ORIGIN AND CHANGES IN CONTINENTAL TURTLE DIVERSITY FROM THE MIOCENE TO HOLOCENE IN THAILAND

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A Dissertation Submitted in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy Program in Palaeontology
Mahasarakham University
September 2013

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ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to all the people who walked with me during a long journey of my Ph.D. It would not have been possible without the kind support and help of many people and organizations. First and foremost, I am deeply grateful to my nice advisors, Asst. Prof. Dr. Komsorn Lauprasert for his advice, encouraged and all supports; and Assoc. Prof. Dr. Julien Claude for his inspired, valuable guidance, and fully supported. My deepest gratitude goes also for to Dr. Haiyan Tong who encouraged me, help me for visiting collection in China and was patient to help and correct my work. She is completing the group who was advising me. I would like to show my greatest appreciation to Dr. Varavudh Suteethorn for his tremendous support, help and also for giving me many chances to see paleontological world. I sincerely thank to Dr. Jeremy Martin for helping at the preparation and for improving my manuscripts, Dr. Suravech Suteethorn, Dr. Jean Le Loeuff, Dr. Eric Buffetaut, Paladej Srisuk, Dr. Arnaud Filoux for their useful suggestions and help.

I am particularly grateful to my thesis committee, Assoc. Prof. Kumthorn Thirakhupt, Dr. Jantima Piyapong, Dr. Suravech Suteethorn and Asst. Prof. Dr. Mongkol Udchachon for their useful suggestion and guidance. I sincerely thank to Dr. Pratueng Jintasakul, Dr. Chavalit Vittayanon, Dr. Benjavun Rattanasathein, Prof. Dr. Hideo Nakaya, Paladej Srisuk, Kannika Pramjai, Dr. Prasit Auetrakulvit and Praon Silapanth for their kindness to allow me studying turtle materials. I am grateful to Assoc. Prof. Kumthorn Thirakhupt at Chulalongkorn University, Fang Zheng, Lu Li at Institute of Vertebrate Paleontology and Paleoanthropology, Shengquan Li, Yueying Chen, Yuezhao Wang, Jianping Jiang at Chengdu Institute of Biology, Prof. Dr. Ren Hirayama at Waseda University, Dr. Akio Takahashi at Okayama University of Science, Prof. Dr. Hideo Nakaya at Kagawa University and Dr. Yuichiro Yasukawa at University of the Ryukyus, Dr. Gunther Köhler, Dr. Rainer Brocke at Senckenberg Museum, Frankfurt and Dr. Walter Joyce at Tübingen University for their kindness and providing comparative materials. I would like to acknowledge the help of Prof. Dr.Ren Hirayama for his support, providing accommodation during my stay in Japan and comparative materials and literatures. I would like to thank Teppei Sonoda for sharing the turtle literatures, discussion and his help. I would like to gratefully acknowledge the help of Dr. Stephan F.K. Schaal for providing useful information for visiting turtle collections in Senckenberg Museum, Frankfurt and also his encouragement. Natasha Vitek kindly sent me several pictures of trionychid for my work and I greatly appreciated her help.

I would also like to convey thanks to Palaeontological Research and Education Centre, Faculty of Science, Mahasarakham University, Sirindhorn Museum, Northeastern Research Institute of Petrified Wood and Mineral Resources, Chiang Muan Mine, Mae Moh Mine, Chavalit Vidthayanon Collection of Zoology, Ren's collection, Institute of Vertebrate Paleontology and Paleoanthropology, Chengdu Institute of Biology, Waseda University, Tohoku University, Tübingen University and Senckenberg Museum, Frankfurt for providing facilities during work. I also wish to express my gratitude towards Tawit Poopradit who taught me Thai turtles, Nikorn Wongchai, Dr. Phornphen Chantasit, Kamonlak Wongko, Linda Acker, Jutta Oelkers-Schaefer and Marton Rabi for their help and took care during studied turtle specimens.

Special thanks also to the persons who took part in field works, i.e., Athiwat Wattanapitukskul, Kamonlak Wongko, Jeeranan Sutthijan, Siripa Pongsaentong , Sila Saitong, Saksiri Soonchan and Wattana Wongsub. I also deeply thank to Chotima Yamee, Dr. Nareerat Boonchai, Dr.Yupa Thasod, Dr. Rattanaporn Hunta, Chalida Laojumpon, Suchada khamha, Ployphan Chittarach, Namosaurus, Sakchai Juanngam, Jaroon Duangkrayom, especially PRC members and my friends. I am grateful for their constant cheerful and help. My special thanks also to Dr. Uthumporn Deesri who guidance and encouragement.

An honorable mention goes to my beloved family. This thesis is dedicated for my best mother who took care of me during her all life and my great father for his understandings and full support during hard and happy times of my life. I thank to my younger brother who was cheerful, my aunt for all her support, my grandfather who was waiting for me growing up and everyone in our relatives. I appreciated to Phrathepwimonyan for his support our family. Without helps of the particular that mentioned above, I would face many difficulties while doing this.

Finally, the funding of this research was granted by Science Achievement Scholarship of Thailand.

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ABSTRACT

Understanding the origin and changes in continental turtle diversity from the Miocene to Holocene in Thailand requires a complete study on the anatomy of living and fossil turtles in this area.

The morphology of shells and plastron of trionychid turtles from Thailand and adjacent territory is described in detail in this work, a taxonomical key being provided. In Testudinoids, the systematic and the morphology of problematic cryptic species within the genera *Malayemys* and *Cyclemys* is discussed. A geometric study of *Malayemys* shows that the morphological characters based on stripe color pattern of the head are not congruent with shell morphology in Northeastern Thailand, suggesting that a redefinition of taxonomic entities should be done in this genus.

The fossils examined in this study include three Miocene localities which consist of Ban Na Sai, Lumphun Province; Mae Moh, Lampang Province and Chiang Muan locality, Phayao Province, two Plio-Pleistocene localities including Khok Sung and Tha Chang, Nakhon Ratchasima Province, and five Holocene localities composed of Khok Farang, Buriram Province; Thammamonkol cave, Phetchaburi Province; Taling Tong, Sukhothai Province; Raksai cave, Phetchaburi Province and Kheet Khin, Saraburi Province. Twenty one taxa can be recognized, some belonging to new species (Miocene localities), some belonging to living forms (Plio-Pleistocene and Holocene).

The Miocene documents the first appearance of fossil trionychid record during the tertiary of Thailand and that this group was already well diversified at that time. A new species of *Cuora*, *Cuora chiangmuanensis* nov. sp. (Naksri *et al*., 2013) is described from Chiang Muan locality and provide new information on the origin of living species in this genus, linking morphologically taxa from Southeast Asia and those from Eastern Asia. It is also the earliest record of the genus in 11-12 Ma (Middle Miocene or early Late Miocene) suggesting that Asian box turtles started to be present in Southeast Asia as soon as the Miocene. In the Plio-Pleistocene, giant tortoises refered to ?*Megalochelys* have been found in Tha Chang locality. The Plio-Pleistocene locality of Khok Sung displays a very important turtle diversity, similar to current day species. Among them some have disappeared from Northeastern Thailand and suggest an evolution of the hydrogeologic system. Holocene species are all assigned to living species of Southeast Asia. Association of turtles and archaeological remains comes often from the fact that these animals were often used by human subsistent.

Overall this study demonstrate that the biogeography and distribution of living turtle evolved until recently, certainly associated with environmental changes.

Key words: Origin, Turtle, Diversity, Miocene, Plio-Pleistocene, Holocene, Thailand

ชื่อเรื่อง	ต้นกำเนิดและการเปลี่ยนแปลงความหลากหลายของเต่าบนภาคพื้นทวีปสมัยไมโอซีนถึงโฮโลซีนในประเทศไทย
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บทคัดย่อ

การเข้าใจถึงจุดกำเนิดและการเปลี่ยนแปลงความหลากหลายของเต่าบนภาคพื้นทวีปจากสมัยไมโอซีนถึงโฮโลซีนในประเทศไทยจำเป็นต้องศึกษาข้อมูลที่สมบูรณ์ของสัณฐานวิทยาของเต่าปัจจุบันและซากดึกดำบรรพ์ในพื้นที่ประเทศไทย

การศึกษาครั้งนี้ได้บรรยายรายละเอียดสัณฐานวิทยาของกระดองหลังและกระดองท้องของตะพาบในประเทศไทยและประเทศใกล้เคียง รวมถึงการสร้างรูปวิธานที่ใช้จัดจำแนก ตำแหน่งอนุกรมวิธานและสัณฐานวิทยาของเต่าชนิดที่มีปัญหาสัณฐานวิทยาใกล้เคียงกันในสกุล *Malayemys* และ *Cyclemys* ซึ่งจัดอยู่ในเต่ากลุ่ม Testudinoid ได้มีการอภิปรายในการศึกษาในครั้งนี้ จากการศึกษา Geometrics ของเต่าในสกุล *Malayemys* แสดงให้เห็นว่าลักษณะสัณฐานวิทยาโดยอาศัยรูปแบบของแถบสีบนหัวของเต่าไม่เป็นไปตามลักษณะสัณฐานวิทยาของกระดองเต่าในภาคตะวันออกเฉียงเหนือของประเทศไทย ซึ่งควรมีการให้คำนิยามการจัดจำแนกลักษณะของเต่าในสกุลนี้ใหม่

ซากดึกดำบรรพ์ที่ทำการศึกษาในครั้งนี้มีแหล่งซากดึกดำบรรพ์สมัยไมโอซีน สามแหล่ง ประกอบด้วยแหล่งบ้านนาทราย จังหวัดลำพูน แม่เมาะ จังหวัดลำปาง และเชียงม่วน จังหวัดพะเยา แหล่งซากดึกดำบรรพ์สมัยไพลโอ-ไพลสโตซีน ซึ่งมีแหล่งโคกสูงและท่าช้าง จังหวัดนครราชสีมา และแหล่งซากดึกดำบรรพ์สมัยโฮโลซีน จำนวนห้าแหล่ง ประกอบไปด้วยแหล่งโคกฝรั่ง จังหวัดบุรีรัมย์ ถ้ำธรรมมงคล จังหวัดเพชรบุรี ตลิ่งทอง จังหวัดสุโขทัย ถ้ำรากไทร จังหวัดเพชรบุรี และขีดขิน จังหวัดสระบุรี

เต่าจัดจำแนกได้ทั้งหมด จำนวน 21 ชนิด พบเต่าชนิดใหม่ (ในแหล่งสมัยไมโอซีน) และบางชนิดพบว่าเป็นเต่าปัจจุบัน (ในแหล่งสมัยไพลโอ-ไพลสโตซีน)

สมัยไมโอซีนปรากฏซากดึกดำบรรพ์ตะพาบในระหว่างยุคเทอร์เชียรีของประเทศไทย และกลุ่มนี้ได้มีความหลากหลายตั้งแต่เวลานั้นเป็นต้นมา เต่าชนิดใหม่ในสกุล *Cuora*; *Cuora chaingmuanensis* (Naksri *et al*., 2013) ได้มีการบรรยายจากแหล่งเชียงม่วน และให้ข้อมูลใหม่เกี่ยวกับจุดกำเนิดของเต่าปัจจุบันของสกุลนี้ เป็นชนิดที่มีสัณฐานวิทยาเชื่อมโยงกันระหว่างเอเชียตะวันออกเฉียงใต้และเอเชียตะวันออก และยังเป็นบันทึกข้อมูลเต่าในสกุลนี้ที่เก่าแก่ที่สุดเมื่อ 11-12 ล้านปีก่อน (สมัยไมโอซีนตอนกลาง หรือ ไมโอซีนตอนปลายช่วงต้น) ซึ่งแสดงให้เห็นว่าเต่าหับเอเชียได้เริ่มปรากฏในเอเชียตะวันออกเฉียงใต้

สมัยไพลโอ-ไพลสโตซีน เต่าบกยักษ์ ซึ่งจัดจำแนกเป็น ?*Megalochelys* ได้พบในแหล่งท่าช้าง แหล่งไพลโอ-ไพลสโตซีนในแหล่งโคกสูง พบว่ามีความหลากหลายที่สำคัญ คือพบเต่าชนิดเดียวกันกับเต่าปัจจุบันกลุ่มของเต่าเหล่านี้ บางชนิดได้หายไปจากภาคตะวันออกเฉียงเหนือ ซึ่งแสดงให้เห็นถึงวิวัฒนาการของระบบแม่น้ำ ส่วนในสมัยโฮโลซีน เต่าที่พบทุกชนิดเป็นเต่าปัจจุบัน ความเกี่ยวข้องของเต่าและหลักฐานทางโบราณคดีได้เกี่ยวข้องกับความจริงที่ว่าสัตว์เหล่านี้ได้ถูกนำมาใช้สำหรับการดำรงอยู่ของมนุษย์

จากข้อมูลในการศึกษาครั้งนี้แสดงให้เห็นว่าการกระจายตัวทางชีวภูมิศาสตร์และการกระจายตัวของเต่าปัจจุบันได้มีวิวัฒนาการมาจนกระทั่งถึงปัจจุบันซึ่งเกี่ยวข้องโดยตรงกับการเปลี่ยนแปลงของสภาพแวดล้อม

คำสำคัญ: ต้นกำเนิด; เต่า; ความหลากหลาย; ไมโอซีน; ไพลโอ-ไพลสโตซีน; โฮโลซีน; ประเทศไทย

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CHAPTER 1

INTRODUCTION

1.1 Background

Thai turtle diversity consists nowadays of 30 species belonging to 7 families including Geoemydidae, Testudinidae, Emydidae, Platysternidae, Cheloniidae, Dermochelyidae and Trionychidae. However, the paleogeographic origin and the stratigraphic range of these Thai species or genera are poorly known. This is partly due because the fossil record for turtles is poorly known in the Cenozoic of Southeast Asia. It is therefore necessary to improve our knowledge in this region of the world to assess palaeontological or evolutionary questions regarding modern taxa of turtles.

Studies on fossil turtles in Thailand have started since the 80's thank to the collaboration between Thai and French teams. Most studies have mainly focused on the Mesozoic for documenting vertebrate ecosystems along with dinosaur discoveries (Tong *et al*., 2006; Tong *et al*., 2009a; Tong *et al*., 2009b). Several species have been described ranging in age from the Late Triassic to the Early Cretaceous. All these past communities of turtles are rather distant in terms of systematic and ecology from modern communities. Apart from the Mesozoic, Cenozoic turtles were only reported recently and descriptions of new species have been done first for Palaeogene taxa (Claude *et al*., 2007). In particular, three taxa are described from the Late Eocene-Early Oligocene of Krabi Basin, Krabi Province: *Mauremys thanhinensis*, *Hardella siamensis*, and a testudinid turtle (Claude *et al*., 2007). In addition, there is a report of geoemydid turtles in the late Oligocene Nong Ya Plong locality in Petchabun Province (Tong *et al*., 2006, Naksri *et al*., 2012). These studies have helped to better understand the turnover of turtle diversity in Southeast Asia through geological time, but do not help very much for understanding the geographic distribution of nowadays modern turtles. Modern communities can be only understood with the light of more recent events. These events can be inferred from modern populations with the help of molecular markers (e.g., DNA), archaelological data, or morphometrics but at present no such studies (or very few) have been done on turtles in Thailand.

Only fossils can give indication of possible local or global extinction and are exact data when they are correctly assigned. Furthermore, fossils can help to calibrate molecular data based on DNA rate of evolution (see Lourenco *et al.*, 2012). Studies on various organisms often estimate that the stratigraphic range for a given species extinction is less than 10 million years (Raup, 1981), therefore fossils coming from archeological sites or the Neogene localities are of prime interest to investigate events that can likely explain current day distribution and diversity.

