *Calsoyasuchus*, which are long-snouted goniopholidids, based on the characters of the upper jaw. Furthermore, the specimens of *Eutretauranosuchus*, up to this day, are known only from North America. Some differences are observed when we compare KPS-1 and *E. delfsi* (CMNH 8028), i.e., the third and the fourth dentary alveoli of KPS-1 are more contiguous than that of *Eutretauranosuchus* (Fig. 4-8D) and resemble that of "*G.*" *phuwiangensis*. The dorsal margin of "*G.*" *phuwiangensis* and KPS-1 exhibits an undulation of the dentary stronger than that of *E. delfsi*. In addition, the convexity at the tenth and eleventh dentary alveoli of the Thai "*Goniopholis*" is also stronger than that of *E. delfsi* (Buffetaut and Ingavat, 1983). For these reasons, this study considers to preclude the reference of KPS-1 to the genus *Eutretauranosuchus*.

The specimen from Khok Pha Suam, KPS-1, shows a combination of characters on the dentary that have only been described for "*Goniopholis*" *phuwiangensis*, although these characters are not found in the European *Goniopholis* (*G. crassidens*, *G. simus*, and *G. baryglyphaeus*). These features are as follow: 1) anterior portion of the tooth row does not show a marked angulation; 2) absence of a strong outward protrusion of the lateral margin at the level of the third and the fourth dentary alveoli; 3) presence of dentary curvatures in both lateral and vertical planes. With these characters, KPS-1 is considered as belonging to the same genus as "*Goniopholis*" *phuwiangensis*. Based on the obscured relationships of the Thai, European and North American *Goniopholis* as well as the absence of the lower jaw of *Siamosuchus*, it should be suitable for the time being to consider KPS-1 as an uncertain genus "*Goniopholis*". Additional material, especially the upper jaw, is required to clear the taxonomic affinities of KPS-1 and of the Thai "*Goniopholis*" form.

Based on the strong undulation of its lateral margin on a vertical plane, KPS-1 can be distinguished from "*Goniopholis*" *phuwiangensis* and the other species of *Goniopholis*. The first and the second convexities of KPS-1 are about twice as high as its concavity whereas in "*Goniopholis*" *phuwiangensis* and the other species of *Goniopholis* the proportion between the maximum height of convexity and concavity is significantly less than that of KPS-1. Additionally, the ornamentation on the lateral surface of KPS-1 is faintly sculptured whereas that of "*G.*" *phuwiangensis* and the other species of *Goniopholis* is heavily sculptured. These two characters, therefore, are sufficient to validate the specimen from Khok Pha Suam as a new species.

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Benton and Clark, 1988

FAMILY GONIOPHOLIDIDAE Cope, 1875

"Goniopholis" sp. B

(Fig. 4-13)

Specimen— NRRU-A 1791 (Fig. 4-13A to C), a part of the left dentary, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province.

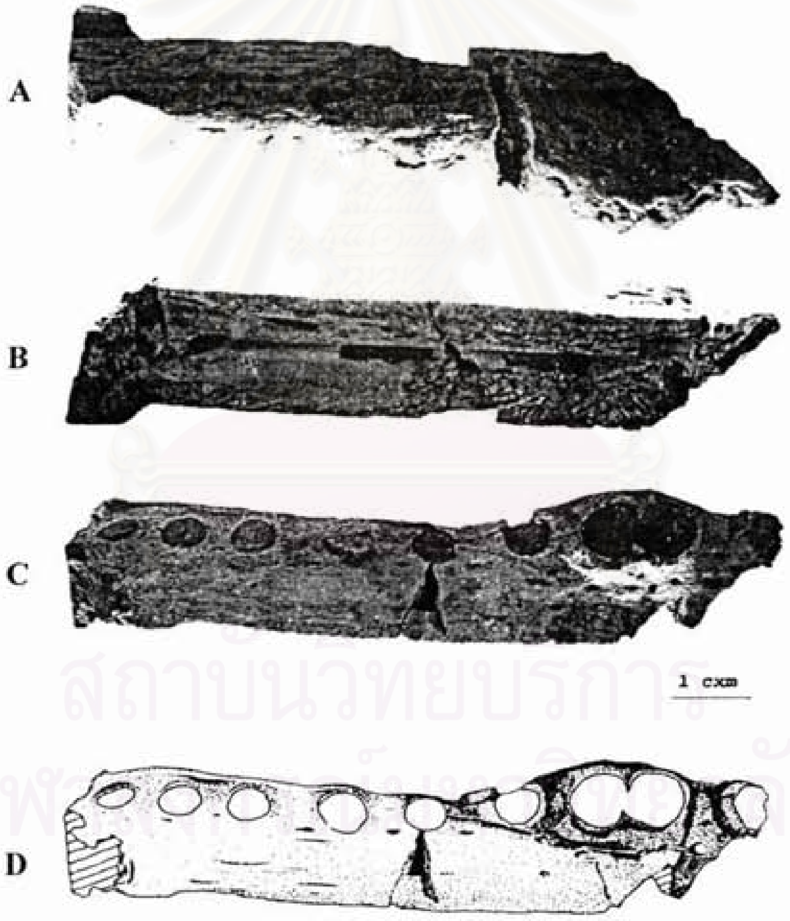


Fig. 4-13 "*Goniopholis*" sp. B, NRRU-A 1791, a part of the left dentary, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province in A: ventral view; B: medial view; C: dorsal view and D: drawing of the dorsal view.

Description: The specimen is an anterior part of the left dentary, which is about 9.4 mm long. Its anterior extremity and posterior part are lacking. Nine dentary alveoli, the second to the tenth ones, can be counted on the dorsal surface of this specimen. These alveoli are almost equal in mesiodistal diameters, which are about 5 mm, except the third and the fourth ones, which are larger than the other dentary teeth, with a diameter of about 7 mm. The second to the third and the fourth to the ninth dentary alveoli are separated by unequal interalveolar septums whereas the third and the fourth are contiguous as shown in Fig. 4-13 A.

In dorsal view, the lateral margin of NRRU-A 1791 shows two convexities. The first convexity is located around the third and the fourth dentary alveoli. The second convexity can be observed at the eighth to the tenth dentary alveoli, although the posterolateral margin of NRRU-A 1791 is broken. A row of vascular foramina are visible along the medial margin of the tooth row.

Medially, the Meckelian groove is found at the level of the fourth and the fifth dentary alveoli. The surface exhibits the usual striations, which radiate from a distinct Meckelian groove. The posterior end of the dentary symphysis is recognized at the level between the sixth and the seventh dentary alveoli. The splenial is not preserved, but the sutural surface for the splenial is visible at the level of the seventh to the tenth dentary alveoli. However, it is not possible to determine whether the splenial is involved in the dentary symphysis. In lateral view, NRRU-A 1791 shows a convexity at the level of the third and the fourth dentary alveoli. The lateral surface of this specimen shows sculptured ornamentation, made of small pits in the anterior region and longitudinal distinct grooves and ridges in the posterior region. These longitudinal grooves and ridges also extend to the ventral surface of the specimen, which is relatively flattened.

Discussion: The general shape of NRRU-A 1791 resembles that of "*Goniopholis*" *phuwiangensis*, the specimen from the Sao Khua Formation, and the Khok Pha Suam specimen, KPS-1 ("*Goniopholis*" sp. A) from the Khok Kruat formation. These specimens share the enlarged and contiguous third and fourth dentary alveoli as well as the protrusion of the lateral margin of these dentary alveoli, which are diagnostic characters of the family Goniopholididae and Pholidosauridae (Buffetaut and Ingavat, 1983). The beginning of the sutural surfaces for the splenial at the level of the seventh dentary alveolus indicates that NRRU-A 1791 possesses a short dentary symphysis, and it can be attributed to a broad-snouted crocodilian of the family Goniopholididae (as mentioned for "*Goniopholis*" *phuwiangensis*), i.e., *Goniopholis*, *Siamosuchus* and *Eutretauranosuchus*.

The Ban Saphan Hin specimen and the other Thai "*Goniopholis*" can be distinguished from *Eutretauranosuchus* (CMNH 8028) by the presence of a contiguous third and fourth dentary alveoli as well as a strong convexity at the region of the tenth and eleventh dentary alveoli. In addition, *Siamosuchus*, a new Thai broad-snouted goniopholidid, should be excluded from the taxonomic comparison because it shows no element in common with the Ban Saphan Hin specimen.

The best phylogenetic position for the Khorat specimen, NRRU-A 1791, at the present stage is within the genus "*Goniopholis*" the same genus as for the other Thai "*Goniopholis*" specimens, based on a combination of characters that have been found only in "*G.*" *phuwiangensis* and "*Goniopholis*" sp. A as follow: 1) anterior portion of the tooth row does not show a marked angulation; 2) absence of a strong outward protrusion of the lateral margin at the level of the third and the fourth dentary alveoli; 3) presence of dentary curvatures in both lateral and vertical planes. The lack of the lower jaw of *Siamosuchus* and the extremely ambiguous relationships among Thai, European and North American *Goniopholis* are the reasons why this study attributes NRRU-A 1791 to an uncertain genus "*Goniopholis*".

The general shape of this specimen is similar to "*G.*" *phuwiangensis* and KPS–1, but comparisons between NRRU-A 1791 and the Khok Pha Suam specimen, and "*G.*" *phuwiangensis* show some differences. The dentary symphysis of NRRU-A 1791, ending at the level between the sixth and the seventh dentary alveoli, is shorter than that of "*G.*" *phuwiangensis*, which ends at the level of the seventh dentary alveolus. This character cannot be evaluated in KPS-1 because the medial part of the Khok Pha Suam specimen is not preserved. The position of the vascular foramina of NRRU-A 1791, particularly at the level of the fifth dentary alveolus to its posterior part, is closer to the medial margin of the tooth row (Fig. 4-13D) than that of "*G.*" *phuwiangensis* and KPS-1. Moreover, this specimen can be distinguished from the Khok Pha Suam specimen based on the vertical curvature difference between the maximum convexity height and the maximum concavity height. The Khok Pha Suam specimen has a more important vertical curvature difference than that of NRRU-A 1791 and "*G.*" *phuwiangensis*. These reasons are sufficient to validate the specimen from Ban Saphan Hin as a new species, "*Goniopholis*" sp. B. Additional and complete material is required to solve the phylogenetic position of this specimen as well as that of the genus "*Goniopholis*" in the Khok Kruat Formation.

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

(Fig. 4-14)

Specimen— NRRU-A 1216 (Fig. 4-14), a part of the right jugal, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province.

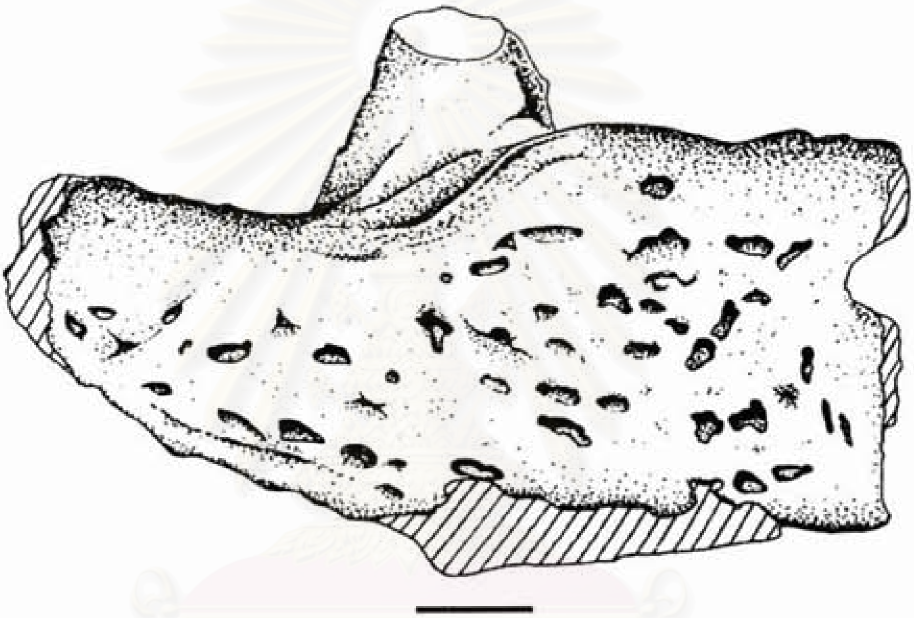


Fig. 4-14 NRRU-A 1216, a part of the right jugal of a mesoeucrocodylian, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province. Scale bar represents 1 cm.

Description: NRRU-A 1216 is a robust jugal without the anterior and posterior extremities. Its medial surface is crushed and obscured because of matrix covering whereas the ventral surface is not preserved. In lateral view, the surface shows deep and heavy sculptures. The anterior portion of the specimen is about twice as high as its posterior portion, which is slender and rod-liked in shape. In dorsal view, a part of the ascending process of the unsculptured postorbital bar is preserved, and situated medially from the lateral margin of the specimen. The anteroposterior diameter of the postorbital bar is 11 mm. An elliptical foramen, about 6 mm in anteroposterior diameter, is recognized at the posterior end of the postorbital bar.

Discussion: The presence of the postorbital bar, situated medially to the lateral margin of the jugal, is a diagnostic character to attribute NRRU-A 1216 to the Crocodyliformes. In addition, the specimen can be diagnosed as a mesoeucrocodylian, based on heavy sculptures on its lateral surface and the size of the anterior portion of the jugal, which is about twice as high as its posterior portion. With only an incomplete jugal, it is not possible to determine a more inclusive taxonomic level for this specimen. Additional material is required.

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

FAMILY *insertae sedis*

Khoratosuchus nov. gen.

Khoratosuchus jintasakulii nov. sp.

(Fig. 4-15)

Specimen— NRRU-A 1803 (Fig. 4-15A and B), holotype, a nearly complete cranium, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province.

Description and Discussion— see Lauprasert et al. (memoir) in Chapter V.

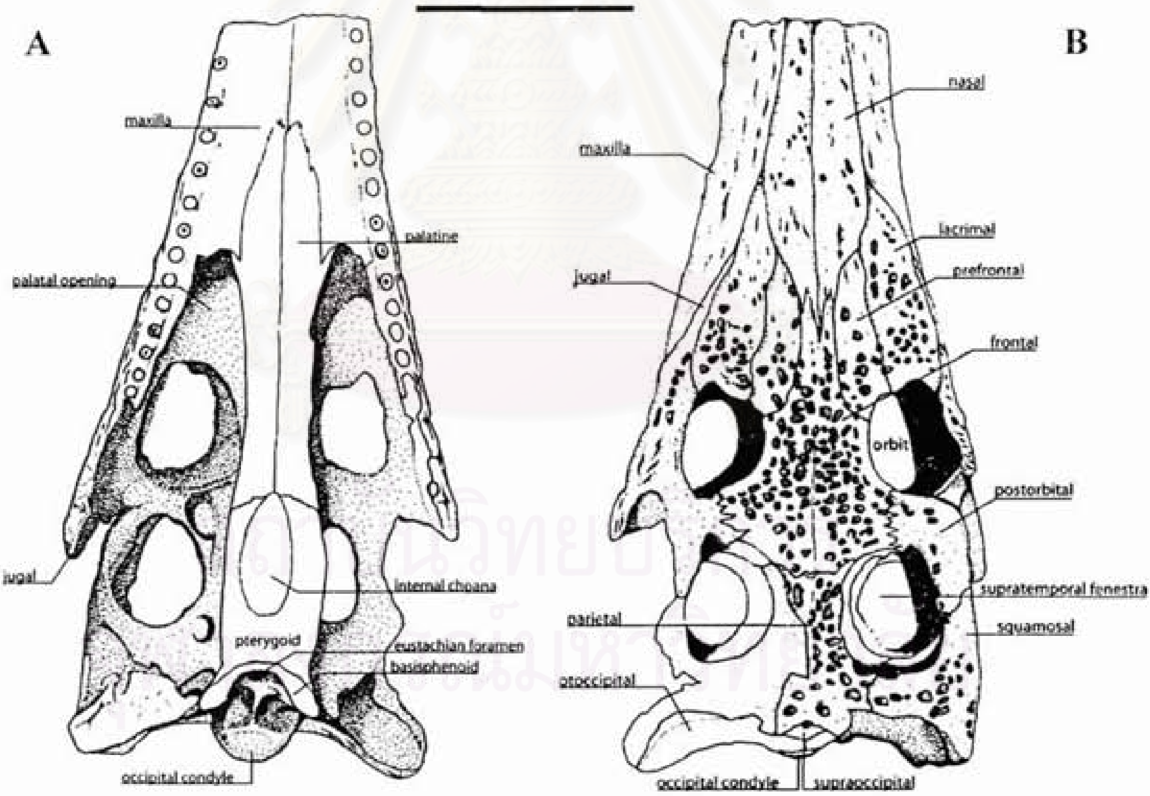


Fig. 4-15 *Khoratosuchus jintasakulii* nov. gen et. sp, NRRU-A 1803, holotype, a nearly complete cranium, from Ban Saphan Hin, Muang District, Nakhon Ratchasima Province in A: ventral view and B: dorsal view. Scale bar represents 5 cm.

CHAPTER V

A NEW NEOSUCHIAN CROCODILE, *KHORATOSUCHUS JINTASAKULII* GEN. ET SP. NOV., FROM THE LATE EARLY CRETACEOUS (APTIAN/ ALBIAN) OF NORTHEASTERN THAILAND

Abstract: A new elongate and slender-snouted neosuchian, *Khoratosuchus jintasakulii* gen. et sp. nov., is described from the late Early Cretaceous Khok Kruat Formation. This discovery represents the youngest and most advanced Mesozoic crocodile known in northeastern Thailand on the basis of the following cranial features: the situation of the internal choanae, which is relatively posterior and almost enclosed by the pterygoid; the lateral margin of the maxilla is relatively straight without lateral constrictions; the dorsal surface of the skull lacks ridges and fossae; maxillary teeth are homodontous; and the anterior end of the jugal and prefrontal terminate at the same level. The specimen bears resemblances to Chinese and European derived neosuchians and also suggests a close relationship between the late Early Cretaceous neosuchians of China, Europe and Southeast Asia.

Introduction

In the past twenty-five years, the Khorat Group in Thailand has yielded a rich assemblage of continental vertebrate faunas, including various dinosaurs, pterosaur, crocodyliforms, turtles, actinopterygian fishes, and hybodont sharks (Buffetaut and Ingavat, 1980, 1983; Buffetaut and Suteethorn, 1998, 1999; Buffetaut et al., 2003a; Tong et al., 2003, 2005; Cavin et al., 2003, 2004; Cuny et al., 2003, 2006; Lauprasert et al., submitted). However, only three taxa of crocodyliforms from the Phu Kradung and Sao Khua Formations have been described. They include "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980, "*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983, and *Siamosuchus phuphokensis* Lauprasert et al., submitted.

In the summer of 2004, a Thai-French expedition had an opportunity to visit the collection of the Museum of Petrified Wood and Mineral Resources, Nakhon Ratchasima province. Several vertebrate fossils from the Ban Saphan Hin locality were housed in the museum. One of the discovered material shows an interesting crocodyliform skull and is described here as the fourth crocodilian taxa of the Khorat Plateau.

Fig. 5-1 Geographic position of the Ban Saphan Hin locality (shaded star), Nakhon Ratchasima Province, Thailand.

Geological Setting

Khoratosuchus jintasakulii was found at Ban Saphan Hin, Nakhon Ratchasima Province. The specimen was embedded in reddish-brown mudstone containing pebbles, silcretes and calcretes. The Ban Saphan Hin locality is currently considered as belonging to the Khok Kruat Formation, the uppermost formation of the Khorat Group of northeastern Thailand (Carter and Bristow, 2003; Meesook, 2000), which consists of reddish-brown, fine- to medium-grained sandstone, siltstone, mudstone and conglomerates, indicative of a meandering river depositional environment (Meesook, 2000; Racey *et al.*, 1996, Tong *et al.*, 2005).

The Khok Kruat Formation is currently dated as late Early Cretaceous (Aptian-Albian) by the occurrence of the freshwater hybodont shark *Thaiodus ruchae,* which is also known from the Aptian-Albian Takena Formation of the Lhasa block of Tibet (Cappetta, *et al.*, 1990) and by palynomorphs suggesting an Aptian age (Sattayarak, *et al.*, 1991, Racey *et al.*, 1994, 1996). Besides crocodiles, this formation has also yielded remains of various vertebrates, including hybodont sharks (Cuny *et al.*, 2003, 2006), semionotiform fishes, turtle (Tong *et al.*, 2005), diverse dinosaurs and pterosaurs (Buffetaut *et al.* 2003a, b).

Material and Methods:

A part of the crocodile upper jaw (NRRU-A 1803), without premaxillae, external naris, quadratojugal, and ectopterygoid, was discovered by Dr. Pratueng Jintasakul, Director of the Museum of Petrified wood and Mineral Resources of Nakhon Ratchasima, where the specimen is housed. The museum is situated about 5 km in northeast of the fossil locality. Preparation was made at the Sahatsakhan

Dinosaur Research Center, Kalasin Province by pneumatic air-pen and 10% formic acid solution bath. The specimen is well preserved. Sutures and surface of the skull are well defined in both dorsal and palatal views. No postcranial remains of this specimen were found.

A phylogenetic analysis was carried out, based on 102 characters, to resolve the position of the new taxon. Character 1 and characters 3 to 100 were taken from the data matrix of Lauprasert *et al.* (submitted), character 2 was modified from Sereno *et al.* (2001). Two additional characters were included in this analysis (Appendix I; characters 101 and 102). All characters were treated as unordered. The data matrix contains 31 taxa of Mesoeucrocodylia and 3 outgroup taxa, which consist of *Protosuchus*, *Hemiprotosuchus*, and *Orthosuchus*. *Pholidosaurus*, and *Rugosuchus* were added to this study to determine the affinities of long-snouted crocodilians and advanced neosuchians, respectively. The data matrix was run using PAUP, Version 4.0b10 for 32-bit Microsoft Windows, using a random, stepwise addition, heuristic search algorithm. There are 99 parsimony-informative characters and 4 parsimony-uninformative characters.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Walker, 1970

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Clark in Benton and Clark, 1988

KHORATOSUCHUS gen. nov.

Etymology: "*Khorat*" Referring to an informal name of Nakhon Ratchasima Province, where the holotype was collected and Greek *souchos*, for crocodile.

Type species: *Khoratosuchus jintasakulii*, sp. nov.

Diagnosis: An elongate and slender-snouted crocodilian distinguished from other neosuchians in having the following apomorphies: choana almost situated in pterygoid; palatines extending back and forming the anterior margins of the choana; maxilla relatively straight without lateral constrictions; flat dorsal surface of skull lacking ridge and fossa; homodont maxillary teeth; anterior end of jugal and prefrontal terminated at the same level.

KHORATOSUCHUS JINTASAKULII, sp. nov.

Holotype: NNRU-A 1803; partial upper jaw represented by part of maxillae, part of nasals, lacrimals, prefrontals, frontal, postorbitals, squamosals, parietal, quadrates, occipital surface of the skull and part of pterygoid.

Locality and Horizon: Ban Saphan Hin, Amphoe Muang, Nakhon Ratchasima Province, Thailand; Khok Kruat Formation, late early Cretaceous (Albian-Aptian).

Etymology: "*jintasakulii*" to honor Dr. Pratueng Jintasakul, Director of the Museum of Petrified wood and Mineral Resources of Nakhon Ratchasima, who allowed us to study the specimen.

Diagnosis: Same as for the genus diagnosed above.

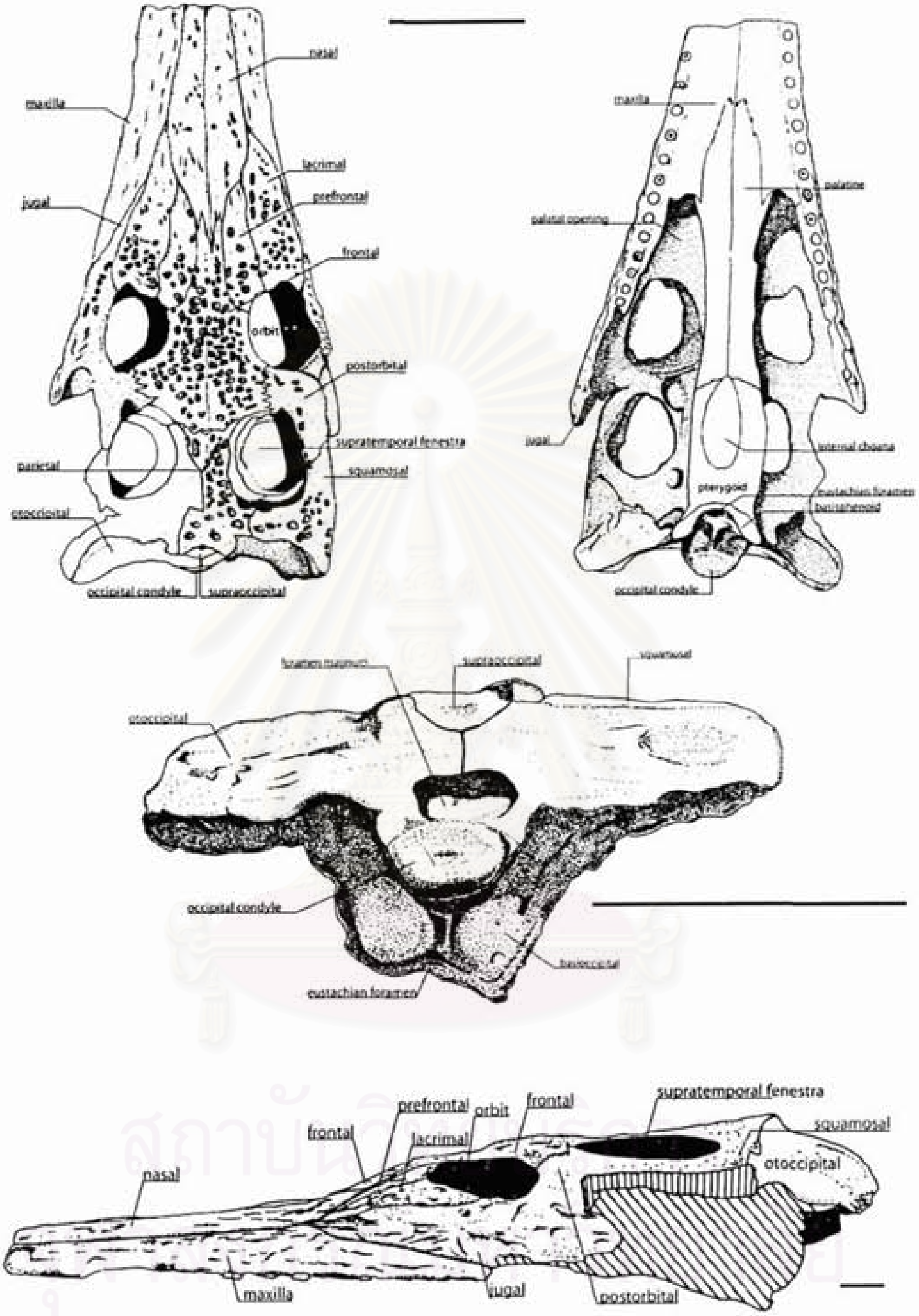


Fig. 5-2 Skull of *Khoratosuchus jintasakulii*, gen. et sp. nov., nearly complete cranium (NNRU-A 1803), holotype, in A: dorsal view, B: palatal view, C: occipital view, and D: lateral view. Scale bars equal 5 cm.

Description

Skull

Form and proportions: NNRU-A 1803 is a partial cranium with a total length of 191 mm. Because the premaxillae and cranial part of the maxillae are not preserved, it is rather difficult to determine the original total length of the specimen. From the cranial end, the straight lateral margin of the rostrum widens gradually caudally. There is no evidence of contact between premaxillae and maxillae, at the preserved tip of the specimen. It seems unlikely that the specimen would be a short-snouted crocodilian. Its frontal, showing craniocaudal suture at the caudal portion, indicates that the skull belongs to a young adult crocodile (Wu et al., 1996a). In dorsal aspect, the surface of this specimen is moderately sculptured, particularly from the caudal margin of the skull to the cranial margin of the orbits. In front of the orbits, the rostrum is slightly sculptured on its surface. Its maximum width at the cranial edges of the orbits is 75 mm long. The cranial table of the specimen is nearly rectangular. Lateral part of the left postorbital, left squamosal and caudal part of the parietal are crushed. It seems that the left side of the specimen was compressed and rather extended laterally. However, their shape can be reconstructed by comparing with the right side. In occipital view, all bones, except quadrates are well preserved. Ventrally, the matrix was removed and the specimen shows clear sutural contact as well as the internal choana and maxillary teeth. The morphological measurement of NNRU-A 1803 are given in Table 5-1.

Maxilla: Part of the maxillae are preserved without their cranial portions. They are 115 mm in length. Dorsally, the right maxilla is narrower than the left one, which relatively flattens. The natural width of the maxilla is 11 mm, measured from the right side. The medial surface of the maxilla touches the lateral surface of the nasal. This suture slightly leans caudolaterally to the point of the maximum width of the nasal bones and touches with the cranial margin of the lacrimal at the same level. The suture exhibits a strong caudolateral bend and contacts the lateral margin of the lacrimal, cranial and lateral margins of the jugal in caudal view. The lateral margin of the maxilla is rather straight without any depression. There are several moderate grooves on its lateral surface.

The ventral surface of the maxilla is rather flat. Medially, the palatine processes of maxillae meet each other and run caudally to the cranial margin of the palatine process of palate. The sutural contact leans caudolaterally to the caudolateral edge of the maxilla. This suture also forms the cranial and craniolateral margins of the palatine and that of the palatal vacuity. Thirteen maxillary alveoli are preserved on the right side of the specimen whereas fifteen maxillary alveoli can be counted on the left side, but the last three maxillary alveoli are merged together.

Nasal: The nasal bones are preserved without their cranial parts. The lateral margin of the nasal exhibits a straight suture with the medial margin of the maxilla. This suture begins to curve caudomedially at the point of the maximum width of the nasal towards the medial margins of the lacrimal and prefrontal. Caudomedially, the terminal parts of the nasal unite together and form a wedge, which separates them from the cranial margin of the frontal. In medial view, the nasal bones meet each other craniocaudally. The maximum width of the nasal is 28 mm. Dorsally, the surfaces of the nasal bones are relatively smooth without ornamentation.