The fossil record in the Neogene and Holocene is nearly not investigated in Thailand. There is a report of giant testudinid turtles from Tha Chang sandpits, Nakhon Ratchasima Province (Tong *et al.*, 2006; Naksri, 2007; Claude *et al.*, 2011). There is also a report of a skull in the Pleistocene of Vietnam as well (Bourret, 1941). Turtle are signaled in the Miocene deposits of Northern Thailand, but rarely studied into details (Suteethorn *et al.*, 1990; Nakaya *et al.*, 2002; Songtham *et al.*, 2003; Srisuk, 2005; Tong *et al.*, 2006). They are rarely mentioned in archeological studies and when they are, they are often not described into details (Auetrakulvit, 2004). Although they are rarely mentioned, Cenozoic turtles have been found in many localities throughout of Thailand in both lignite mines and sandpits during paleontological excursions but few of them have been studied in detailed especially in the Miocene epoch. In addition, several Pleistocene-Holocene sub-fossil turtles are known from archeological localities and caves.

It is necessary for studying the systematic fossil and sub-fossil turtles to well know the osteology of living turtles (see for instance the work of Gaffney, 1979). This is especially true for the diverse families inhabiting Southeast Asia such as Trionychidae or Geoemydidae. In my master dissertation, I have already provided a description of geoemydids and testudinids anatomy for the species occurring in Thailand; there is, however, still a need to better document the anatomy of Trionychids.

In Thailand, some species of geoemydid turtles can be difficult to recognize, and have been the object of systematic revision during the last 10 years, thanks to the help of soft anatomy, color pattern or molecular data (this is particularly true for the species of the genus *Malayemys* and *Cyclemys* (Brophy, 2004; Stuart *et al.*, 2001) and were not considered into detail in my master dissertation. However, their identification in the fossil record depends on soft anatomy and no detailed study of their carapace or bone shape have been done. There is therefore a need to describe whether these species can be recognized from skeletal anatomy if one wish to refer fossils to them. Furthermore, finding differences in osteological character may contribute to better define these taxonomic units. In accurately investigating the morphological difference among different populations, one could better document of divergence between species in these groups. For these cases, the use of morphometrics should allow to quantify and precisely depict differences between populations and species. It will be a complementary tool to anatomical descriptions.

The first and second objectives of this research are to describe and quantify anatomical differences of skeleton of Indochinese living turtles. These parts should give birth to an osteological catalogue and morphometric studies and reference frame between morphologically close species. This should be help as a tool for study systematic of fossil and sub-fossil turtles in Indochina. The third objective is to screen the fossil record of continental turtles from the Miocene to Holocene. This should allow to provide an overview of Thai turtle diversity through time. This inventory will be necessary for the fourth and last objective of this study: understanding historical features (e.g., climate change, human activities) that could have affected the diversity and the geographic distribution of turtles in Thailand.

1.2 Objectives

1.2.1 To describe and quantify anatomical differences of shells in closely related species or between populations in Indochinese-Thai living turtles

1.2.2 To constitute of a comparative catalogue of reference shells of living trionychid turtles in Thailand

1.2.3 To identify the fossil record of continental turtles of the Neogene to Quaternary in Thailand and in order to find first occurrences of Thai living genera or species

1.2.4 To better understand the historical features (including human activities) determining the diversity and the geographic distribution of turtles in Thailand

1.3 Scope of the study

This work concerns the shell anatomy and evolution of living, fossil and sub-fossil turtles collected from both field trips and available in osteological and palaeontological collections. The first part of the work is to describe or to quantify anatomical differences of shells in closely related species or between populations in Indochinese-Thai living turtles, genus *Malayemys* with a geometric morphometric approach and to constitute of a comparative shells catalogue of Thai living trionychid turtles. Information obtained from this part will help for describing and compare fossil turtles with their living relatives. The second part hinges on taxonomy and geographical distribution of the Neogene to Quaternary turtles in order to understand historical features that have determined the current day diversity and geographic distribution of turtles in Thailand. The work was conducted in Palaeontological Research and Education Centre, Maha Sarakham Province; Sirindhorn Museum, Kalasin Province; Chiang Muan Mine Museum, Phayao Province; Mae Moh Mine Museum, Lampang Province; Thai turtle laboratory at Chulalongkorn University, Bangkok, and collections of other countries.

1.4 Significance of the study

The results from this study have provided

1.4.1 Descriptive anatomical differences in shell morphology for populations of the genus *Malayemys* in Thailand

1.4.2 A comparative catalogue of trionychid turtle shells in Thailand

1.4.3 Knowledge fulfillment on diversity of the Neogene to Quaternary turtles in Thailand

1.4.4 Knowledge on the changes of turtle diversity and assesses origin and evolutionary features of the living turtles in Thailand

CHAPTER 2

LITERATURE REVIEW

2.1 Diversity of living turtles in Thailand

Seven on the thirteen living families of turtles are living in Thailand: Testudinidae, Geoemydidae, Emydidae, Platysternidae, Trionychidae, Cheloniidae, and Dermochelyidae. The first four families are belonging to the Testudinoidea superfamily, the largest extant group of turtles (Claude *et al.*, 2003). Platysternidae were included in this superfamily rather recently based on molecular analysis (Cervelli *et al.*, 2003; Krenz *et al.*, 2005; Parham *et al.*, 2006).

Testudinidae of Thailand includes *Manouria emys*, *Manouria impressa* and *Indotestudo elongata*. All are terrestrial.

In Thailand, Geoemydidae are freshwater (FW) and semi-terrestrial turtles (ST), which include the following species: *Cuora amboinensis* (FW), *Cuora mouhotii* (ST), *Siebenrockiella crassicollis* (FW), *Malayemys subtrijuga* (FW), *Malayemys macrocephala* (FW), *Melanochelys trijuga* (FW), *Batagur baska* (FW), *Batagur borneoensis* (FW), *Heosemys annandalii* (FW), *Cyclemys atripons* (FW), *Cyclemys oldhami* (FW), *Heosemys spinosa* (ST), *Heosemys grandis* (FW) and *Notochelys platynota* (FW). The presence of *Melanochelys* in Thailand is questionable, but this species is known in Myanmar and close to the border. A new species of *Malayemys*, *M. macrocephala* (FW), was proposed by the recent work of Brophy in 2004. In previous work the diversity of *Cyclemys* in Southeast Asia was particularly unclear and these species were often referred to the *Cyclemys* complex since differences among them were not clear (Stuart *et al.*, 2001). More recently Fritz *et al.*(2008) analyzed genotypes of several specimens including holotypes, revealing that seven species could be identified in Southeast Asia and South Asia including *Cyclemys dentata*, *C. atripons*, *C. pulchristriata*, *C. oldhamii*, *C. gemeli*, *C. fusca*, *C. enigmatica*; two of them are known in Thailand: *Cyclemys atripons* and *C. oldhami*. The turtle taxonomy working group (2011) reported *Cyclemys dentata* in Thailand, but there is no clearly identified *C. dentata* in Southern Thailand according to our knowledge.

Emydidae is represented by only one introduced freshwater species, *Trachemys scripta.*

Platysternidae is presented only one native freshwater species, *Platysternon megacephalum*.

Six species of Trionychidae (all freshwater) are present in Thailand: *Amyda cartilaginea*, *Chitra chitra*, *Chitra vandijki, Dogania subplana*, *Pelochelys cantorii* and one introduced species, *Pelodiscus sinensis*.

Cheloniidae are represented by *Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata* and *Lepidochelys olivacea* and are all marine turtle.

Dermochelyidae is represented by *Dermochelys coriacea,* which is also marine.

2.1.1 Literature overview of living turtles in Thailand

2.1.1.1 Testudinidae Batsch, 1788

1) *Intotestudo elongata* (Blyth, 1854)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.*(2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This terrestrial species lives in tropical evergreen and deciduous forest on hills, mountains or high plateaus (Ernst & Barbour, 1989), it likes relatively cool and humid areas (Nutaphand, 1980). It is mostly herbivorous. It feeds on herbaceous leaves, fruits, flowers, mushrooms, grass, carcass, food particles and animal excrement (Sriprateep *et al.*, 2013). Juveniles can sometimes eat earthworms (Stuart *et al.*, 2001). The clutch size is composed of two to five eggs and is laid two to three times between July to October (Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Nepal, Bangladesh, and Northeastern India, Myanmar, Laos, Thailand, Cambodia, and Vietnam to Penang, Malaysia (Ernst & Barbour, 1989).

Conservation statuship: CITES; Appendix II.; IUCN Red List: Endangered A1cd+2cd (2012).

2) *Manouria emys* (Schlegel & Müller, 1844)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.*(2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This terrestrial species lives in tropical evergreen forest at low to mid elevations (Stuart *et al.*, 2001; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006) and prefers moist situations and also shallow mountain streams. It spends much of its time burrowed into moist soil or under leaf litter (Ernst & Barbour, 1989). It is herbivorous and feeds on leave, mushrooms, bamboo shoots, banana trunks and figs (Stuart *et al.*, 2001). Aquatic plants such as tubers and lotus are also foods (Nutaphand, 1980). The clutch size of this species is about five to fifty eggs and is laid twice a year (Nutaphand, 1980; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Bangladesh, and Myanmar, Western and Southern Thailand and Malaysia to Sumatra, Borneo, and the Indo-Australian Archipelago (Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Endangered A1cd+2cd (2012).

3) *Manouria impressa* (Günther, 1882)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.*(2001); Bonin, Deveaux, & Dupré (2006); Naksri (2007).

Biology: This is a terrestrial species, found on hills covered by evergreen forest over 800 m elevation. It is herbivorous and it eats, mainly mushrooms, bamboo shoots and some fruits (Stuart *et al.*, 2001; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006). The clutch size in natural nest is about 8-10 eggs (Wanchai *et al.*, 2013).

Geographic distribution: Cambodia, China (Yunnan), Laos, Malaysia (West), Myanmar, Thailand (Western, Southern, Central), Vietnam (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1acd, B1+2acd (2012).

2.1.1.2 Geoemydidae Theobald, 1868

1) *Batagur baska* (Gray, 1831)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species lives in tidal areas of the estuaries of large rivers but during breeding season, ranges far upstream in these rivers (Ernst & Barbour, 1989). It is omnivorous and feeds on leaves, shoots, and fruits of mangroves and other waterside plants, clams and other small animals (Stuart *et al.*, 2001; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006). The clutch size is up to 13-34 eggs per time. Females can nest can up to three times a season (Ernst & Barbour, 1989).

Geographic distribution: Bangladesh (Sundarbans), India (Sundarbans), Indonesia (Sumatra), Thailand (Southern Peninsula, formerly widespread in all estuarine areas), Vietnam, Cambodia, Malaysia and Myanmar (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix I;
IUCN Red List; Critically Endangered A1cd (2012).

2) *Batagur borneoensis* (Schlegel & Müller, 1844)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: Adults of this aquatic species live mainly in estuaries and tidal area. Juveniles live in freshwater portions of these same rivers (Ernst & Barbour, 1989; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006). It is usually found in brackish water around estuaries (Nutaphand, 1979). It is herbivorous, feeding on leaves, shoots and fruits of mangroves and other waterside vegetable (Stuart *et al.*, 2001). The clutch size is about 15 to 25 eggs and is laid three times a year (Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Extreme Southern Thailand southward through Malaysia to Sumatra and Borneo (Ernst & Barbour, 1989).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Critically Endangered A1bcd (2012).

3) *Cuora amboinensis* (Riche, 1801)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This semi aquatic species is found in streams and marshes in lowland forest, in rice paddies and in mangrove creeks (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). It is often found on land far from water (Ernst & Barbour, 1989). It is omnivorous; feeding on terrestrial and aquatic plants, mushrooms, worms, snails, and crustaceans (Stuart *et al.*, 2001). This species has three or four clutches a year, usually composed of only two to three eggs (Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Bangladesh, Brunei, India, Indonesia, Malaysia, Myanmar, Philippines, Singapore, Thailand (Northern, Western, Southern, Central Plain), Laos, Vietnam, and Cambodia (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1d+2d (2012).

4) *Cuora mouhotii* (Gray, 1862)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006); Naksri (2007).

Biology: This terrestrial species, usually lives in forested hill areas but is occasionally lowland and swamp areas (Stuart *et al.*, 2001; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006). It is omnivorous, feeding usually on vegetable but also on animals with a preference for snails (Stuart *et al.*, 2001; Ernst & Barbour, 1989). It lays one to three eggs in a clutch.

Geographic distribution: India (Assam), China (Hainan), Vietnam westward to Northern Thailand and Myanmar (Ernst & Barbour, 1989; Stuart *et al.*, 2001)

However, the presence of this species in Thailand today is still questionable.

Conservation statuship: CITES; - ;
IUCN Red List; Endangered A1d+2d (2012).

5) *Cyclemys atripons* Iverson & McCord, 1997

Description: see Fritz *et al.*(2008); Bonin, Deveaux & Dupré (2006)

Biology: Probably close to *Cyclemys oldhami*

Geographic distribution: Southeastern Thailand, including the Koh Chang and Koh Kut islands; Southwestern Cambodia (Fritz *et al.*, 2008).

Conservation statuship: CITES; - ;
IUCN Red List; not evaluated.

6) *Cyclemys oldhami* Gray, 1863

Description: see Fritz *et al.* (2008); Bonin, Deveaux & Dupré (2006)

Biology: This semi aquatic species is found on hills in forested area, often in small streams or under dead leaves. It is omnivorous. It lays 4 to 5 clutches of 2 to 4 eggs each a year (Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Central and Southern Myanmar (Burma), Central and Northern Thailand, Laos, Northern Cambodia, Northern and Central Vietnam, perhaps neighboring Southern China (Fritz *et al.*, 2008).

Conservation statuship: CITES; - ;
IUCN Red List; not evaluated.

7) *Heosemys grandis* (Gray, 1860)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006); Naksri (2007).

Biology: This aquatic species is found in streams and freshwater marshes at low to mid elevation. It is omnivorous and feeds on fruits, vegetable, and animal matter. The clutch is composed from 4 to 8 eggs (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Western, Southeastern, and Peninsular regions), Laos, Vietnam, Cambodia, Malaysia (Peninsula) and Myanmar (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1d+2cd (2012).

8) *Heosemys spinosa* (Gray, 1830)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: Juveniles are more terrestrial than adults (Mertens, 1971 in Ernst & Barbour, 1989). Adults often wanders on land in cool, humid, shaded areas, and often hides under plant debris or clumps of grass (Ernst & Barbour, 1989). It is mostly herbivorous (mostly eating fruits) but likes insect and worms (Stuart *et al.*, 2001; see also in Pritchard, 1979; Bonin, Deveaux & Dupré, 2006). The clutch size varies from one to three eggs (Ernst & Barbour, 1989).

Geographic distribution: Peninsular Thailand, Brunei, Indonesia (Banka, Kalimantan, Mentawei, Sumatra), Malaysia , possibly Myanmar, Philippines (Mandanao), and Singapore (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Endangered A1bcd (2012).

9) *Heosemys annandalii* (Boulenger, 1903)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species lives in marshes, ponds, and other slow moving or still water bodies at low elevation. It can also tolerate brackish water. It is mostly herbivorous feeding on water-lily leaves and tubers, floating plants, and overhanging vegetation but can rarely eat worms and insects (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Central, Southern, South-Eastern), Cambodia, Vietnam and Malaysia (Ernst and Barbour, 1989).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Endangered A1cd+2d (2012).

10) *Malayemys subtrijuga* Schlegel and MÜller, 1884

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Brophy (2004); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species inhabits slow-moving water bodies with soft bottoms and aquatic vegetation. It is also found in ponds, canals, small streams, marshes, and rice field (Ernst and Barbour, 1989). It is carnivorous feeding on freshwater snails and occasionally small mussels and shrimp (Stuart *et al.*, 2001). Females lay four to six eggs in a clutch.

Geographic distribution: Mae Kong river basin (Northeastern and Eastern Thailand), Thailand (Northeastern), Laos, Vietnam, Cambodia (Brophy, 2004).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1d+2d (2012).

11) *Malayemys macrocephala* Gray, 1859

Description: see in Brophy, 2004

Biology: see *Malayemys subtrijuga*

Geographic distribution: Chao Phraya and Mae Klong river basins, coastal area of Southeastern Thailand and Malay Peninsula (Brophy, 2004)

Conservation statuship: CITES; - ;
IUCN Red List; not evaluated

12) *Melanochelys trijuga* (Schweigger, 1812)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: It is a species mainly found a freshwater inhabiting in clean ponds, streams and rivers; but it occasionally can be found on land far from water. It is omnivorous. It is mainly feeding on plants. It also has scavenging habit. It lays ten eggs in a clutch (Pritchard, 1979; Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Peninsular India, Northern Bangladesh, Central Myanmar, Sri Lanka, Maldives and Chagos Islands. It probably occur in Nepal (Ernst & Barbour, 1989) and along the border of Thailand and Myanmar for the subspecies *Melanochelys trijuga edeniana* (Nutaphand, 1979).