Lacrimal: The lacrimals of the specimen are relatively long and moderately wide, i.e. 57 mm long and 17 mm wide in average. The cranial tip tapers cranially, separating the maxilla laterally from the nasal medially. From the caudal end to three-fifths of its length, the lacrimal is bordered by the prefrontal medially and jugal laterally. Its caudal margin shows a distinct concavity forming a notch and the cranial wall of the orbit. The left lacrimal has a slightly convex dorsal surface. Ventrally, the opening of the lacrimal duct is not visible, because of matrix covering.

Prefrontal: Both prefrontals are 40 mm long and 10 mm wide. The prefrontal margins taper cranially towards the medial margin of the lacrimal. The caudolateral margin of the prefrontal forms the craniomedial wall of the orbit. One-third of its medial margin is articulated with the nasal cranially and two-thirds with the frontal caudally. In ventral view, the lateral portion of the right prefrontal pillar is exposed from the matrix. It is located medially at the cranial margin of the orbit and extends to the dorsal surface of the palate.

Frontal: The dorsal surface of the frontal is slightly concave, particularly at the interorbital region. Its surface is also marked with deep sculptured ornamentations. Cranially, the lateral margins of the frontal taper cranially and form a "W"–shaped sutural contact with the prefrontal and nasal. The frontal extends to the prefrontal craniolaterally with a concave suture and forms the medial wall of the orbit laterally. Caudolaterally, the frontal is articulated with the postorbital by a zigzagged suture and forms the craniomedial edge of the supratemporal fenestra. Its caudal margin extends into one-fourth of the supratemporal fenestra. The median suture on the caudodorsal surface is visible and indicates that this specimen should be a young adult individual.

This suture gradually fades out and disappears at the interorbital surface. In ventral view, two strong ridges form a craniocaudal groove, 5 mm wide, at the midline. Its cranial end is impossible to determine, because it is covered by the matrix.

Parietal: The left portion of the parietal is crushed at the left caudal margin. In dorsal view, the surface of the parietal is heavily sculptured as in the frontal. The cranial margin of the parietal contacts the frontal with a concave suture. Its lateral margin forms two-third of the depth of the medial and caudomedial portions of the supratemporal fenestra. Caudally, the parietal sends a lateral process to contact the squamosal. Its caudal margin is slightly concave at the midline of the skull and contacts the craniodorsal margin of the supraoccipital.

Postorbital: The right postorbital is completely preserved, while the left one presents only its cranial portion and descending process. Its craniolateral corner makes the cranial table sub-rectangular in shape. The cranial margin of the postorbital forms the caudal edge of the orbit. In medial view, the postorbital sends a process to contact the frontal and forms the cranial wall of the supratemporal fenestra. The curvature of its mediocaudal margin forms the craniolateral wall of the supratemporal fenestra. In caudal view, the postorbital contacts the squamosal with an oblique suture, which runs caudally from a craniolateral to caudomedial direction. In dorsal view, the surface of the right postorbital is slightly abraded. Consequently, it is not possible to observe its ornamentation. In ventral view, the descending process of the postorbital is rather robust and thick. Its diameter is approximately 11 mm.

Squamosal: The left squamosal is crushed and distorted whereas the right one is abraded on the craniodorsal surface. It is a triradial bone that consists of cranial, medial and caudolateral processes. In dorsal view, the squamosal sends a cranial process, which is rather straight and slightly bent craniomedially, to contact the postorbital. In medial view, the cranial and medial processes form the caudomedial wall of the supratemporal fenestra. The medial process is bounded by the lateral margin of the parietal. In caudal view, its ventral margin is widely connected with the craniodorsal surface of the otoccipital. Laterally, the caudolateral process extends downward and overlaps with the otoccipital process caudally. The sculpture on the dorsal surface of the squamosal is similar to that of the parietal.

Quadrate: Both quadrates show only the tips of their craniomedial ends that form the caudoventral part of the supratemporal fenestrae. In dorsal view, it contacts the ventral surface of the parietal medially and squamosal laterally.

Jugal: The right jugal is nearly complete, lacking only its caudal end. It is more complete than the left one. In lateral view, the jugal contacts the medial margin of the maxilla cranially by an oblique suture, which runs cranially from a caudoventral to craniodorsal direction. The cranial process of the jugal is about twice as broad as the caudal process. In dorsal view, the jugal is located beside the lateral margin of the cranial table. The jugal tapers cranially and wedges between the lacrimal and maxilla. The cranial tip of the jugal is at the same level as that of the prefrontal. Medially, the jugal contacts two-thirds of the lacrimal caudally and also forms the lateral margin of the orbit. At the caudal end of the orbit, the jugal displays an unsculptured ascending process, which leans lateromedially and forms the ventral part of the postorbital bar.

Its shape is relatively flat mediolaterally and broad craniocaudally. A foramen forms a moderate elongated opening, 7mm long, at the caudal end of the ascending process. The suture between the ectopterygoid and jugal is invisible. The ventral surface of the jugal is smooth.

Supraoccipital: The supraoccipital is broadly rectangular in shape. Dorsally, it can be observed as a small semi-circular shape on the skull roof that contacts the caudal margin of the parietal. In occipital view, its surface is almost completely abraded except on its lateral and ventral margins, which are well preserved. The supraoccipital is bounded by the otoccipital laterally and ventrally whereas the dorsolateral margin of the supraoccipital is bordered by the parietal.

Otoccipital: The paired wings of the otoccipital slightly extend caudolaterally. In occipital view, the dorsal margin of the otoccipital contacts the ventral margin of the cranial table. The otoccipital surface, from dorsal to ventral, gradually protrudes caudally with an angle of approximately 30 degrees to the vertical axis. The ventral edge of the otoccipital forms a transversal ridge beyond the dorsal margin of the occipital condyle. Its surface becomes nearly vertical at the level of the occipital condyle. The lateral margin of the right process is rounded whereas the left process is crushed. In lateral view, the otoccipital extends laterally and reaches the lateral margin of the squamosal. At its lateral tip, the dorsal surface of the otoccipital is overlapped by the ventrolateral surface of the squamosal. In medial view, its dorsal surface is bordered by the ventral surfaces of the supraoccipital and parietal. Medially, the otoccipitals contact each other 8 mm along the midline of the skull, separating the supraoccipital from the dorsal margin of the foramen magnum. Below this suture, the medial margin is widely concave and forms the wall of the foramen magnum. The wedge-shaped process on the lateroventral margin of the foramen magnum is not evident. The suture between the otoccipital and basioccipital is not possible to observe because the surface is relatively worn.

Basioccipital: The basioccipital is situated in a nearly vertical plane. It entirely forms the occipital condyle, which has a sub-circular articular facet. In occipital view, the bone is bounded by the foramen magnum dorsally and the otoccipital dorsolaterally. Its lateral margin is rather thick and robust. The ventral part of the occipital condyle presents a well-developed medial crest through the dorsal margin of the eustachian foramen. This crest separates two strong lateral depressions. The medial eustachian foramen can be observed in the caudoventral part of the basioccipital margin. It looks like a broad invert "v" shape. The lateral eustachian tubes are visible laterally from the medial eustachian foramen at the ventrolateral margin of the basioccipital. They are dorsoventrally compressed and about 2 mm in lateromedial diameter.

Basisphenoid: In occipital view, the basisphenoid is exposed at the ventral margin of the basioccipital because the posterior margin of the pterygoid is lacking. Its dorsal margin forms the ventral wall of the medial eustachian foramen and of the lateral eustachian tubes. Ventrally, the caudal margin of the basisphenoid is concave cranially. The basisphenoid rostrum is not preserved.

Supratemporal fenestra: The supratemporal fenestrae are oval in shape. Their dorsal surface is placed at the same level to that of the cranial table. The medial wall of the fenestrae is formed by the contact among the lateral surface of the parietal, the craniodorsal surface of the quadrate, and the dorsolateral surface of the laterosphenoid. In dorsal view, the supratemporal fenestrae are bordered craniolaterally by the postorbital, craniomedially by the frontal, medially and caudomedially by the parietal, and caudolaterally by the squamosal. Their opening size is nearly equal to that of the orbit.

Infratemporal fenestra (Fig. 3B): Lacking of the quadratojugal and caudal portion of the jugal, the reconstruction of the infratemporal fenestra is not possible. However, the remains of the jugal indicate that the cranial part of the infratemporal fenestra is rather flat dorsoventrally and elongated in shape.

Internal Choana: The internal choana is oval in shape, 29 mm long and 14 mm wide. It is bordered by the palate cranially, about 6 mm wide, whereas the lateral and caudal margins are enclosed by the pterygoid. The internal choana seems unlikely to be divided by a septum.

Pterygoid: In dorsal view, the cranial process of the pterygoid is a very thin bar. It extends craniodorsally to overlap the dorsal surface of the palatine ventrally. It also forms the caudal part of the dorsal roof of the narial passage. Laterally, the pterygoid flanges are broken. Caudally, the pterygoid forms the base of the braincase for half of its total length.

In ventral view, only the medial surface of the pterygoid is preserved, which is about 39 mm in length and 25 mm in width, since the pterygoid wings are lacking. The pterygoid contacts the caudal margin of the palate cranially whereas its posterior margin is broken, baring the ventral part of the basisphenoid. Craniomedially, the pterygoid is concave caudally and forms the lateral and caudal walls of the internal choana for about two-thirds of its length.

Laterosphenoid: The laterosphenoids are partly preserved on both sides. Their dorsal parts widely contact the frontal and parietal medially and the postorbital laterally. In lateral view, its surface forms the craniolateral part of the braincase. Caudally, the caudoventral margin of the laterosphenoid forms the cranial and craniodorsal margins of a moderate foramen, which is corresponding to the cranial nerve 5th. This foramen is about 9 mm in craniocaudal length and 6 mm in dorsoventral length. Its caudal part also shows sutural connections with the prootic caudoventrally and quadrate caudodorsally. The laterosphenoid bridge is not preserved in this specimen.

Palatine: The palatine is elongated in shape, and 99 mm in length. Its ventral surface is smooth and rather convex at the middle of its length. Cranially, it contacts the maxilla by a suture that extends caudolaterally to the craniomedial margin of the palatal fenestra. The caudal margin of the palatine contacts the pterygoid caudolaterally and the internal choana caudomedially.

In dorsal view, one-third of its length is overlain by the ventral surface of the pterygoid caudally. Cranially, at the end of the overlapping, the palatine contacts the descending process of the prefrontal in its caudal portion.

Suborbital fenestra: In ventral view, the suborbital fenestra tapers cranially in shape. Its cranial and lateral margins are formed by the palatal process of the maxilla whereas its medial margin is bordered by the palatal process of the palatine. The caudal margins of these openings are lacking at both sides, because the ectopterygoids are not preserved. The width of the cranial margin of a suborbital fenestra is approximately half the width of its caudal portion.

Dentition: Most of the cranial region of the maxillae and the whole premaxillae are missing. Therefore only fifteen alveoli can be counted in each maxilla from the caudal end of the maxilla forward. Only the bases of the crowns of some teeth are preserved. They are all circular in cross-section and show a size similar to that of the alveoli. The mesiodistal diameter of each alveolus is about 4 mm, and they are separated from each other by the same distance. The tooth row is rather straight.

Table 5-1 Measurement of the cranium of *Khoratosuchus jintasakulii* gen. et sp. nov.

Skull	Measurement (mm)
Skull length, tip of rostrum to caudal margin of the occipital condyle (preserved)	192
Length of rostral part of skull, from tip of rostrum to cranial tip of orbit	97
Maximum width of cranial table, at caudal margin of squamosal	89
Length of nasal bones, as preserved	85
Length of parietal	44
Length of frontal	68
Maximum width of frontal	43
Maximum width of parietal	32
Length of right orbital	30
Width of right orbital	28
Length of left orbital	30
Width of left orbital	29
Width of interorbital	24
Width of intertemporal fenestrae	15
Length of cranial table	70
Width of right supratemporal fenestra	25
Maximum width of right squamosal, as preserved	27
Height of occipital surface, supraoccipital to basioccipital	42
Width of occipital surface, at otoccipital process	40
Height of occipital surface, supraoccipital to ventral of occipital condyle	28
Height of occipital condyle	11
Width of occipital condyle	20
Height of supraoccipital	10
Width of supraoccipital	26
Height of foramen magnum	7
Width of foramen magnum	15

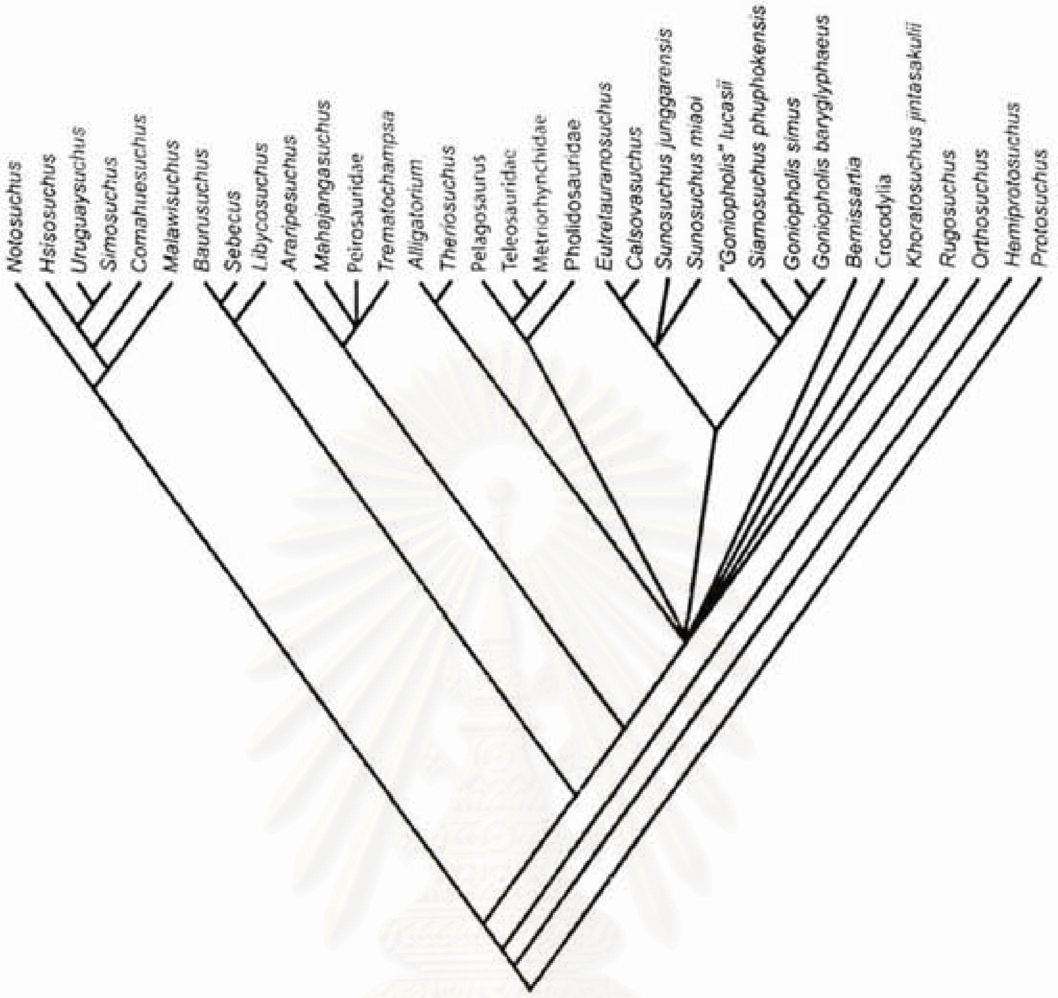


Fig. 5-3 Strict consensus tree of 66 equally most parsimonious trees (length = 316 steps, consistency index (CI) = 0.418, and retention index (RI) = 0.625) derived from the analysis of 102 characters in 31 taxa of Mesoeucrocodylia and 3 outgroup taxa, which consist of *Protosuchus*, *Hemiprotosuchus* and *Orthosuchus*.

COMPARISON AND DISCUSSION

The strict consensus tree (Fig. 5-3) shows that *Khoratosuchus jintasakulii*, Atoposauridae, Goniopholididae, *Rugosuchus*, *Bernissartia*, the Eusuchia, and Longirostrine Forms (see definition in Clark, 1994; Wu et al., 1997, 2001a), illustrated by *Pelagosaurus*, Teleosauridae, Metriorhynchidae, and *Pholidosaurus*, form an unresolved monophyletic group, representing the Neosuchia (Benton and Clark, 1988). All members of this clade share an unambiguous diagnostic character, which is the dorsal part of the postorbital possessing anterior and lateral edges (28[0])

Although the maxilla of *Khoratosuchus jintasakulii* is relatively slender and long, it does not mean that the specimen is included in the Longirostrine Forms. On the contrary *K. jintasakulii* can be rejected from the Longirostrine Forms on the basis of the following characters. The rostrum of the Thai specimen is wider than its height and longer than the remainder of the skull (3[2], 103[2]) whereas that of the Longirostrine Forms is nearly tubular in shape and is also much longer than the remainder of the skull (3[1], 103 [4]). The quadratojugal of *K. jintasakulii* extends dorsally as a broad sheet contacting most of the postorbital portion of the postorbital bar (19[0]). On the contrary, the Longirostrine Forms possess a narrow quadratojugal, which extends to contact only a small part of the postorbital bar (19[1]). In addition, the internal choana of the Thai neosuchian is mostly bordered by pterygoids, but its most anterior margin is bordered by palatines (102[2]). For Longirostrine Forms, the internal choanae are entirely bordered by palatines, or half palatine and half pterygoid (101[1]). The position of the internal choana of *K. jintasukulii* is an important diagnostic character that precludes the Thai neosuchian from belonging to the families Atoposauridae or Goniopholididae (Wu et al., 1997), which share this feature with the Longirostrine Forms. It also suggests that the Thai specimen is phylogenetically closer to the derived neosuchians and the Eusuchia than to the family Goniopholididae (Wu et al., 2001a). Furthermore, the absence of the basisphenoid on the palatal surface is another good diagnostic character that can be used to distinguish *K. jintasakulii* from the other two families.

Currently, the Eusuchia are diagnosed as a monophyletic group based on a single synapomorphy (Clark, 1986; Ortega et al., 2000; Wu et al., 2001a), which is that the internal choanae are entirely situated into the pterygoids. On the contrary, the anteromedial tip of the internal choana of the Thai neosuchian is formed by the palatine. This character indicates that *K. jintasakulii* is not a member of the Eusuchia.

The new crocodyliform from Thailand is comparable with derived neosuchians like *Bernissartia fagesii* Dollo, 1883 from the Lower Cretaceous of Europe (Fig. 2 in Buscalioni and Sanz, 1990); *Shamosuchus* spp. from the Upper Cretaceous of Mongolia (Figs.17 and 19 in Efimov, 1988); and an unnamed taxon (= "Glen Rose form" of Clark in Benton and Clark, 1988) described from two skulls from the Lower Cretaceous of North America (Fig. 6E in Langston, 1973), on the basis of the situation of the internal choanae, which are mostly restricted by the pterygoids. *K. jintasakulii* was also compared with *Shamosuchus* spp. and the "Glen Rose form" in order to understand the phylogenetic position of the Thai new crocodyliform, although the latter two taxa were not included in the ingroups of our phylogenetic analysis.

The skull of *K. jintasakulii* resembles that of a Chinese crocodyliform, *Rugosuchus nonganensis* from the late Early Cretaceous of Nenjiang Formation, northeastern China, which shows peculiar cranial features (Figs. 3A, 3B and 4 in Wu et al., 2001a). Both of them share an elongate and slender skull, and the lateral margins of their maxillae are relatively straight. However, *Khoratosuchus* can be separated from *Rugosuchus* by the following cranial characters: 1) the maxillary teeth are homodontous based on the sub-conical shape of the base of the preserved crowns;

2) the dorsal surfaces of the frontal and parietal are smooth, without any median ridge; 3) the dorsal surface of the maxillae lacks a series of fossae; 4) the suborbital fenestrae are larger whereas the interfenestral region of the palatines is much smaller; 5) the internal choanae is almost entirely formed by the pterygoid; and 6) the supraoccipital has no vertical ridge along the midline of its occipital surface.

In addition to the internal choana of *K. jintasakulii* being more posterior in position than seen in *Bernissartia fagesii*, and *Shamosuchus* spp., the following cranial characters can distinguish the Thai crocodyliform from those taxa: 1) the skull of *K. jintasakulii* is more slender than those two taxa, which are relatively broader and stouter; 2) the dorsal surface of the frontal and parietal lacks a median ridge along the midline whereas *B. fagesii* has a median ridge on the concave frontal surface. The frontal and parietal of *Shamosuchus* spp. are often partially ridged along the dorsal midline; 3) the lateral margin of the maxilla is relatively straight without any strong constrictions as commonly seen in *B. fagesii* and *Shamosuchus* spp.

Moreover, the following additional characters can distinguish *K. jintasakulii* from *B. fagesii*: the interorbital region is broader than the interfenestral region; the occipital surface of the supraoccipital is smooth; and the ventral border of the orbit is concave and does not rise as a rim-like edge. The jugal of *K. jintasakulii* lacks a longitudinal ridge on the lateral surface and the interfenestral region of the palatines is longer and much smaller than that of *Shamosuchus* spp. These features also exclude the Thai specimen from *Shamosuchus* spp. Only the posteroventral view of the skull of the "Glen Rose Form" is available for comparison (fig. 6E in Langston 1973).

Except for the position of the internal choana that can be compared, the other features, as mentioned above, are unknown for the "Glen Rose Form."

According to the above comparisons, it is clear that the new crocodyliform from Thailand cannot be referred to any previously known taxa. Additionally, based on the following cranial features: the relatively straight and elongate lateral margin of the maxilla; the absence of a median ridge along the flat dorsal surface of the frontal and parietal; the internal choana entirely situated into the pterygoid; and the relatively flat, wider than long snout, it is sufficient to erect the new taxon *Khoratosuchus jintasakulii* for this Thai crocodyliform. These diagnostic characters also suggest that *K. jintasakulii* may be closer to the Eusuchia than the Chinese derived neosuchian, *Rugosuchus*.

Khoratosuchus jintasakulii is the first crocodyliform from the Aptian-Albian Khok Kruat Formation to be described from a skull and also represents the most advanced form among all the crocodyliforms of the Khorat Group. Previous works have already described three taxa of Thai neosuchians i.e., "*Sunosuchus*" *thailandicus* (Buffetaut and Ingavat, 1980) from the Phu Kradung Formation, "*Goniopholis*" *phuwiangensis* (Buffetaut and Ingavat, 1983) and *Siamosuchus phuphokensis* (Lauprasert et al., submitted) from the Sao Khua Formation. The discovery of *K. jintasakulii* does not increase only the diversity of the neosuchian crocodilians from the Mesozoic Era of the Khorat Group, but also represents the most advanced form of non-eusuchian crocodilians in Southeast Asia.

An additional specimen from Ban Saphan Hin is part of a left dentary (NRRU-A 1791). It clearly shows that the specimen belongs to a short-snouted crocodyliform on the basis of its short symphysis, suggesting a different taxon from *K. jintasakulii*. As these crocodilians were found from the same assemblage, it indicates that Ban Saphan Hin appears as a very interesting locality for the study of the late Early Cretaceous vertebrate fossils, in particular crocodyliforms.

CHAPTER VI

CROCODYLIFORM TEETH FROM THE MESOZOIC KHORAT PLATEAU

Abstract

Crocodyliform teeth from the Phu Kradung, Sao Khua, and Khok Kruat Formations are described and categorized. The tooth specimens are divided into seven morphotypes on the basis of shape (size and curvature) of the crown, ridge ornamentation, and the presence of serration. Morphotypes I, II, and IV are considered as teeth of Goniopholididae whereas morphotype VI and VII show some characters that can be diagnosed as *Theriosuchus* and *Peipehsuchus teleorhinus* Young, 1948, respectively. Morphotype III and V, which are different from the others, are attributed to indeterminate crocodyliforms.

Key words: crocodyliformes, tooth morphology, Goniopholididae, Khorat Group

Introduction

Fossil excavations in the non-marine Mesozoic sediment of the Khorat Plateau have yielded a succession of vertebrate faunas (Buffetaut et al., 2003; Cuny et al, 2003). For the fossil crocodilians, although cranial and postcranial skeletons are rare, numerous isolated teeth were discovered during the field surveys and field excavations, more than twenty five years ago, by the Franco-Thai team of palaeontologists. All materials are housed in the collection of the Sahatsakhan Dinosaur Research Centre. Many crocodilian teeth from the Mesozoic Khorat Plateau show the typical goniopholidid pattern, corresponding to the descriptions of Owen (1841, 1878), Salisbury et al., (1999), Averianov, (2000), Schwarz, (2002), and

Maisch et al., (2003). In addition, some teeth are different from the goniopholid pattern based on their shape, crenulation, and ridge ornamentation. So far, the diversity of the neosuchian crocodilians, particularly the members of the families Goniopholididae and Atoposauridae from the Khorat Plateau, is increasing (Lauprasert et al., submitted). Moreover, there was no previous works about the Thai neosuchian tooth morphology. Therefore, their study is very important to fulfill the knowledge of the Thai neosuchians.

Material and method

There are 158 isolated crocodilian teeth being studied. They were acquired from direct surface collecting, for the large specimens, and screened-washing sediment using 5 and 17 mm mesh-sized sieves (Cuny et al., 2003), for the small specimens. Specimens were collected from three formations of the Khorat Group, i.e., the Phu Kradung, Sao Khua and Khok Kruat Formations (Fig. 6-1), and were investigated under stereomicroscope to categorize morphotype differences on the basis of shapes (size and curvature) of the crowns, ridge ornamentations, and the presence of serrations. All specimens are housed in the Sahatsakhan Dinosaur Research Centre (SDRC), Kalasin Province.

Geological Settings

Carter and Bristow (2003) divided the Khorat Group, from base to top, into five formations, i.e., the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, and Khok Kruat Formations, using detrital zircon thermochronology. The Phu Kradung Formation ranges in age from the late Jurassic to early Cretaceous. At the present stage, there is no direct evidence to determine the precise age of the Phra Wihan, Sao

Khua, and Phu Phan Formations. Therefore, these three formations should be considered as ante-Aptian in age. The Khok Kruat Formation, as the top formation of the Khorat Group, has the best age determination, ranging from Aptian to Albian, on the basis of the occurrence of freshwater hybodont shark (Cappetta, *et al.*, 1990) and palynomorphs (Sattayarak, *et al.*, 1991, Racey *et al.*, 1994, 1996).

So far, all fossil crocodile remains in the Khorat Plateau, northeastern Thailand, were obtained from only three formations of the Khorat Group, i.e., the Phu Kradung, Sao Khua and Khok Kruat Formations. These three formations represent non-marine Mesozoic rocks, accumulated with red clays, siltstones, and sandstones, which contains abundant vertebrate remains, including crocodiles, dinosaurs, turtles, bony fishes and sharks. The Khorat Group, a part of the Indochina Block, collided with South China as early as the late Permian based on palaeogeographic and geotectonic studies (Metcalfe, 1998; Buffetaut et al., 2003). This indicates that the Khorat Group of Thailand was a part of the mainland Asia continent during its deposition.

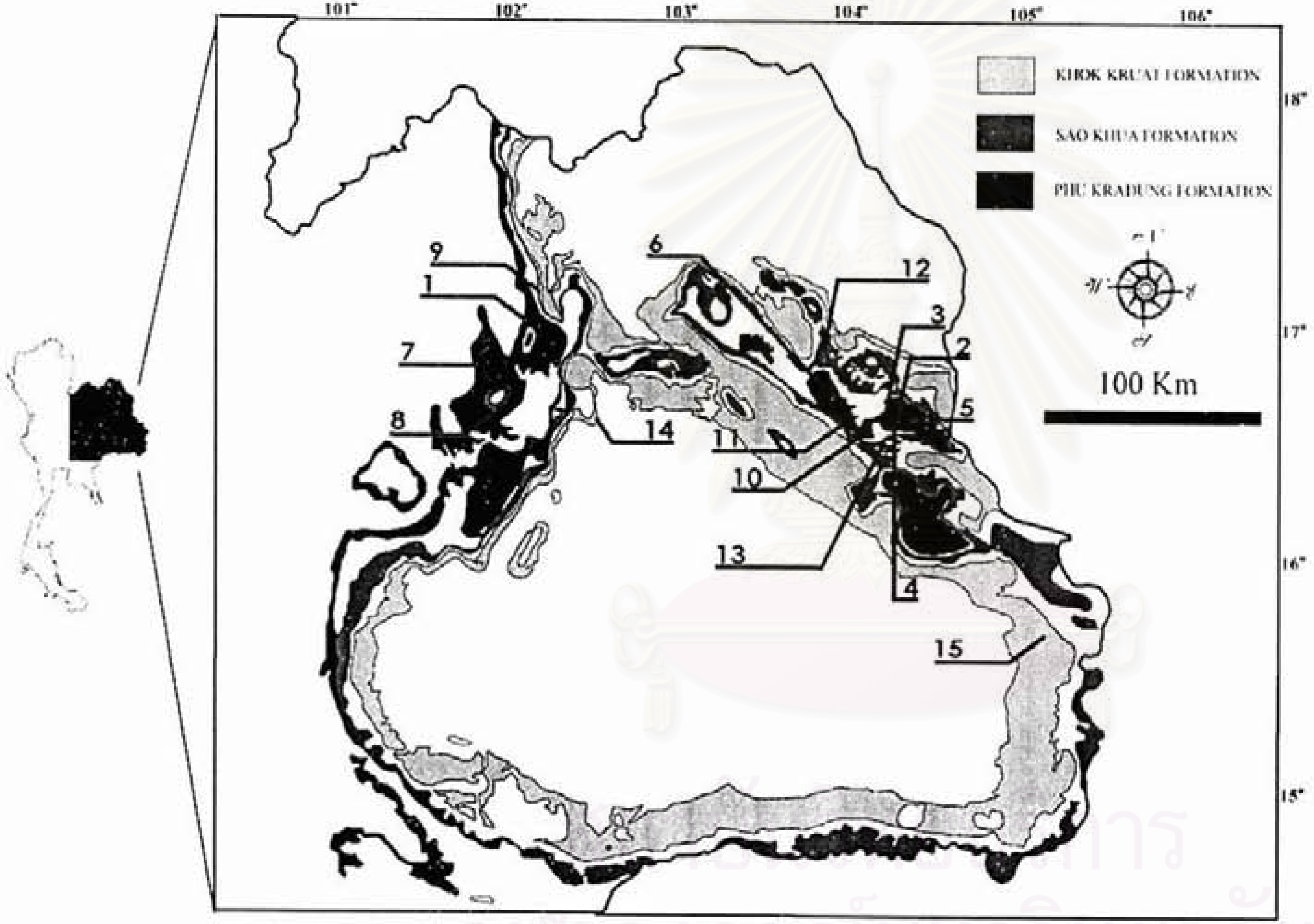
SYSTEMATIC DESCRIPTION

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

? Goniopholididae Cope, 1875



Study sites:

1= Chong chat (Nongbualumpoo),
2= Dan Kerng (Mukdahan),
3= Dan Luang (Mukdahan),
4= Pilot Site (Mukdahan),
5= M3(18) (Mukdahan),
6= Ban Khok Sanam (Kalasin),
7= PW 1A (Khon Kaen),
8= Phu Pra Tu Tee Ma (Khon Kaen)
9= Nb6 (Nongbualumpoo)
10= Khok Kong (Kalasin)
11= Phu Phak (Kalasin)
12= Phu Phok (Sakon Nakhon)
13= Nong Sung (Mukdahan),
14= Ban Samran (Khon Kaen)
15= Khok Pha Suam (Ubon Ratchathani)

Note:

1-6 represent the Phu Kradung Formation
7-13 represent the Sao Khua Formation
14-15 represent the Khok Kruat Formation

Fig. 6-1 Geological map of the Khorat Plateau

Morphotype I

Material: n= 28

Localities- Phu Kradung Formation: Dan Luang, Dan Kerng, and Pilot Site,
Mukdahan province; Khok Sanam, Kalasin province.
Sao Khua Formation: PW 1A, Khon Kaen province.
Khok Kruat Formation: Ban Samran, Khon Kaen province and Khok
Pha Suam, Ubon Ratchathani province.

These teeth are robust, high and conical in shape, with numerous ridges on the lingual (9 to 33) and labial (10 to 38) sides (Fig. 6-2A). A complete specimen of this morphotype indicates that the largest Thai crocodilian tooth, 18 mm in diameter and 38 mm in height, of the Khorat Plateau is also included in this category. On the contrary, the smallest tooth of this morphotype is 5 mm in diameter and 8 mm in height. The specimens mostly show a number of well-developed apicobasal ridge, more abundant on the labial side than on the lingual side, but some specimens exhibit an equal number of ridges on both sides. The cross-section of this morphotype is circular to subcircular (slight labiolingual compression, which probably characterizes more anterior teeth). This morphotype possesses both straight and slightly labiolingually curved teeth. The root is usually not set off from the crown. The crown is stout while the apex forms a rounded to obtuse triangle in shape. Two carinae are present on the crown. They are strongly distinct at the apical region, but become less developed near the root. The mesiodistal carinae define two different plans with the axis of the tooth and form a lingual angle of nearly 180 degrees. Consequently, the surface of the lingual side is nearly equal to that of the labial side. The crown surface is covered by straight ridges, which are parallel to each other on most of their length, and disappear before reaching the carina. The ridges and furrows are more angular near the root than near the apex, where they are rather rounded. There are some intercalated ridges at the base of the crown and on the apical area. The apex also displays irregular enamel wrinkles, which finally reach the carinae with an angle of about 20 degrees, and form crenulations. Few teeth of this morphotype display flat and vertical occlusion surfaces. All these teeth belong to a caniniform morphotype.

Partially preserved teeth of the lower jaw of "*Sunosuchus*" *thailandicus* fit rather well with this morphotype, although some appear slightly slender. Unfortunately the apical part of the teeth is not preserved in the Thai "*Sunosuchus*", which makes the taxonomic attribution of these specimens ambiguous. However, these teeth are different from those of *Sunosuchus junggarensis*, which are more slender and covered by thinner ridges (Wu et al., 1996a). In addition, the teeth of this morphotype are relatively stouter than the teeth of *Sunosuchus miaoi* (Young, 1948).

Morphotype II

Material: n= 68

Localities- Phu Kradung Formation: M 3(18) and Pilot Site, Mukdahan province; Nong Mek, Kalasin province.

Sao Khua Formation: Nb6, Nongbualumpoo province; Nong Sung, Mukdahan province; Khok Kong and Phu Phak, Kalasin province; Phu Pra Tu Tee Ma and PW1A, Khon Kaen province; Phu Phok, Sakon Nakhon province.

Khok Kruat Formation: Khok Pha Suam, Ubon Ratchathani province.

Morphotype II is the most abundant teeth found in this study. The base of the crown of these teeth is slender and conical in shape whereas the apex is acutely pointed (Fig. 6-2B and 2C). The specimens of this morphotype show various sizes, from 5 to 28 mm in height, and distinctive ridges on the lingual side (6 to 21 ridges) and the labial side (7 to 23 ridges). The distribution of the ridges between the labial and lingual surfaces is similar to that of morphotype I, but some specimens possess more ridges on the lingual side than on the labial side. The cross-section of the teeth is circular. The teeth exhibit either straight or slightly lingually curved crown. The crowns are divided into labial and lingual sides by mesial and distal carinae, descending from the apices to the base of the crowns. In lingual aspect, the apex forms an angle less than 180 degrees. The carinae are gradually better developed, becoming higher and stouter from the base of the crown to the apex, and form crenulations. The ridges are angular, straight, and parallel to each other on almost the entire crown. Apically, the ridges gradually bend inward in the carina direction, forming an angle of about 20 degrees on the lingual side and 30 degrees on the labial side. These ridges disappear before reaching each carina. The furrows and ridges of this morphotype are weaker than those of the morphotype I. Intercalated ridges and enamel wrinkles may or may not be present either at the base of the crown or on the apical region.

In some specimens (Fig. 6-2C), the mesial and distal margins or the carinae give flange-like crests and are separated from the central part of the crown by broad and shallow grooves. This is particularly apparent on the lingual face. The root of this morphotype is almost not set off from the crown except when the teeth show a slight constriction between the base of the crown and the apex of the root.

Morphotype III

Material: n= 24

Localities- Phu Kradung Formation: M 3(18) and Pilot Site, Mukdahan province.

Sao Khua Formation: PW1A, Khon Kaen province; Khok Kong, Kalasin province.

The crowns of morphotype III are slender and high in shape, as seen in morphotype II (Fig. 6-2D). This morphotype can be distinguished from the others by the mesiodistal compression at the base of their crowns, which probably characterizes the most anterior teeth of the rostrum. The maximum labiolingual length at the base of the crown is about twice its mesiodistal length. The teeth are curved labiolingually and possess strong elliptical shape in cross section. The root is not set off from the crown. The lingual and labial sides of the crown are separated by obtuse carinae.

The teeth of this morphotype show various sizes from 13 to 33 mm in height and distinctive ridges on the lingual side (9 to 14 ridges) and the labial side (10 to 22 ridges). The labial side possesses more ridges than the lingual side. The carinae divide the teeth into two plans and form a lingual angle of about 95 degrees. The teeth are covered by finely angular ridges and furrows at the apical area. They are gradually rougher and broader in apicobasal direction. At the base of the crown, the ridges of this morphotype are rather more worn than those of the morphotype I and II. No intercalated ridge occurs in this morphotype whereas the enamel wrinkles appear close to the base of the crown.

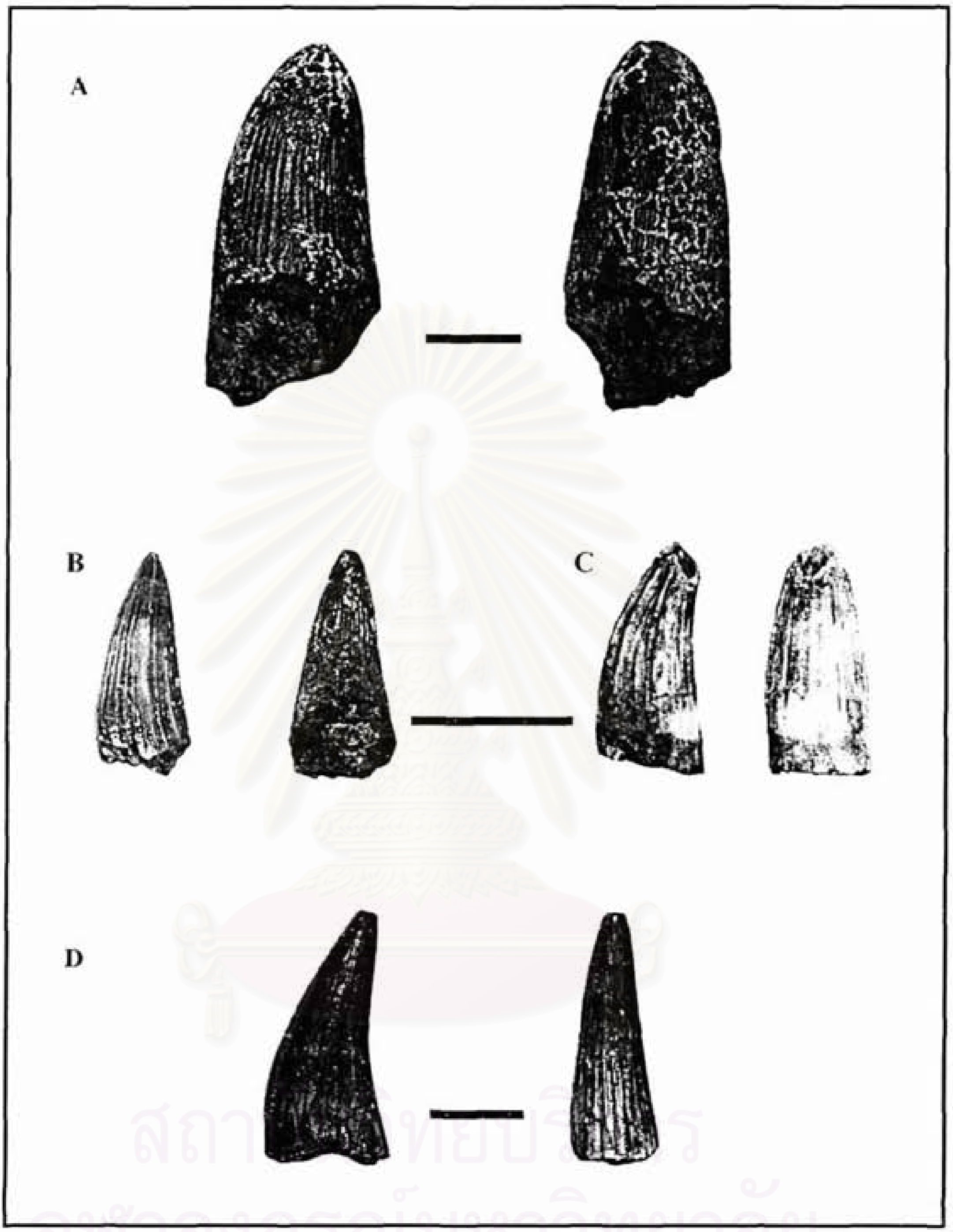


Fig. 6-2 Mesoeucrocodylia indet., the carina view (on the left side of each picture) and lingual view (on the right side of each picture) of teeth specimens from the Khorat Group, ranging in age from the late Jurassic to early Cretaceous. A: morphotype I. B and C: morphotype II. D: morphotype III. All scale bars represent 10 mm

Morphotype IV

Material: n=16

Localities- Phu Kradung Formation: Dan Luang, Mukdahan province

Sao Khua Formation: Khok Kong, Kalasin province.

Khok Kruat Formation: Khok Pha Suam, Ubon Ratchathani province.

The teeth have a roughly triangular shape in labial or lingual views with an acutely pointed apex (Fig. 6-3A). The cross-section at the base of the crown is rather elliptical, because the teeth are slightly compressed labiolingually. The height of the specimens ranges from 3 to 11 mm whereas their mesiodistal length ranges from 3 to 7 mm The teeth are faintly curved lingually. The crown surface is traversed by two sharp carinae at the mesial and distal margins. These carinae, without any serration or crenulation, are distinct, rising and sharp close to the apex. The crown surface is covered by longitudinal and parallel ridges on most of their length. The number of the ridges on the lingual surface (6 to 21 ridges) is fewer than that on the labial one (10 to 31 ridges). The furrows are relatively shallow. Their roots are not set off from the crowns.

The base of the crown is swollen and the connection between the crown and the root is marked by a constriction. The teeth of this morphotype possibly represent the intermediate between the anterior and the most anterior of the posterior teeth.

Morphotype V

Material: n=10

Locality-Khok Kruat Formation: Khok Pha Suam, Ubon Ratchathani province.

The crown of these teeth is relatively short, either with a nearly equal height and length, or slightly higher than long (Fig. 6-3B). The range of the crown height is 4 to 8 mm while the mesiodistal diameter is 3 to 7 mm The base of the crown is bulbous, being convex in both surfaces. The labial face is more convex than the lingual face, which is flatter than the lingual face of the morphotype IV. A marked constriction is present at the base of the crown. The surface of the crown is ornamented with medium to coarse ridges and grooves of broadly parallel orientation. The ridge number on the lingual side ranges from 15 to 23 whereas that of the labial one ranges from 18 to 30. The mesial and distal carinae are worn without any sign of serrations. This morphotype is elliptical in cross-section at the base of the crown.

The apex of the crown is very blunt. The anteroposterior length of this morphotype is greater than its height. This morphotype shows a constriction at the region between the base of the crown and root. These small teeth suggest a probable diet of very hard prey such as crustaceans and molluscs (Russell, 1975; Massare, 1987). These teeth can be attributed to the most posterior series.

Mesoeucrocodylia Whetstone and Whybrow, 1983

Atoposauridae

Morphotype VI

Material: n= 9

Localities- Phu Kradung Formation: Chong Chat, Nongbualumpoo province.

Sao Khua Formation: Phu Phok, Sakon Nakhon province and
Phu Wiang, Khon kaen province.

Nine specimens of this morphotype plus the dentary teeth of CCC-1 from Chong Chat, PPC-2 from Phu Phok, and PWC-2/1 from Phu Wiang are relatively short, with a height nearly equal to the length (Fig. 6-3C). The lingual side of this morphotype is flat or slightly convex, whereas its labial surface is more convex. The apex is acutely pointed whereas the base is elongated mesiodistally. The crowns are strongly labiolingually compressed. Therefore, the teeth are elliptical to strongly elliptical shaped in cross-section. The lingual surface is equally separated from the labial surface by mesial and distal sharp carinae, descending from the apex to the base of the crown close to the crown-root constriction. The surface of the teeth is ornamented with fine parallel ridges and grooves except the marginal ridges that bent inward to the carinae.

The well preserved teeth exhibit festooned crenulations on the mesial and distal carinae. These crenulations are the prolongation of the enamel ridges. They are formed by anastomising and irregular ridges issued from the main body of the crown (Prasad et al., 2002) which is an important diagnostic character of the Atoposauridae's teeth.

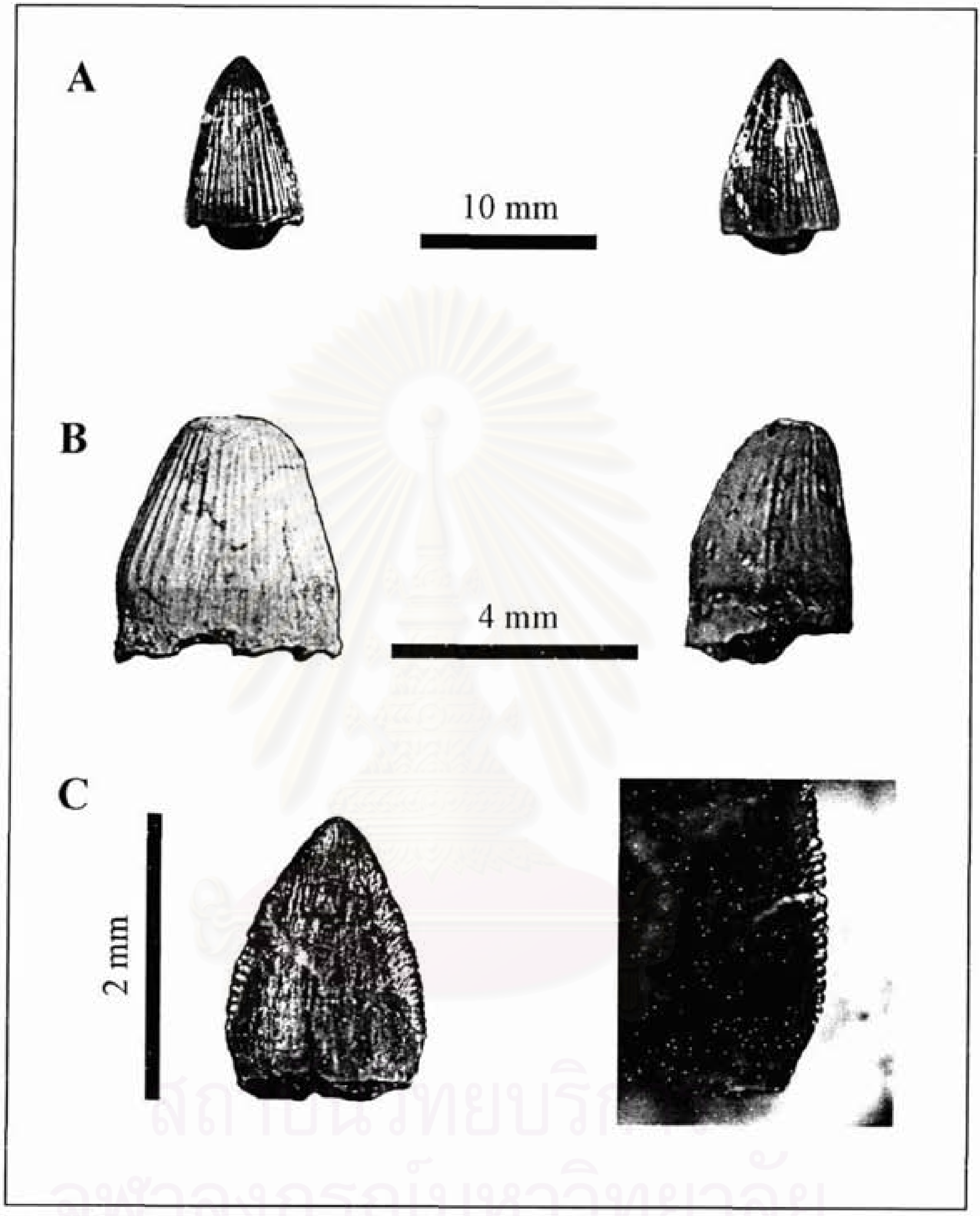


Fig. 6-3 Mesoeucrocodylia indet., the carina (on the left side of each picture) and lingual views (on the left side of each picture) of teeth specimens from the Khorat Group, ranging in age from the late Jurassic to early Cretaceous. A: morphotype IV. B: morphotype V., C: attributed to the genus *Theriosuchus*.

Mesoeucrocodylia Whetstone and Whybrow, 1983

? Teleosauridae

Cf. *Peipehsuchus teleorhinus* Young, 1948

Morphotype VII

Material: (n= 3)

Locality- Phu Kradung Formation: Khok Sanam, Kalasin province.

The teeth of morphotype VII are remarkably slender and conical in shape (Fig. 6-4B). A specimen of this morphotype is well preserved, showing a root and an almost complete crown on the lingual side. The root is not set off from the crown. The teeth are slightly curved lingually. At the base of the crown, this morphotype is subcircular in cross-section (slightly labiolingual compression). The labial and lingual surfaces are equally divided by anterior and posterior carinae, forming a lingual angle of about 180 degrees. The crown surface is covered with very thin and numerous ridges on the lingual side (27 to 48 ridges) and labial side (35 to 42 ridges). The ridges are relatively straight and extend from the base to the tip of the crown.

In carina view, the ridges do not reach the carina on the lingual side, but they are parallel to the crest whereas the ridges on the labial side are gradually bending and touching the carina, forming an angle of about 20 degrees, except the relatively straight ridges on the mesial area. The typical ridge ornamentation of these teeth has been found in a tooth of a Teleosauridae, *Peipehsuchus teleorhinus* Young, 1948 (Fig. 6-4A). This taxon is known from the Red Beds of Maanshan Formation, which is up to now considered as being in the late Early Jurassic of the Szechuan Province, China (Lucas, 2001). This study would tentatively refer the morphotype VII teeth to the genus *Peipehsuchus*, in the family Teleosauridae on the basis of the similarities in their ridge ornamentations and shapes.

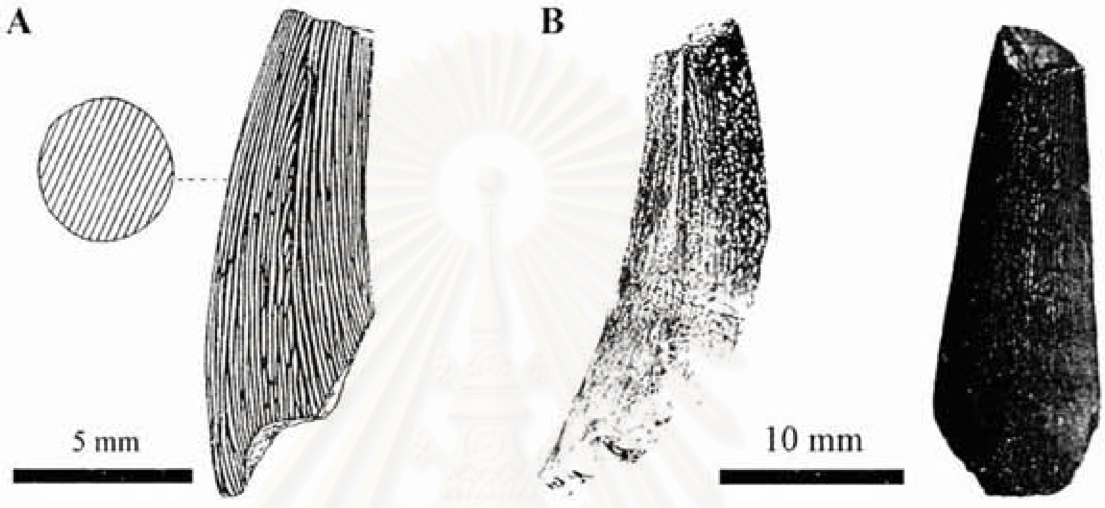


Fig. 6-4 A tooth of *Peipehsuchus teleorhinus* referenced by Young (1948); in A: carina view and cross-section. B: a tooth representing morphotype VII in carina view on the left side and lingual views on the right side, cf. *Peipehsuchus teleorhinus* from Kalasin province, Phu Kradung Formation. A: from Young (1948).

Conclusion and Discussion

Primitive forms of crocodilian dentition are made of relatively high, acutely pointed and non-serrated teeth. These forms are different only in height, i.e., higher caniniform teeth and shorter posterior teeth (Prasad et al., 2002). Apparently, the Mesozoic crocodilian teeth under discussion exhibit a variation of shapes and some morphotypes from the Khorat Group belong to heterodont dentitions. The collection includes high, robust teeth with a rounded cross-section (Morphotype (M) I); slender and conical or labiolingually compressed teeth with acutely pointed apex (M II); slender and strongly mesiodistally compressed teeth (M III); sub-triangular teeth with elliptical cross-section and acutely pointed apex (M IV); short and blunt teeth with mesiodistally long apex (M V); lanceolate labiolingually compressed teeth with elliptical to strongly elliptical cross section and serrated carinae formed by the lateral prolongation of the enamel ridges (M VI), and slender and conical teeth with an unusual ridge ornamentations (M VII).

The crocodyliform teeth under discussion can be classified into five taxa: Goniopholididae, *Theriosuchus*, cf. *Peipehsuchus teleorhinus*, and two indeterminate crocodyliform. Morphotype I, II, and IV are relatively widespread. They were found in all studied formations (Phu Kradung, Sao Khua and Khok Kruat Formations). These morphotypes were compared closely with those of the goniopholidid teeth described and illustrated in the works of Owen (1841, 1878, 1879), Young (1948), Buffetaut and Ingavat (1980, 1983, 1984), Hua et al. (1993), Wu et al. (1995), Goodwin et al. (1999), Salisbury et al. (1999), Averianov (2000), Schwarz (2002), Maisch et al. (2003). The Thai crocodyliform teeth show resemblance in shape and ridge ornamentation with teeth of the family Goniopholididae, which bears well developed carinae, ridges and furrows (Owen, 1841; Salisbury et al., 1999; Averianov, 2000; Schwarz, 2002). Maisch et al. (2003) mentioned a "heterodontous" new *Sunosuchus* specimen, a generic taxon of the family Goniopholididae, from the Upper Toutunhe Formation (Middle Jurassic, ?Bathonian-Callovian) of northwestern China. The specimens of Maisch and his colleagues exhibits several isolated teeth with pointed, strongly curved, almost non-carinate anterior, and strongly carinate, bulbous and heavily striated, small posterior teeth. The former features can be categorized into morphotype II of this study whereas the latter can be categorized into morphotype IV.

The type of the genus *Goniopholis* is characterized by thick and robust teeth with subcircular cross-section at the base of the crown (Owen, 1878, 1879), indicating the anterior teeth. Teeth specimens of morphotype I show all the characters described by Owen (1841, 1878) for the genus *Goniopholis*. Nevertheless, it is difficult to identify isolated teeth of goniopholidids at a generic level. In addition, complete skulls of goniopholidids are up to now lacking. Therefore, morphotype I, II, and IV are appropriately diagnosed as being the teeth of the family Goniopholididae, which seem to have been rather opportunistic, generalized piscivorous to carnivorous freshwater crocodiles (Maisch et al., 2003). The appearance of these three morphotypes also confirms the existence of the family Goniopholididae throughout the Mesozoic Era in the Khorat Group of Thailand.

Two morphotypes show specific characters, which have been found within known taxa, i.e., morphotype VI and VII. The former morphotype resembles teeth of a dwarf mesoeucrocodylian, *Theriosuchus*, whereas the latter morphotype was considered to have close affinities to those of a Chinese taxon, *Peipehsuchus teleorhinus* Young, 1948. The stratigraphic correlation of the morphotype VI, ranging in age from the late Jurassic Phu Kradung Formation to early Cretaceous Sao Khua Formation (Ante-Aptian), corresponds with the European *Theriosuchus*. In addition, the morphotype VII from the Phu Kradung Formation is reminiscent of a teleosaurid, *Peipehsuchus teleorhinus* Young, 1948, which is known from the late Early Jurassic

Red Beds of Szechuan in China, on the basis of the pattern of their ridge ornamentations. *Peipehsuchus teleorhinus* had been originally attributed to the family Pholidosauridae (Young, 1948). At the present time, it is considered as belonging to the family Teleosauridae as confirmed by the discovery of a complete skull (Li, 1993). The exact relationships between the Thai and Chinese teleosaurids, from a palaeobiogrographical point of view, are difficult to assess with only some isolated teeth. Moreover, there is a long hiatus between the late Triassic Nam Phong and late Jurassic Phu Kradung Formations, with a lack of deposition of sediments. Therefore, there is nothing to compare with the late Early Jurassic Teleosauridae of China. However, the discovery of teleosaurid teeth in the non-marine sediment of the Phu Kradung Formation and in China may indicate that *Peipehsuchus* is a marine crocodilian that could certainly survive in freshwater or brackish environments. It is one of the very few teleosaurids known from non-marine deposits.

The specimens of morphotype III show strongly mesiodistally compressed teeth. For a dietary opinion, the curve of the apical region of morphotype III is similar to that of morphotype II, which is acutely pointed and bent lingually. This indicates that they were used for the same function, i.e., piercing and seizing soft prey. Comparisons with the previous works, as mentioned above, show that this morphotype cannot be classified in any of the goniopholidid teeth since mesiodistally compressed teeth have never been mentioned before in this family. Therefore, it is probable that this morphotype does not belong to a Goniopholididae. The ridge ornamentation of this morphotype is more obtuse than that of *P. teleorhinus*. This difference also suggests that morphotype III is unique to the Mesozoic Khorat Plateau. For these reasons, the teeth of morphotype III are considered as belonging to an indeterminate crocodyliform for the time being. The recognition of morphotype III only in the Phu Kradung and Sao Khua Formations can be depicted as the existent range for this indeterminate crocodyliform, from the late Jurassic to the ante-Aptian.

The teeth of morphotype V obviously belong to the posterior series. The apex of morphotype V is relatively blunt whereas the crown is robust. These features suggest that the teeth had been used for crushing preys. However, its shape does not bear a resemblance to the Goniopholididae teeth that were described in previous works. The sizes of these teeth are too large to be the teeth of the dwarf crocodilian *Theriosuchus* and too small to be a posterior series of morphotype III. The teeth of *Peipehsuchus teleorhinus* are known only in the Phu Kradung Formation and in the late Early Jurassic Maanshan Formation of China, whereas morphotype V is recognized only in the Khok Kruat Formation. Therefore, this study considers that the teeth of morphotype V belong to an indeterminate crocodyliform which existed from the Aptian to the Albian. Complete material, especially skull and dentition, is indeed required to allow more accurate identification and understanding of its exact affinities.

The teeth from the late Jurassic Phu Kradung Formation (cf. *Peipehsuchus teleorhinus*) and Early Cretaceous Sao Khua Formation (*Theriosuchus*) generally resemble those of Chinese assemblage from the late Early Jurassic Red Beds of Szechuan (Young, 1948) and Mongolian assemblage from the Lower Cretaceous of Inner Mongolia (Wu et al., 1996b), respectively. Apart from *Peipehsuchus teleorhinus*, another interesting long-snouted crocodyliform from the late Jurassic Phu Kradung Formation is "*Sunosuchus*" *thailandicus*, which was described on the basis of a nearly complete lower jaw by Buffetaut and Ingavat (1980). However, the teeth of this specimen are poorly preserved, showing only the base of the preserved crowns. This long-snouted goniopholidid shows a great resemblance to *Sunosuchus miaoi* Young, 1948 from the Late Jurassic Xiangtang Formation of Gansu Province, northern China (Young, 1948), *Sunosuchus shartegensis* Efimov, 1988 from the Upper Jurassic of Shar Teg in Outer Mongolia (Efimov, 1988), and *Sunosuchus junggarensis* Wu et al., 1996 from the Shishugou Formation of Pingfengshan in the Eastern Junggar Basin, Inner Mongolia (Wu et al., 1996a). These evidences demonstrate close affinities between Thai, Central and Eastern Asia from the Middle to Late Jurassic.

Theriosuchus remains has been reported only in the European region from the Late Jurassic (Kimmeridgian) to the Early Cretaceous (Barremian) (Schwarz and Salisbury, 2005), until Wu and his colleagues (1996b) described the material from the Early Cretaceous of the Ordos Basin of Inner Mongolia. The discovery of *Theriosuchus* teeth from the Phu Kradung and Sao Khua Formations confirms the wide distribution of this genus throughout Southeast Asia since the late Jurassic. It was a widespread crocodilian group.