The presence of this species in Thailand is questionable.

Conservation statuship: CITES; - ;
IUCN Red List; Lower Risk/near threatened (2012).

13) *Notochelys platynota* (Gray, 1834)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This semi aquatic species lives in streams and slow moving or still bodies of shallow water in lowland wet evergreen forest. It is mostly herbivorous feeding on fruits and plants but it can also eat invertebrates (insect, snails, larvae). The clutch size varies from two to six eggs. (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Southern and Eastern), Indonesia (Sumatra, Banka, Java, Kalimantan), Malaysia, Myanmar (Tenasserim), and Singapore (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1cd+2cd (2012).

14) *Siebenrockiella crassicollis* (Gray, 1830)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species lives in slow moving or still bodies of freshwater at low elevations including ponds, canals, ditches and swamps. It is omnivorous feeding on aquatic invertebrates, carrion and plants (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). This species lays one or two eggs in three or four clutches during a season covering from April until June (Ernst & Barbour, 1989; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Northern, Central and Peninsular), Laos, Vietnam (Southern), Cambodia, Indonesia (Sumatra, Banka, Java, Kalimantan), Malaysia (Peninsular and Sarawak), Myanmar (Tenasserim), and Singapore (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1cd+2cd (2012).

2.1.1.3 Plastysternidae Gray, 1869

1) *Platysternon megacephalum* Gray, 1831

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species lives in rocky streams in forest to mid to high elevation. It is carnivorous, eating Snails, crabs, fish, prawn, worms, frogs and tadpoles. Each clutch contains about one or two eggs (Pritchard, 1979; Ernst & Barbour, 1989; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Northern, Western, Northeastern), Laos, Vietnam, China (Southern, Hainan, and Hong Kong) and Myanmar (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Endangered A1d+2d (2012).

2.1.1.4 Emydidae Rafinesque, 1815

1)*Trachemys scripta* (Schoepff, 1792)

Description: see in Smith (1931); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006); Naksri (2007).

Biology: This aquatic species occurs in freshwater ponds and lakes, and is widely introduced in temple ponds, city parks, reservoirs and canals. It is omnivorous and eats plants, fruit, small animals and carrion. Several clutches of two to 25 eggs are laid each season (Pritchard, 1979; Ernst & Barbour, 1989; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: introduced in Thailand, Cambodia. Native to Southern United states, established in many temperate and tropical regions of the world including China, Hong Kong, Myanmar, and Singapore (Stuart *et al.*, 2001).

Conservation statuship: CITES; -
IUCN Red List; Least Concern (2012).

2.1.1.5 Trionychidae Gray, 1825

1) *Amyda cartilaginea* (Boddaert, 1770)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006).

Biology: This aquatic species lives in various water bodies, from marshes and estuaries to mountain streams. It can be found in rivers, ponds, swamps and oxbow lakes near to large rivers (Ernst and Barbour, 1989). It is omnivorous and feeds on insects, crabs, prawns, snails, clams, fish, carrion, fruit and seeds (1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). This species lays three or four clutches in each year containing four to ten eggs (Nutaphand, 1980; Ernst and Barbour, 1989).

Geographic distribution: Thailand, Laos, Vietnam, Cambodia, Brunei, Indonesia, Malaysia, Myanmar and Singapore (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Vulnerable A1cd+2cd (2012).

2) *Chitra chitra* (Nutaphand, 1986)

Description: see in Smith (1931); Bourret (1941); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006).

Biology: This aquatic species lives in large rivers with clear water and sandy bottoms. It is carnivorous and eats fish and sometimes prawns(Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Mae Klong Basin), possibly Malaysia (Peninsular) and Indonesia (Java) (Stuart *et al.*, 2001) and also Mae Ping River in Thailand (Kitimasak and Thirakhupt, 2002).

Conservation statuship: CITES; Appendix II;
IUCN Red List; Critically Endangered A1cd, B1+2c (2012).

3) *Chitra vandijki* (McCord and Pritchard, 2003)

Description: see in McCord and Pritchard (2002)

Biology: It is probably close to *Chitra chitra*

Geographic distribution: Myanmar and Thailand (Turtle Taxonomy Working Group, 2011; Kitimasak, 2002)

Conservation statuship: CITES; Appendix II;

IUCN Red List; not evaluated.

4) *Dogania subplana* (Geoffroy, 1809)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: This aquatic species lives in most freshwater bodies from lowland marshes to streams at mid elevations. It often hides under rocks and large stones (Ernst & Barbour, 1989). It is carnivorous, eating snails and other aquatic invertebrates. A clutch contains three to seven eggs (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Western and Peninsular regions), Brunei, Indonesia (Java, Kalimantan, Sumatra), Malaysia, Myanmar (Tenasserim), Singapore, possibly Philippines (Stuart *et al.*, 2001).

Conservation statuship: CITES;- ;

IUCN Red List; Lower Risk/least concern (2012).

5) *Pelochelys cantorii* Gray, 1864

Description: see in Smith (1931); Bourret (1941); Pritchard (1979); Nutaphand (1979); Stuart *et al.* (2001); Bonin, Deveaux & Dupré (2006).

Biology: This aquatic species lives in rivers and estuaries and tidal area. It is carnivorous, feeding on fish, prawn, and crabs. Females lay a clutch a year of about 30 eggs. (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006).

Geographic distribution: Thailand (Southern and Eastern), Laos, Vietnam, Cambodia, Bangladesh, China (Southeastern and Hainan), India, Indonesia, Malaysia, Myanmar, Papua New Guinea (North coast) and Philippines (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix II;

IUCN Red List; Endangered A1cd+2cd (2012)

6) *Pelodiscus sinensis* (Wiegmann, 1835)

Description: see in Smith (1931); Bourret (1941); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: This aquatic species lives in slow moving or still bodies of freshwater including rivers, lakes, ponds, canals, and creeks (Ernst & Barbour, 1989). It is omnivorous and its foods consist in prawns, crabs, snails, clams, frogs, fish, insects, and sometimes plant seeds (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). The clutch size varies from fifteen to at least twenty-eight eggs and the female may nest two to four times per year (Ernst and Barbour, 1989).

Geographic distribution: Introduced species in Thailand, Vietnam. Native in China (including Hainan), Japan, the Koreas, Russia (Ussuriland), and Taiwan. This species is widely breed throughout Asia, where introduced animals are likely to establish populations (Stuart *et al.*, 2001).

Conservation statuship: CITES; - ;
IUCN Red List; Vulnerable A1d+2d (2012)

2.1.1.6 Cheloniidae Oppel, 1811

1) *Caretta caretta* (Linnaeus, 1758)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: Adults occur mainly in coastal marine waters, while juveniles may be associated with floating weed masses in open sea. It enters bays, lagoons, salt marshes, creeks, and the mouths of large rivers. This species also shares its nesting beaches with other sea turtles (Ernst & Barbour, 1989). It is carnivorous, mainly eating bottom-living animals such as snails, clams and other mollusks, crabs, sea urchins, sponges and fishes (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). The clutch usually contains sixty-four to two hundreds eggs and is laid in one time (Ernst and Barbour, 1989).

Geographic distribution: Thailand (wanders into Northern Gulf of Thailand), Vietnam, Cambodia. Worldwide in tropical and subtropical seas. Nests in China (Southern), Japan, Australia (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix I;
IUCN Red List; Endangered A1abd (2012).

2) *Chelonia mydas* (Linnaeus, 1758)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: This species lives in shallow coastal marine water, particularly sandy areas supporting sea grass beds. It produces nests mainly on gentle sandy beaches. It shares its nesting beaches with all other sea turtles (Ernst & Barbour, 1989). It is herbivorous, feeding on sea grasses and algae (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). Females of this species nest every two or three year. It nest several times each season and twelve to two hundred and thirty-eight (normally one hundred to one hundred and fifty) eggs are laid (Ernst & Barbour, 1989).

Geographic distribution: Worldwide in tropical and subtropical marine waters, including throughout Asia and Thailand (Andaman Sea and Gulf of Thailand). Nesting beaches in Asia known from Myanmar, Malaysia, Indonesia, and the Philippines (Stuart *et al.*, 2001).

Conservation statuship: CITES; Appendix I;
IUCN Red List; Endangered A2bd (2012).

3) *Eretmochelys imbricata* (Linnaeus, 1766)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al*. (2001); Bonin, Deveaux & Dupré (2006).

Biology: This species inhabits in tropical coral reefs. It can be found in shallow coastal waters and small narrow creeks and passes or even deep waters (Ernst & Barbour, 1989). It is omnivorous and eats sponges, tunicates, sea anemones, mollusks and algae (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). It is often nests on small beaches with coarse sand or gravel, and may lay three to four clutches of 50 to 200 eggs every nesting season.

Geographic distribution: Worldwide in tropical and subtropical oceans (Stuart *et al.*, 2001) including Thailand (Andaman Sea and Gulf of Thailand)

Conservation statuship: CITES; Appendix II;
IUCN Red List; Critically Endangered A2bd (2012).

4) *Lepidochelys olivacea* (Eschscholtz, 1829)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: This species inhabits mainly coastal marine waters, but can sometimes be seen offshore in waters up to 200 m in depth. It is omnivorous, feeding on crabs, lobsters and other crustaceans, fish, tunicates, mollusks, jellyfishes, and algae (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006). It produces nest in large aggregations on remote sandy beaches when nesting. The clutches are about thirty to one hundred and sixty-eight eggs and are laid three to four time during the nesting season (Ernst and Barbour, 1989).

Geographic distribution: Tropical and subtropical seas worldwide including Thailand (Andaman Sea and Gulf of Thailand), Vietnam, Cambodia. Nests in Asia in India, Malaysia, and Myanmar (Stuart *et al.*, 2001)

Conservation statuship: CITES; Appendix I;
IUCN Red List; Vulnerable A2bd (2012).

2.1.1.7 Dermochelyidae Fitzinger, 1843

1) *Dermochelys coriacea* (Vandelli, 1761)

Description: see in Smith (1931); Bourret (1941); Taylor (1970); Pritchard (1979); Nutaphand (1979); Ernst and Barbour (1989); Stuart *et al.* (2001); Bonin, Deveaux, & Dupré (2006).

Biology: This species is pelagic and lives in deep ocean waters. It sometimes enters the shallow waters of bays and estuaries (Ernst & Barbour, 1989). It is carnivorous and predates on jellyfish and tunicates (Pritchard, 1979; Stuart *et al.*, 2001; Bonin, Deveaux & Dupré, 2006. It produces nests on sandy beaches with an unobstructed approach from deep water. The normal clutch size is 50-170 eggs and is laid several times during the nesting season (Ernst and Barbour, 1989).

Geographic distribution: Worldwide in tropical, subtropical, and occasionally temperate seas (Stuart *et al.*, 2001), including Thailand (nests on Andaman coast), Vietnam, Cambodia.

Conservation statuship: CITES; Appendix I;
IUCN Red List; Critically Endangered A1abd (2012)

2.2 Literature overview of fossil turtles in Thailand

In Thailand, fossil turtle remains are known in sediments from both the Mesozoic and Cenozoic eras ranging in age from the Late Triassic to the Holocene. Mesozoic turtles were first described starting from the 1980s when Thai-French Teams investigated the Mesozoic continental fossilized ecosystems. Most Mesozoic turtles that have been discovered come from non-marine beds of the Khorat Plateau, in Northeastern Thailand but one taxon has been discovered in Southern peninsula of Thailand (Tong *et al.*, 2002; Tong *et al.*, 2006). Apart from the Mesozoic, Cenozoic beds have yielded fossil turtles thanks to coal and sand mining activities. Several caves and archeological localities have also yielded sub-fossil turtles. However, these turtles have received less attention.

2.2.1 Mesozoic fossil turtles in Thailand

Mesozoic turtles have been found mostly in the Khorat Plateau (part of Indochina Block), Northeastern Thailand more than 30 years ago by Thai-French Teams. The record ranges from the Late Triassic to the Early Cretaceous in age.

2.2.1.1 Late Triassic

The Late Triassic Huai Hin Lat Formation has yielded one of the oldest turtles in the world, *Proganochelys ruchae* (Proganochelyidae) (Broin *et al.*, 1982; Broin, 1984).

2.2.1.2 Middle Jurassic

Siamochelys peninsularis (Cryptodira) was discovered at the Mab Ching locality, Nakhon Si Tammarat Province, Southern peninsula of Thailand, Shan-Thai Block (Tong *et al.*, 2002).

Most Mesozoic turtles are from the Khorat Group which consists of five formations including Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, Khok Kruat formations ranging from bottom to top (Racey *et al.*, 2009). Turtles were found in the Phu Kradung, Sao Khua, and Khok Kruat formations.

2.2.1.3 Late Jurassic-Early Cretaceous

The Late Jurassic-Early Cretaceous, Phu Kradung Formation has yielded a large trionychoid turtle, *Basilochelys macrobios* (Cryptodira, Trionychoidea), which type locality is in Mukdahan Province (Tong *et al.*, 2009a; 2009b). The details of

B. macrobios are given in Appendix III. Apart from this, new material from Phu Noi, Kalasin Province has been discovered and is currently under study, several isolated bones have also been found in several other localities.

2.2.1.4 Early Cretaceous

The adocid turtle *Isanemys srisuki* was discovered in Kalasin and Khon Kaen provinces and described on the basis of more than 20 shells (Tong, Buffetaut & Suteethorn, 2006). In the same formation, isolated elements have allowed to identify the carettocheyid *Kizylkumemys* sp. (Tong *et al.*, 2006). Testudines indet. has been reported from Koh Kut, Trat Province (Cuny *et al.*, 2010).

At least three taxa species are known from the Khok Kruat Formation. The first is a carttochelyid and was named *Kizylkumemys koratensis*. It was found in Ban Saphan Hin, Nakhon Ratchasima Province and Khok Pha Suam, Ubon Ratchathani Province (Tong *et al.*, 2005). In addition, the adocid turtle, *Shachemys* sp. has also been found from these two localities. Moreover, a few fragment trionychid shell has been collected near Nakhon Ratchasima Province (Tong *et al.*, 2009b).

An overview of Mesozoic turtles in Thailand is detailed in Tong *et al.*, 2009b (see Appendix IV).

2.2.2 Cenozoic fossil turtles in Thailand

By comparison with the Mesozoic, Cenozoic turtles are represented by a fewer reports. Tong *et al* (2006) reported an overview of the fossil turtles Cenozoic turtles in Thailand. The publication is given in Appendix V.

2.2.2.1 Late Eocene- Oligocene

The first description is from the Late Eocene-Early Oligocene of Krabi Basin. There are three taxa of turtles including two new geoemydids, *Mauremys thanhinensis* and *Hardella siamensis* and a possible testudinid (Claude, Tong & Suteethorn, 2007). This information indicates that these modern families are known at least by the end of the Eocene in South East Asia. The Oligocene turtles from Nong Ya Plong, Petchaburi Province have been preliminary described in my Master thesis (2007) and are identified as two new geoemydid turtles.

2.2.2.2 Neogene

Neogene turtles have been reported by Claude *at al.* (2011) and Tong *et al*. (2006). Two giant tortoises were found in Tha Chang sandpit, Nakhon Ratchasima Province. They were identified as ? *Megalochelys*. Seven taxa of turtles have been recognized from the Early Pleistocene of Khok Sung locality, Nakhon Ratchasima Province including *Batagur* cf. *trivittata* (Duméril and Bibron, 1835), *Heosemys annandalii* (Boulenger, 1903), *Heosemys* cf. *grandis* (Gray, 1860), and *Malayemys* sp., *Chitra* sp., and cf. *Amyda* sp. (Claude *et al.*, 2011). While coal mines of Northern Thailand have yielded a rich diversity of mammals such as Mae Moh, Lampang Province, Chaing Muan, Phayao Province, Na Sai, Lamphun Province, turtles from these areas have been often classified as Testudines indet. in taxonomic lists (e.g., Songtham *et al*., 2003: Nakaya *et al*., 2002). Therefore a taxonomic study of these new turtles is needed for fulfilling knowledge about diversity and origin of living turtle especially in Thailand and Southeastern Asia.