The teeth, which can be characterized as the Goniopholididae teeth, were found in all studied formations. However, identification of goniopholid isolated teeth at the generic level is uncertain because complete dentition of this family is still lacking. However, with the material at hand, it is clear that the Goniopholididae possesses heterodont dentition, indicating opportunistic consumer, generalized piscivorous to carnivorous. Goniopholididae assemblages have been reported from the Early Jurassic to the Late Cretaceous, and are widespread throughout the northern hemisphere, from western North America to Europe and Asia (Buffetaut and Ingavat, 1980, 1983, 1984; Efimov, 1988; Maisch, *et al.*, 2003). The discovery of this family in Thailand is thus not surprising. Although the previous studies on the fossil crocodilians from the Khok Kruat Formation had never reported goniopholidid material before, the teeth of morphotype I, II and IV can still be used to ascertain the existence of the Goniopholididae in the Aptian-Albian Khok Kruat Formation.

CHAPTER VII

DENTAL ENAMEL MICROSTRUCTURE OF CROCODILIANS AND FISH-EATING DINOSAURS

In order to differentiate crocodilian tooth from the fish-eating dinosaur, *Siamosaurus suteethorni*, four anterior teeth of the Early Cretaceous crocodilians from Thailand (n=4; PPC-3 to 6) were selected to study the dental enamel microstructure and to compare with that of teeth of *Siamosaurus suteethorni* (n=2; PPS-1 and 2) from Phu Phok, Tambon Kok Prasil, Phu Phan District, Sakon Nakhon Province, and with a tooth of spinosaurid from Morocco. Studies were done using a Scanning Electron Microscope (SEM), Faculty of Science, Mahasarakham University (see methods of preparation in Chapter III)

PPC 3 to 6 show resemblance in shape and ridge ornamentation with the teeth of the family Goniopholididae, which bear well developed carinae, ridges and furrows (Owen, 1841; Salisbury et al., 1999; Averianov, 2000; Schwarz, 2002). They also exhibit some morphological similarities with the teeth of *S. suteethorni*: both types of teeth are divided by anterior and posterior carinae and show ridges and furrows on their lingual and labial faces. In addition, the surfaces of the teeth are smooth at low magnification (Naksri, 2003). Study of the enamel type of the goniopholidid tooth samples shows various structures. Two major enamel types were observed from the specimens, i.e., columnar enamel and parallel crystallite enamel (Fig. 7B). Crocodilian tooth samples show two zones, which merge into each other. The thicker inner zone exhibits well-defined columnar enamel (Fig. 7D). The limits of this enamel type become less distinct outward, whereas the parallel crystallite enamel appear in the outer zone together with incremental lines (Fig. 7B). The enamel is structured by major divergence and major convergence of the columnar unit (Fig. 7C and D). Ridges on the surface of the examined crocodilian teeth are preformed by a curvature of the enamel dentine junction (EDJ) as shown in Fig. 7A and C.

The tooth samples from the fish-eating dinosaur, *S. suteethorni,* and from the spinosaurid from Morocco also consist of outer parallel crystallite enamel and inner columnar enamel, which were observed in the inner half of the enamel layer (Fig. 7F). The major divergences of columnar unit (Fig. 7H) were clearly recognized at the ridges and carinae. Variable expressions of incremental lines, especially at the outer half of the enamel layer were detected and combined with the parallel crystallite enamel. The ridges and carinae of the *S. suteethorni* teeth resulted from either a curvature of the enamel dentine junction (EDJ) (Fig. 7E) or solely from convergences and divergences of apatite crystals in the enamel layer itself (Fig. 7F and G) (Creech, 2004). However, the ridges of the spinosaurid tooth from Morocco result only from preformation by the dentine.

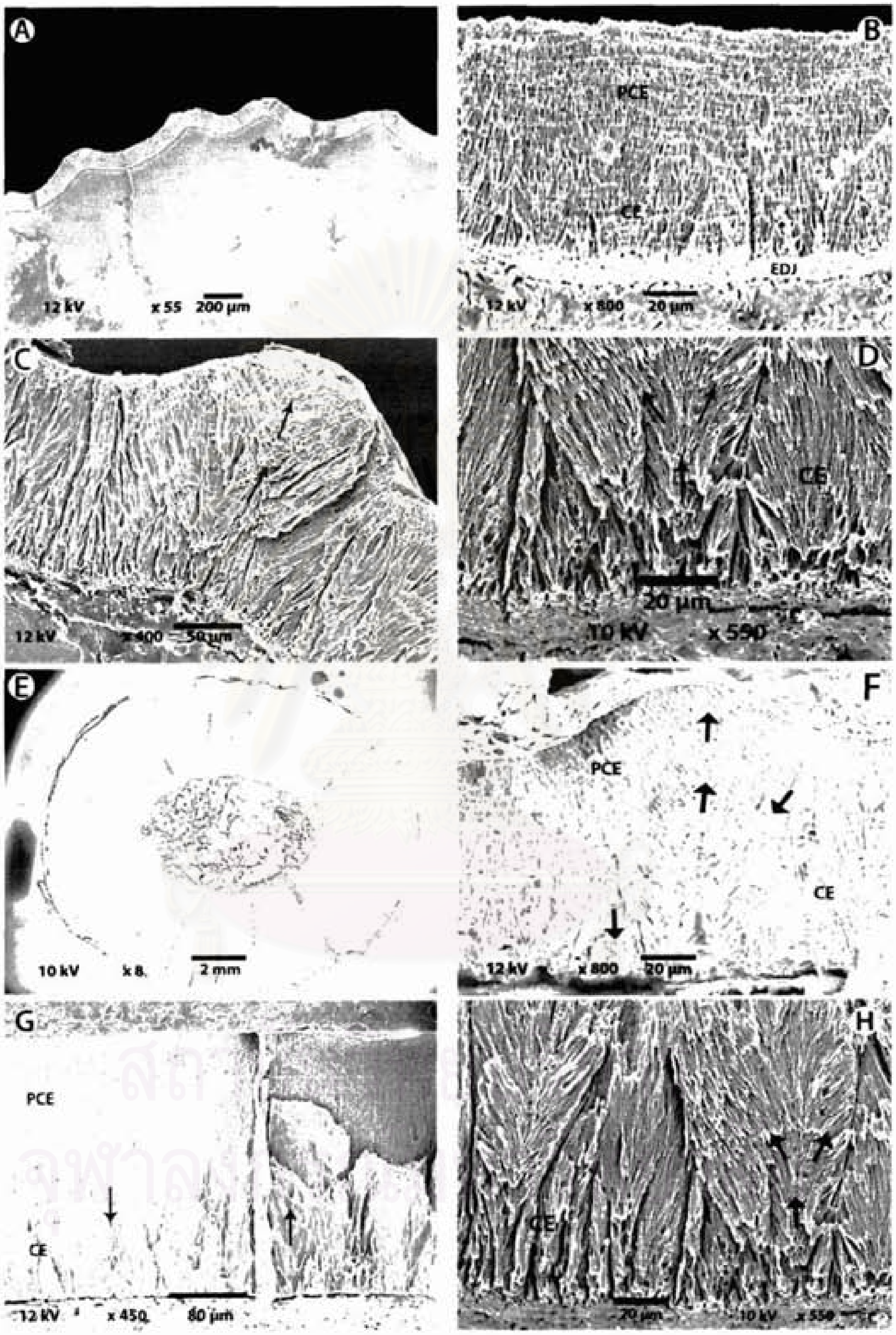


Fig. 7-1 Microstructure of enamel of crocodilian and spinosaurid teeth, all in cross section. A) The ridges on the tooth crown (PPC-5) are preformed by the enamel

dentine junction (EDJ) in crocodilian. B) Enamel of crocodilian tooth (PPC-3) showing columnar enamel (CE) and parallel crystallite enamel (PCE). C) A ridge of crocodilian tooth, showing the major divergence (arrow) bisects the ridge. D) Close-up of the major divergence (arrows) of the columnar enamel in crocodilian tooth. E) The ridges on the tooth crown (PPS-2) are preformed either by the enamel dentine junction (EDJ) or by convergences and divergences of apatite crystals of the enamel layer in *Siamosaurus suteethorni*. E) Close-up of a ridge of *S. suteethorni*. The enamel is structured by major divergence (arrows) and major convergence (inverted arrows). F) Note the transition from columnar enamel (CE) in the inner half of the enamel layer to parallel crystallite enamel (PCE) in the outer half of the enamel layer of a spinosaurid tooth from Morocco. The enamel is also structured by major divergence (arrows) and major convergence (inverted arrows) in the columnar enamel. H) Close-up of the major divergence (arrows) of the columnar enamel in spinosaurid tooth.

The enamel structures of the Early Cretaceous goniopholidid teeth, *S. suteethorni* teeth from Thailand, and the spinosaurid tooth from Morocco are relatively similar. All of them consist of outer parallel crystallite enamel and inner columnar enamel. The resemblance between enamel microstructure of the fish-eating dinosaurs and the Early Cretaceous goniopholidids may suggest a similarity of feeding behavior and mechanical constraints between these animals. Therefore, the absence of long-snouted piscivorous crocodilians in the Sao Khua and Khok Kruat Formations may reflect an ecological replacement of *Siamosaurus suteethorni*, which is unknown before the deposition of the Sao Khua Formation.

CHAPTER VIII

INTERPRETATION OF SEDIMENTATARY ENVIRONMENTS

1. Stratigraphy

Sediments of the Phu Kradung, Sao Khua, and Khok Kruat Formations were observed and recorded in order to interpret the environment of the late Jurassic to early Cretaceous of the Khorat Group in Thailand. The rock lithology and sedimentary structures of three localities of the Phu Kradung Formation (Fig. 8-1) were studied, i.e., Chong Chat (Nongbualumpoo province), Dan Kerng, and Dan Luang (Mukdahan province). The Chong Chat assemblage is close to the contact between the Phu Kradung and Phra Wihan Formations. The fossiliferous bed, which is about 1.3 m thick, consists of maroon mudstones interbedded with grayish white siltstones with poor sorting and scattering sand lenses. Fossil remains from this assemblage contain plant remains, almost entirely preserved *Lepidotes* sp., hybodont shark teeth, crocodilian vertebrae and teeth, dinosaur teeth, and turtle bone fragments.

Dan Luang is situated close to Dan Kerng, about 1 km west from the latter (Fig. 3-2). These sediments were deposited in the upper part of the Phu Kradung Formation. Both of them possess two fossiliferous layers. At Dan Kerng, the lower layer, about 1 m thick, consists of yellowish brown mudstone, scattering with fine sand lenses and calcretes. It is separated from the upper fossiliferous bed by 1 m of sandstone. The upper assemblage is about 1 m thick and contains maroon, fine-grained mudstone. The lower fossiliferous bed of Dan Luang is located in massive sandstone. It is approximately 15 m under the top surface and is separated from the upper fossiliferous bed by 1 m of sandstone beds (Fig. 8-1 C). The upper fossiliferous layer mainly consists of green mudstone with calcareous nodules. This deposit is about 50 cm thick. Based on their preservation, the small fragmentary fossiliferous from the Phu Kradung fossil beds can be interpreted as being further transported or as being buried late during the sedimentary process. Both hypotheses can be confirmed by the discovery of the following disarticulated and fragmentary remains, i.e., a small part of a left dentary of *Theriosuchus* from Chong Chat (Fig. 4-6), another fragment of a left dentary from Dan Kerng (Fig. 4-4), a caudodorsal part of a right surangular from Dan Luang (Fig. 4-5), fragment of turtle shells, crocodilian osteoderms, and many isolated teeth.

Three sites from the Sao Khua Formation were observed (Fig. 8-2). These are PW 1A (Khon Kaen province), Khok Kong (Kalasin province), and Phu Phok (Sakon Nakhon province). This formation has yielded many fossil vertebrate faunas as shown in Appendix II. At the Khok Kong locality, the fossiliferous layer is about 1.5 m thick and underlaid by the massive sandstone of the Phra Wihan Formation. This fossiliferous layer consists of maroon and yellow, fine-to medium-grained mudstones, with calcretes and silcretes. The fossil remains of PW 1A embedded in reddish brown siltstone interbedded with maroon sandstone, with calcretes and silcretes. The fossil bed is only 30 cm thick and 15 m below the base of the Phu Phan Formation. The sediment of PW 1A seems unlikely to have been transported under high energy condition, because this assemblage possesses articulated parts of the dwarf crocodilian specimen, PWC-2/1 to 2/6. On the contrary, the Khok Kong fossiliferous layer exhibits only small fragment of fossil vertebrates such as, isolated pterosaur, crocodilian, and dinosaur teeth, many crocodilian vertebrae, and fish scales. The presence of unrelated taxa from this assemblage may be the result of transport under high energy, from neighbouring areas into the Khok Kong basin.

At Phu Phok, the specimens came from a 1 m thick, maroon and reddish-brown, fine-grained mudstone. There is clear sorting of the sediments with calcrete nodules and nodular silcretes. The Phu Phok fossil bed show well preservation of the crocodilian remains, i.e., some articulated parts of a new goniopholidid (Fig. 4-7), *Siamosuchus phuphokensis*, and an anterior part of a *Theriosuchus* skull (Fig. 4-9). This site has also yield four theropod eggs, some of them with embryo (Buffetaut et al., 2005). These well preserved fossil remains indicate that the fossil assemblage has been deposited *in situ* (Suteethorn, pers comm.).

The Khok Kruat Formation, i.e., Ban Samran (Khon Kaen province), Khok Pha Suam (Ubon Ratchathani province), and Ban Saphan Hin (Nakhon Ratchasima province) were excavated and their sedimentary features were recorded (Fig. 8-3). The Ban Saphan Hin fossiliferous layer is almost at the top of the Khok Kruat Formation. The uppermost part of the fossiliferous bed is about 2 m under the road (top soil). It is overlaid, from base to top, by sandstones, conglomerate, and siltstone beds. The fossiliferous layer consists of granule-grained conglomerates, mixing with pebbles, silt, sand, and clay. The upper conglomerate layer was observed an upward-fining sequence. These features suggest the deposition of sediments in channel of a meandering river, which has commonly occurred in the Khok Kruat Formation (DMR, 1999; Meesook, 2000). The sediment seems to have not been further transported, because a part of an advanced crocodilian cranium, *Khoratosuchus jintasakulii*, still shows the sutural contact on its bones (Fig. 4-15).

Two fossil beds were detected at the Khok Pha Suam locality. The upper fossiliferous layer is about 45 cm thick, and composed of argillaceous sandstones with a thin-bedded marls layer at the top, whereas the lower fossiliferous layer is about 15 cm thick. The fossiliferous layer consists of argillaceous, angular grained sandstones and clayey sand with thin-bedded marls layers at the bottom. It is separated from the upper fossiliferous layer by 30 cm of maroon mudstone bed. The Khok Pha Suam fossiliferous layer has yielded only fragmentary fossils, such as isolated teeth of hybodont sharks, dinosaurs, and crocodilians, turtle shells, bone fragments, and a nearly complete left dentary of "*Goniopholis*" sp. A (Fig. 4-12). All fossil fragments were collected from the mudstone fossiliferous layers. It means that they were transported under high energy condition and deposited in the quiet water or low energy current.

There are two fossiliferous layers at the Ban Samran localities. The lower fossiliferous layer consists of maroon, fine-grained mudstone. It is about 1 m thick and is overlaid by 30 cm thick of reddish-brown, medium-grained and poor sorted sandstone. The fossil crocodilians were not abundant in this site, but it has yielded many isolated teeth and dorsal vertebrae of *Siamosaurus suteethorni*. Some articulated dorsal vertebrae of *S. suteethorni*, found in the lower fossiliferous layer, indicate that sediments have not been transported further. On the contrary, the upper fossiliferous layer indicates that the transportation of the sediments was under higher energy than that of the lower fossiliferous layer, based on the presence of many bone fragments and isolated teeth. The discovery of many complete dorsal vertebrae, showing tall neural spine, of *S. suteethorni* is additional evidence to confirm that this dinosaur is a member of the Spinosauridae (Currie, 1997). However, intensive excavations should also be carried out in this site to look for more complete material of *S. suteethorni* and crocodilian. Further recovery of more material will be a key to better understand the relationship between these animals.

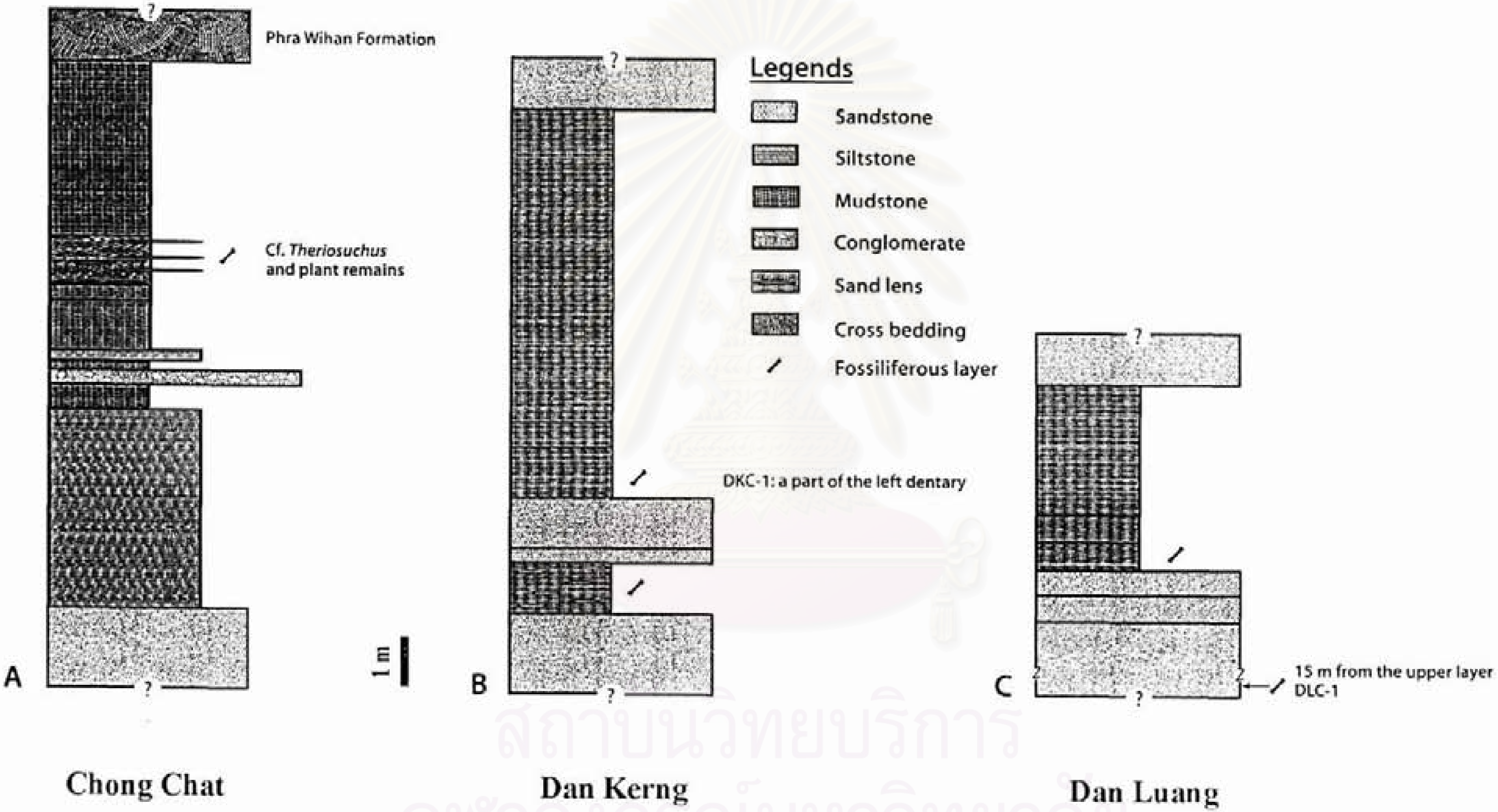


Fig. 8-1 Lithologic column of three fossiliferous sites in the Phu Kradung Formation

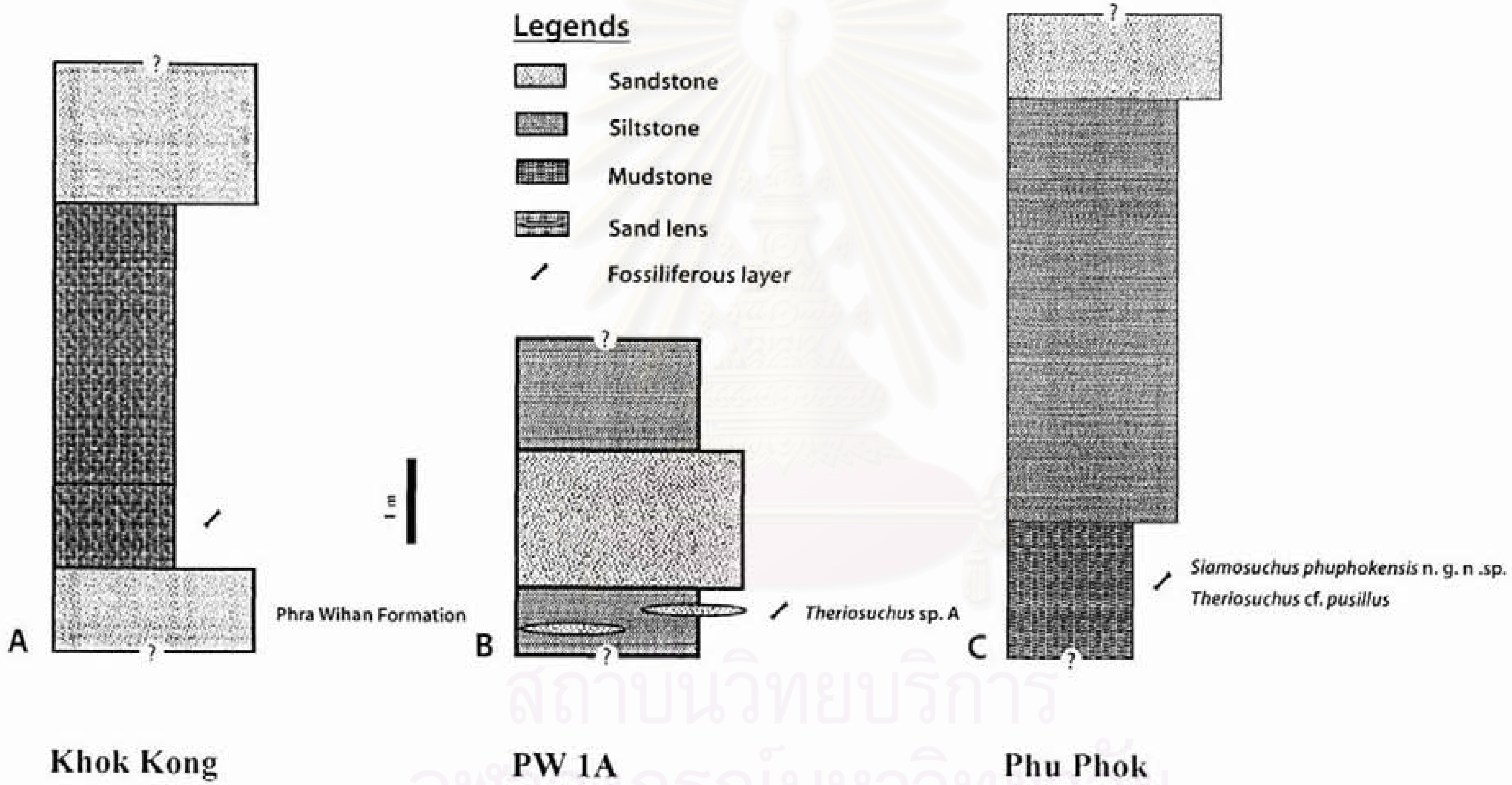


Fig. 8-2 Lithologic column of three fossiliferous sites in the Sao Khua Formation

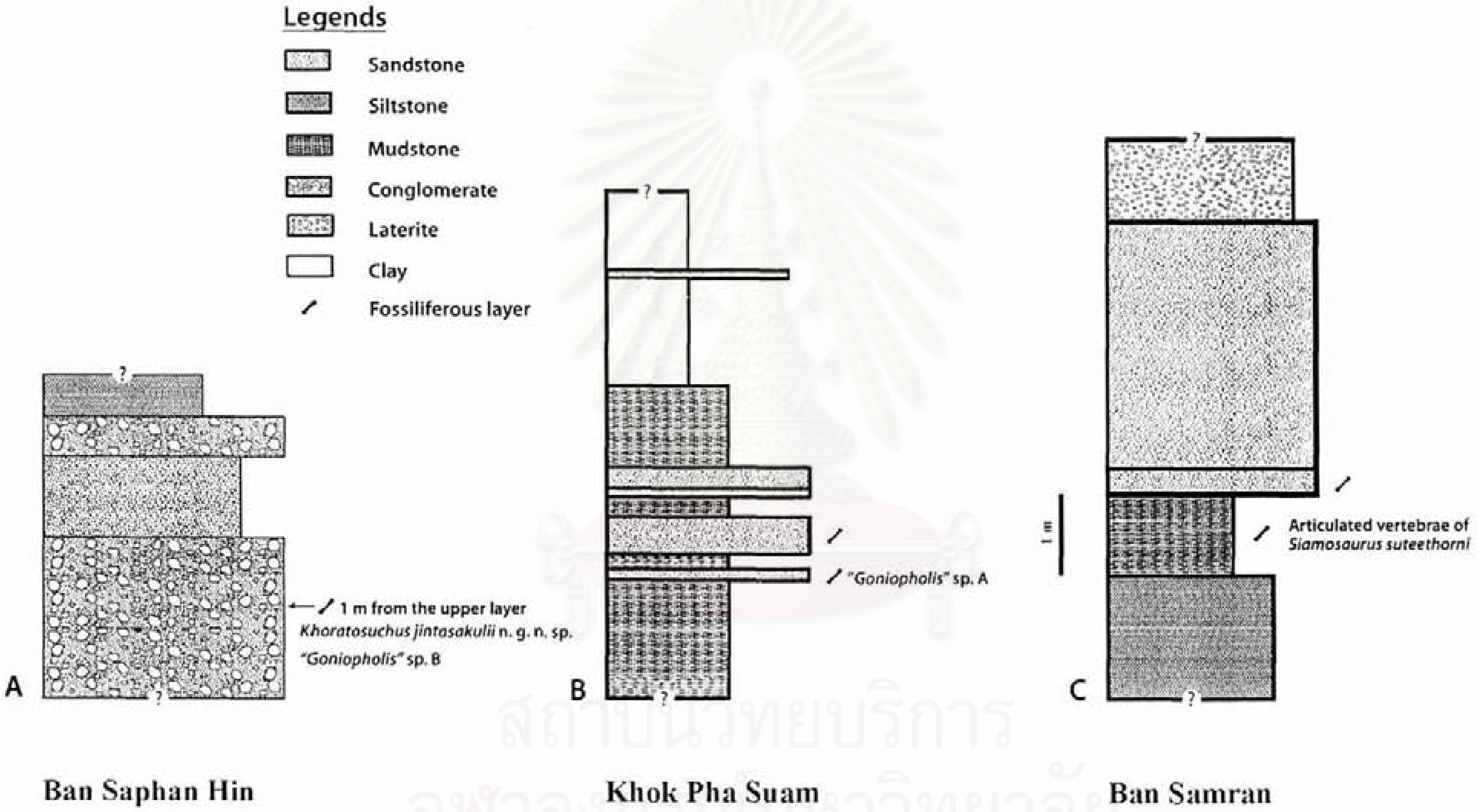


Fig. 8-3 Lithologic column of three fossiliferous sites in the Khok Kruat Formation

2. Correlation inside the Khorat Group

The fossiliferous sites of this study were correlated inside the Khorat Group, based on the stratigraphic data as described earlier (Fig. 8-4).

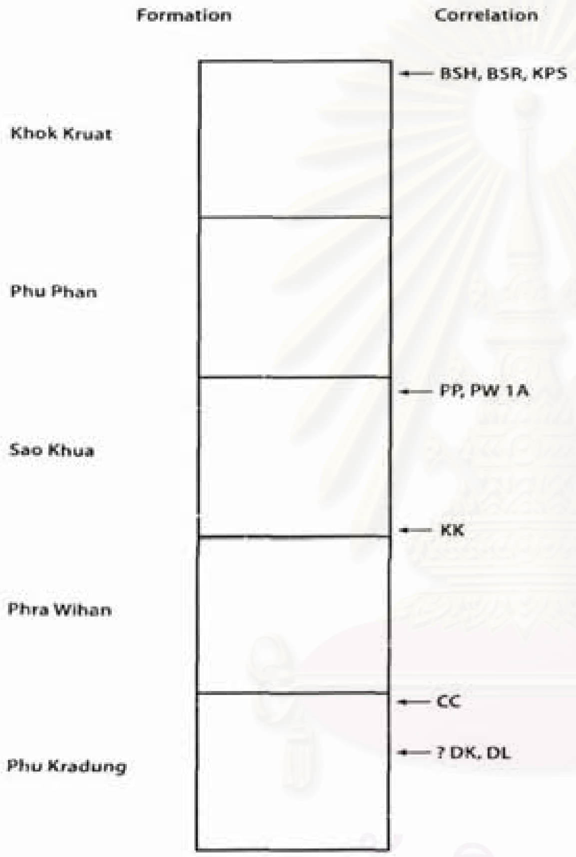


Fig. 8-4 Correlation of nine fossiliferous sites in the Khorat Plateau. Abbreviations: DK, Dan Kerng; DL, Dan Laung; CC, Chong Chat; KK, Khok Kong; PP, Phu Phok; BSH, Ban Saphan Hin; BSR, Ban Samran; KPS,

3. Environmental Deposition

Meesook (2000) reported that woods and plant remains are more abundant in the Phu Kradung Formation than in the Sao Khua and Khok Kruat Formations. The presence of dense coal and plant remains, which often required water for their growth, from the Chong Chat locality can be used to support that the palaeoclimate of the Phu

Kradung Formation is more relatively humid than the Sao Khua and Khok Kruat Formations.

The occurrence of calcretes and silcretes, which are relatively thicker and more predominant in the Sao Khua Formation than in the other formations, suggest that the palaeoclimate of the Sao Khua Formation was more semi-arid than that of the Phu Kradung Formation (Meesook, 2000). Field studies from PW 1A, Khok Kong, and Phu Phok show that the fossil records are mostly embedded in the mudstone beds, which are usually deposited under low energy currents (Selley, 1982). Moreover, some articulated skeletons, indicating no further transport and rapidly burial (Lyman, 1994), of crocodilians and dinosaurs were also found. The presences of articulated skeletons in the mudstone, which is deposited under low energy current, therefore, suggest that the sedimentary deposition of the Sao Khua Formation has taken place in swamps or lakes.

For the Khok Kruat Formation the calcretes and silcretes beds have also been recognized, but not as thick and dominant as those of the Sao Khua Formation. This means that a semi-arid climate continued through the Early Cretaceous in Thailand. Additionally, the most abundant sediments, from Ban Samran and Ban Saphan Hin, are sandstone and conglomerate, which are usually deposited under high energy currents (Lyman, 1994), not mudstone as seen in the Sao Khua Formation. Upward fining sequence in conglomerate was also observed in both localities. The occurrence of upward fining sequence indicates that the sedimentation has been taken place in river channel (Selley, 1982). On the other hand, the presence of the Khok Pha Suam fossil fragments in the mudstone fossiliferous layers can be interpreted that the sedimentation has been transported under high energy and deposited in the quiet water or low energy current.

The lithology and sedimentary structures of each locality can be used to explain the palaeoclimate of each formation as follow: The palaeoclimate of the Phu Kradung Formation was more humid than that of the Sao Khua and Khok Kruat Formations, based on the dense appearance of plain debris and fossil woods (Meesook, 2000). The climate changes, during the Late Jurassic and Early Cretaceous (Meesook, 2001), have probably triggered the increase of dry areas and the decrease of wet areas in the Khorat Plateau. For this reason, it can probably be used to explain that why the ecological niches of the long-snouted crocodilians in the Sao Khua and Khok Kruat Formations have been lately replaced by the fish-eating dinosaurs, *S. suteethorni*, which possessed well locomotory adaptation.

In addition, modern crocodilians are restricted to the tropics and subtropics with a very few warm temperate representatives (Dodd and Stanton, 1999). Thus the presence of abundant crocodilians in the fossil record of the Khorat Plateau indicates that the Indochina block was located under warm temperatures since the late Jurassic Phu Kradung Formation.

CHAPTER IX

CONCLUSIONS

Taxonomy of the Mesozoic crocodilians from the Khorat Plateau

The diversity of the Mesozoic crocodilians from the Khorat Plateau has been increased when compared with previous works. It has, so far, yielded at least six genera and nine species from three families, as shown in Table 9-1. The Phu Kradung Formation has yielded three taxa, i.e., "*Sunosuchus*" *thailandicus* (Goniopholididae), cf. *Peipehsuchus teleorhinus* (Teleosauridae), and cf. *Theriosuchus* sp. (Atoposauridae).

Crocodilian remains from the Early Cretaceous Sao Khua Formation show the highest diversity at specific level. Three genera and four species from two families were described. The first family is the Goniopholididae, which consists of "*Goniopholis*" *phuwiangensis* and *Siamosuchus phuphokensis* whereas the second family, the Atoposauridae, comprises *Theriosuchus* sp. A, and *Theriosuchus* cf. *pusillus*.

Almost all the neosuchian skulls from the youngest Khok Kruat Formation belong to crocodile from the family Goniopholididae except a specimen from Ban Saphan Hin (Nakhon Ratchasima province) belonging to *Khoratosuchus jintasakulii*, which is attributed to a family *incertae sedis*. This formation has yielded two genera and three species, i.e., *Khoratosuchus jintasakulii*, "*Goniopholis*" sp. A, and "*Goniopholis*" sp. B.

Two described taxa "*Sunosuchus*" *thailandicus* Buffetaut and Ingavat, 1980 and "*Goniopholis*" *phuwiangensis* Buffetaut and Ingavat, 1983 were considered as uncertain genera, based on insufficient diagnostic characters. Two genera of the fossil crocodilians were recognized as first records in Thailand, i.e., *Theriosuchus* (from the Phu Kradung and Sao Khua Formations) and *Peipehsuchus* (from the Phu Kradung Formation), on the basis of tooth morphologies and skeletal comparisons.

In addition, two new taxa were described in this study. *Siamosuchus phuphokensis* from the Sao Khua Formation (Sakon Nakhon province) and *Khoratosuchus jintasakulii* from the Khok Kruat Formation (Nakhon Ratchasima province) were erected as new genera and species. Additionally, three specimens, i.e., *Theriosuchus* sp. A, from the Sao Khua Formation (Khon Kaen province), as well as "*Goniopholis*" sp. A (Ubon Ratchathani) and "*Goniopholis*" sp. B (Nakhon Ratchasima province), from the Khok Kruat Formation, possess unique characters, which are sufficient to recognize these taxa as new species.

Evolution, palaeoecological and palaeobiogeographical implications

The Khorat Plateau shows a noteworthy record of the Mesozoic crocodilians. The Phu Kradung, Sao Khua, and Khok Kruat Formations illustrate the evolution of South-East Asian mesoeucrocodylians. A notable difference between the crocodilian assemblages from the Late Jurassic Phu Kradung Formation and the Early Cretaceous Sao Khua and Khok Kruat Formations has been observed. The Phu Kradung Formation has yielded both long-snouted neosuchians and broad, short-snouted *Theriosuchus*. The Sao Khua Formation has yielded only broad, short-snouted neosuchians, while the Khok

Kruat Formation has yielded broad, short-snouted and elongate, slender-snouted neosuchians

The crocodilians from the late Jurassic Phu Kradung Formation illustrate the early stage in the evolution of the Thai Atoposauridae. The discovery of a *Theriosuchus* skull indicates that the distribution of this dwarf Atoposauridae was widespread from Europe through China and Southeast Asia, not only in the European region and Inner Mongolia as previously suggested (Wu et al., 1996b; Schwarz and Salisbury, 2005). It also suggests that Europe and Southeast Asia has already been connected at that time. However, the origin of the connection between these continents is not exactly known, since the lack of deposition of sediments between the late Triassic Nam Phong and late Jurassic Phu Kradung Formations. Therefore, there is no evidence to prove the affinity between the oldest *Theriosuchus* of Europe and the Thai *Theriosuchus*. Comparisons between the Thai and European *Theriosuchus*, which shows the maximum length approximately 550 mm (Schwarz and Salisbury, 2005), suggest that the Thai *Theriosuchus* probably reached a maximum length of about 500 mm. With their small size, the diet of *Theriosuchus* was probably similar to that of all extant crocodilian juveniles, i.e., invertebrates, and possibly small vertebrates such as amphibians and some mammals (Trutnau, 1994). It seems likely that there was little overlap in diet between *Theriosuchus* and adults of larger crocodilians such as, "*Sunosuchus*" in the Phu Kradung Formation, and "*Goniopholis*" and *Siamosuchus*, in the Sao Khua Formation. Therefore, these crocodilians could have lived sympatrically within the same habitat.

The phylogenetic positions of "*Sunosuchus*" *thailandicus* and cf. *Peipehsuchus*, are still obscure, because the former lacks of the complete upper jaw, whereas the latter was described on the basis of isolated teeth. These two taxa thus cannot be used to explain the relationship of the faunas between Southeast Asia and China.

In the Early Cretaceous Sao Khua Formation, no fossil bones of long-snouted crocodilian have been found, despite the fact that numerous crocodilian material has been recovered. This is in accordance with the faunal changes, which took place in the dinosaur assemblages of Southeast Asia, at or close to the Jurassic-Cretaceous boundary (Buffetaut et al., 2001; Le Lœuff et al., 2002). The absence of long-snouted piscivorous crocodilians in the Sao Khua Formation may be caused by the palaeoclimate change from humid environment of the Late Jurassic to semi-arid environment of the Early Cretaceous (see chapter VIII). The ecological niche of long-snouted crocodilians, therefore, has been replaced by *S. suteethorni*, which is unknown before the deposition of the Sao Khua Formation. This hypothesis is supported by the resemblance of the enamel microstructures of *S. suteethorni* and the Mesozoic crocodilians (see chapter VII), indicating the similarity of feeding behavior and mechanical constraints between these animals. *S. suteethorni* also possessed a well locomotory adaptation, which is better than crocodilians. Consequently, in arid environment, this fish-eating dinosaur can certainly access the abundant areas faster than crocodilians. These reasons can be used to explain that why *S. suteethorni* had survived through the Early Cretaceous, where the environment was relatively dry condition.

On the other hand, the Sao Khua Formation has become significantly diverse in broad, short-snouted goniopholidids and atoposaurids such as, "*Goniopholis*" *phuwiangensis*, *Siamosuchus phuphokensis*, *Theriosuchus* sp. A, and *Theriosuchus* cf. *pusillus*. Although the fish-eating dinosaurs appeared in the Sao Khua Formation, it seems likely that there is no competition between *S. suteethorni* and the broad, short-snouted goniopholidids, because the undulation of the jaw margin of the broad, short-snouted goniopholidids has been adapted to hold large and strong prey such as small mammals, and juvenile of dinosaurs, more firmly between the jaws (Iordansky, 1973). It means that the diet of the broad, short-snouted goniopholidids are generally more diverse than that of the long-snouted crocodilians, which its long jaws and narrow snout has been reflected specialization for ichthyophagy (or piscivore) only (Iordansky, 1973).

S. phuphokensis is a new genus among the Goniopholididae, which occurs in the Sao Khua Formation. It can be distinguished from the other genera of Goniopholididae based on the nasal bones that take part in the narial border. This genus was separated from "*G.*" *phuwiangensis* in a recent phylogenetic analysis made by Lauprasert et al. (submitted). The newly discovered goniopholidid demonstrates the diversity of the broad, short-snouted Goniopholididae in the Sao Khua Formation of the Khorat plateau. The type specimen of *Siamosuchus* was collected from the Phu Phok locality, where *Theriosuchus* was found. This also indicates that *Siamosuchus* and *Theriosuchus* can lived sympatrically within the same habitat.

Theriosuchus is absent from the Khok Kruat Formation. The stratigraphic range of this genus is from the Late Jurassic Kimmeridgian to Early Cretaceous Barremian (Owen, 1878; Buscalioni and Sanz, 1988; Brinkmann, 1992; Wu et al., 1996b; Schwarz and Salisbury, 2005). The lack of *Theriosuchus* in the youngest formation of the Khorat Group thus reinforces the idea that the Khok Kruat Formation is not older than Aptian in age.

Many fossils of the broad, short-snouted "*Goniopholis*" have been described from the Khok Kruat Formation. They demonstrate the existence of the Thai "*Goniopholis*" forms throughout the Early Cretaceous of the Khorat Plateau. However, the preservation of these specimens is not adequate for identification at generic or specific levels. Therefore, the affinity between the Sao Khua and the Khok Kruat *Goniopholis* is, at the moment, still ambiguous.

Spinosaurid remains are still abundant in the Khok Kruat Formation, while the long-snouted crocodilian has not yet been found in this formation. Although the youngest and most advanced elongate-snouted neosuchian of Thailand, *Khoratosuchus jintasakulii*, was described, a part of its upper jaw cannot be insisted that it is a long-snouted crocodilian. *K. jintasakulii* skull bears resemblances to the Chinese crocodilian, *Rugosuchus nonganensis*. The lengths of their upper jaw are not significantly long as seen in the other long-snouted crocodilians. In addition, the mandible symphysis of *R. nonganensis* is relatively short, resembling to the other short, broad-snouted crocodilians. Therefore, it seems likely that *K. jintasakulii* is probably not a long-snouted crocodilian. However, the affinity between the Chinese and Thai elongate-snouted neosuchians is still imperfectly known, since the lack of complete material in both taxa to compare each other.

K. jintasakulii is the first crocodilian from the Aptian-Albian Khok Kruat Formation to be described from a skull. The internal choanae are relatively posterior and almost enclosed by the pterygoid. This discovery thus illustrates the evolutionary trend of the internal choanae's position of the neosuchian, which slightly moves posteriorly in advanced form. The occurrence of "*Goniopholis*" in the same assemblage as *K. jintasakulii* suggests that they shared the same resources.

Table 9–1 Checklist of the Late Jurassic to Early Cretaceous crocodilians from the Khorat Plateau. Abbreviation: Fm., Formation; Spec. No., specimen number.

Fm.	Spec. No.	Localities	material	Families	Genera	Species
Khok Kruat	NRRU-A 1803	Ban Saphan Hin Nakhon Ratchasima	part of the cranium	*Incertae sedis*	*Khoratosuchus*	*K. jintasakulii*
	NRRU-A 1791	Ban Saphan Hin Nakhon Ratchasima	part of the left dentary	Goniopholididae	"*Goniopholis*"	"*G.*" sp. B
	NRRU-A 1216	Ban Saphan Hin Nakhon Ratchasima	part of the right jugal (Mesoeucrocodulia)	?	?	?
	KPS-1	Khok Pha Suam Ubon Ratchathani	part of the left mandible	Goniopholididae	"*Goniopholis*"	"*G.*" sp. A
Sao Khua	TF-1478	Phu Wiang Khon Kaen	part of the left dentary	Goniopholididae	"*Goniopholis*"	"*G.*" *phuwiangensis*
	PWC-2/1 to 2/6	Phu Wiang Khon Kaen	incomplete skull and part of the postcranial skeleton	Atoposauridae	*Theriosuchus*	*sp.* A
	PPC-1/1 to 1/88	Phu Phok Sakon Nakhon	fragmented cranium and part of the postcranial skeleton	Goniopholididae	*Siamosuchus*	*S. phuphokensis*
	PPC-2	Phu Phok Sakon Nakhon	nearly complete rostrum and dentaries	Atoposauridae	*Theriosuchus*	*T.* cf. *pusillus*
Phu Kradung	CCC-1	Chong Chat Nong Bua Lam Phu	part of the left dentary	Atoposauridae	Cf. *Theriosuchus*	?
	TF-1370	Phu Phan Khum Nong Bua Lam Phu	nearly complete lower jaw	Goniopholididae or Pholidosauridae	"*Sunosuchus*"	"*S.*" *thailandicus*
	DKC-1	Dan Kerng Mukdahan	middle part of the left dentary	Goniopholididae or Pholidosauridae	?	?
	DLC-1	Dan Luang Mukdahan	caudodorsal part of the right surangular	Goniopholididae or Pholidosauridae	?	?
	K 7A (22); K 7A (34); K 7A (6)	Ban Khok Sanam Kalasin	3 isolated teeth	Teleosauridae	Cf. *Peipehsuchus*	Cf. *P. teleorhinus*

Recommendations and Suggestions

The knowledge about the fossil records from the Khorat Plateau is still incomplete, because its evolutionary history is constrained by numerous conditions, such as the effects of geological processes, the lack of complete material, the bad preservation of some fossils, and the unconformity in geological terms. The following suggestions are recommended:

1) The diversity of the crocodilians from the Mesozoic Khorat Plateau is increasing. This demonstrates that the Mesozoic of Thailand has a huge potential to yield fossil vertebrates, including fossil crocodilians. Therefore, further surveys and excavations should be conducted and expanded to the other parts of the Mesozoic region of Thailand such as the marine Jurassic sediments from southern (Mab Ching, Krabi province) and eastern (Ko Kut, Trad province) Thailand.

2) Because the relationships among the European (*Goniopholis*), North American (*Goniopholis* and *Eutretauranosuchus*), and Thai species ("*Goniopholis*" and "*Sunosuchus*") are still extremely obscure, accession to these specimens is certainly needed in order to understand the affinities of the European, North American, and Thai goniopholidids. Moreover, intensive excavations in the Sao Khua and Khok Kruat Formations are needed for additional complete crocodilian material from the Early Cretaceous.

3) Intensive excavations should also be carried out in the Phu Kradung Formation to look for the cranium of "*Sunosuchus*" *thailandicus*, which is a key to solve the affinity

between the Chinese-Mongolian and Southeastern Asian *Sunosuchus*, and for additional material of *Peipehsuchus*, which is one of the very few teleosaurids known from non-marine deposits.

4) Enamel microstructure of the crocodilian teeth should be studied on the material from the Phu Kradung and Khok Kruat Formations as well. In addition, all tooth morphotypes of the Mesozoic crocodilians should be studied and compared with each other and with the dinosaur teeth. These data are valuable to understand the functional constraints of the Mesozoic archosaurs teeth from Thailand.

5) Research collaboration between Thai and neighbouring countries, such as Laos, China, Cambodia, and Vietnam, are very important to the exploration of the Khorat Group vertebrate palaeontology. A close cooperation with the relevant government agencies, such as the Department of Mineral Resources, the Royal Forest Department, Tourism Authority of Thailand etc., to carry out field researches is also needed.

6) The fossil patrimony of Thailand has a high potential in world commercial trade. Several fossil assemblages were illegally excavated and destroyed by local people. Therefore, laws to protect the fossil remains are immediately needed.

7) At present, palaeontological research programmes in Thailand are almost conducted by foreign institutes of palaeontology, owing to the lack of Thai palaeontologists. It is, thus, necessary for Thailand to pay more attention to research

programmes on the fossil patrimony of Thailand. These include teaching and practicing palaeontology in the Thai universities from the Bachelor Degree and up.

Furthermore, financial support should be allocated to such activities by the Thai government with close cooperation with international institutes of palaeontology on research programmes and/ or advanced study for the Thai students.

The Department of Mineral Resources of Thailand, as the competent authority regarding palaeontological resources, should enact laws concerning enforcement of the possession and transaction of palaeontological resources.

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APPENDICES

APPENDIX I

Additional characters of the phylogenetic analysis in Chapter V.

Characters 1 and 3–100 were taken from the data matrix of Lauprasert et al. (submitted) (See Appendix III) and character 2 was modified from Sereno et al. (2001). Characters 101 and 102 were added. All characters were treated as unordered. Coding for character states: 0 (ancestral), 1, 2, and 3 (derived), "?" (unknown state).

2. (Modified from Sereno et al., 2001) Rostrum narrow and rectangular (parallel-sided) (0), or broadening gradually (subtriangular) (1), or broad and rectangular (parallel-sided) (2).

101 (Modified from Wu et al., 2001) Internal choanae bordered by maxillae only (0), or either by palatines or half palatine and half pterygoid (1), or by almost all of pterygoids (2), or by pterygoids only (3).

102. (Modified from Wu et al., 2001) Snout wider than high and shorter than remainder of skull (0), or wider than high and longer than remainder of skull (1), or very much wider than high and longer than remainder of skull (2), or much wider than high and wider than long (3), or nearly tubular and much longer than remainder of skull (4).

Distribution of the character-states for 102 characters among 31 Mesoeucrocodylia taxa and 3 outgroups considered in the analyses.

	10	20	30	40	50	60	70	80	90	100	
outgroups											
Protosuchus	0000000100	0000?10000	0000000000	0?00000000	0000000000	000?100100	1001000000	000?000000	00000000?1	000?000000	00
Hemiprotosuchus	?00??0?0??	????00000	0??00?0000	0?????0000	?0?0000000	?00??0?1??	??01?????0	????0?0?0?	00000000?1	000?0?0000	00
Orthosuchus	100?000000	1?00000000	0000000000	0000?00010	001000?0?0	00000?00?0	0000000000	000?000010	00000000?0	1000000000	00
ingroups											
Notosuchus	?12?001011	0100101000	1?010?0100	1001?00000	021000110?	?00??4?10?	100?0??1?0	0?0???????	0??0?00001	201?100000	10
Baurusuchus	0000001001	??00?01000	??010?0100	???1?1??21	021000?10?	02?114?101	10010?????	0?????????	0?1??00111	2???1000?0	11
Libycosuchus	?10?001011	??00?01000	0?010?0100	?001??00?1	021010?1??	0?0??4?001	?1000????0	0?0???????	??1??00???	20????00?0	10
Sebecus	1000?01011	0000?01010	1?011?0?00	0011010 0?1	021000?1?0	0201041001	11000????0	?00???????	0010?001?1	2001100000	11
Pelagosaurus	111?011011	0011020111	0110000010	0011000020	1110010011	1111?20001	2100001010	0000000101	000001001	1001000000	14
Teleosauridae	011?011011	0011000110	0110000010	0001000?0	1110011 0?1	1111?2?001	2100011010	000?000100	000001001	100?000000	14
Metriorhynchidae	011?011011	0011?20111	0110000010	0001000?0	1110011 0?1	1111?20011	2100011010	000?????1?	00000100?	1001000000	14
Mahajangasuchus	1?????????	?????????	?????????	?????????	?????????	????14110?	???010?111	100021 1???	111111001?	?0??000??0	??
Peirosauridae	112?111021	1?002?10?0	0101 1?0100	001101002?	02?00001??	?1110???0?	1?1???????	?????????	?????11?1?	????1000?0	12
Hsisosuchus	102??????1	1?00?10000	0101?00100	0011000020	010000 0??2	?01111?00?	1?10000?0?	????0?0000	0?00000??0	100?000000	11
Trematochampsa	112?0010?1	00??201??0	0101 1?0100	001?????21	02?0?001??	?01??4????	1?????????	100011????	111?1100?	??0?0000?0	12
Uruguaysuchus	011?0??01?	??00??1??1	???????1?1	0?11?00021	?????????	?000????0?	?1001??1??	?????????	?11??0???	111?2100?0	11
Malawisuchus	012?00?011	0100?01100	1001?011?0	0011?00000	?1??00???0	?10103100?	101?1?????	100??????1	??0??0???2	221?1100?0	11
Comahuesuchus	00??0??011	1?00?????0	10????????	0001????2?	?????????	1?0?0???0?	11100?????	?????????	??00??00??	20??0?00?0	1?
Simosuchus	1120101010	1?00?10000	11010?0100	0012?10011	?111000?0	010013110?	01000????1	000?111?00	0?20?00002	21102100?0	11
Araripesuchus	1121011021	0100201000	0001100100	0?01000011	02?000?100	000104?001	1110101110	10001?0???	0100111001	10101000?0	11
Alligatorium	112101?13?	0000?00010	00011?00?1	?10??00??	0??000???0	0?0??3?010	1?20100110	????0?0010	0000011001	20????0?00	13
Theriosuchus	112101?031	0100100010	1101110001	010100002?	0?1000??00	0101?3?010	1120100110	011?000010	0000011001	1001000000	13
Phoiidosaurus	111??11011	??11?01111	01011?0000	1001100011	12101?111?	1201?20???	2?0???11?0	??0??0???1	??0??0???0	1000000000	14
Calsoyasuchus	112?010031	0210?0???0	0001?10000	???2?200??	?????????	1000??????	?12???????	?????????	??1??????1	1??1??1110	12
Eutretauranosuchus	112??1?0?1	0010201010	01011?00?0	00020200?1	021010?1??	110003?000	1120101??0	??0?00????	000011001	1001001110	12
"Goniopholis" lucasii	112?01?031	??10?01010	01011?0000	0001?000?1	0210101 1?0	1200?3?01?	112010?1?0	?00?000?0?	000011001	1001002000	12
Sunosuchus junggarensis	112?010031	1?10?01010	0101110000	0001120021	021010?102	1200?31001	11201??11?	1000000?01	?????????	10?1??1010	12
Sunosuchus miaoi	112??????1	????010?0	00011?0000	0001?200??	0?????????	??00????0?	?????????	???00????	?10??00???	??011?1010	12
Siamosuchus phuphokensis	112001?03?	0?00?01010	0?0110000?	0011????11	00?010?1??	12????????	?12????110	1000000?00	?00???1??1	1?0?0?2??0	12
Goniopholis simus	112?011031	0010?01010	01011?0000	0011?000?1	00??1??1?0	120013100?	112???????	?????0????	1?0??11001	1?010?2?01	12
G. baryglyphaeus	112?01?031	0010101010	0101110000	0011?????1	00?010?1??	120??3?01?	112??????0	1000000?00	1?0??11??1	1?0?0?2??1	12
Khoratosuchus jintasakulii	112??1???1	00??1010?0	0101100000	0011?000??	???010?1??	?201??????	??0???????	?????????	??????1??1	1?010?0?00	22
Rugosuchus nonganensis	112?11?031	0010?01010	11011?0000	1011?00021	?2101001??	?20?02?01?	110???????	???01??10	1?0??0?100	1000010000	22
Bernissartia	112?111031	??00?01010	0?011?0000	?001??0011	02?010?1??	120??3?010	?12010?1?0	0002011000	0000011001	1001000000	22
Eusuchia	1120111031	0000201010	0101110000	0001001111	0210101101	1201021001	1110101111	1111011001	0000011001	1001000000	32

APPENDIX II

Check list of vertebrate faunas from the Mesozoic of the Khorat Plateau

The Phu Kradung Formation

Class	Subclass	Order	Suborder	Family	Taxonomy
Reptilia/ Sauropsida	Diapsida	Saurischia	Sauropoda	Euhelopodidae	Euhelopodid
			Theropoda	Therizinosauroidea	*Therizinosaur*
		Ornithischia	Thyreophora	Stegosauridae	*Stegosaur*
			Cerapoda		Ornithopod indet.
		Crocodyliformes	Mesoeucrocodylia	Goniopholididae	*Sunosuchus thailandicus*
				Atoposauridae	*Theriosuchus* sp.
		Squamata			Lizard indet.
	Anapsida	Testudines (Chelonia)			Turtle indet.
	Synapsida	Therapsida	Cynodontia	Tritylodontidae	? Tritylodontidae
Osteichthyes	Actinopterygii	Semionotiformes		Semionotidae	Lepidotes sp.
					Lepidotes buddhabutrensis
					Semionotiformes indet.
	Sarcopterygii	Dipnoi			Cf. *Ferganaeratodus*
Chondrichthyes	Elasmobranchii	Hybodontiformes		Hybodontidae	*Hybodus* sp. C
					Acrodus sp.
				Lonchidiidae	*Lonchidion* sp.

The Sao Khua Formation

Class	Subclass	Order	Suborder	Family	Taxonomy
Reptilia	Diapsida	Saurischian	Sauropoda	Euhelopodidae	reminiscent of Chinese forms such as *Euhelopus* and *Mamenchisaurus*
				Nemegtosauridae	*Phuwiangosaurus sirindhornae*
			Theropoda	Spinosuaridae	*Siamosaurus suteethomi*
					Spinosaurids
				indet.	teeth of a more usual type
				Tyrannosauridae	*Siamotyrannus isanensis*
				Ornithomimidae	Early ornithomimosaur
				Compsognathidae	Compsognathidae
				-	Tiny fossil eggs of theropod dinosaurs
		Pterosauria	Pterodactyloidea	Ornithocheiridae	Ornitjocheirid
		Crocodyliformes	Mesoeucrocodylia	Goniopholididae	*Goniopholis phuwiangensis*
					Siamosuchus phuphokensis
				Atoposauridae	*Theriosuchus* cf. *pusillus*
					Theriosuchus new sp.
	Anapsida	Testudines	Cryptodira	Trionychoidae	Adocid-like trionychoids: Freshwater
					trionychoid indet.
Osteichthyes	Actinopterygii	Amiiformes		Sinamiidae	Halecomorph (Amia and relatives)
		Pycnodontiformes		Pycnodontidae	Pycnodont indet.
Chondrichthyes	Elasmobranchii	Hybodontiformes		Hybodontidae	*Hybodus* sp.
					Hybodus sp. A
					Hybodus sp. B
				Ptychodontidae	*Heteroptychodus steinmanni*
				Lonchidiidae	*Lonchidion khoratensis*
					Parvodus sp.
					Isanodus paladeji

The Khok Kruat Formation

Class	Subclass	Order	Suborder	Family	Taxonomy
Reptilia	Diapsida	Saurischian	Sauropoda	Nemegtosauridae	*Phuwiangosaurus* and *Nemegtosaurus*
					Nemegtosaurid
			Theropoda	Spinosuaridae	middle-sized theropods; including a possible *deinonychosaur*
					Siamosaurus suteethorni
		Ornithischian	Cerapoda	Iguanodontidae	Iguanodontids
				Psittacosauridae	*Psittacosaurus sattayaraki*
		Crocodyliformes	Mesoeucrocodylia	*insertae sedis*	*Khoratosuchus jintasakulii*
				Goniopholididae	"*Goniopholis*" sp. A
					"*Goniopholis*" sp. B
	Anapsida	Testudines			?? Carettochelyid: Freshwater (unpublished)
					one other species (Family indet.)
Osteichthyes	Actinopterygii	Semionotiformes		Semionotidae	*Lepidotes*
Chondrichthyes	Elasmobranchii	Hybodontiformes		Hybodontidae	*Hybodus* sp.
				Ptychodontidae	*Heteroptychodus steinmanni*
				incertae sedis	*Thaiodus ruchae*
					New genus and species #1
					New genus and species #2
					New genus and species #3

APPENDIX III

Siamosuchus phuphokensis, a new goniopholidid from the Early Cretaceous (ante-aptian) of northeastern Thailand

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Keywords: Crocodylia, Northeastern Thailand, Early Cretaceous, phylogeny

Abstract – A new taxon of a broad-snouted goniopholidid, *Siamosuchus phuphokensis*, gen. et sp. nov., was discovered in the Sao Khua Formation (Ante-Aptian), northeastern Thailand. The specimen is described on the basis of an incomplete skeleton showing the premaxillae, maxillae, nasals, left lacrimal, frontal, left jugal, right postorbital, caudal part of the cranial table, most of the right part of the postcranial skeleton, and several heavily sculptured osteoderms. *S. phuphokensis* is distinguished from the other broad-snouted goniopholidids on the basis of the following: penetration of the nasals in the narial border; presence of a robust and high median ridge on the interorbital surface; lateral margin of the frontal forms the medial edge of the orbit; supraoccipital exhibits a wide pentagonal shape. A phylogenetic analysis using 101 characters for 29 Mesoeucrocodylia taxa and 3 outgroup taxa supports the monophyly of the family Goniopholididae. In addition, the Thai specimen forms a clade with the European *Goniopholis*. Based on our strict consensus tree, the genus *Goniopholis* should be restricted to the European *Goniopholis* only.

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Un nouveau Goniopholididés, *Siamosuchus phuphokensis,* du Crétacé inférieur (anté-Aptien) du Nord Est de la Thaïlande.

Mots-clés: Crocodylia, Thailande, Crétacé inférieur, Phylogénie

Résumé – Un nouveau taxon de crocodile Goniopholididés brévirostre, *Siamosuchus phuphokensis,* n. g., n. sp., a été découvert dans la Formation Sao Khua (anté-Aptien) du Nord Est de la Thaïlande. Le spécimen est décrit sur la base d'un squelette incomplet comprenant les prémaxillaires, maxillaires, nasaux, lacrymal gauche, frontal, jugal gauche, postorbitaire droit, partie caudale du toit cranien, la plupart du squelette postcranien droit, et plusieurs ostéodermes fortement ornementés. *S. phuphokensis* se distinguent des autres Goniopholididés brévirostres sur la base des caractères suivants: Participation des nasaux à la bordure de la narine; présence d'une ride médiane haute et robuste à la surface interorbitaire; le bord latéral du frontal forme le bord médial de l'orbite; le supraoccipital a la forme d'un large pentagone. Une analyse phylogénétique basée sur la distribution de 101 caractères chez 29 taxa de mésoeucrocodiles et trois outgroups confirme la monophylie de la famille des Goniopholididés. De plus, le spécimen thaïlandais forme un clade avec les *Goniopholis* européens. Sur la base de notre arbre de strict consensus, le genre *Goniopholis* n'inclut que les formes européennes.