2.2.2.3 Holocene

Holocene turtles are known from archeological localities and caves (Auetrakulvit, 2004). Archeological localities in northeastern Thailand often found two species of turtles including *Malayemys subtrijuga* and *Indotestudo elongataga* (Thotsarat and Kitngam, 2004) which are common species in the present. However, most of them have not been studied in detail yet. They can, however, document recent fluctuations of turtle species biogeography and possibly could help to better understand the relationship between human activities and turtle diversity.

CHAPTER 3

A GEOMETRIC MORPHOMETRIC INVESTIGATION ON THE SHELL SHAPE VARIATION OF *MALAYEMYS* IN THAILAND

3.1 Introduction

Some species of geoemydid turtles in Thailand are particularly difficult and problematic to recognize. They have been the object of systematic revision during the last 10 years, with the help of soft anatomy, color pattern or molecular data. In Thailand, this concerns especially the species of the genera *Malayemys* and *Cyclemys*. The infrageneric evolutionary units found in these genera are often found in different places suggesting the role of allopatry during speciation.

In the past, *Malayemys* was considered as monotypic with the nominal species *Malayemys subtrijuga*. In 2004, Brophy found that variation of head color patterns was strong enough for considering two species of *Malayemys*; *Malayemys subtrijuga* Schlegel and Müller, 1884 and *Malayemys macrocephala* Gray, 1859. Skeletal differences between these two sister species remain, however, not defined; in addition the role of hybridation is not assessed on these two species.

Nutaphand (1979) considered two species of *Cyclemys* in Thailand: *Cyclemys dentata* (Gray, 1831) and *Cyclemys tcheponensis* (Bourret, 1939). In previous work the diversity of *Cyclemys* in Southeastern Asia was particularly unclear and these species were often referred to the *Cyclemys* complex since morphological differences and geographical respective range for each described species were not clear (Stuart, *et al*., 2001). More recently Fritz *et al*. (2008) analyzed genotypes of several specimens including holotypes, revealing that seven species could be identified in Southeastern Asia; two of them are considered in Thailand: *Cyclemys atripons* Iverson & McCord, 1997 and *Cyclemys oldhami* Gray, 1863. The differences between these two species based on DNA and morphology which includes shell outline, maximum size, color, carapace and plastron pattern and throat color. *Cyclemys atripons* distributes in Southeastern Thailand (Koh Chang and Koh Kut islands) and Southwestern Cambodia while *C. oldhami* has a wider range including Central and Southern Myanmar, Central and Northern Thailand, Laos, Northern Cambodia, Northern and Central Vietnam and possibly China (Fritz *et al.*, 2008).

Malayemys is a common genus which can be found in a wide range through out the country. It is simple to find it in Northeastern and Central plain of Thailand because this turtle is sold in the market all the year for cultural and believe reasons. Some Thai people believe that releasing a turtle is as a kind of making a merit that may confer a longer life. For this reason many of these turtle are released in temple basins.

Cyclemys is more difficult to find in Thailand, the species is rare and it is difficult to investigate its variation together with geographical variation. Therefore, this study concentrates itself on the *Malayemys* genus for which larger sample size can be studied. The shell will be considered here as the phenotype of interest, in order to see whether geographical variation in this structure is related to stripe patterns, and if the distribution of morphotype entities (if any) follow the ones found in Brophy (2004)

The genus *Malayemys* is found in lowland freshwater areas of Thailand, Laos, Cambodia, Southern Vietnam, Northern Malay Peninsula, and Java (Brophy, 2004; Ernst and Barbour, 1989; Nutaphand, 1979).

Brophy (2004) in analyzing geographical variation of phenotypic character of this genus a discovered that two forms of *Malayemys* occurred allopatrically in lowland areas of mainland Southeast Asia. Brophy (2004) suggested that these two forms can be assigned to two distinct species, *Malayemys subtrijuga* Schlegel and Müller, 1884 and *Malayemys macrocephala* Gray, 1859. *M. subtrijuga* would be restricted in the Mekong River basin while *M. macrocephala* will live in the Chao Phraya and Mae Klong river basins, coastal area of Southeastern Thailand, in the Malay Peninsula and Indonesia.

The characters found by Brophy (2004) concern coloration patterns of the head (see Figure 1). Six or more nasal strips and narrow a infraorbital strip characterizes *M. subtrijuga* while *M. macrocephala* has four or less nasal strips and a wide infraorbital strip. The shell shape difference patterns between these two species have not been depicted into details yet but just partially by Brophy (2004).

Molecular studies are classical tool for investigating genomic differentiation among individuals, and ultimately for delimiting species. However, phenotypes and geographical distribution are also important character to consider evolving units.

Recently, Guillot *et al.*, 2012 proposed the method to jointly analyze geographical, genetic and phenotypic data for delimiting taxa.

In turtle biology, geometric morphometrics have been used for quantifying differences between ecological and taxonomic groups (Claude *et al.*, 2003, 2004), as for addressing morphofunctional hypotheses (Rivera and Claude, 2008) or at a lower scale to address taxonomic problems concerning cryptic species (Chiari and Claude, 2011; 2012). These methods allow to depict and quantify subtile shape change and have demonstrated their power in the field of turtle taxonomy (eg., Chiari and Claude, 2012): they should therefore be useful for distinguishing shell patterns in closely species like the one known in the genus *Malayemys* and *Cyclemys*.

Many softwares have been developed for performing with morphometrics. Among them, R is probably the more integrated plateform allowing to work from data acquisition to data management, to data treatment, to finally statistical analyses and graphic display (Claude, 2008; R Core development team, 2010).

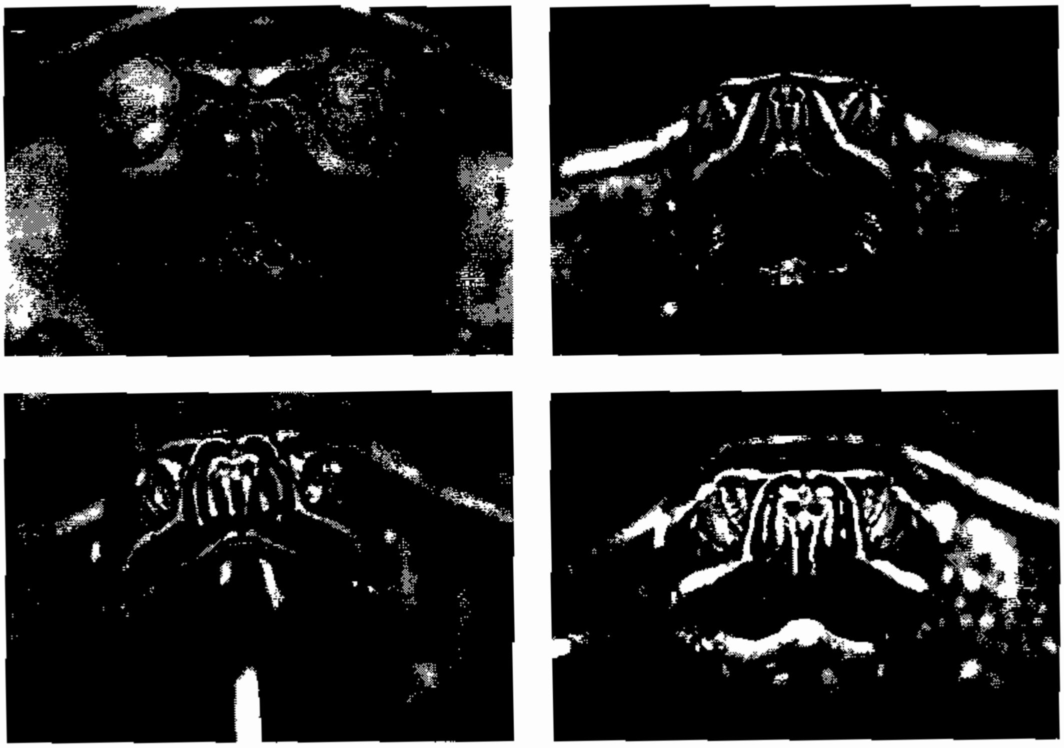


Figure 1 *Malayemys* photographs; *M. macrocephala* exhibiting nasal stripes two (left top) and four (right top) and *M. subtrijuga* exhibiting nasal stripes six (left below) and seven (right below) (Brophy, 2004: Fig. 1 and 2, p. 67).

3.2 Methods

3.2.1 Localities and sampling

All specimens from 13 provinces representing 4 of 8 major drainage basins of Thailand were sampled. Sample localities (Figure 2) include Mae Nam Mun basin (Buriram, Surin and Ubon Ratchathani provinces), Mae Nam Chi basin (Chaiyaphum, Maha Sarakham, Roi Et and Yasothon provinces), Mae Nam Khong basin (Mukdahan, Loei and Nakhon Phanom provinces), and Mae Nam Chao Phraya basin (Uthai Thani, Nakhon Sawan, and Singburi provinces). Number of sampling individuals of *Malayemys* species for carapace and plastron are shown in Table 3.1 and 3.2, respectively.

Table 3.1 Sampling effort for *Malayemys* carapace according to sex, species and localities; species identification is priorly based on Brophy (2004).

Species Locality (province)	*Malayemys macrocephala*				*Malayemys subtrijuga*			
	Number of sampling individuals							
	Male	Female	Juvenile	Sum	Male	Female	Juvenile	Sum
1. Buriram (BR)	5	6	-	11	1	9	-	10
2. Surin (SR)	-	2	-	2	8	9	-	17
3. Ubon Ratchathani (UB)	6	9	7	22	2	3	2	7
4. Chaiyaphum (CY)	9	10	1	20	-	-	-	-
5. Maha Sarakham (MH)	25	7	1	33	-	-	-	-
6. Roi Et (RE)	6	3	-	9	-	-	-	-
7. Yasothon (YT)	25	22	12	59	-	-	-	-
8. Mukdahan (MD)	3	3	3	9	-	-	-	-
9. Loei (LO)	6	1	-	7	-	-	-	-
10. Nakhon Phanom (NP)	21	10	11	42	-	-	-	-
11. Uthai Thani (UT)	8	10	-	18	-	-	-	-
12. Nakhon Sawan (NS)	14	24	1	39	-	-	-	-

Table 3.1 (continued)

Species Locality (province)	*Malayemys macrocephala*				*Malayemys subtrijuga*			
	Number of sampling individuals							
	Male	Female	Juvenile	Sum	Male	Female	Juvenile	Sum
13. Singburi (SB)	2	13	1	16	-	-	-	-
Summary	131	119	37	**287**	11	21	2	**34**
Sampling individuals for carapace	**321**							

Table 3.2 Sampling efforts for *Malayemys* plastron according to sex, species and localities; species identification priorly based on Brophy (2004).

Species Locality (province)	*Malayemys macrocephala*				*Malayemys subtrijuga*			
	Number of sampling individuals							
	Male	Female	Juvenile	Sum	Male	Female	Juvenile	Sum
1. Buriram (BR)	7	7	-	14	4	11	-	15
2. Surin (SR)	-	2	-	2	10	9	-	19
3. Ubon Ratchathani (UB)	6	10	8	24	2	3	2	7
4. Chaiyaphum (CY)	10	11	2	23	-	-	-	-
5. Maha Sarakham (MH)	23	8	1	32	-	-	-	-
6. Roi Et (RE)	6	3	-	9	-	-	-	-
7. Yasothon (YT)	27	21	13	61	-	-	-	-
8. Mukdahan (MD)	3	4	4	11	-	-	-	-
9. Loei (LO)	6	1	-	7	-	-	-	-
10. Nakhon Phanom (NP)	24	13	11	48	-	-	-	-
11. Uthai Thani (UT)	10	13	-	23	-	-	-	-
12. Nakhon Sawan (NS)	14	25	1	40	-	-	-	-
13. Singburi (SB)	2	13	1	16	-	-	-	-
Summary	139	130	41	310	16	23	2	41
Sampling individuals for plastron	**351**							

Specimens with strong abnormalities are excluded from the sample.

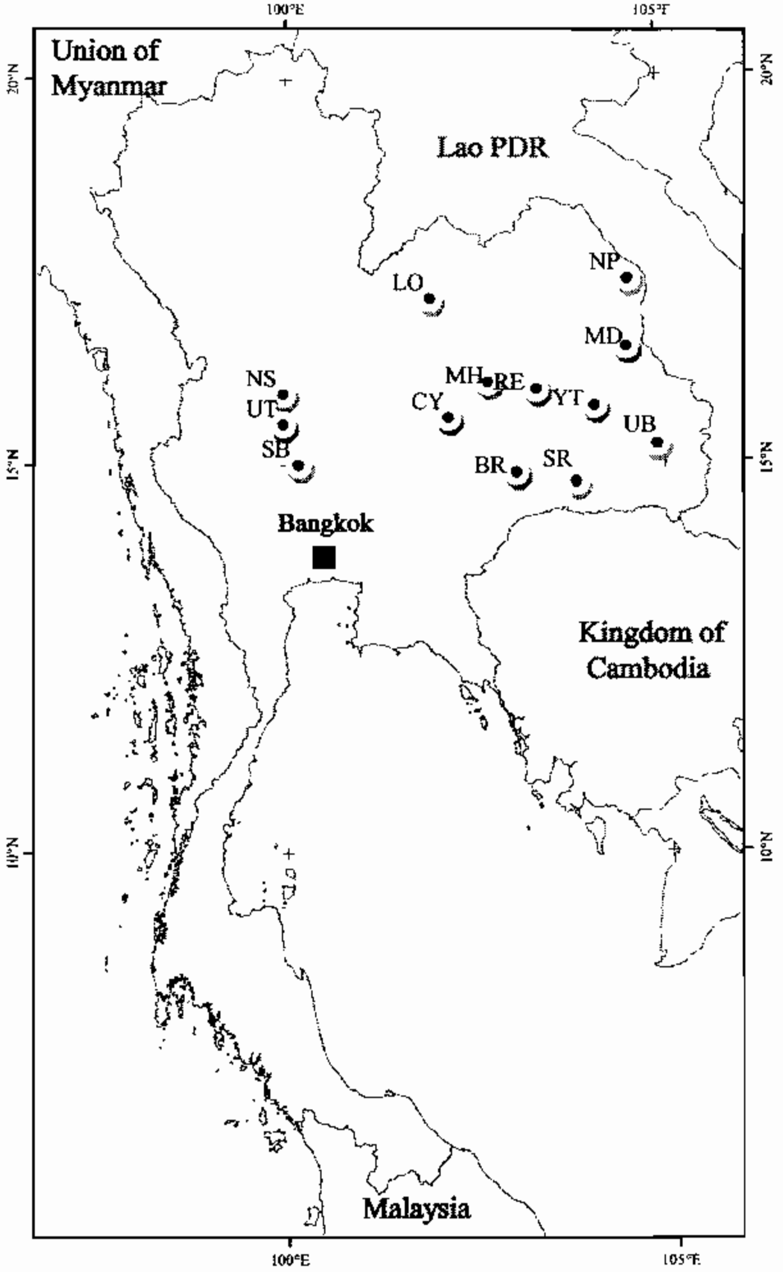


Figure 2 Localities where *Malayemys* were sampled indicated by black dot (●).

3.2.2 Landmark data

Landmarks are identified for the carapace and plastron of turtles (modified from Claude *et al.*, 2003). These landmarks are mostly located between epidermal scutes covering the carapace and plastron and are defined as follows.