Introduction

Fossils of crocodiles are common in the non-marine sediments of the Khorat Plateau (northeastern Thailand), especially in the Sao Khua Formation. Since the early 1980s, they have fossil record has been studied extensively by a joint Thai-French palaeontological program. Two genera of the family Goniopholididae have been recorded [Buffetaut and Ingavat, 1980, 1983]. In 1980, a crocodile jaw fragment from the Phu Kradung Formation (Late Jurassic to basal Cretaceous) was identified as *Sunosuchus thailandicus* [Buffetaut and

Ingavat, 1980]. Prior to this discovery, the genus *Sunosuchus* was known only from the continental Jurassic of North-Central China. Recently, its distribution has been extended to Mongolia, Kirghisia [Averianov, 2000], and northeastern Thailand. The second Thai goniopholidid, *Goniopholis phuwiangensis,* was based on a left dentary bone found in the Sao Khua Formation at Phu Wiang, Khon Kaen province in northeastern Thailand [Buffetaut and Ingavat, 1983]. Recently, the age of the Sao Khua Formation is now considered as Early Cretaceous in age [Racey *et al.,* 1996; Carter and Bristow, 2003]. In addition, the joint Thai French Palaeontological project discovered cranial and postcranial elements of a brevirostrine Mesozoic crocodile during excavations in the Sao Khua Formation at the Phu Phok locality, Sakon Nakhon Province in northeastern Thailand [Buffetaut *et al.*, 2003b]. This specimen is described in the present paper.

Currently, the family Goniopholididae consists of five valid genera: *Goniopholis* Owen, 1841; *Sunosuchus* Young, 1948; *Vectisuchus* Buffetaut and Hutt, 1980; *Eutretauranosuchus* Mook, 1967; and *Calsoyasuchus* Tykoski *et al.*, 2002. Goniopholidids have been reported from the Early Jurassic to the Late Cretaceous and are widespread throughout the northern hemisphere, from western North America to Europe (England, France, Germany, Belgium, and Portugal), and Asia (Kirghisia, Mongolia, China, and Thailand) [Buffetaut and Ingavat, 1980, 1983, 1984; Efimov, 1988; Maisch, *et al.*, 2003; Mook, 1967; Salisbury *et al.*, 1999; Schwarz, 2002; Tykoski *et al.*, 2002; Wu *et al.*, 1996]. The taxonomic status of this family, however, is still not well defined, and a revision of the North American "*Goniopholis*" and of *Sunosuchus* is required [Buffetaut and Ingavat, 1983; Schwarz, 2002; Wu *et al.*, 1996].

Abbreviations

Institutional—The Natural History Museum, London; **GZG,** Geoscience Centre of the University of Göttingen; **IPB,** Institut für Palaontologie der Universität Bonn; **IPFUB,** Institut für Palaontologie der Freien Universität Berlin; **IRSNB,** Institut Royal des Sciences Naturelles de Belgique; **SDRC,** Sahatsakhan Dinosaur Research Centre

Anatomical—bo: basioccipital, **bsph**: basisphenoid, **cap**: capitulum, **cau**: caudal, **cond occ**: occipital condyle, **cq**: cranioquadrate canal, **cr B**: quadrate crest B, **cr C**: quadrate crest C, **cr int**: interorbital crest, **cra**: cranial, **cra pro**: craniolateral process, **eu**: eustachian foramen, **For m**: foramen magnum, **For pot**: posttemporal foramen, **For sqot**: squamosootoccipital foramen, **fst**: supratemporal fenestra, **fti**: infratemporal fenestra, **hy**: hypapophysis, **j**: jugal, **l**: lacrimal, **m 1- m 18**: maxillary alveoli 1 to 18, **max**: maxilla, **mdep**: maxillary depression, **na**: nasal, **ne**: external naris, **no**: notch at the suture between premaxilla and maxilla, **Or**: orbit, **ot**: otoccipital, **p**: parietal. **pmx**: premaxilla, **pm 1- pm 5**: premaxillary alveoli 1 to 5, **prezy**: prezygapophysis, **po**: postorbital, **po bar**: postorbital bar, **postzy**: postzygapophysis, **q**: quadrate, **qj**: quadratojugal, **r**: ridge, **so**: supraoccipital, **sq**: squamosal, **tub**: tuberculum.

Geological Setting

The Sao Khua Formation, a part of the Khorat Group, is underlain by the Phra Wihan Formation and overlain by the Phu Phan Formation. It is an accumulation of non-marine red clays, siltstones, and sandstones, containing abundant vertebrate remains. On the basis of stratigraphic correlations of the various formations of the Khorat Group, mainly based on palynomorphs and vertebrate fossils, the Sao Khua Formation has been considered Ante-Aptian in age and is probably not basal Cretaceous [Buffetaut *et al.*, 2003a; Racey *et al.*, 1996]. Its exact age, however, remains difficult to determine, and more data, particularly from palynology, are needed to better assess it.

The Phu Phok fossils have been found on a slope of the Phu Phan Mountain Range in Sakon Nakhon Province, northeastern Thailand (fig. 1). The exact location of this site can be obtained on request from the authors or from the staff of the SDRC. The outcrop of this locality consists of a reddish-brown siltstone, 5 m thick, showing a clear sorting of the sediments with scattered pebbles inside. The crocodilian remains came from the lower part of this outcrop, which is mixed with calcrete nodules and nodular silcretes.

The Sao Khua Formation was deposited in a very extensive floodplain with low energy meandering rivers [Mesook, 2000; Mouret *et al.*, 1993]. This environment explains the partially articulated status of the fossil under study. Other vertebrate remains also discovered at this locality include teeth of *Siamosaurus suteethorni* and other theropods, theropod dinosaur eggs [Buffetaut *et al.*, 2003a; 2005a], a pterodactyloid pterosaur tooth [Buffetaut *et al.*, 2003b], shell fragments of 2 undescribed taxa of turtles (Claude, pers. com.), abundant scales, centra and jaws of an amiid fish (L. Cavin, pers.com.), a number of isolated teeth of indeterminate fishes, and *Heteroptychodus steinmanni* teeth [Cuny *et al.*, 2003].

(fig. 1)

Materials and Methods

The specimens described here are housed at the Sahatsakhan Dinosaur Research Center, Kalasin Province. Preparation of the fossils was difficult because the bone surfaces are somewhat delicate and were mostly enclosed in matrix. Most of the matrix was removed using a pneumatic air-pen. Specimens were then treated with a 10% formic acid solution. However, these treatments proved insufficient to completely clean the specimens. This was especially evident on the ventral surface of the rostrum. Consequently, some bone sutures cannot be observed. Several isolated parts of the upper jaw are well preserved. The cranial rostrum is preserved as three pieces including the premaxillae, external naris, nasals, maxillae, left lacrimal. Caudally, the squamosals and caudal part of the parietal are preserved in association with the occipital portion of the skull. Ventrally, the pterygoids are missing. The left jugal, right postorbital and right frontal are also preserved, but as disarticulated bones. The skull is slightly compressed dorsoventrally and extended caudolaterally on the right side. The sutures between the cranial bones are often difficult to trace. The ventral surface of the skull, the choanae, and the cranial palatal openings are not preserved. The lower jaw is not preserved. Most of the limb and girdle bones of the right side are preserved.

(fig. 2)

Systematic Palaeontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Goniopholididae Cope, 1875

Siamosuchus, gen. nov.

Type species—*Siamosuchus phuphokensis*, sp. nov.

Etymology— *Siamosuchus*, "Siam", in reference to the ancient name of Thailand, and the Greek *souchos*, derived from the Egyptian word for crocodile.

Diagnosis—As for the species, by monotypy.

Siamosuchus phuphokensis, sp. nov.

(figs. 2-6)

Holotype— PPC 1/1, cranial portion of a rostrum, including premaxillae, external nares, part of maxillae and nasals.

Type series— PPC 1/2– 88, parts of maxillae, nasals, left lacrimal, frontal; part of left postorbital; part of left jugal; part of caudal cranial table; postcranial skeleton represented by isolated vertebrae, femur, tibia-fibula, humerus, radius-ulna, pelvic girdles, and dorsal and ventral osteoderms.

Etymology— *phuphokensis*, "Phu Phok" in reference to the locality in which the holotype has been found.

Locality and Horizon— Sao Khua Formation, Early Cretaceous (Ante-Aptian), Phu Phok, Kok Prasil Sub-district, Phu Phan District, Sakon Nakhon Province.

Diagnosis— Distinguished from all other broad-snouted goniopholidids by the following combination of characters: the nasal bones take part in the narial border; the frontal exhibits a well-developed ridge along the midline; the lateral margin of the frontal forms the medial edge of the orbit; the supraoccipital exhibits a wide pentagonal shape.

(fig. 3)

Morphological Description

Skull

Form and proportions: The reconstructed skull length is about 420 mm, of which the rostral part forms about 270 mm or 64% (fig. 2A-D and 3A-C). This indicates that *Siamosuchus phuphokensis* belongs to a brevirostrine (short-snouted) crocodilian. The rostrum is flattened dorsoventrally. A regular pattern (fig. 2A and C) of moderate sculpturing is present from the caudal part of the skull to the maxillae and premaxillae. The tip of the rostrum is rounded and abruptly constricted at the suture between the premaxilla and the maxilla, which forms a strong notch in the lateral margin. Dorsally, the rostrum exhibits undulating lateral margins, showing at least three convexities and two concavities that widen gradually caudally. The maximum width of the rostrum cannot be estimated, as the caudal portion of the maxilla is lacking. The remaining part of the cranial table is nearly rectangular and terminates caudolaterally with the rounded process of the squamosal. Cranial measurements are given in Table 1.

(tabl. 1)

External naris (fig. 2A and 3B): The external naris shows a sub-circular aperture that opens dorsally on the rostrum. Its craniomedial and medial margins are formed by the premaxillae and are somewhat thickened and raised above the level of neighboring bones of the rostrum. Its caudal part is formed by the nasal bones, which extend into the naris for about three-fifth of its length.

Premaxilla (fig. 2A and B): This bone is about twice as long as wide. The length of the premaxillary bar is about one third of its width. Its cranial surface is about 25 mm high medially, which is rather higher than the nearby surfaces. The premaxillae are enlarged to form a swollen rostral tip that is wider than high. The lateral margins are convex. They show their maximum curvature at the level of the fourth premaxillary teeth and are caudally constricted. Just after the fifth premaxillary teeth, the specimen presents a deep notch on each side. The notch is 19.2 mm long. The suture between the premaxilla and the maxilla is oblique, running mediodorsally from the ventral part of the premaxilla-maxilla notch to the level of the fourth maxillary teeth. Medially, at the caudal end of the premaxillary bar, the premaxillae are concave and contact the nasals at the level of the caudal end of the external naris. At the caudal end of the external naris, the premaxillae are apparently separated from each other by the nasal bones, which are 9 mm wide. The caudodorsal process of the premaxilla is wedged between the maxilla and the nasal.

Maxilla (fig. 2A and B): The maxilla is relatively long and dorsoventrally compressed. The cranial and craniomedial surfaces of the maxilla contact the premaxilla dorsolaterally. Dorsally, the lateral margin of the maxilla forms two convex waves, with the maximum curvature at the level of the fifth and eleventh maxillary teeth. Two concavities are also visible, with the maximum indentation at the level of the first and eighth maxillary teeth. The lateral surface of the maxilla presents a typical maxillary depression. The cranial margin of the right depression is above the eleventh maxillary tooth and its caudal margin is above the fifteenth maxillary tooth. The left depression is crushed and distorted. Its shape is somewhat oblong. The surface and the internal structure of the right depression are indistinct, because it is covered by matrix and bone fragments. The medial surface of the maxilla makes contact, along most of its length, with the lateral surface of the nasal. The caudomedial part of the maxilla is broken on the right side, while it is displaced on the left side. The left maxilla shows a suture between the medial edge of the maxilla and the lateral margin of the lacrimal, which is concave. On the ventral surface, the secondary palate is incompletely preserved, only the cranial part which consists of the palatine processes of the premaxilla and a part of the maxilla is present, excepting the caudomedial portion. Identification of their sutures is difficult, because of numerous matrix filled cracks and fractures.

Nasal (fig. 2A): The cranial ends of the nasal bones are well preserved, but the caudal ends are broken. The cranial processes of the nasals wedge in between the premaxillae and their cranial tips enter the narial aperture over a length of about 21 mm. The cranial tip of the nasal bones is 2 mm wide and gradually increases its width until it reaches the level of the fourth maxillary tooth. At this point, the nasal bones are 26 mm in width and maintain this width up to their caudal extremity. Along their length, they separate the premaxillae and maxillae dorsally. The dorsal surfaces of the nasal bones meet each other medially along a simple edge-to-edge connection. In ventral view, the caudal part of the nasal cavity is visible because the maxilla is crushed inward (fig. 2B).

Lacrimal (fig. 2A): A portion of the left lacrimal is preserved over a length of approximately 54 mm. It is located at the level of the maxillary depression. The cranial and the lateral margins make contact with the maxilla mediolaterally. The medial portion is broken. The caudolateral edge contacts the jugal. The caudal margin slightly protrudes and forms the cranial margin of the orbit.

Postorbital (fig. 2E): An isolated right postorbital is preserved. Its cranial and caudal margins are missing. Medially, the curve of its caudomedial edge forms the craniolateral edge of the supratemporal fenestra. In dorsal aspect, the craniolateral corner makes the cranial table rectangular in shape. Sculpture on the dorsal surface of the postorbital continues downward to the postorbital bar, which is broken in its ventral part. Its diameter is approximately 10 mm.

Frontal (fig. 2G): A portion of the frontal that forms the caudal part of the left orbital margin is preserved. This frontal fragment is 42 mm in length and extends craniolaterally. Its cranial and caudal margins are broken away as well as the portion of the right orbital margin. It bears a robust and high median ridge (fig. 3B), which is 30 mm craniocaudally and 8 mm in maximum width. Ventrally, the bone is fragmentary and poorly preserved.

Parietal (fig. 2C): The preserved parietal fragment lacks a cranial margin. The remaining cranial portion appears at the level of the caudomedial part of the supratemporal fenestra and indicates the caudal edge of the latter. It abruptly widens at the caudal end and forms approximately one-third of the caudal margin of the cranial table. The 21 mm long suture with the squamosal is nearly straight at the middle of the caudal margin of the supratemporal fenestra. Dorsally, the surface is slightly concave and is covered by a regular pattern of sculpturing consisting of rounded pits about 2-5 mm in diameter. Caudally, the parietal margin contacts with the dorsal surface of the supraoccipital ventrally. The parietal exhibits a caudocranial curve at the middle of the caudal border. Two curves, which are smaller than the former, are formed by the parietal caudolaterally and the squamosal caudomedially. The latter curves overhang the posttemporal fenestrae.

Squamosal (fig. 2C): The squamosal is a triradiate bone. The cranial margins of these bones are destroyed. The preserved craniomedial margin forms the caudolateral border of the supratemporal fenestra. In lateral aspect, the squamosal is obviously straight and bends downward overlapping the otoccipital process caudally. It forms the roof of the recessus oticus externus. The squamosal presents a broad process caudomedially. This process contacts the lateral margin of the parietal. They form the roof of the posttemporal fenestra. Caudally, its margin is widely connected with the craniodorsal surface of the otoccipital. A caudolateral process is broken and exposes the cranioquadrate canal [Iordansky 1973; canalis quadratosquamosootoccipital in Salisbury *et al.* 1999] at the contact between the cranial surface of the otoccipital and the medial surface of the quadrate. Dorsally, the lateral margin of the squamosal is nearly straight. Sculpture on the dorsal surface of the squamosal is similar to that of the parietal. Ventrally, the caudal edge of the squamosal forms the roof of the squamosootoccipital foramen [Salisbury *et al.*, 1999].

Jugal (fig. 2F): Part of the left jugal is preserved as an isolated bone. The cranial and caudal parts of the bone are not preserved and it is thus difficult to reconstruct its actual shape. The specimen is slightly deformed. The remaining cranial portion shows the lateral wall of the orbit and the remaining caudal process indicates the cranioventral position of the infratemporal fenestra. These two openings are divided by a dorsally ascending process, which forms the lower part of the postorbital bar. This process is 25 mm in length and 10 mm in diameter and slightly displaced lateromedially. The suture between this process and the postorbital process is not preserved. In the medial view, a short dorsal process of the ectopterygoid is observed, connecting with the jugal caudodorsally. Its most caudal part is not preserved.

Quadrate (fig. 2C and D): The right quadrate is well preserved. Its cranial end extends craniomedially to the temporal fossa. The medial surface of the quadrate contacts the cranial surface of the otoccipital process and the lateral surface of the basisphenoid. The mandibular condyle is situated at the caudal margin of the quadrate and the caudolateral corner of the skull is at the same level as the foramen magnum. This condyle is weakly bent and forms a broad and robust articular surface that is 52 mm in mediolateral width. The articular surface is oriented caudoventrally. It is subdivided into two parts by an oblique furrow, running from the caudoventral to the craniodorsal extremities. There is a strong ridge on the dorsal surface of the quadrate that runs in craniomedial direction. The lateral portion of the condyle is nearly straight whereas the medial portion twists slightly downward and faces caudoventrally. The foramen aereum is not visible.

In dorsal aspect, the quadrate forms the floor of the temporal fossa with the ventral part of the squamosal and the cranial part of the otoccipital process. The cranioquadrate canal is observed along the medial edge and continues caudally on the quadrate, as a shallow sulcus. The dorsal surface of the quadrate is smooth, without sculpturing. In ventral aspect, the cranial surface presents four well developed crests (A, A´, B and C) for insertion of the tendons and aponeuroses of the mandibular adductor muscles [Iordansky, 1973].

Quadratojugal (fig. 2C): The medial portion of the quadratojugal is preserved. This fragment contacts the lateral margin of the quadrate by a simple suture, which reaches the lateral edge of the squamosal. This suture is obscured on the ventral surface. The dorsal surface of the caudolateral corner shows an ornamentation consisting of 2-3 pits.

Supraoccipital (fig. 2C and D): This bone exhibits a wide pentagonal shape. Its dorsal edge inclines craniodorsally to contact the caudal margin of the parietal. The caudolateral margin forms the ventromedial margin of the posttemporal fenestra. On the occipital surface, the supraoccipital is faintly concave near the ventral margin. Ventrally, the V-shaped margin of the supraoccipital is bordered by the dorsomedial edge of the otoccipital (fig. 3A).

Otoccipital (fig. 2C and D): Salisbury *et al.* [1999], referred to the otoccipital as included between exoccipital and opisthotic. Laterally, it forms a large paroccipital process, which is somewhat round and stout. In cranial aspect, this process contacts with the medial surface of the quadrate and thus forms the ventral wall of the cranioquadrate canal and is covered by the caudolateral process of the squamosal. Dorsally, the otoccipital forms the ventral border of the squamosootoccipital foramen laterally and of the posttemporal fenestra medially (fig. 3A). It also contacts the lateroventral margin of the supraoccipital dorsomedially. The medial edges of the otoccipital contact each other for about 11 mm along the midline of the skull and separate the supraoccipital from the dorsal margin of the foramen magnum. Below this suture, the medial margin extends laterally, forming the dorsal edge of the foramen magnum. At the lateroventral margins of the foramen magnum, there are two small wedge-shaped processes, which protrude caudally. Between these processes a distinct shallow sulcus runs into the foramen magnum. These processes and sulcus are bounded by the occipital condyle ventrally. On both sides of the occipital condyle, the suture between the otoccipital and the basioccipital runs dorsoventrally in cranial direction to the ventral margin of the otoccipital. Ventrally, the occipital contacts the dorsal edge of the basioccipital.

Three foramina are recognized on the surface of the otoccipital: the foramen caroticum posterius, the foramen vagi, and the foramen corresponding to the XIIth cranial nerve [Iordansky, 1973]. The first and second foramina are laid along the ventrolateral margin. The third is located beside the medial margin at the same level as the dorsal edge of the occipital condyle (fig. 3A).

Basioccipital (fig. 2D and 3A): The basioccipital is placed in a nearly vertical plane. It entirely forms the occipital condyle, which has a subcircular articular facet. In occipital aspect, this bone is bordered by the foramen magnum dorsally and forms a somewhat stout ridge with the otoccipital dorsolaterally. A narrow tuberosity extends along its lateral margins. The ventral part of the occipital condyle presents well-developed pendulous tubera and a medial crest for the insertion of neck muscles [Gasparini and Buffetaut, 1980]. The medial crest gradually extends laterally and reaches 20 mm in its maximum width above the eustachian foramen. This crest separates two lateral depressions. The medial eustachian foramen can be observed at the caudoventral end of the basioccipital margin. In addition, the eustachian tube is exposed on the cranial surface of the basioccipital, because the basisphenoid is not preserved. The average diameter of the eustachian tube is about 5 mm, expanding to 10 mm at the ventral opening of the foramen. On each lateral edge of the eustachian foramen (fig. 2D), two grooves are present. They are identified as the lateral eustachian foramina.

Foramen magnum (fig. 2D and 3A): The foramen magnum is ovoid. Its dorsal and lateral walls are formed by the ventromedial borders of the otoccipital that separates the foramen magnum from the supraoccipital. Ventrally, the foramen magnum is bounded by the occipital condyle.

Supratemporal fenestra (fig. 2C and 3B): The caudal edge of the supratemporal fenestrae is present. The remaining portions of the parietal and squamosal enclose it. The preserved portion of the caudal margin of the supratemporal fenestra indicates its moderate size. Its diameter is approximately 40 mm. Using the postorbital to reconstruct the shape of this fenestra indicates that it was relatively rounded.

Infratemporal fenestra (fig. 3B): The somewhat triangular shape of the infratemporal fenestra can be reconstructed from the right jugal fragment and right postorbital.

Posttemporal fenestra (fig. 2C, D and 3A): The posttemporal fenestra is shaped like an inverted triangle. Dorsally, it is bounded by the lateroventral surface of the parietal. Its ventral edge is formed by the dorsolateral margin of the supraoccipital that contacts the dorsomedial margin of the otoccipital. It appears only on the occipital surface, because it is covered by the squamosal in dorsal view.

Squamosootoccipital foramen (fig. 2C, D and 3A): This foramen is partially separated from the posttemporal fenestra by the dorsal margin of the otoccipital. It is smaller than the posttemporal fenestra. The right squamosootoccipital foramen is situated 35 mm away from the midline of the caudal skull. It is bounded by the squamosal dorsally and the otoccipital ventrally.

Dentition

Teeth: Three teeth are associated with this specimen. They are preserved *in situ*, on the left maxilla. The first is in the third maxillary alveolus, but its crown is completely broken and the remaining portion is poorly preserved. The two others are replacement tooth not fully erupted and are present in the fourth and sixth maxillary alveoli and present only their crown tips. The tooth in the fourth maxillary alveolus is rather robust and conical in shape with numerous fine ridges. The cross section of the tip of the crown is circular. It shows a strong carina in a mesiolingual position while the tooth in the sixth maxillary alveolus has been obscured by matrix.

Pattern of dentition: The ventral part of the premaxilla and maxilla are rather obscured by crushing. The dentition pattern of the rostrum, however, can be reconstructed from the alveoli (fig. 2B and 3C). Twenty-four alveoli can be counted on the right side of the rostrum. The premaxilla presents five alveoli. The tooth sockets indicate that the third and fourth premaxillary teeth are similar in size. These two are the largest premaxillary teeth (tabl. 2).

The first and the second alveoli also have a similar size, but they are smaller than the third and fourth. The smallest premaxillary alveolus is the fifth. The first and second alveoli are separated from each other by a moderate cavity, like the third and fourth alveoli. The most caudal portion of the maxilla is broken, and nineteen alveoli can be counted on this bone. Six of them on the caudal portion are eroded but parts of their labial edges remain partially intact. The alveolar outline indicates that the maxillary teeth gradually increase in size, from the first through the fifth teeth. The fourth and fifth maxillary teeth are equal in size to each other and are the largest teeth on the maxilla. At the sixth maxillary alveolus, the diameter of the alveoli starts to decrease as shown in tabl. 2.

The alveolar size is related to the curvature of the rostrum in both lateral and vertical views. In dorsal aspect, the lateral edge of the Phu Phok rostrum exhibits three convexities. The first convexity is situated at the level of the fourth premaxillary alveolus. The second convexity reaches its maximum at the level of the fifth maxillary alveolus, which suggests that the largest tooth on the maxillary was there as well. Reconstruction of the skull indicates that the third convexity, which is the largest, is recognized at the level of the eleventh maxillary alveolus as shown in fig. 3C.

(tabl. 2)

Postcranial skeleton

Vertebral column: The vertebral column is represented by 34 articulated and isolated amphicoelous vertebrae as follows:

Cervical vertebrae (fig. 4A-D): The second to ninth cervical vertebrae are preserved, although some are incomplete. The axis (fig. 4A-C) is recognized on the basis of a typically shaped centrum, articulating with a large odontoid process cranially. In cranial view, the surface of the axis is 25 mm high and 29 mm wide. Its craniocaudal length, including the odontoid process, is 49 mm. The preserved neural spine indicates that its dorsal edge is somewhat broad craniocaudally and 3 mm thick lateromedially. The prezygapophyses of the axis are missing and the postzygapophyses are obscured, because they are distorted and covered by the matrix. Ventrally, there is a median ridge expanding caudocranially (fig. 4B), disappearing before the odontoid process. In craniodorsal aspect, the odontoid reveals a lateral wing-like process (fig. 4C) on each side. The third to sixth cervical vertebrae were articulated with the axis *in situ*. Their centra are cylindrical in shape, about 23–25 mm in average width, 26–28 mm in average length and 28–29 mm in average height. The parapophyses are situated below the suture between the centrum and neural arch. All parapophyses are relatively semicircular in cross section. The diapophyses of the third and fourth cervical vertebrae are also semicircular in cross section whereas the remaining processes are elliptical in shape. The hypapophysis is clearly visible at the cranioventral margin and extends caudally to a half of the ventral length of the centrum. The seventh and eight cervical vertebrae articulate together, but their neural arches are missing. The shape of their centra are similar to the former cervical centra, except that the parapophysis is more elliptical and longer in the seventh cervical vertebra and becomes perpendicular to the previous parapophysis in the eighth. The ninth cervical vertebra (fig. 4D) has a clearly preserved neural arch and exhibits a neural canal measuring 17 mm in width and 10 mm in height. Its parapophysis is elliptical in cross section and also perpendicular to the long axis of the centrum. The prezygapophyses are short and high in shape. The orientation of their articular facets is dorsomedial while the articular facets of the postzygapophyses are ventrolateral. The section of the diapophyses is triangular in shape and its cranial margin connects with the caudal margin of the prezygapophysis. The neural spine is ventrodorsally higher than craniocaudally long.

Dorsal vertebrae (fig. 4E): The first and second dorsal vertebrae are recognized on the basis of the position of their parapophyses across the suture between the centrum and neural arch

[Wu *et al.*, 1996] and the appearance of their hypapophyses. Their general shape is similar to that of the caudal cervical vertebrae, especially the eighth cervical vertebra. The first dorsal vertebra is not well preserved, lacking the neural arch. Its parapophysis is considerably larger than that of the second dorsal vertebra, which exhibits a broad neural spine in a craniocaudal direction. Based on the absence of a hypapophysis, six of the preserved vertebrae are identified as dorsal vertebrae from position 3–10. Their interzygapophysial width (between the lateral margins of the zygapophyses) is 35 mm in average. These six dorsal vertebrae have cylindrical centra 30–40 mm in length, longer than the centra of the cervical vertebrae. The diapophyses are elliptical and dorsoventrally flattened in section. The determination of their precise position is relatively difficult, because most of them are dorsoventrally compressed and their neural arches have collapsed. Three lumbar vertebrae are recognized by having a zygapophysis width that is equal to the distance between the extremities of the pre- and postzygapophyses, this distance being about 46–50 mm. This is longer and wider than in any other cervical or dorsal vertebrae. Their broad and stout neural spines are caudocranially directed (fig. 4G).

Caudal vertebra (fig. 4H and I): Fifteen caudal vertebrae are identified by long and narrow centra. The hemal arch is not evident. The most cranial caudal vertebra shows a deep and distinct groove craniocaudally, which is absent in the cervical and dorsal vertebrae. The neural spine is broadly expanded caudocranially. The pre- to postzygapophysis length is 45-56 mm, slightly longer than in the lumbar vertebra. In contrast, however, the zygapophysis width is narrower than in the other vertebrae (1.9-2.6 mm wide). Centra of five terminal caudal vertebrae (fig. 4I) are also preserved. They present long and narrow centra about 22–33 mm long and 10–13 mm wide. The ventral surfaces of these vertebrae are strongly concave.

Rib (fig. 4F): Partial left and right cervical ribs are preserved. Both the cranial and caudal processes are destroyed. On the left rib, only the capitulum is present, whereas both tuberculum and capitulum are preserved on the right one. Unfortunately, they cannot be fitted with any preserved cervical vertebrae. The cross section of the right capitulum is somewhat circular and larger than that of the left one. This suggests that the former should be placed more caudally than the latter. In addition, the tuberculum of the right rib is elliptical, slender, and smaller than the right capitulum.

(fig. 4)

Forelimb

Humerus (fig. 5D): The right humerus bears a well-developed deltopectoral crest. The bone is 167 mm long. The proximal end is transversely elongated and slightly medially curved. Its proximal transverse width is 52 mm. The shaft is nearly circular in cross section and dorsoventrally compressed close to the distal end. The outer surface is generally similar to that of the extant *Crocodylus porosus*. There is an incision at its distal end, forming two condyles for the radius and ulna. Its distal transverse width is 48 mm.

Radius (fig. 5F): Two portions of the right radius are preserved, but they cannot be fitted together. The proximal articular surface is expanded craniocaudally, measuring 24.4 mm in width. Its proximal surface is kidney-shaped. The shaft of the radius is compressed lateromedially. The distal articular surface is 20.6 mm wide. In distal view, the condyle is slightly lateromedially bent and narrows at the facet for the carpus.

Ulna (fig. 5E): The left ulna is preserved, except for the distal end. The transversal proximal end is 39.4 mm wide. At the level of the proximal condyle, the lateral edge is relatively narrow and extends lateromedially to contact the radius at the medial margin. This ulna also possesses a concave surface at the caudolateral edge. Its shaft is craniocaudally compressed and has an oblong shape in cross section.

Pelvic girdle

Ilium (fig. 5C): The cranial, caudal, and dorsal margins of the left ilium are eroded whereas the right one is completely preserved. The dorsal blade is arched and has a thin margin. The preacetabular to postacetabular length [anatomical terminology according to Wu, *et al.*, 1996] is 103 mm, and the maximum height of the ilium is 63 mm. The preacetabular process is relatively short and knob-like. This process is projected forward at the same level as the edge of the cranial ischium facet. The postacetabular process is curved caudodorsally and possesses a large dorsoventral blade. Ventrally, the facets for the ischium are oriented ventromedially. Their length is 28 mm for the cranial facet and is 29 mm for the caudal facet. A semicircular space, which is 6 mm long, separates the facets.

Pubis (fig. 5C): The proximal portion of the right pubis is preserved. It is 26.6 mm long and 16 mm wide. Its lateral surface is slightly convex whereas its medial surface is weakly concave.

Hindlimb

Femur (fig. 5A): The right femur presents a well-developed proximal head. The shaft of this massive femur is sigmoid and 200 mm long. Its proximal end forms a transverse articular surface for the acetabulum, 51.3 mm long and 28 mm wide. In caudal view, the fourth trochanter protrudes markedly close to the proximal end. Its dorsal end is 69 mm from the proximal margin. The distal end is turned rather caudally and upward. The distal articular region is 45 mm in width. It is also divided into a medial and a lateral condyle by an incision. The medial condyle is smaller than the lateral one.

Tibia and fibula (fig. 5B): The right tibia and fibula are preserved in connection. The lengths of these bones are 149 mm and 143.3 mm respectively. The robust tibia is situated more cranially than the slender fibula. Dorsally, the proximal articular surface of the tibia is broad. Its shape is more or less pentagon, 40 mm wide and 33 mm long. The proximal condyle of the fibula is somewhat elliptical in shape. It is 22 mm in width and 11 mm in length. Their shafts are weakly curved mediolaterally. The distal end of the tibia is subtriangular in shape whereas that of the fibula is trapezoidal. The distal articular surface of the tibia is 25 mm in width and 24 mm in length whereas that of fibula measures 23 mm in width and 16 mm in length.

Metatarsal (fig. 5G): Parts of the proximal and distal ends of the right metatarsal II are present. The preserved elements indicate that the metatarsal is dorsoventrally compressed. The proximal transverse width is 28.5 mm and its length is 12.3 mm. Its proximal articular surface is broad medially whereas its lateral margin is narrow and markedly convex. The distal condyle is 17 mm in width and 13 mm in length and shows a strongly developed incision at the midline that separates the distal condyle into two articular surfaces.

(fig. 5)

Osteoderms (fig. 6A-H)

The dorsal and ventral osteoderms are ornamented with round, slightly ovoid and deep pits, having a maximum diameter usually between 2 and 5 mm on the outer surface and 1 and 2 mm in depth. Six distinct paravertebral shields are observed (fig. 6A). These osteoderms are placed along the midline of the presacral region. They are recognized by the presence of a lateral ridge, a craniolateral process, and a smooth facet cranially [Wu *et al.*, 1996]. Paravertebral shields are rectangular in shape, about 65–73 mm in average width and 30–42 mm in average length. On the cranial margin, these osteoderms possess an articular facet 6–7 mm long and a narrow depressed facet along the caudal margin of the ventral surface. These characters indicate an imbrication between the cranial and caudal margins of the dorsal osteoderms. The craniolateral processes of these specimens are almost always broken at their tip. Only two of the six paravertebral shields are well preserved. Their craniolateral processes are 14 mm and 16 mm in length respectively and are dorsoventrally flatten. Dorsally, their cranial tips are rounded and obtuse. The longitudinal depression on the ventrolateral surface fits together with the craniolateral process. Medially, they present a sutural area to contact the dorsal osteoderms on the other side whereas the lateral margins are smooth. The surface from the lateral portion to the lateral ridge curves ventrally away from the dorsal edge at an angle of approximately 35°. Ventrally, the osteoderms are covered with a reticular pattern of fine striae.

A dorsal osteoderm presents a strongly keeled ridge on its dorsal surface and the cranial articular facet is 6 mm long (fig. 6C). It is identified as one of the most cranial among the postsacral osteoderm.

Ten caudodorsal osteoderms are also recognized on the basis of the absence of a craniolateral process (fig. 6D). At the cranial margin, the smooth facet is about 4–6 mm in length, somewhat smaller than on the paravertebral osteoderms. These facets create an area of overlap with the more cranial osteoderms. Dorsally, they exhibit a lateral ridge more developed than on the paravertebral shields. The ridges run caudocranially and disappear before reaching the cranial articular facet. The shape of these osteoderms is rectangular, ranging from 59 to 65 mm in width and from 42 to 43 mm in length. The sculptured ornamentation on the dorsal surface is made of deep ovoid pits about 1–5 mm in diameter.

Two osteoderms appear to be different form the above. An osteoderm is recognized as a nuchal osteoderm on the basis of its small size, leaf-shaped outline, and strongly keeled dorsal ridge (fig. 6G). Additionally, based on comparison with *Sunosuchus junggarensis* [Wu *et al.*, 1996], another small osteoderm with a shape similar to that of the nuchal osteoderm (fig. 6H), but lacking a strong and keel-like dorsal ridge, is identified as a limb osteoderm.

Two plates, one of eight and the other of seven ventral osteoderms are affixed together by their dorsal face. These osteoderms, and two isolated ventral scutes, vary in shape (square, pentagonal, hexagonal). All of them, except one of the isolated ones, lack a smooth facet along the craniodorsal margin, but possess articular facets on all sides, characteristic of the more medial ventral osteoderms [Wu *et al.*, 1996]. A ventral osteoderm presents articular facets on two sides and lacks the smooth facet along the craniodorsal margin (fig. 6E). It is recognized as coming from the craniolateral corner of the right side of the ventral shield [Wu *et al.*, 1996, Fig.13].

(fig. 6)

Comparison and Discussion

A phylogenetic analysis was carried out, based on 101 characters, to resolve the position of the new taxon. Most of the characters (1 to 98) were taken from the data matrix of Tykoski *et al.* [2002] and one character was taken from Wu *et al.* [2001; character 99]. Two characters were added (see Appendix 1; characters 100 and 101). Some characters were modified as following: 21 characters were re-polarized, based on their distribution in outgroups, and one character was amended by adding one more state (character 97). Characters 15, 34, 42, 52, 61, and 97 were treated as ordered. The data matrix contains 29 taxa of Mesoeucrocodylia and 3 outgroup taxa, which consist of *Protosuchus*, *Hemiprotosuchus*, and *Orthosuchus*. The taxa include 27 Mesoeucrocodylia taxa listed by Tykoski *et al.* [2002]. Additionally, *Sunosuchus miaoi*, *Goniopholis simus*, *G. baryglyphaeus*, and *Siamosuchus phuphokensis* were added to this study to determine the affinities of *S. phuphokensis* among the Goniopholididae. An undescribed crocodile skull from the Khok Kruat Formation (Aptian/Albian) at Khorat, herein referred to the Khorat specimen, was also included in this analysis. Its full description will be the subject of a subsequent paper

[Lauprasert *et al.*, in prep.]. The data matrix was run using PAUP, Version 4.0b10 for 32-bit Microsoft Windows, using a random, stepwise addition, heuristic search algorithm. There are 93 parsimony-informative characters and 8 parsimony-uninformative characters.

(fig. 7)

The strict consensus tree shows that *Eutretauranosuchus delfsi*, *Calsoyasuchus valliceps*, *Sunosuchus junggarensis*, *S. miaoi*, the North American broad-snouted goniopholidid (*"Goniopholis" lucasii*), the European broad-snouted goniopholidids (*G. simus* and *G. baryglyphaeus*), and *Siamosuchus phuphokensis* belong to a monophyletic group representing the family Goniopholididae. They are unambiguously diagnosed by only one character, the "maxillary depression (97.1 to 2)", which is located dorsomedially on the lateral surface of the maxillae [Buffetaut 1982, 1986]. In addition, two equivocally diagnostic characters involve the choana divided by a septum (54.1), and the nasal that does not take part in narial border (13.1).

The appearance of the very narrow and elongate cranial palatal fenestra (99.1) or secondary choana is a unique character [Buffetaut, 1986; Witmer, 1995] for the non broad-snouted goniopholidids: *Eutretauranosuchus*, *Calsoyasuchus*, and *Sunosuchus*. In this analysis, these taxa form a clade, but it is unclear whether or not *Sunosuchus* is monophyletic, due to many missing characters. *Sunosuchus thailandicus* was described by Buffetaut and Ingavat [1980] on the basis of a nearly complete lower jaw whereas *Sunosuchus shartegensis* shows only a partial skull and jaws [Efimov, 1988]. Therefore, more material of *Sunosuchus miaoi*, *S. thailandicus*, and *S. shartegensis* is necessary to resolve the phylogenetic affinities of this genus. *Eutretauranosuchus* and *Calsoyasuchus* from North America are united unambiguously by the palatine forming palatal shelves that do not meet (34.2); long anterior process of pterygoids that contact the maxillae craniomedial to primary choanae (98.1)

[Tykoski *et al.*, 2002]; and the presence of an antorbital fenestra (99.1). These features can be used to separate them from the genus *Sunosuchus*.

Concerning North American "*Goniopholis*", "*G.*" *lucasii* shows unclear relationships with the others, although it shares two synapomorphies with *Siamosuchus phuphokensis* and the European forms as follows: maxillary depressions located at the level of the maximum width of the nasals (97.2), and a typical ridge or crest present on their interorbital surfaces (101. 1 and 3). Salisbury [1999] mentioned the possibility that all North American forms ("*G.*" *stovalli*, "*G.*" *lucasii*, "*G.*" *gilmorei*, and "*G.*" *felix*) may belong to the genus *Eutretauranosuchus*, which is not really long-snouted in shape as *Calsoyasuchus* and *Sunosuchus*, based on their palatal structure. Tykoski *et al* [2002] also recognized the retention of an antorbital fenestra in *E. delfsi* and probably also in "*G.*" *felix*, which is unknown in any other broad-snouted goniopholidids. For the above reasons, the North American forms seem clearly to be separated from the other broad-snouted goniopholidids. In addition, our phylogenetic tree also shows that the North American forms do not belong to the *Goniopholis* clade (see below). A revision of the taxonomic status of the North American broad-snouted taxa is necessary.

Siamosuchus phuphokensis and the European goniopholidids (*Goniopholis simus* and *G. baryglyphaeus*) form a clade. The Thai specimen is the sister group of the European goniopholidids. These three taxa share two synapomorphies, which distinguished them from "*G.*" *lucasii*: exposure of the cranioquadrate canal on the dorsal surface of the quadrate (42.0) [Salisbury, 1999; Schwarz, 2002], and the caudal margin of the squamosal extending caudally as a long process (33.1).

Goniopholis simus and *G. baryglyphaeus* form a clade, which shows the following combination of characters: a broadly marked U-shaped crest on their interorbital surface (101.3), and prefrontal and postorbital separating the lateral margin of the frontal from the medial edge of the orbit (100.1). Morphological observation on BMNH 41098, IPB R359, and IPFUB Gui Croc1 specimens show that their dentary symphysis end at the level of the 6th tooth. They also present a distinct angulation of the tooth row at the level of the 3rd tooth. These characters are similar to the characters of BMNH 37972, BMNH 1807, and BMNH 3220, referable to *G. crassidens*, the type specimen of *Goniopholis*. Consequently, the genus *Goniopholis* should be restricted to *G. crassidens, G. simus*, and *G. baryglyphaeus* only, which are known from the Middle Jurassic to Early Cretaceous of European [Owen, 1841; Salisbury, 1999; Schwarz, 2002].

Siamosuchus phuphokensis shows a nasal that takes part in the narial border (13.0). This character is unknown in any other goniopholidids. It also presents a more distinct median ridge than in "*G.*" *lucasii* on the interorbital surface (101.1). Comparison between *S. phuphokensis* and the European forms shows that the supraoccipital of *S. phuphokensis* exhibits a wide pentagonal shape, while in *G. baryglyphaeus* and *G. simus* it is subtrapezoidal and triangular, respectively. Considering the comparisons made above, the differences between *Siamosuchus phuphokensis* and the other goniopholids are sufficient to justify the erection of a new genus and species.

"*Goniopholis*" *phuwiangensis* is a taxon defined by Buffetaut and Ingavat [1983] on the basis of a partial left dentary from the Sao Khua Formation of northeastern Thailand. Although they come from the same formation, comparison between *Siamosuchus phuphokensis* and "*Goniopholis*" *phuwiangensis* is impossible because there are no elements in common. "*G.*" *phuwiangensis* was defined by the length of its dentary symphysis and the angulation of the tooth row. The dentary symphysis of "*G.*" *phuwiangensis* ends at the level of the 7th tooth (without the splenial symphysis) whereas the symphysis of the European *Goniopholis* is shorter, ending at the level of the 6th tooth. The dentary symphysis of *E. delfsi* ends at the same level as that of the Phuwiang specimen and at the level of the 8th tooth when the splenial symphysis is included. Moreover, "*G.*" *phuwiangensis* does not present a marked angulation of the tooth row. This character is also similar to *E. delfsi*. These comparisons and the results of our phylogenetic analysis indicate that "*G.*" *phuwiangensis* does not belong to the genus *Goniopholis* and it seems likely that "*G.*" *phuwiangensis* exhibits a dentary morphology closer to that of the North American, *Eutretauranosuchus delfsi* than to that of the European goniopholidids. However, more material is needed to clear the relationships and taxonomic status of "*G.*" *phuwiangensis*.

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Appendix 1

List of characters used in the phylogenetic analysis. Characters 1–98 were taken from the data matrix of Tykoski *et al.* (2002) and character 99 was taken from Wu *et al.* (2001). Characters 100 and 101 were added. Characters 15, 34, 42, 52, 61 and 97 were treated as ordered. Coding for character states: 0 (ancestral), 1, 2, and 3 (derived), "?" (state unknown).

1. External surface of cranial and mandibular bones smooth (0) or heavily sculptured with deep grooves and pits (1).
2. Rostrum narrow anterior to orbits, broadening abruptly at orbits (0) or broad throughout (1).
3. Rostrum higher than wide (0), or nearly tubular (1), or wider than high (2).
4. Premaxilla forms at least ventral half of internarial bar (0) or forms little, if any, of internarial bar (1).
5. Premaxilla narrow anterior to naris (0) or broad similar in width to part lateral to naris (1)
6. Dorsal part of premaxilla vertical, naris laterally oriented (0) or dorsal part of premaxilla nearly horizontal, naris dorsolaterally or dorsally oriented (1)
7. Palatal parts of premaxillae do not meet posterior to incisive foramen (0) or meet posteriorly along contact with maxillae (1)
8. Premaxilla and maxilla sutured along butt joint (0) or Premaxilla loosely overlying maxilla on face (1)
9. Premaxilla and maxilla with broad, laterally open notch between maxilla and premaxilla (0), or broad contact on face, rostrum does not narrow at contact (1), or rostrum constricted at contact with premaxilla and maxilla, forming narrow slit (2) or rostrum constricted at contact, forming broad, laterally directed concavity (3).
10. Posterior ends of maxillae do not meet on palate anterior to palatines (0) or ends do meet

(1).

11. Nasals contact lacrimal (0) or do not (1)
12. Lacrimal contacts nasal along medial edge only (0), or on medial and anterior edges (1), or along anterior edge only (2).
13. Nasal takes part in narial border (0) or does not (1).
14. Nasal contacts premaxilla (0) or does not (1).
15. Descending process of prefrontal does not contact palate (0), or contacts palate (1), or contacts palate in robust suture (2).[Ordered]
16. Postorbital medial to jugal (0), or postorbital anterior to jugal on postorbital bar, (1), or postorbital lateral to jugal (2).
17. Anterior process of jugal as broad as posterior process (0) or about twice as broad as posterior process (1).
18. Jugal transversely flattened beneath infratemporal fenestra (0) or rod-shaped beneath fenestra (1).
19. Quadratojugal extends dorsally as a broad sheet contacting most of the postorbital portion of postorbital bar (0), or narrows dorsally, contacting only a small part of postorbital (1).
20. Frontals narrow between orbits (similar in breadth to nasals) (0) or are broad, about twice nasal breadth (1).
21. Dorsal surface of frontal and parietal flat (0) or with narrow midline ridge (1).
22. Frontal extends slightly or not at all (0), or extends well into supratemporal fossa (1).
23. Supratemporal roof with dorsal flat ''skull table'' developed, with flat shelves extending laterally beyond quadrate contacts (0) or complex dorsal surface (1).
24. Postorbital bar weak, lateral surface sculptured (if skull sculptured) (0) or postorbital bar robust, unsculptured (1).
25. Postorbital bar transversely flattened, unsupported by ectopterygoid (0) or postorbital bar

columnar, supported by ectopterygoid (1).

26. Vascular opening on lateral edge of dorsal part of postorbital bar absent (0) or present (1).
27. Postorbital bar without anterolateral process (0) or with anterolateral process (1).
28. Dorsal part of postorbital with anterior and lateral edges only (0) or with anterolaterally facing edge (1).
29. Dorsal part of postorbital bar constricted, distinct from dorsal part of postorbital (0) or dorsal end of postorbital bar broadens dorsally, continuous with dorsal part of postorbital (1).
30. Bar between orbit and supratemporal fossa broad and solid, with broadly sculptured dorsal surface (0) or bar narrow, with sculpturing on anterior part only (1).
31. Postparietal (dermosupraoccipital) a distinct element (0) or not distinct (fused with parietal?) (1).
32. Posterodorsal corner of squamosal squared off, lacking extra ''lobe'' (0), or with unsculptured ''lobe'' (1).
33. Posterior edge of squamosal nearly flat (0) or posterolateral edge of squamosal extending posteriorly as a long process (1).
34. Palatines do not meet on palate below narial passage (0), or meet ventral to narial passage, forming part of secondary palate (1), or form palatal shelves that do not meet (2). [Ordered]
35. Pterygoid restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0) or quadrate ramus of pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).
36. Choana of moderate size, less than one-fourth of skull breadth (0), or choana extremely large, nearly half of skull breadth (1), or choana (secondary choana) very narrow and

elongate, more than three times longer than wide (2). [Ordered]

37. Pterygoids do not enclose choana (0) or enclose choana (1).
38. Choana situated near anterior edge of pterygoid (or anteriorly) (0) or in middle of pterygoid (1).
39. Quadrate with three or more fenestrae on dorsal and posteromedial surfaces (0), or without fenestrae (1), or with single fenestra (2).
40. Posterior edge of quadrate broad medial to tympanum, gently concave (0) or posterior edge narrow dorsal to otoccipital contact, strongly concave (1).
41. Dorsal, primary head of quadrate articulates with squamosal, otoccipital, and prootic (0) or with prootic and laterosphenoid (1).
42. Quadrate, squamosal, and otoccipital do not meet to enclose cranioquadrate passage (0), enclose cranioquadrate passage near lateral edge of skull (1), or meet broadly lateral to passage (2). [Ordered]
43. Pterygoid ramus of quadrate with deep groove along ventral edge (0) or with flat ventral edge (1).
44. Ventromedial part of quadrate contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (0), or does not contact otoccipital (1).
45. Basisphenoid exposed on ventral surface of braincase (0) or virtually excluded from ventral surface by pterygoid and basioccipital (1).
46. Basioccipital without well-developed bilateral tuberosities (0) or with large, pendulous tubera (1).
47. Cranial nerves IX–XI pass through common large foramen vagi in otoccipital (0) or cranial nerve IX passes medial to nerves X and XI in separate passage (1).
48. Otoccipital with large ventrolateral part ventral to paroccipital process (0) or without large ventrolateral part (1).

49. Mastoid antrum extends through transverse canal in supraoccipital to connect middle ear regions (0) or does not extend into supraoccipital (1).

50. Two large palpebrals present (0), or one small palpebral present in orbit (1), or one large palpebral present (2).

51. External naris divided (0) or confluent (1).

52. Antorbital fenestra about half the diameter of orbit (0), or much smaller than orbit (1), or absent (2). [Ordered]

53. Supratemporal fenestrae equal in length or much shorter than orbits (0) or much longer than orbits (1).

54. Choana confluent (0) or divided by septum (1).

55. Dentary does not extend beneath fenestra (0) or extends posteriorly under mandibular fenestra (1).

56. Retroarticular process short, robust and ventrally situated (0), or absent (1), or posterodorsally curving and elongate (2), or posteroventrally projecting and paddle-shaped (3), or posteriorly projecting from ventral part of mandible and attenuating (4).

57. Prearticular present (0) or absent (1).

58. Dorsal edge of surangular flat (0) or arched dorsally (1).

59. Mandibular fenestra present (0) or absent (1).

60. Insertion area for M. pterygoideus posterior does not extend onto lateral surface of angular (0) or extends onto lateral surface of angular (1).

61. Splenial not involved with symphysis (0), or involved slightly in symphysis (1), or involved extensively in symphysis (2). [Ordered]

62. Posterior two premaxillary teeth much longer than anterior teeth (0) or similar in size (1).

63. Maxillary teeth homodont, with lateral edge of maxilla straight (0), or teeth enlarged in middle of tooth row, with edge of maxilla extending outward at these loci (1), or teeth

enlarged and edge of maxilla curved in two waves (''festooned'') (2).

64. Anterior dentary teeth opposite premaxilla-maxilla contact no more than twice the length (0) or more than twice the length of other dentary teeth (1).

65. Dentary teeth posterior to tooth opposite premaxilla-maxilla contact homodont (0) or enlarged opposite smaller teeth in maxillary tooth row (1).

66. Anterior scapular edges more strongly concave than posterior edge (0), or symmetrical in lateral view (1).

67. Coracoid no more than half the length of scapula (0) or about equal in length to the scapula (1).

68. Anterior process of ilium similar in length to posterior process (0) or one-quarter or less the length of the posterior process (1).

69. Pubis rod-like, without expanded distal end (0) or with expanded distal end (1).

70. Neural spine on posterior cervical vertebrae as broad as those on anterior cervical vertebrae (0) or anteroposteriorly narrow, rod-like (1).

71. Cervical vertebrae without well-developed hypapophyses (0) or with well-developed hypapophyses (1).

72. Cervical vertebrae amphicoelous or amphiplatyan (0) or procoelous (1).

73. Trunk vertebrae amphicoelous or amphiplatyan (0) or procoelous (1).

74. All caudal vertebrae amphicoelous or amphiplatyan (0), or first caudal vertebra biconvex, with other caudal vertebrae procoelous (1), or all caudal vertebrae procoelous (2).

75. Dorsal osteoderms rectangular, broader than long (0), or square (1), or rounded, ovate (2).

76. Dorsal osteoderms with anterolateral process laterally on anterior edge (0) or with straight anterior edge (1).

77. Dorsal osteoderms arranged in two parallel, longitudinal rows (0) or in more than two longitudinal rows (1).

78. Tail completely surrounded by osteoderms (0) or with dorsal osteoderms only (1).

79. Osteoderms absent from ventral part of trunk (0) or present (1).

80. Osteoderms with longitudinal keels on dorsal surfaces (0) or without keels (1).

81. Surangular forms only lateral wall of glenoid fossa (0) or surangular forms approximately one-third of the glenoid fossa (1).

82. Anterior margin of femur linear (0) or anterior margin of femur bears flange for coccygeofemoralis musculature (1).

83. Teeth without carinae, or with smooth carinae (0) or teeth serrated (1).

84. Dentary smooth lateral to seventh alveolus (0) or dentary with large occlusal pit lateral to seventh alveolus (1).

85. Scapular blade no more than twice the length of the scapulocoracoid articulation (0) or scapular blade very broad and greater than twice the length of the scapulocoracoid articulation (1).

86. Dorsal edge of dentary straight (0) or dorsal edge of dentary sinusoidal, with two concave waves (1).

87. Compressed dentary (0) or transversely expanded dentary, almost as wide as high (1).

88. Lateral surface of dentary continuous, without longitudinal groove (0) or lateral surface of dentary with longitudinal groove (1).

89. Splenial thin posterior to symphysis (0) or splenial robust posterodorsal to symphysis (1).

90. Prefrontals narrow and long (0), or broad (1), or narrow and short (2).

91. Snout narrow and shorter than the remainder of the skull (0), or long relatively (1), or broad and shorter than the remainder of the skull (1).

92. Posterior cheek teeth not multicusped (0), multicusped with cusps in single row (1), or multicusped with cusps in more than one row (2).

93. Occipital condyle in posterior position (0) or posteroventral position (1).

94. Vomer exposed (0) or not exposed (1) on palate.

95. Posterior cheek teeth conical (0), or laterally compressed (1), or strongly spatulate (2).

96. Cheek teeth not constricted at base of crown (0) or constricted (1)

97. Maxillary depressions absent (0) or present caudally to the level of the maximum width of nasals (1), or present at the level of the maximum width of nasals on lateral surface of maxilla (2). [Ordered]

98. Long anterior processes of pterygoids that contact the maxillae anteromedial to primary choanae absent (0) or present (1).

99. Anterior palatal fenestra absent (0) or present (1)

100. Lateral margins of frontal form a part of medial edge of orbits (0) or do not contact medial margin of orbits (1)

101. Interorbital flat (0) or with median ridge (1) or deeply grooved ventrally (2) or with broadly marked U-shaped (semi-lunar ridge) interorbital crest (3)

Appendix II

Distribution of the character-states for 101 characters among 29 Mesoeucrocodylia taxa and 3 outgroups considered in the analyses.

	10	20	30	40	50	60	70	80	90	100	
outgroups											
Protosuchus	0000000100	0000?10000	0000000000	0?00000000	0000000000	000?100100	1001000000	000?000000	00000000?1	000?000000	0
Hemiprotosuchus	?00??0?0??	?????00000	0??00?0000	0?????0000	?0?0000000	?00??0?1??	??01?????0	????0?0?0?	00000000?1	000?0?0000	0
Orthosuchus	100?000000	1?00000000	0000000000	0000?00010	001000?0?0	000?0?00?0	0000000000	000?000010	00000000?0	1000000000	0
ingroups											
Notosuchus	?12?001011	0100101000	1?010?0100	1001?00000	021000110?	?00??4?10?	100?0??1?0	0?0???????	0??0?00001	201?100010	0
Baurusuchus	0000001001	??00?01000	??010?0100	???1?1??21	021000?10?	02?014?101	10010?????	0?????????	0?1??00111	2???1000?0	0
Libycosuchus	?10?001011	??00?01000	0?010?0100	?001??00?1	021010?1??	0?0??4?001	?1000????0	0?0???????	??1??00???	20????00?0	0
Sebecus	1000?01011	0000?01010	1?011?0?00	00110100?1	021000?1?0	0200041001	11000????0	?00???????	0010?001?1	2001100000	0
Araripesuchus	1121011021	0100201000	0001100100	0?01000011	02?000?100	000004?001	1110101110	10001?0???	0100111001	10101000?0	0
Alligatorium	112101?13?	0000?00010	00011?00?1	?10???00??	0??000???0	0?0??3?010	1?20100110	????0?0010	0000011001	20????0?00	0
Theriosuchus	112101?031	0100100010	1101110001	010100002?	0?1000??00	0100?3?010	1120100110	011?000010	0000011001	1001000000	0
Pelagosaurus	111?011011	0011020111	0110000010	0011000020	1110010011	1110?20001	2100001010	0000000101	0000001001	1001000000	0
Teleosauridae	011?011011	0011000110	0110000010	00010000?0	11100110?1	1110?2?001	2100011010	000?000100	0000001001	100?000000	0
Metriorhynchidae	011?011011	0011?20111	0110000010	00010000?0	11100110?1	1110?20011	2100011010	000?????1?	000000100?	1001000000	0
Eutretauranosuchus	112??1?0?1	0010201010	01011?00?0	00020200?1	021010?1??	110103?000	1120101??0	??0?00????	0000011001	1001001110	0
"Goniopholis" lucasii	112?01?031	??10?01010	01011?0000	0001?000?1	02101011?0	1201?3?01?	112010?1?0	?00?000?0?	0000011001	1001002000	1
Bernissartia	112?111031	??00?01010	0?011?0000	?001??0011	02?010?1??	120??3?010	?12010?1?0	0002011000	0000011001	1001000000	0
Crocodylia	1120111031	0000201010	0101110000	0001001111	0210101101	1200021001	1110101111	1111011001	0000011001	1001000000	0
Mahajangasuchus	1?????????	??????????	??????????	??????????	??????????	???14110?	???010?111	1000211???	111111001?	?0??000??0	0
Peirosauridae	112?111021	1?002?10?0	01011?0100	001101002?	02?00001??	?1100???0?	1?1???????	??????????	?????11?1?	????1000?0	0
Hsisosuchus	100??????1	1?00?10000	0101?00100	0011000020	0100000??2	?01011?00?	1?10000?0?	????0?0000	0?00000??0	100?000000	0
Trematochampsa	112?0010?1	00??201??0	01011?0100	001?????21	02?0?001??	?01??4????	1?????????	100011????	1111?1100?	??0?0000?0	0
Uruguaysuchus	011?0??01?	??00??1??1	???????1?1	0?11?00021	??????????	?001????0?	?1001??1??	??????????	?11??0????	111?2100?0	0
Malawisuchus	010?00?011	0100?01100	1001?011?0	0011?00000	?1??00???0	?10003100?	101?1?????	100??????1	??0??0???2	221?1100?0	0
Comahuesuchus	00??0??011	1?00?????0	10????????	0001????2?	??????????	1?0?0???0?	11100?????	??????????	??00??00??	20??0?00?0	0
Simosuchus	1120101010	1?00?10000	11010?0100	0012?10011	?1110010?0	010113110?	01000????1	000?111?00	0?20?00002	21102100?0	0
Sunosuchus junggarensis	112?010031	1?10?01010	0101110000	0001120021	021010?102	1201?31001	11201??11?	1000000?01	??????????	10?1??1010	1
Sunosuchus miaoi	11???????1	?????010?0	00011?0000	0001?200??	0?????????	??01????0?	??????????	????00????	?10??00???	??011?1010	0
Calsoyasuchus	112?010031	0210?0???0	0001?10000	???2?200??	??????????	1001??????	?12???????	??????????	??1??????1	1??1??1110	2
Siamosuchus phuphokensis	112001?03?	0?00?01010	0?0110000?	0011????11	00?010?1??	12????????	?12????110	1000000?00	?00???1??1	1?0?0?2??0	1
Goniopholis simus	112?011031	0010?01010	01011?0000	0011?000?1	00??1??1?0	120113100?	112???????	?????0????	1?0??11001	1?010?2?01	3
G. baryglyphaeus	112?01?031	0010101010	0101110000	0011?????1	00?010?1??	120??3?01?	112??????0	1000000?00	1?0??11??1	1?0?0?2??1	3
Khorat specimen	112??????1	00??1010?0	0101100000	0011?000??	????10?1??	?200??????	??0???????	??????????	??????1??1	1?010?0?00	0

Figure captions

Légende des figures

Fig. 1: Geographic position of the Phu Phan locality, Sakon Nakhon Province, Thailand.