Carapace (Figure 3)

1 and **2**-scale bar; **3**-anterior left end of the cervical; **4**-posterior left end of the cervical; **5**-anterior lateral left end of the 1st vertebral; **6**- intersection between first and second vertebrals and first left pleural; **7**- intersection between first and second left pleurals and second vertebral; **8**-intersection between second and third vertebral and second left pleural; **9**-intersection between second and third left pleurals and third vertebral; **10**-intersection between third and fourth vertebrals and third left pleural; **11**-intersection between third and fourth left pleurals and fourth vertebral; **12**-intersection between fourth and fifth vertebrals and fourth left pleural; **13**-intersection between fourth and fifth vertebrals and left marginal scute; **14**-intersection between third and fourth vertebrals and left marginal; **15**-intersection between second and third vertebrals and left marginal; **16**-intersection between first and second vertebrals and left marginal; **17**- anterior right end of the cervical; **18**- posterior right end of the cervical; **19**- anterior lateral right end of the 1st vertebral; **20**- intersection between first and second vertebrals and first right pleural; **21**- intersection between first and second right pleural and second vertebral; **22**- intersection between second and third vertebrals and second right pleural; **23**- intersection between second and third right pleurals and third vertebral; **24**-intersection between third and fourth vertebrals and third right pleural; **25**- intersection between third and fourth right pleurals and fourth vertebral; **26**- intersection between fourth and fifth vertebrals and fourth right pleural; **27**- intersection between fourth and fifth vertebrals and right marginal; **28**- intersection between third and fourth vertebrals and right marginal; **29**- intersection between third and fourth vertebrals and right marginal; **30**-intersection between first and second vertebrals and right marginal; **31**-Intersection between the lateral margin and the first and second left marginal; **32**-Intersection between the first and second left marginals and first pleural; **33**-intersection between the lateral margin and the second and third left marginal; **34**-intersection between the second and third left marginals and first pleural; **35**-intersection between the lateral margin and tenth and eleventh left marginal; **36**-

intersection between tenth and eleventh left marginals and fourth left pleural; **37-** intersection between the lateral margin and eleventh and twelfth left marginal; **38-** intersection between eleventh and twelfth left marginals and fifth vertebral; **39-** intersection between the lateral margin and first and second right marginal; **40-** intersection between first and second right marginals and first right pleural; **41-** intersection between the lateral margin and second and third right marginal; **42-** intersection between second and third right marginals and first right pleural; **43-** intersection between the lateral margin and tenth and eleventh right marginal; **44-** intersection between tenth and eleventh right marginals and fourth right pleural; **45-** intersection between the lateral margin and eleventh and twelfth right marginal; **46-** intersection between eleventh and twelfth right marginals and fifth vertebral; **47-** intersection between twelfth marginal and fifth vertebral; **48-**intersection between twelfth marginal and posterior carapace margin.

Plastron (Figure 4)

1 and **2**-scale bar; **3-** anterior contact between gulars; **4**-contact between right gular, and left and right humerals; **5**-contact between right humeral and left and right pectorals; **6**-contact between right abdominal and left and right humerals; **7**-contact between right femoral and left and right abdominals; **8**-contact between right anal and left and right femorals; **9-** posterior end of the plastron at the contact between anals; **10-** most lateral contact between right humeral and gular; **11**-most lateral contact between right humeral and pectoral; **12**-posteriormost right end of the axillary notch; **13-** anteriormost contact between right plastral and carapace scutes at the right anterior plastral lobe; **14-** lateral contact between right pectoral, abdominal scutes and marginals; **15**-anteriormost contact between plastral and carapace scutes at the right posterior plastral lobe; **16-** posteriormost right end of the inguinal notch; **17-** most lateral contact between right abdominal and femoral scutes; **18**-most lateral contact between right femoral and anal; **19-** most posterior right end of the xiphiplastron; **20-** contact between left gular, and left and right humerals; **21-** contact between left humeral and left and right pectorals; **22-** contact between left abdominal and left and right humerals; **23-** contact between left femoral and left and right abdominals; **24-** contact between left anal and left and right femorals; **25-** most lateral contact between left humeral and gular; **26-** most lateral contact between left humeral and pectoral; **27-**

posteriormost left end of the axillary notch; **28-** anteriormost contact between left plastral and carapace scutes at the right anterior plastral lobe; **29-** lateral contact between left pectoral and abdominal scutes and marginals in contact; **30-** anteriormost contact between plastral and carapace scutes at the left posterior plastral lobe; **31-** posteriormost left end of the inguinal notch; **32-** most lateral contact between left abdominal and femoral scutes; **33-** most lateral contact between left femoral and anal; **34-** most posterior right end of the xiphiplastron.

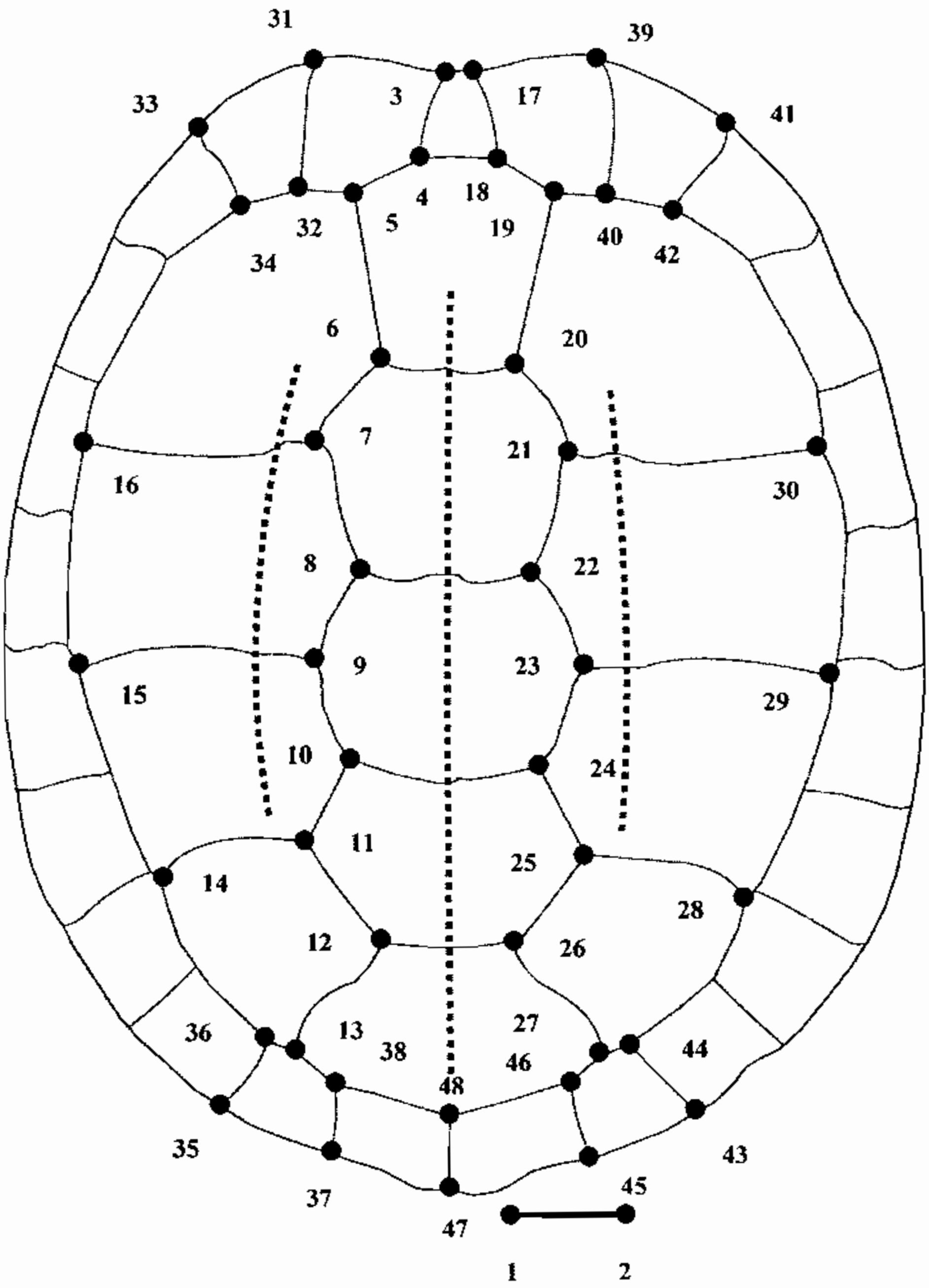


Figure 3 Landmarks located on the *Malayemys* carapace in dorsal view (modified from Claude *et al.*, 2003). Full lines indicate sulci of epidermal scutes and dotted line indicated central and lateral keels.

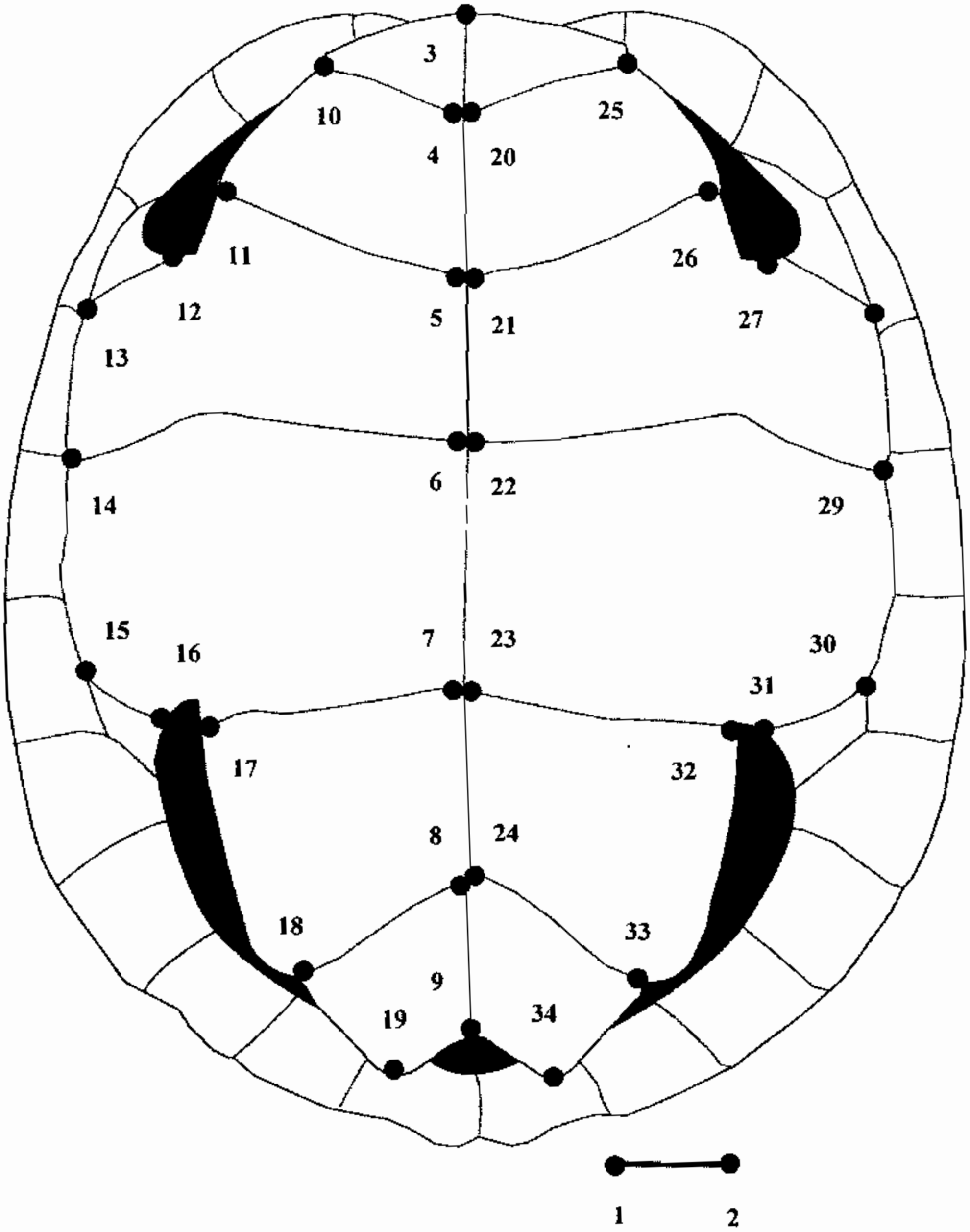


Figure 4 Landmarks located on the *Malayemys* plastron in the ventral view (modified from Claude *et al*., 2003). Full lines indicated sulci of epidermal scutes.

3.2.3 Digitization of landmarks

In order to obtain landmark coordinates, specimen were first photographed. In this aim, each specimen was positioned on flatten area with scale bar. Three views were photographed by a digital camera: frontal view of the head (in order to have an information about the stripe pattern defining the two species according Brophy classification in 2004), external view of the carapace and the plastron. The specimen were positioned so that their coronal plans were always parallel to the cameral length at a focal distance above 50 cm from the camera to avoid lateral deformation as much as possible. In order to estimate error with positioning of the camera or of the specimens two replicates for each individual were taken for carapace and plastral view. In order to generate a photo bank, all pictures were later labeled with a name of six characters; the first correspond to a number specifying the replicate and the picture (carapace or plastron). 1 or 2 are used to specify the carapace replicate; 3 or 4 for the plastron replicate, the picture of the head received the 5 value. The second and third characters indicate the provinces abbreviations, the fourth and fifth letters indicate the specimen ID for a given locality, the last sixth letter indicate the sex (F: female, M: male, J: Juvenile). For instance, 1 MH 05 F means carapace of the fifth of female turtle from Maha Sarakham locality.

Forty six and thirty two anatomical landmarks of the carapace and plastron respectively were digitized directly on pictures together with a scale bar. Landmarks on labeled photos were digitized together with a scale for calibrating the size of pictures. All coordinates have been acquired using TPSDIG version 2.16 (Rohlf, 2004). The landmarks correspond to the intersections between epidermal scutes for both carapace and plastron (see Figure 3 and Figure 4). Bookstein provided three types of landmarks: type I represent discrete juxtapositions of tissues; type II representing local maximum of curvature and; Type III representing extremal points (Booksteins, 1991). All the landmarks used here were considered as type I and II in Booksteins's nomenclature of landmarks classification. Most were of the I type, but landmarks for both axlliary and inguinal notches and the end of xiphiplastron are of the II type.

Morphometric procedure: for obtaining shape information from landmark raw coordinates, a procrustes superimposition was performed on the whole set of configurations for the carapace and the plastron. Size was defined by the centroid size (the square root of the sum of squared distances from each landmark to the centroid of the configuration of landmarks for a specimen (Bookstein, 1991)) and was also considered in further analyses (eg., for considering possible allometries, or analyzing size variation between localities). All specimens were superimposed together following the partial generalized procrustes superimposition (Dryden and Mardia, 1998; Claude, 2008). The algorithms and routines in R are given in Claude (2008). In order to perform later statistical analysis the landmark coordinates were projected into the euclidean shape space by an orthogonal projection (see Dryden and Mardia, 1998; Claude, 2008). These transformed coordinates were later used as variables for later analyses. It should be however reminded that four degrees of freedom are lost during the superimposition. Therefore there will be 4 null dimensions in that shape space. In order to remedy to this problem the non Null principal components of a PCA were considered as shape variables.

3.2.4 Statistical analyses

Percentage of the size measurement error was computed using one-way analysis of variance (ANOVA) on centroid size of all replicated specimens. It was calculated from the mean squares and cross products corresponding to the specimen and residual sources of variation following the Procrustes Anova approach described in Claude *et al.* (2003) (see also Klingenberg and McIntyre, 1998).

A principal components analysis was performed on averaged configurations for each individuals (average of the two replicates) and ordination of individuals was plotted on the first two PCs. To understand which shape features were involved (sex, putative species), reconstruction of extreme morphologies along PC was obtained for Procrustes data. The effects of sex and localities are estimated by ANOVA on centroid size carapace and plastron. Similarly a multivariate linear model was applied on shape with the sex, locality, and size variable as well as the interactions. Effects were tested by using a multivariate analysis of variance between the effect and the residual variance of the model. Because of in balance between groups, univariate (for size) and multivariate (for shape) analyses of variance were using type II sums of squares (and cross products). In order to visualize differences between populations, a linear discriminant analysis on the whole set of individuals was performed, considering population as grouping factor. On this canonical analysis, population where plotted and it was visually checked whether the stripe pattern was coincident with the ordination based on morphology. In order to avoid confounding effect of sex, the same analysis was performed for each sex and excluding juveniles. These analysis were performed with R.2.15.2.

3.3 Results

3.3.1 Measurement error

The percentage of measurement error for carapace is 1 % for centroid size and 9.5 % for shape. For plastron, the percentage of measurement error is less than 1 % (0.6) for centroid size and 8.9 % for shape. The specimen factor is significant. It indicates that interindividual shape and variations are more effective than variation between replicated measurements on the same individual.

3.3.2 Analysis of principal components of shape variation (PCA)

3.3.2.1 *Carapace*

The projection of individuals on eigenvectors is shown in Figure 5. The PCA first plan on carapace shows that variation overlap between populations overlaps on PC1 and PC2. There is, however, clearly a difference between sexes, females having lower scores on PC1 and PC2, while males have higher scores on these two PCs. The first principal component (PC1) explained 24.7% of the total variance. On PC1, variation corresponds to carapace shapes that are narrower anteriorly and wider posteriorly with narrower vertebral scutes for higher scores opposed to carapace shapes that are wider anteriorly and narrower posteriorly for lower scores a relatively narrower anteriorly with wider vertebral scutes (see Figure 5, right top). The second principal component (PC2) explained 11.4% of the total variance. On PC2, variation corresponds to carapace shapes with anteriorly wide vertebral scutes and long anterior marginal scutes opposed to carapace shapes that display anteriorly narrow vertebral scutes with short anterior marginal scutes (see Figure 5, right below).

3.3.2.2 *Plastron*

On the principal components analysis on plastron (Figure 6), PC1 represents 29.1% of the total variance. On this axis, shape variation opposes plastrons with longer anterior lobes and short anal scutes, relatively narrow pectorals and abdominals (lower scores) to plastrons with shorter anterior lobes, and larger anal scutes, with wider pectoral and abdominal scutes (higher scores). On PC2 (16.1% of the total variance), shape variation opposes plastron with short gulars, short humerals, and short anal scutes, and longer bridge area (lower scores), with plastron with longer gulars, humerals and anal scutes, wider posterior plastral lobes and shorter bridge area (larger scores) (see Figure 6, right top).

There is an important overlap between population for plastron variation for these two PCs. However, sex dimorphism is expressed on these shape components of variation, females have higher scores on PC1 and lower scores on PC2 by comparison to males which would mean that females would have a shorter anterior plastral lobe and a wider posterior plastral lobes than males.

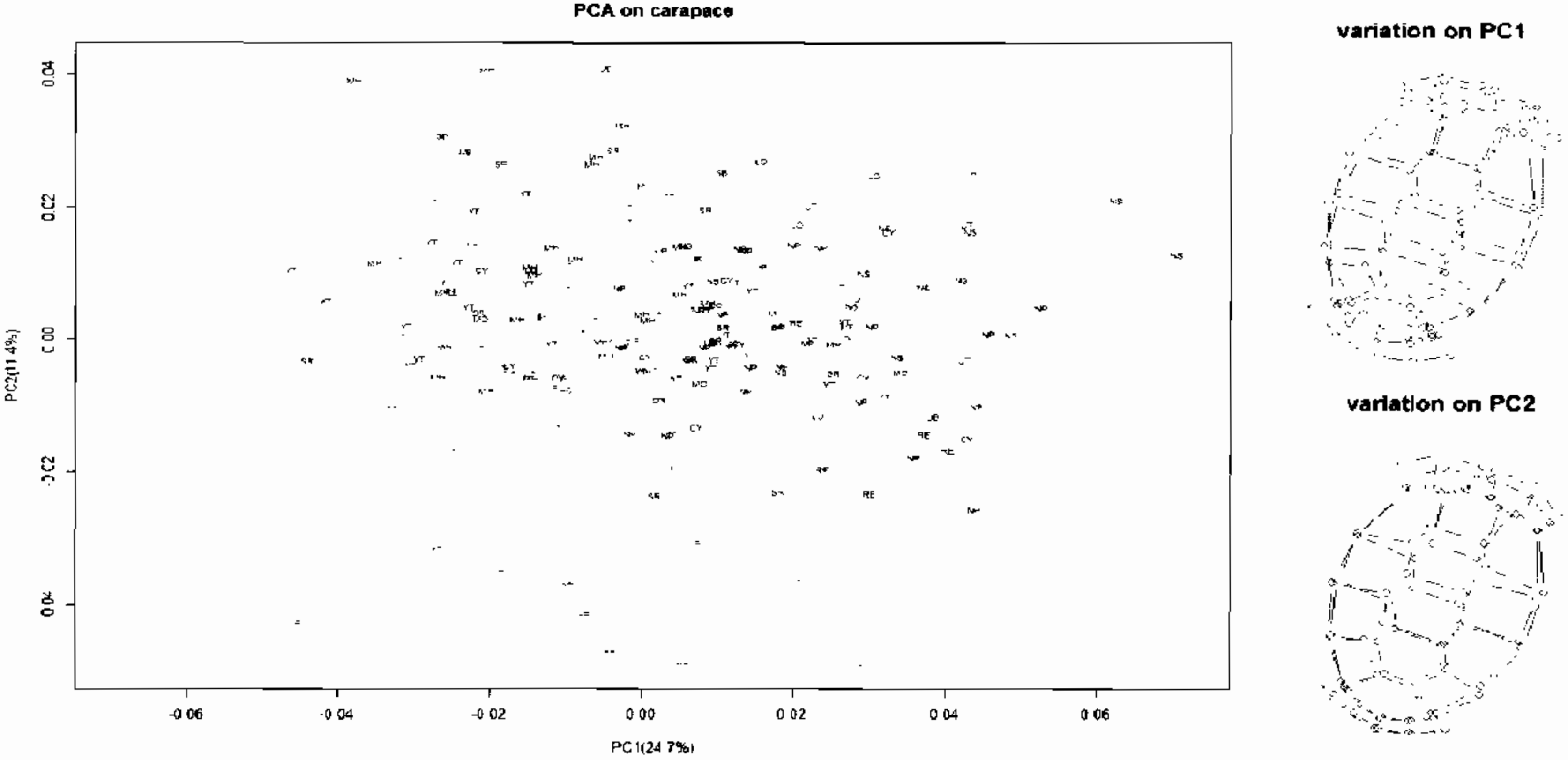


Figure 5 PCA on carapace, localities are displayed with different abbreviations of sample provinces (in Table 3) while colors represent sex (red: female, blue: male, grey: juvenile individuals), patterns of variation on PC1 and PC2 are exhibited on the right side of the plot; purple corresponding to maximal scores, green to minimal ones.

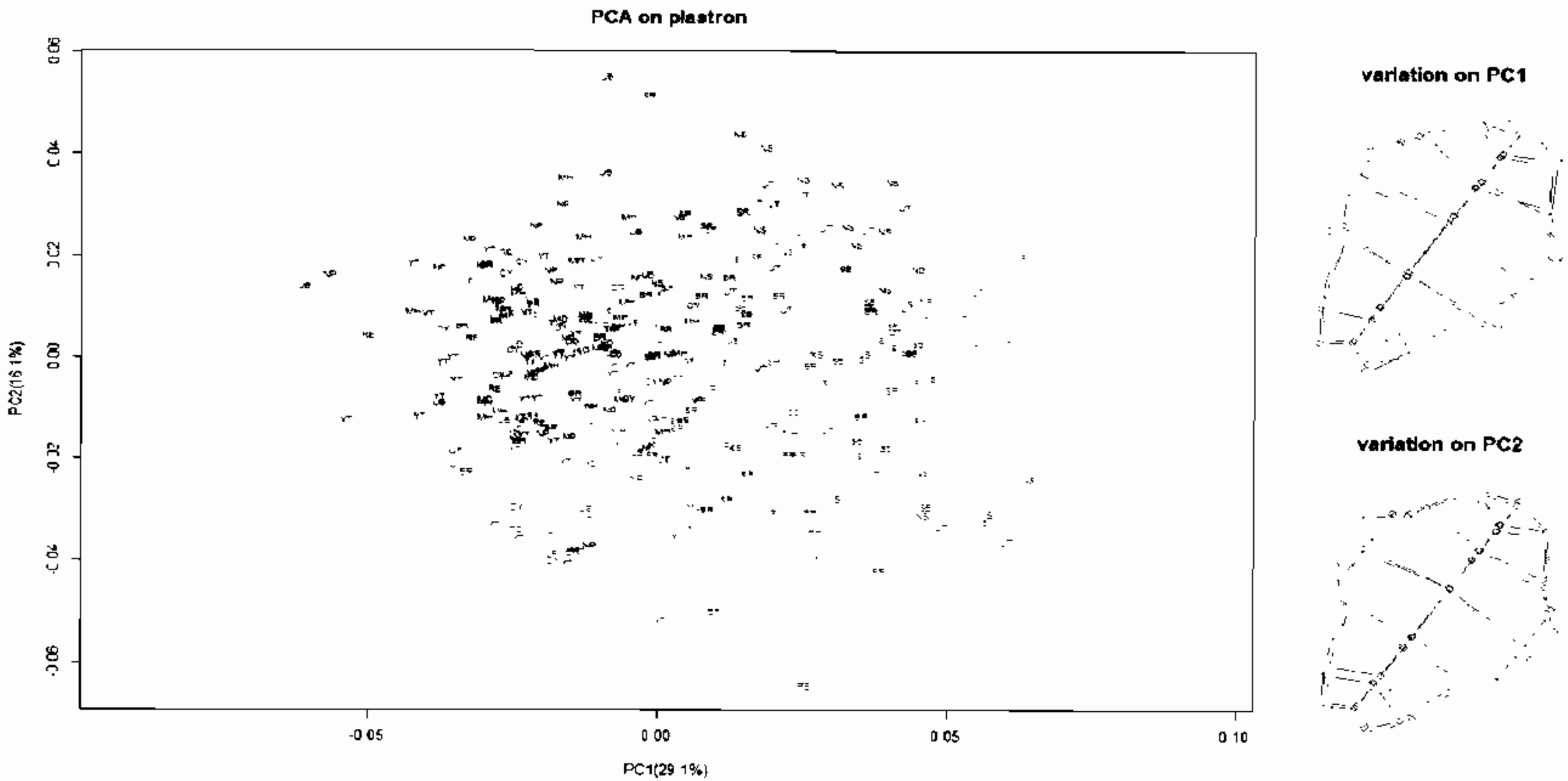


Figure 6 PCA on plastron, localities are displayed with different abbreviations of sample provinces (in Table 3) while color represent sex (red: female, blue: male, grey: juvenile), patterns of variation on PC1 and PC2 are exhibited on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

3.3.3 Differences between localities and sexes

3.3.3.1 *Carapace*

There are size differences between localities and between sexes, sex size dimorphism is not the same between localities (significant interaction see Table 3.4). On Figure 7, males are usually smaller than females and there is a variation in size between localities. Sex and locality have a significant effect on shape variation (Table 3.3). In addition, there is a significant interaction between these two factors, which mean that sex dimorphism in shape is not the same between localities.

According to the Manova test reported in Table 3.5 and incorporating size, carapace shape is related with sex, size, and localities, and the significant interaction between three factors indicate that there are differences is sex shape dimorphism between localities, and growth is not the same between sexes.

Table 3.3 Manova on shape variation explained by non null principalcomponents (loc: localities, sex: sex).

Factor	Df	Pillai	approx F	num df	den df	P-value
Loc	12	6.1632	2.1599	1056	2160	< 2.2e-16 ***
Sex	1	0.7763	6.6627	88	169	< 2.2e-16 ***
Loc:Sex	12	4.1860	1.0957	1056	2160	0.04124 *

Table 3.4 Size variation on Anova (Type II tests) of individual centroid size carapace.

Factor	SS	Df	F value	P-value
Loc	2215.4	12	5.1928	8.46e-08 ***
Sex	3964.4	1	111.5091	< 2.2e-16 ***
Loc:Sex	1272.0	12	2.9816	0.0006426 ***
Residuals	9101.3	256		

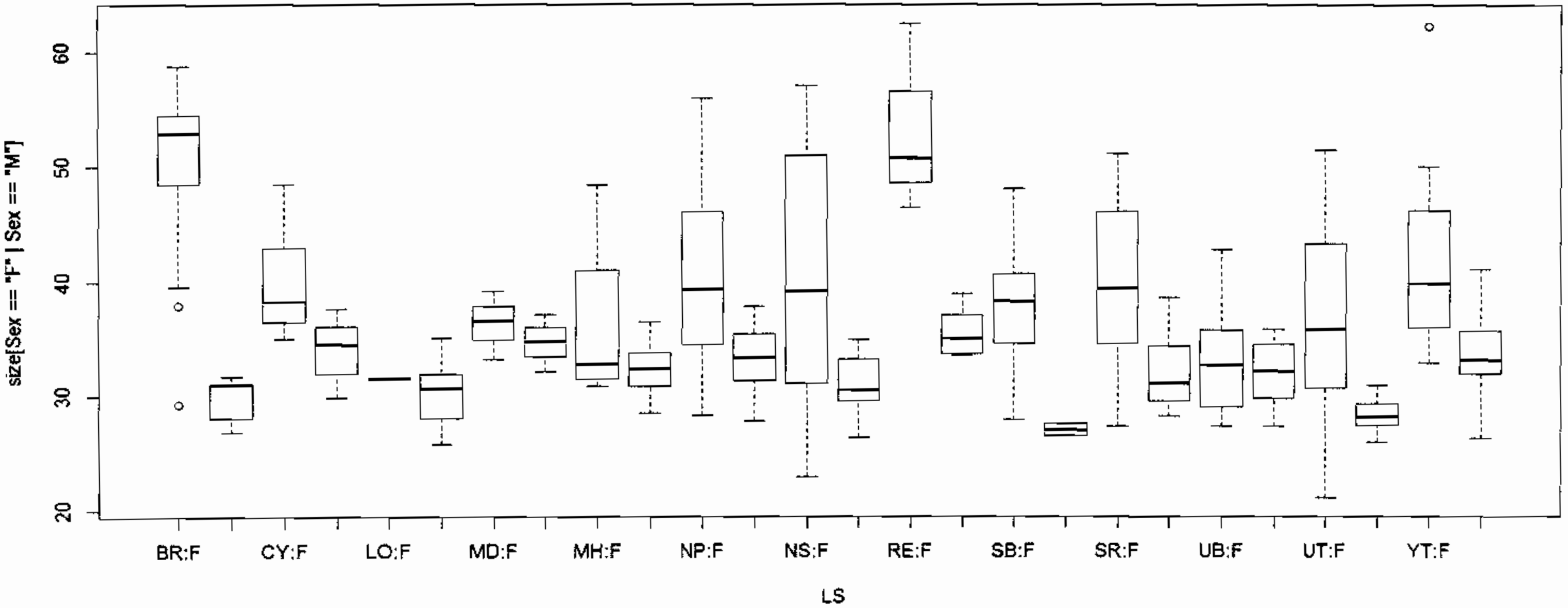


Figure 7 Box plot of *Malayemys* carapace size variation between sexes and localities: BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon.

Table 3.5 Type II MANOVA on shape variation described by non null principal components.

Factor	Df	test stat	approx F	num Df	den Df	P-value
Sex	1	0.17580	25.7024	2	241	7.620e-11 ***
Loc	12	0.63053	9.2851	24	484	< 2.2e-16 ***
Size	1	0.20165	30.4355	2	241	1.639e-12 ***
Sex:Loc	12	0.16058	1.7605	24	484	0.0149793 *
Sex:Size	1	0.02272	2.8017	2	241	0.0626834
Loc:Size	12	0.20413	2.2923	24	484	0.0005321 ***

3.3.3.2 *Plastron*

There are significant size differences between localities and between sexes (Table 3.7). In addition the significant interaction between these factors shows that sex size dimorphism is not the same between localities. Sex and locality have an effect on shape variation of plastron significantly (see Table 3.6), moreover there is an interaction between these two factors, which means that sex dimorphism in shape is not the same between localities. When size is considered in the Manova, shape is significantly explained by size, sex and localities and sex and size also interact, showing that there are differences in allometric growth between sex.