Fig. 1: Situation géographique de la localité de Phu Phan, Province de Sakon Nakhon, Thaïlande.

Fig. 2: Skull of *Siamosuchus phuphokensis*, gen. et sp. nov., Partial rostrum (PPC 1–1 [holotype], PPC 1–2 and 1–3) in A: dorsal view, and B: palatal view. Caudal part of the cranial table (PPC 1–8) in C: dorsal view, and D: occipital view. E: right postorbital (PPC 1–6) in lateral view. F: left jugal (PPC 1–5) in lateral view. G: incomplete frontal (PPC 1–4) in dorsal view. Scale bar equals 5 cm.

Fig. 2: Crâne de *Siamosuchus phuphokensis*, n. gen. et n. sp., Rostre partiel (PPC 1-1 [holotype], PPC 1-2 et 1-3) en A: vue dorsale, et B: vue ventrale. Partie caudale du toit cranien (PPC 1-8) en C: vue dorsale, et D: vue occipitale. E: postorbitaire droit (PPC 1-6) en vue latérale. F: Jugal gauche (PPC 1-5) en vue latérale. G: frontal incomplet (PPC 1-4) en vue dorsale. Barres d'échelles: 5 cm.

Fig. 3: A reconstruction of the skull of *Siamosuchus phuphokensis*, gen. et sp. nov., A: occipital view, B: dorsal view, and C: palatal view. Scale bar equals 5 cm.

Fig. 3: Reconstitution du crâne de *Siamosuchus phuphokensis*, n. gen. et n. sp. en A: vue occipitale, B: vue dorsale, et C: vue ventrale. Barres d'échelle: 5 cm.

Fig. 4: Post cranial skeleton of *Siamosuchus phuphokensis*, gen. et sp. nov., Axis to 6th cervical vertebra (PPC 1–18) in A: lateral view, B: ventral view, and C: cranial view showing the odontoid process. D: 9th cervical (PPC1–21) vertebra in cranial view. E: 2nd dorsal

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vertebra (PPC 1–23) in cranial view. F: cervical ribs (PPC 1–41 and 1–42) in lateral view. G: lumbar vertebrae (PPC 1–25 and 1–26) in dorsal view. H: cranial caudal vertebrae (PPC 1–31, 1–33, and 1–34) in lateral view. I: distal caudal vertebrae (PPC 1–36 to 1–40) in lateral view. Scale bar equals 5 cm in A–B and D–I; 1 cm in C.

Fig. 4: Squelette postcranien de *Siamosuchus phuphokensis,* n. gen. et n. sp., Série vertébrale de l'axis jusqu'à la sixième vertèbre cervicale (PPC 1-18) en A: vue latérale, B: vue ventrale, et C: vue craniale, montrant le processus odontoïde. D: Neuvième vertèbre cervicale (PPC 1-21) en vue craniale. E: Deuxième vertèbre dorsale (PPC1-23) en vue craniale. F: Côtes cervicales (PPC 1-41 et 1-42) en vue latérale. G: Vertèbres lombaires (PPC 1-25 et 1-26) en vue dorsale. H: Vertèbres caudales craniales (PPC 1-31, 1-33 et 1-34) en vue latérale. I: Vertèbres caudales distales (PPC1-36 à 1-40) en vue latérale. Barres d'échelle: A-B et D-I: 5 cm, C: 1 cm.

Fig. 5: Fore and hind limbs of *Siamosuchus phuphokensis*, gen. et sp. nov.; A: right femur (PPC 1–9) in cranial view. B: right tibia and fibula (PPC 1–11) in cranial view. C: right ischium and ilium (PPC 1–12) and a partial pubis (PCC 1–19) in lateral view. D: right humerus (PPC 1–10) in ventral view. E: left ulna (PPC 1–14) in caudal view. F: part of the right radius (PPC 1–16) in lateral view. G: part of a right metatarsal (PPC 1–17) in dorsal view. Scale bar equals 5 cm.

Fig.5: *Siamosuchus phuphokensis,* n. g. et n. sp.; A: Fémur droit (PPC 1-9) en vue craniale. B: Tibia et fibula droit (PPC 1-11) en vue craniale. C: Ischion et ilion droit (PPC 1-12) ainsi qu'une partie du pubis (PPC 1-19) en vue latérale. D: Humérus droit (PPC-10) en vue ventrale. E: Ulna gauche (PPC 1-14) en vue caudale. F: Radius droit incomplet (PPC 1-16) en vue latérale. G: Métatarse droit incomplet (PPC 1-17) en vue dorsale. Toutes les barres d'échelles: 5 cm.

Fig. 6: Dorsal and ventral osteoderms of *Siamosuchus phuphokensis*, gen. et sp. nov.; A: paravertebral shields (PPC 1–48 to 1–51) in dorsal view. B: ventral osteoderms from the middle region (PPC 1–62) in ventral view. C: the most cranial postsacral osteoderm (PPC 1–54) in dorsal view. D: dorsocaudal osteoderms (PPC1–55 and 1–56) in dorsal view. E: craniolateral corner of the right side of the ventral armour (PPC 1–64) in ventral view. F: a hexagonal ventral osteoderm (PPC 1–63) in ventral view. G: an osteoderm of the neck region (PPC 1–65) in dorsal view. H: a limb osteoderm (PPC 1–66) in dorsal view. Scale bar equals 5 cm in A–F; 1 cm in G–H.

Fig. 6: Ostéodermes de *Siamosuchus phuphokensis* n. g. et n. sp.; A: Ostéodermes paravertébraux dorsaux (PPC 1-48 à 1-51) en vue dorsale. B: ostéodermes ventraux (PPC 1-62) de la partie centrale du ventre en vue ventrale. C: Premier ostéoderme postsacral (PPC 1-54) en vue dorsale. D: Ostéodermes dorso-caudaux (PPC 1-55 à 1-56) en vue dorsale. E: Coin craniolatéral de la partie droite du plastron ventral (PPC 1-64) en vue ventrale. F: Ostéoderme ventral hexagonal (PPC 1-63) en vue ventrale. G: Ostéoderme du cou (PPC 1-65) en vue dorsale. H: Ostéoderme des membres (PPC 1-66) en vue dorsale. Barres d'échelle: A-F: 5 cm, G-H: 1 cm.

Fig. 7: Strict consensus tree of 30 equally most parsimonious trees (length = 286 steps, consistency index (CI) = 0.447, and retention index (RI) = 0.643) derived from the analysis of 101 characters in 29 taxa of Mesoeucrocodylia and 3 outgroup taxa, which consist of *Protosuchus*, *Hemiprotosuchus* and *Orthosuchus*.

Fig. 7: Arbre de strict consensus des 30 arbres les plus parcimonieux obtenus (longueur: 286 pas, index de consistence = 0,447, Index de retention = 0,643) par l'analyse de 101 caractères au sein de 29 taxa de mésoeucrocodiles et de 3 outgroups (*Protosuchus, Hemiprotosuchus* et *Orthosuchus*).

Table captures

Légende des tableaux

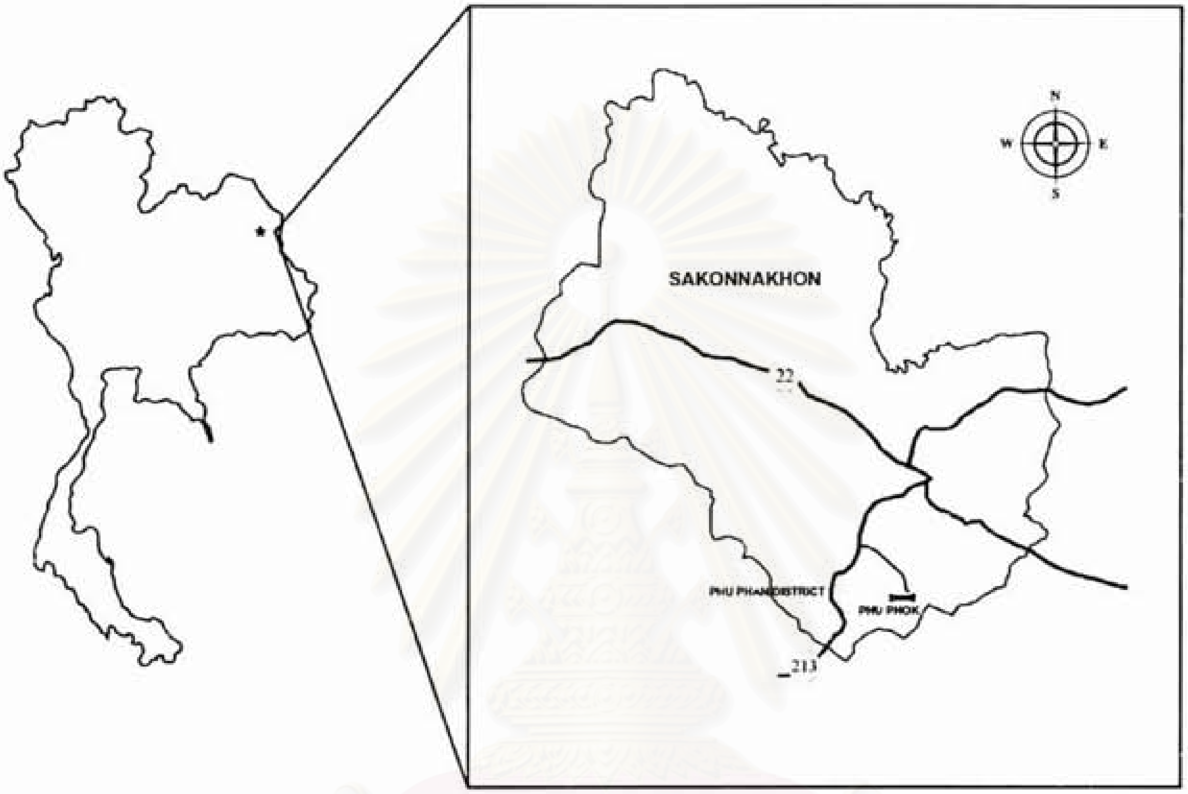
Table 1: Measurement of the skull of *Siamosuchus phuphokensis* gen. et sp. nov.

Tableau 1: dimensions du crane de *Siamosuchus phuphokensis* n. g. et n. sp.

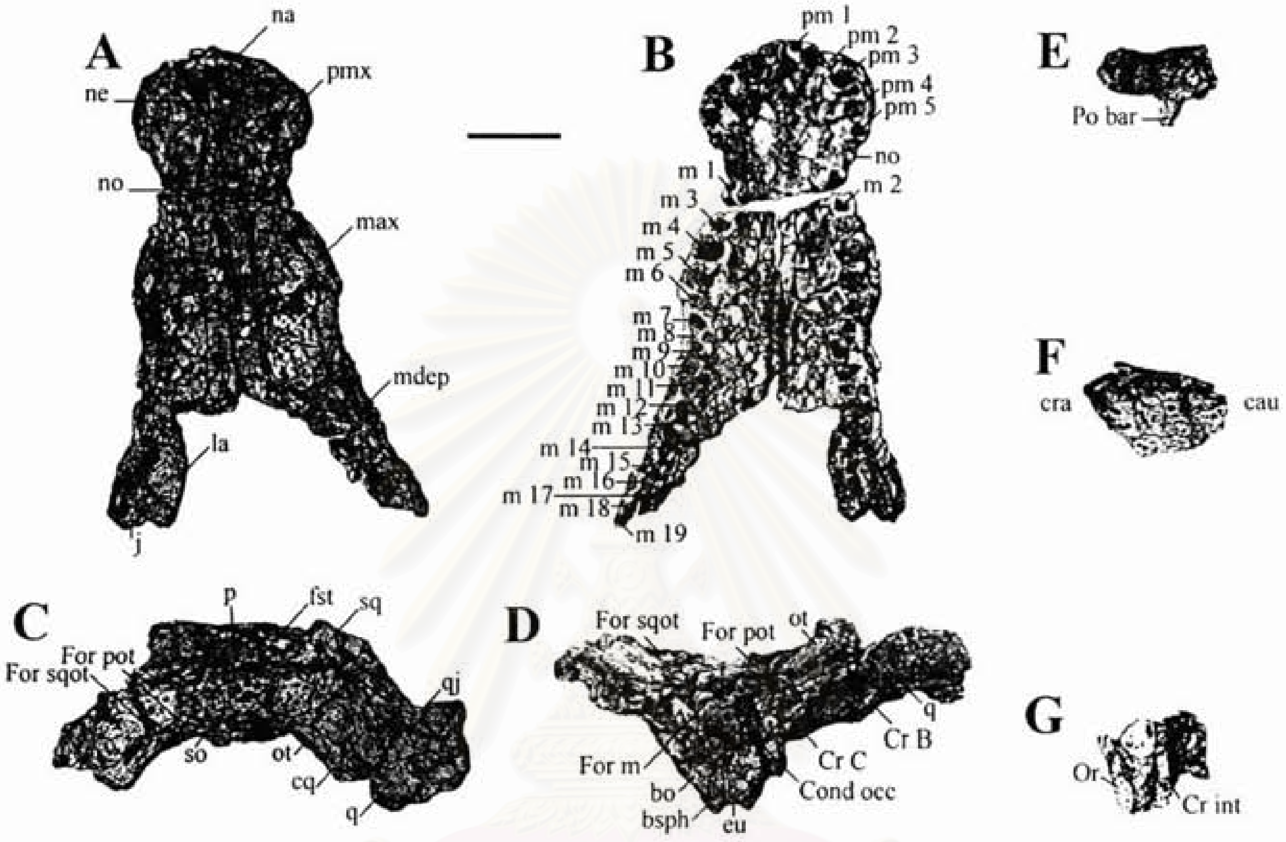
Table 2: Rostral alveoli measurements of *Siamosuchus phuphokensis* gen. et sp. nov.

Tableau 2: Dimensions des alvéoles du rostre de *Siamosuchus phuphokensis* n. g. et n. sp.

Figure–1



Figure–2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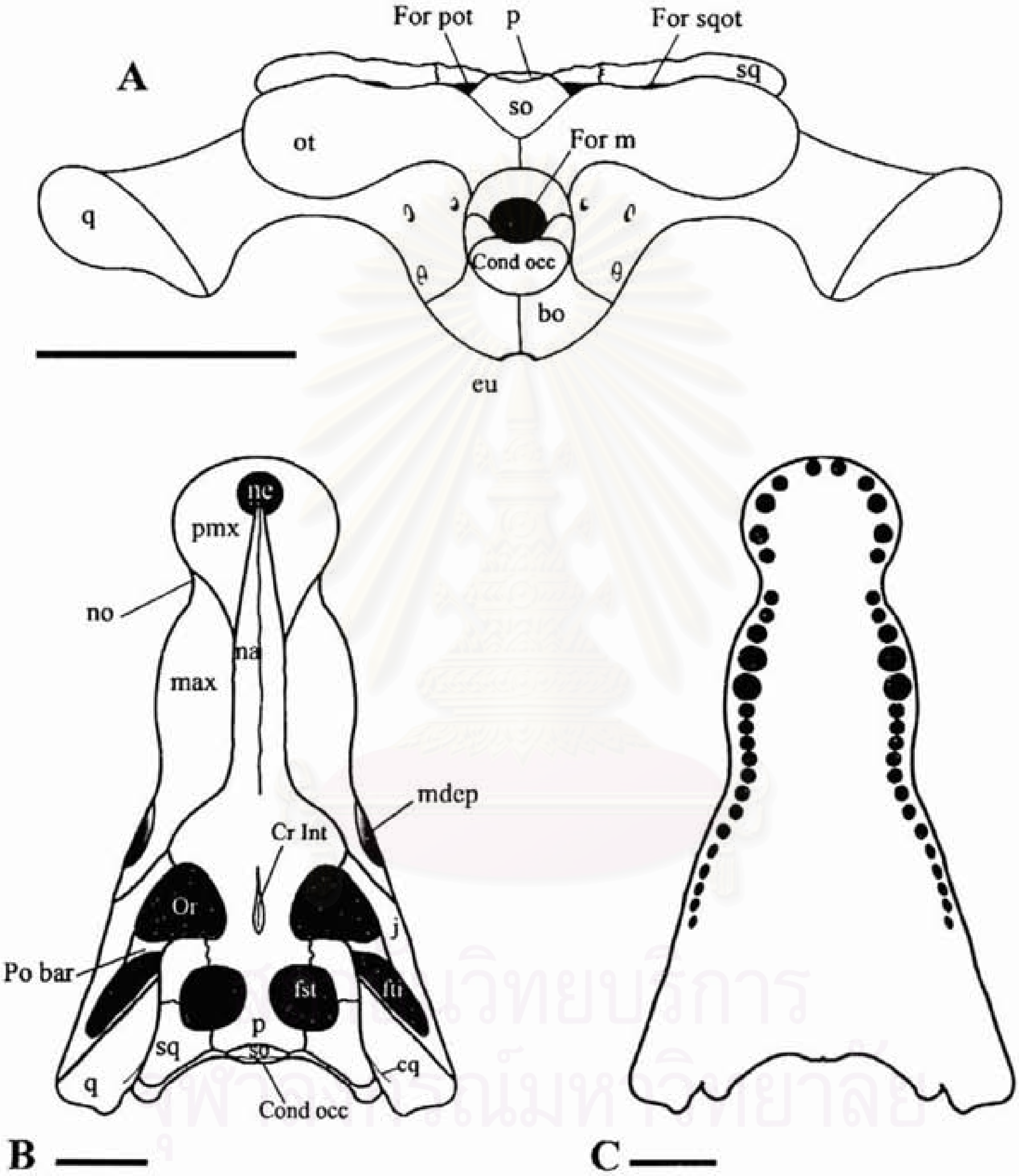
Figure–3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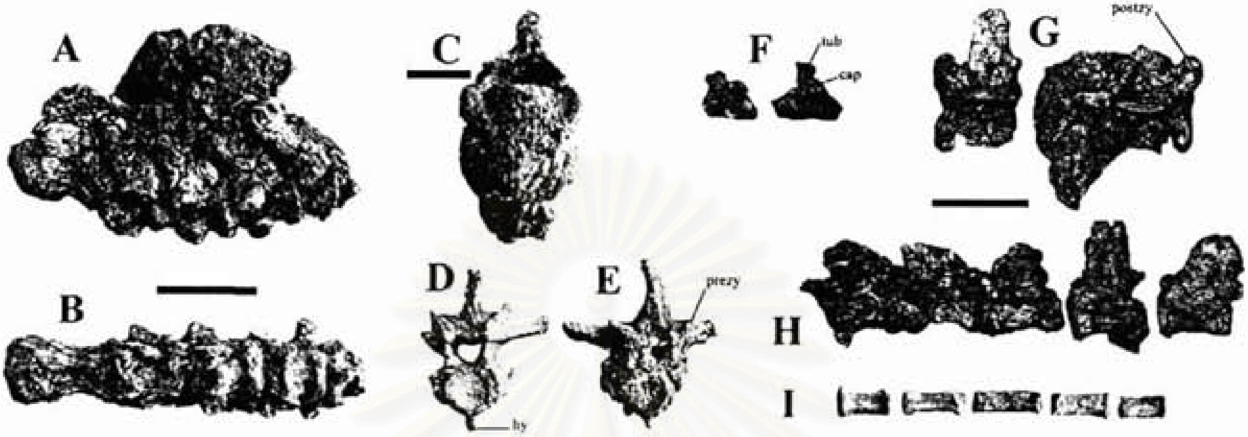
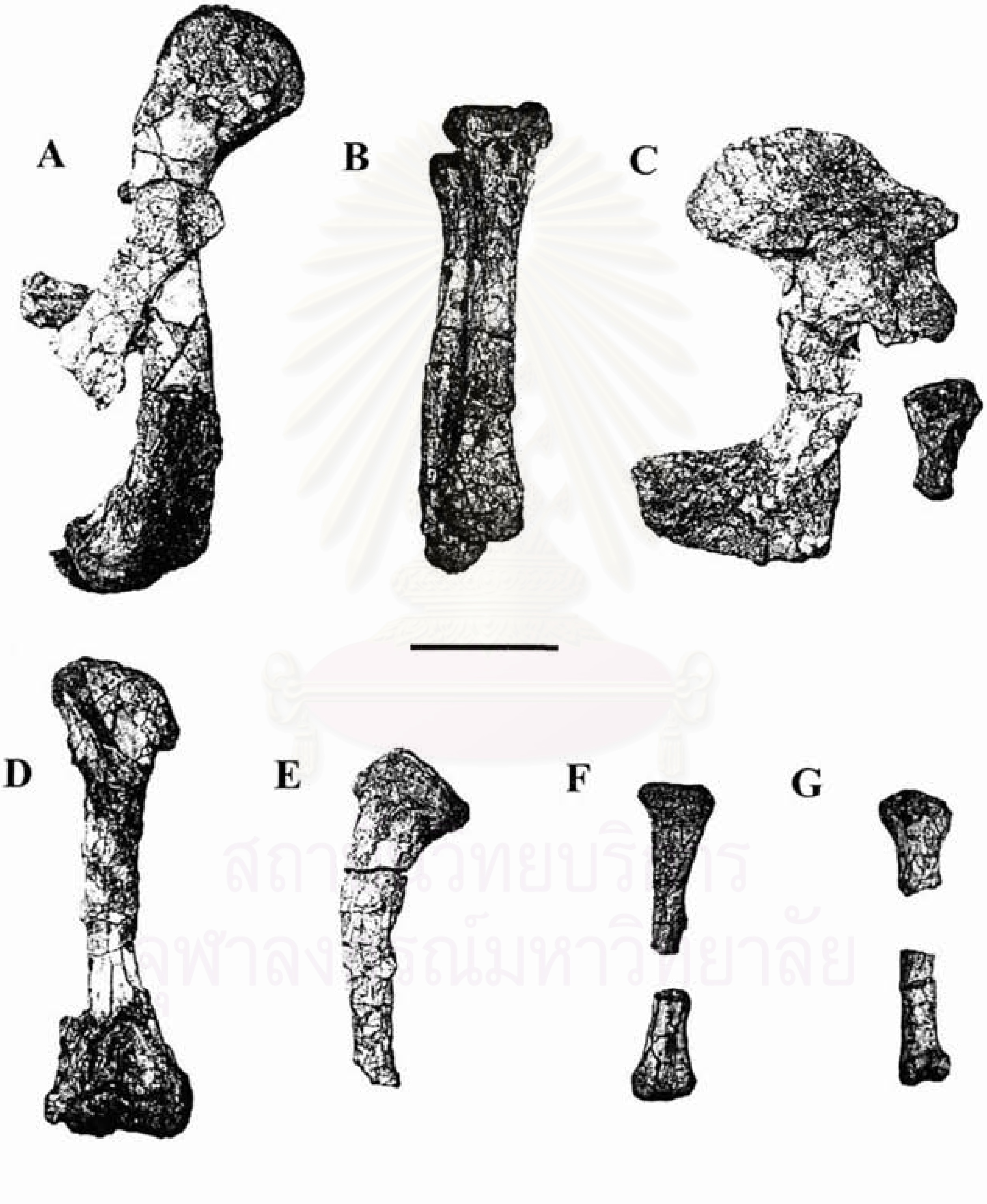
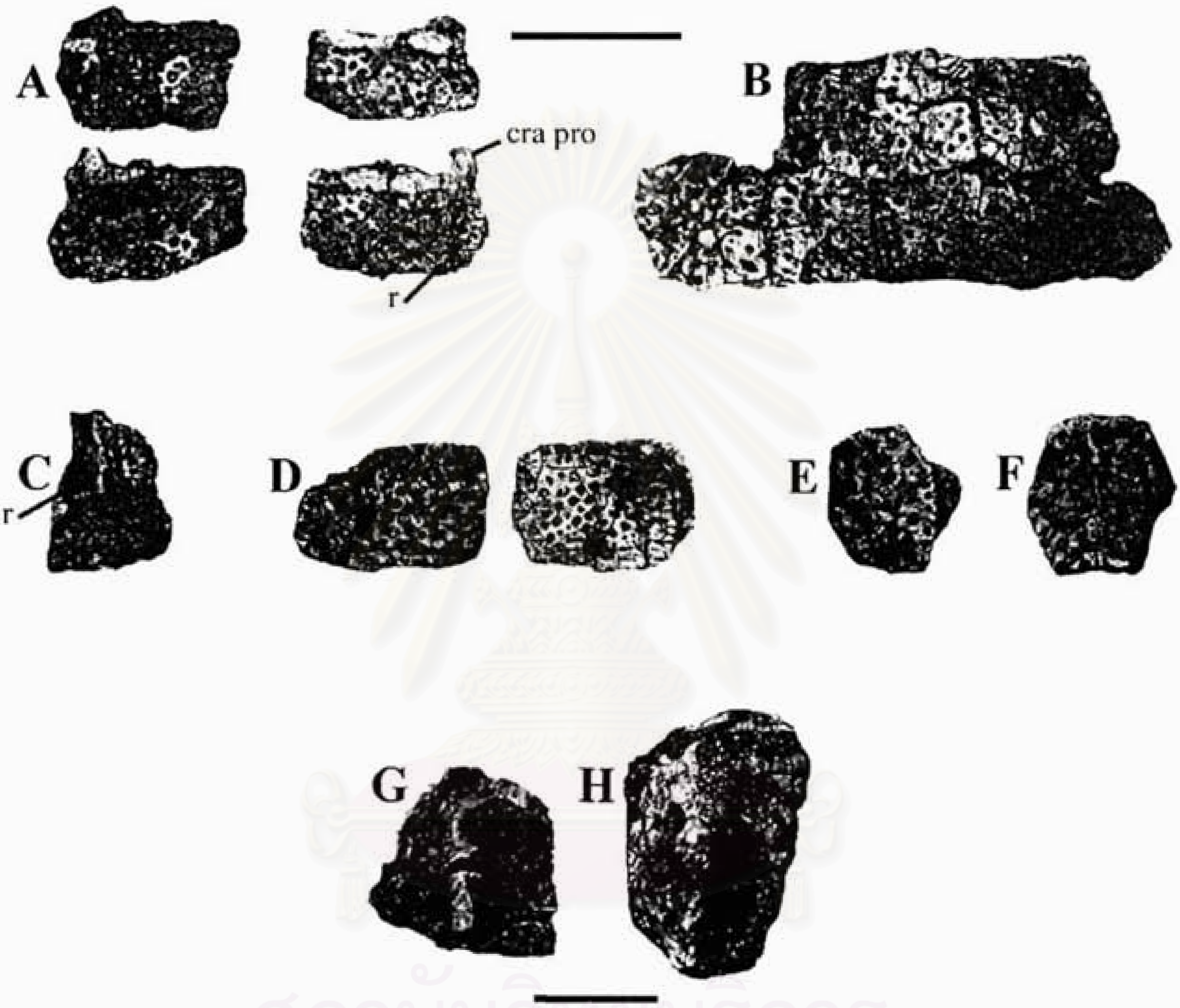
Figure–4



Figure–5



Figure–6



Figure–7


Goniopholididae
Protosuchus
Hemiprotosuchus
Teleosauridae
Pelagosaurus
Metriorhynchidae
Libycosuchus
Baurusuchus
Sebecus
Notosuchus
Malawisuchus
Uruguaysuchus
Simosuchus
Araripesuchus
Trematochampsa
Mahajangasuchus
Peirosauridae
Khorat specimen
Alligatorium
Theriosuchus
Eutretauranosuchus
Calsoyasuchus
Sunosuchus junggarensis
Sunosuchus miaoi
"Goniopholis" lucasii
Siamosuchus phuphokensis
Goniopholis simus
Goniopholis baryglyphaeus
Bernissartia
Crocodylia
Hsisosuchus
Comahuesuchus

Table–1

Skull	Measurement (mm)
Skull length, tip of rostrum to caudal margin of the occipital condyle (reconstructed)	420
Length of rostral part of skull, from tip of rostrum to cranial tip of orbit	270
Maximum width of cranial table, at caudal margin of squamosal	118.6
Width of external naris	34
Length of external naris	29
Length of cranial end of nasal bones, where enter in external naris	21
Length of nasal bones, as preserved	160.5
Length of premaxilla bar	18.5
Maximum width of left premaxilla	49
Length of left premaxilla	106
Width across premaxilla-maxilla notch	63.6
Length of right premaxilla-maxilla notch	19.2
Height of right maxillar depression	16
Length of right maxillar depression	39.6
Length of caudal part of cranial table, as preserved	60.5
Width of right supratemporal fenestra (reconstructed)	33
Maximum width of right squamosal, as preserved	40
Maximum width of parietal	41
Height of occipital surface, supraoccipital to basioccipital	76
Width of occipital surface, at otoccipital process	128
Height of occipital surface, supraoccipital to ventral of occipital condyle	47
Height of occipital condyle	18
Width of occipital condyle	21
Height of foramen magnum	15.5
Width of foramen magnum	18

Table–2

	Right Premaxilla					Right Maxilla																		
No.	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
mm	7	7	11	11	6	7	9	10	13.8	13.8	8.5	8	8	8	8	7	7	7	7	7	7	6	6	5

BIOGRAPHY

Mr. Komsorn Lauprasert was born on August 30th, 1973 in Bangkok. He graduated his Bachelor's degree of science in Fisheries (Aquaculture) in 1994 from the Faculty of Fisheries, Kasetsart University. He continued his graduated study for Master's degree of science in Zoology at the Department of Biology, Faculty of Science, Chulalongkorn University in 1996. He was awarded a year scholarship by the University Development Committee (UDC), Ministry of University Affairs in 1999. After that he was awarded the scholarship by the Royal Golden Jubilee Ph. D. Program of the Thailand Research Fund for his Ph. D. study in Biological Sciences Program, Faculty of Science, Chulalongkorn University since 2002. At the present, he works as a lecturer at the Department of Biology, Faculty of Science, Mahasarakham University, Thailand.