Table 3.6 Shape variation on Anova of principle components.

Factor	Df	Pillai	approx F	num df	den df	P-value
Loc	12	4.5672	2.3964	720	2808	< 2.2e-16 ***
Sex	1	0.7116	9.1690	60	223	< 2.2e-16 ***
Loc:Sex	12	2.7305	1.1488	720	2808	0.008395 **

Table 3.7 Size variation on Anova (Type II tests) of individual centroid size carapace.

Factor	SS	Df	F value	P-value
Loc	1760.5	12	6.4556	3.756e-10 ***
Sex	3077.2	1	135.4054	< 2.2e-16 ***
Loc:Sex	804.0	12	2.9482	0.0006966 ***
Residuals	6408.6	282		

Table 3.8 Shape variation on Type II MANOVA of shape principle components.

Factor	Df	test stat	approx F	num Df	den Df	P-value
Sex	1	0.26188	47.365	2	267	< 2.2e-16 ***
Loc	12	0.72978	12.831	24	536	< 2.2e-16 ***
size	1	0.15077	23.702	2	267	3.346e-10 ***
Sex:Loc	12	0.10507	1.238	24	536	0.20135
Sex:size	1	0.02698	3.702	2	267	0.02596 *
Loc:size	12	0.11274	1.334	24	536	0.13378

3.3.4 Structuration of the shape space

3.3.4.1 *Carapace*

Two groups can clearly be identified on the canonical analysis based on carapace shape and using population as factor. The first group is from the central plain with the population of Singburi, Uthai Thani, and Nakhon Sawan, and the second group contain all the populations from Northeastern Thailand (see Figure 8). Sex does not affect the ordination of populations (independent analysis were done according of each sex and display the same result). Northeastern Thailand and central plain populations do not overlap: one can conclude that the practice of selling and releasing turtle does not impact the biogeography of this turtles at interregional scale.

The stripe color pattern (Figure 9) does not match with this grouping. Indeed in populations of Surin, Ubon and Buriram, several individuals where found with the *M. subtrijuga* and *M. macrocephala* stripe pattern. These individuals do not form any grouping structure between or within these populations suggesting that stripe head color patter do not match carapace morphological variation. The Northern population, displaying the "*macrocephala*" pattern in Northeastern Thailand are morphologically all classified with individuals displaying the *"subtrijuga"* pattern and the central plain populations are all classified in *M. macrocephala*. The population from Surin, Ubon and Buriram, are closer to north eastern population of the North than populations of the central plain and should then belong to the same group. Differences in carapace morphology between Northeastern Thailand and central plain do not reflect differences between species identified by stripe pattern. The mixed pattern of the population in the South of Northeastern Thailand could be the result of a possible introgression between the two species in the South of Northeastern Thailand; or may correspond to a third geographical group. The head shape pattern of North of Northeastern population may be a feature that is shared by the central plain populations independently of their classification in terms of carapace variation. Molecular sequencing could be a solution to know exactly what happened, it would also be necessary to sample more population that are composed at 100% of *M. subtrijuga* morphotype, and these populations should therefore not overlap with *M. macrocephala* that are found in the North of Northeastern Thailand.

On LD1 (axis that discriminate Northeastern populations from the central plain, the higher scores (in purple and corresponding to Northeastern populations, show carapace shapes with a larger cervical scute, and with a first vertebral scute margin that is as long posteriorly as anteriorly; by contrast populations with lower scores (from the central plain), displaying smaller cervical scute, more emarginated anterior margin of the carapace and a first vertebral scute that is wider anteriorly than posteriorly.

On LD2, variation is more subtile, with carapace having longer anterior marginal and first vertebral scutes opposed to populations that show shorter anterior marginal scutes, and shorter first vertebral scute (Buriram, Surin, Ubon Ratchathani, where *M. subtrijuga* stripe pattern were found).

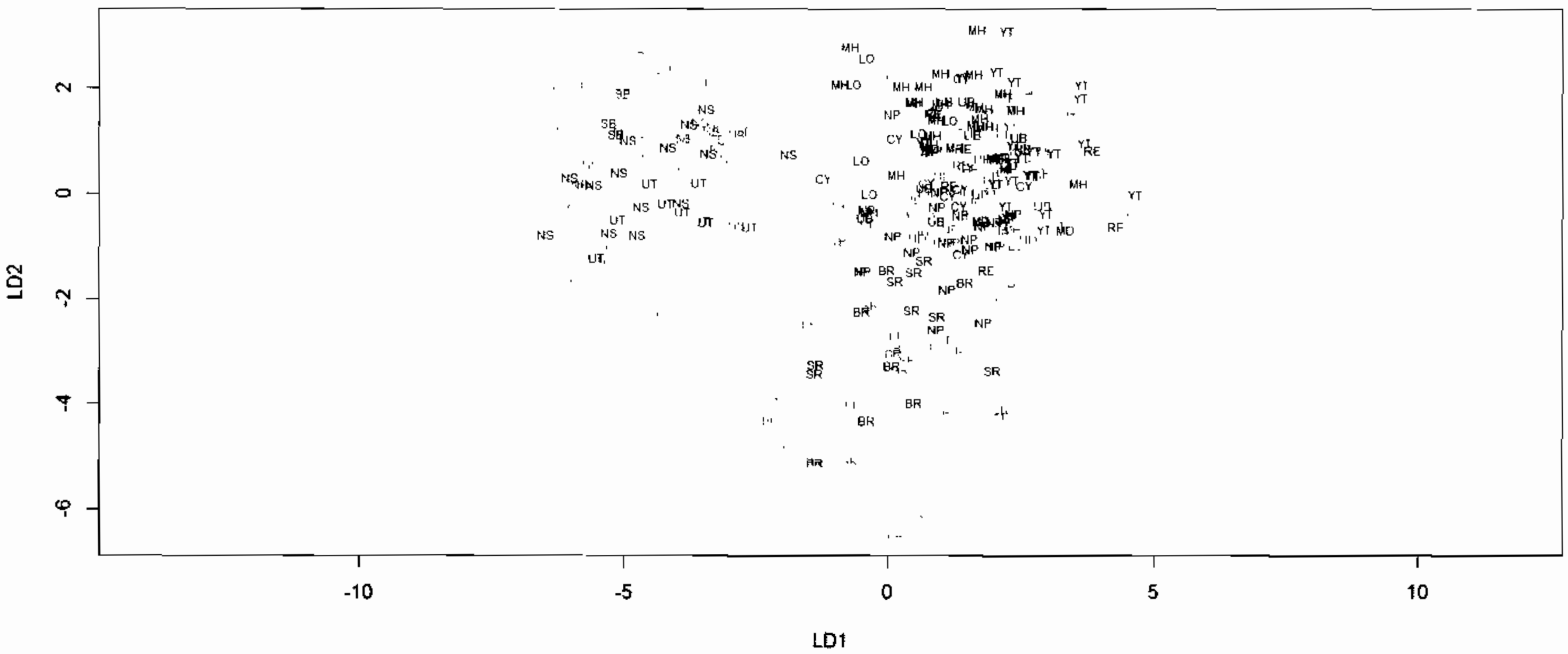


Figure 8 Linear discriminant analysis plot of *Malayemys* carapace (colors indicate sex: blue, male; red, femal; grey: juveniles) in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon.

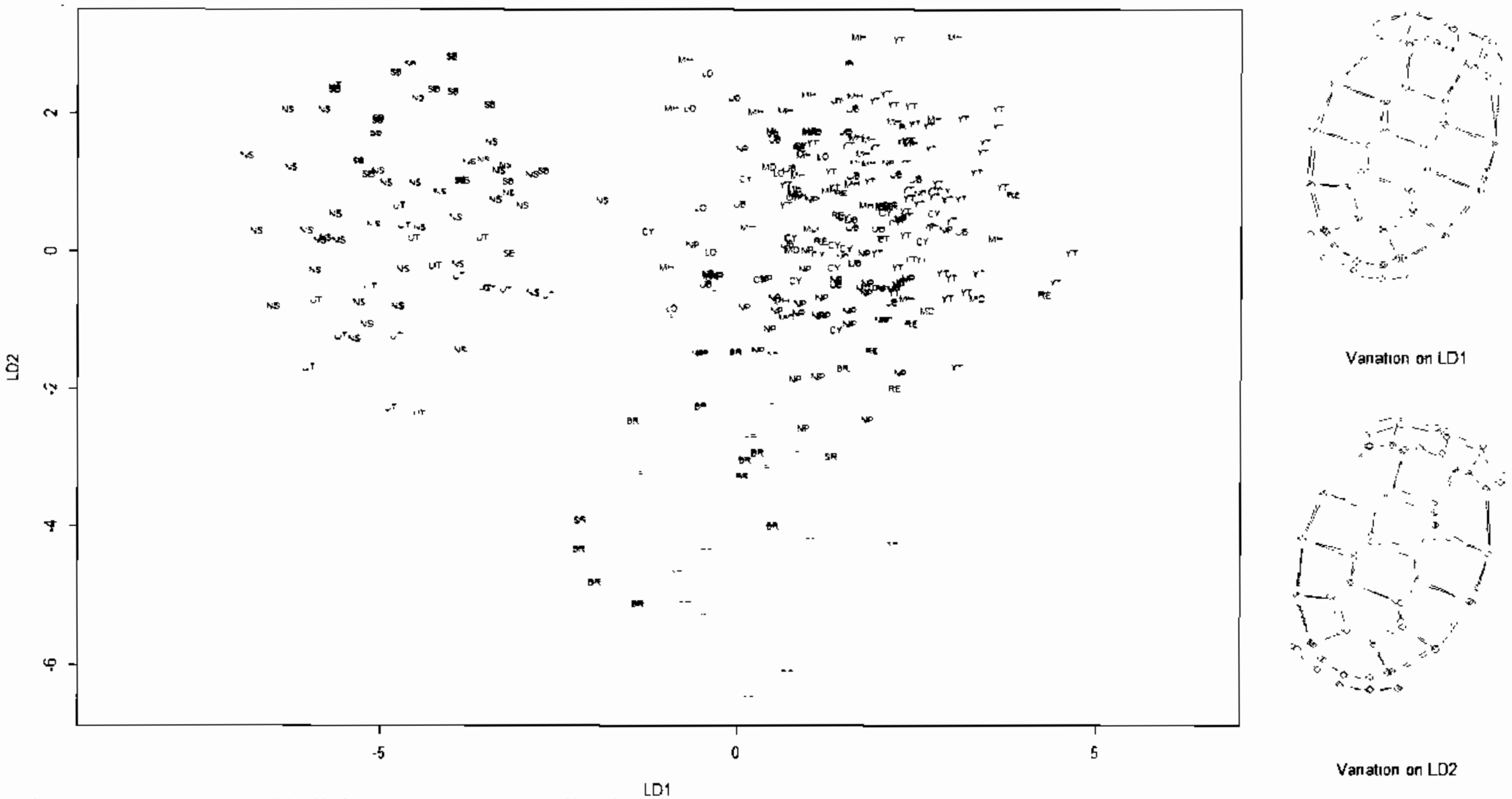


Figure 9 Ordination of individuals on the linear discriminant analysis of carapace shape on population. Colors indicate strip pattern: black, *macrocepala*; red, *sutrijuga* in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

3.3.4.2 *Female carapace*

There are 140 females identified in the data set. On the lda plot for females, three groups are clearly distinct, one containing turtles from the central plain, one containing turtles from Surin, Roi Et, Loei and Buriram, and the other containing the other Northeastern localities (see Figure 10). Turtles with the *M. subtrijuga* stripe pattern are either in one or the other group of the Northeastern turtles, but do not form a single group. Carapace shapes variation is better understood in regard of geography on LD1. This, however, does not match well with stripe pattern, indicating that this character seems to be not related with population differentiation. This further suggest that carapace differences may be correct to identify taxa rather than stripe differences; even so it should be molecularly tested.

Morphological variation was drawn along canonical axes to describe in which respect populations differ (Figure 10, right of the plot). On LD1 (axis that discriminate Northeastern populations from the central plain), the higher scores (in purple), corresponding to Northeastern populations, show carapace shapes with a larger cervical scute, and with a first vertebral scute margin that is as long posteriorly as anteriorly; by contrast populations with lower scores (from the central plain), display smaller cervical scute, more emarginated anterior margin of the carapace and a first vertebral scute that is wider anteriorly than posteriorly. On LD2, variation is more subtile, with carapace having longer anterior marginal and first vertebral scutes, wider carapaces, opposed to populations that show shorter anterior marginal scutes, and shorter first vertebral scute and narrower carapace (Buriram, Surin, Roi Et, Loei).

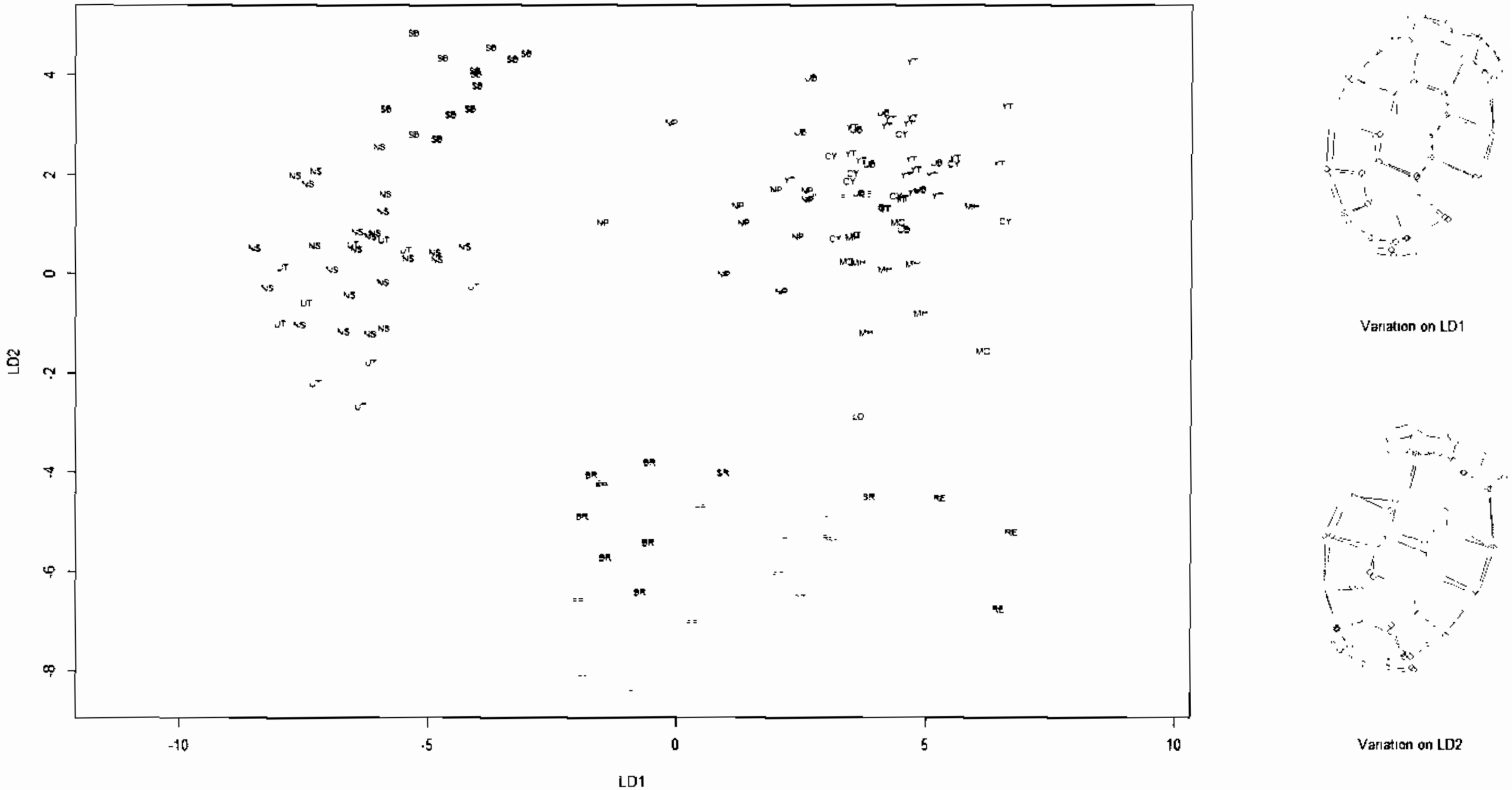


Figure 10 Ordination of female individuals on the linear discriminant analysis of female carapace shape on population. Colors indicate strip pattern: black, *macrocepala*; red, *subtrijuga* in the following localities: BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan; MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

3.3.4.3 *Male carapace*

There are 142 males identified in the data set. On the lda plot for males (Figure 11), four groups are clearly distinct, one containing turtles from the central plain (higher scores on LD1), one containing turtles from Surin, Loei and Buriram (lower scores on LD2), one containing turtles from Chaiyaphum, Roi Et and Mukdahan (higher scores on LD2) and the other containing the other Northeastern Localities (median scores on LD2). Turtles with the subtrijuga stripe pattern are either in one or the other group of the Northeastern turtles, but do not form a single group. Carapace shapes variation is better understood in regard of geography on LD1. This, like females, does not match well with stripe pattern, indicating that this character seems to be not related with population differentiation according to stripe pattern. This further suggest that carapace differences may be correct to identify taxa rather than stripe differences; even so it should be molecularly tested.

On LD1 (axis that discriminate Northeastern populations from the central plain), the lower scores (in green and corresponding to Northeastern populations), show carapace shapes with a larger cervical scute, and with a first vertebral scute margin that is as narrower anteriorly; by contrast populations with lower scores (from the central plain), displaying smaller cervical scute, more emarginated anterior margin of the carapace and a first vertebral scute that is wider anteriorly than posteriorly. On LD2, variation is really subtile, with carapace being a bit wider for lower scores (Singburi, Loei, Buriram, Surin), opposed with carapace a bit longer for higher scores (Chaiyaphum, Mukdahan, Roi Et) (Figure 11).

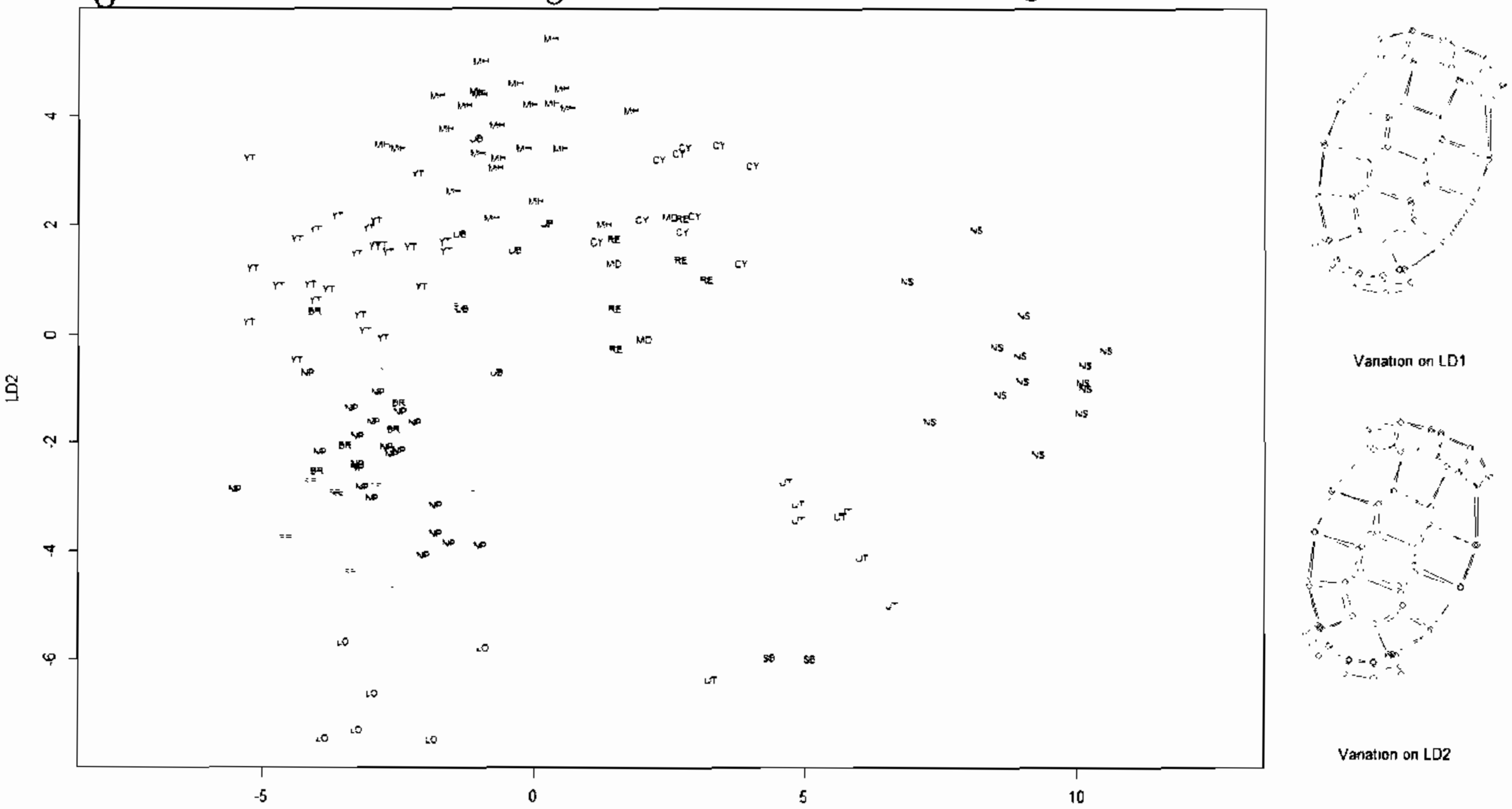


Figure 11 Ordination of male individuals on the linear discriminant analysis of male carapace shape on population. Colors indicate strip pattern: black, *macrocepala*; red, *subtrijuga* in the following localities: BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan; MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

3.3.3 Plastron

On the lda plot, several populations partially overlap on each others, however, two groups can clearly be identified, one group from the central plain with the population of Singburi, Uthai Thani, and Nakhon Sawan, and the other group with the populations from Northeastern Thailand (Figure 12). Sex does not affect the ordination of populations. In addition, because Northeastern Thailand and population from the central plain do not overlap, one can also conclude that the effect of turtle relocation by sellers in the market has no impact on turtle distribution at interregional scales.

Carapace shapes that are more closer to the central plain are for population which stripe pattern correspond to *subtrijuga* (South of Northeastern Thailand) occupying a position that is between the population from Northeastern and Central plain which the stripe pattern correspond to *macrocephala*. This does not seem logic since the population having subtrijuga should diverge more from the others and should be found in one of the extreme. However, one can understand that easily, if it suppose that population from south Northeastern Thailand are all *macrocephala*. This may explain that populations from the South of Northeastern Thailand may in part introgressed with population from belonging to *macrocephala* (present in Southeastern Thailand).

Morphological variation was drawn along canonical axes to describe in which respect populations differs (Figure 13, right of the plot).

Form stripe pattern, on LD1 (axis that discriminate Northeastern populations from the Central plain, lower scores (in green and corresponding to Northeastern populations) correspond to plastron shapes with longer anterior plastral lobes and gular scutes, shorter anal scutes, narrower pectoral and abdominal scutes extending on a less extent laterally while higher scores (in purple and corresponding to central plain populations) correspond to plastrons with shorter anterior plastral lobes and gular scutes, longer anal scutes and wider pectoral and abdominal cutes extending laterally on the bridge. On LD2, variation is more subtile, related to the length of the pectoral scute, and does not seem to easily differentiate one group of population from the others.

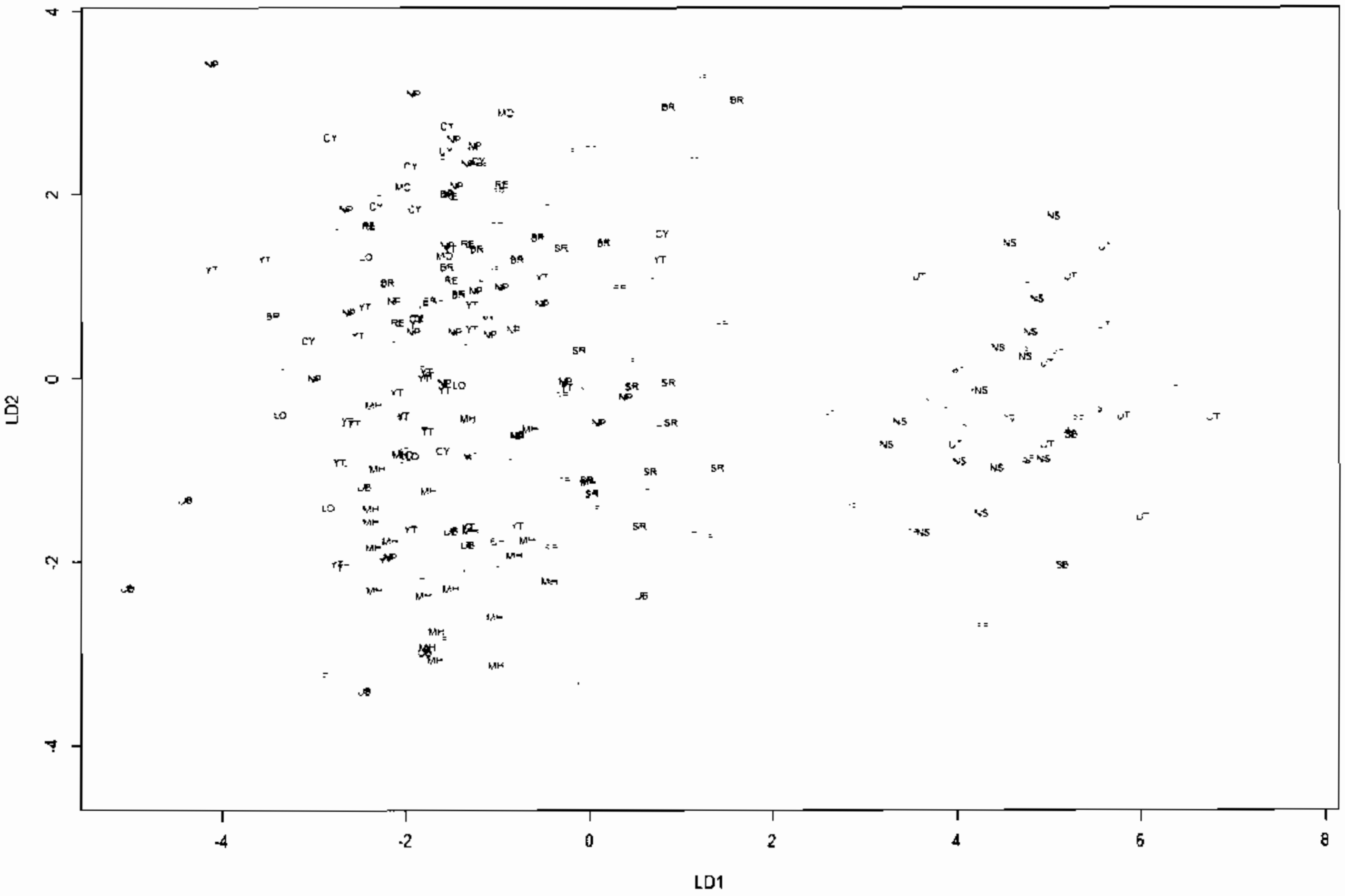


Figure 12 Linear discriminant analysis of *Malayemys* plastron (colors indicate sex: blue, male; red, female) in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon.

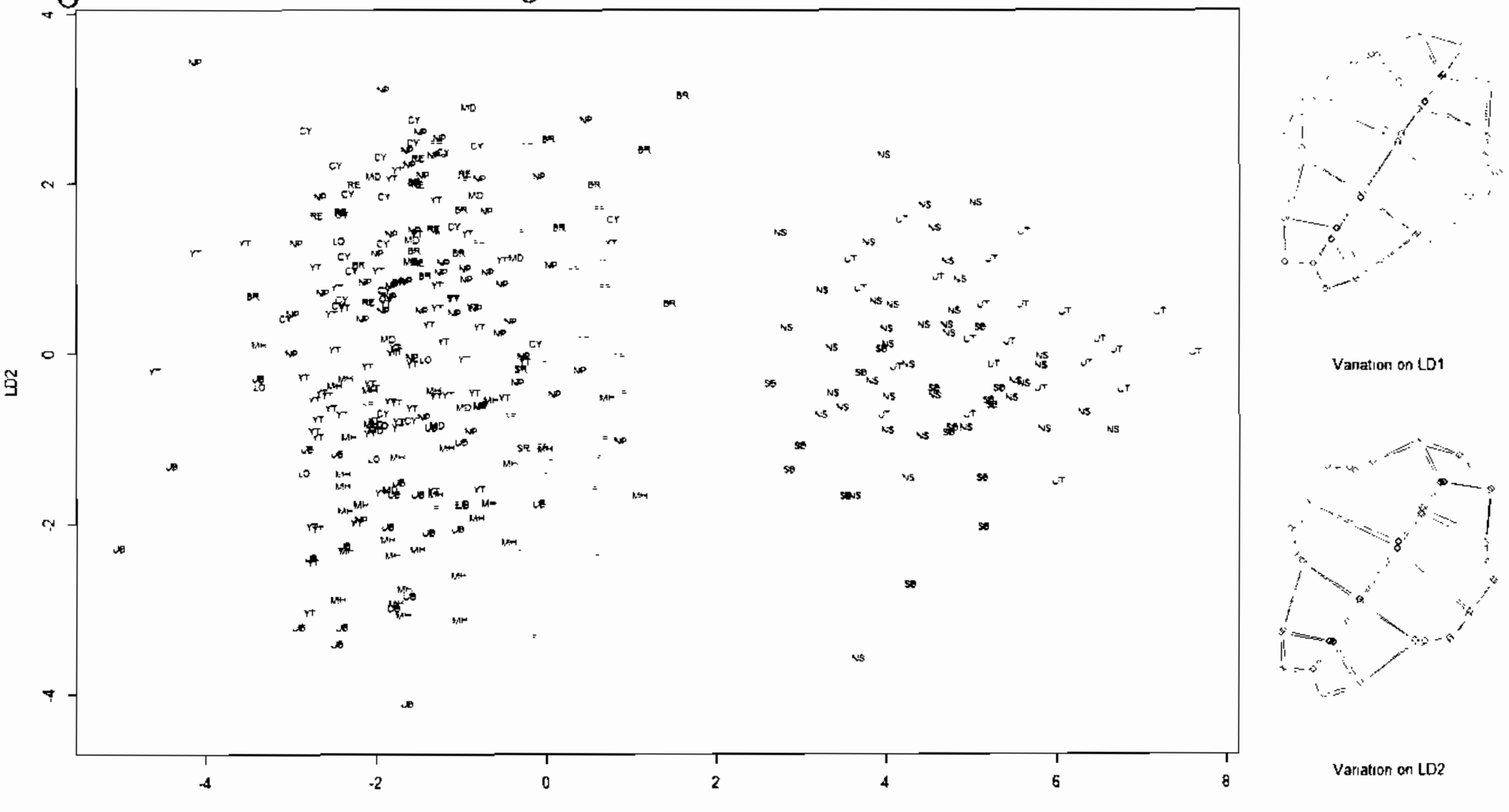


Figure 13 Ordination of individuals on the linear discriminant analysis of plastron shape on population. Corlors indicate strip pattern: black, *macrocepala*; red, *sutrijuga* in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

In order to avoid confounding effect of sex and age, the same analysis was performed independently on each sex.

3.3.4.5 *Female plastron*

There are 153 females identified in the data set. On the lda plot for females (Figure 14), two groups are clearly distinct, one containing turtles from the central plain (higher scores on LD1), and the other containing Northeastern population. In the second group, turtles from Surin, Loei, Roi Et, Buriram and Ubon Ratchathani, have usually higher scores on LD2 than other turtle from Northeastern Thailand, there is, however, an overlap between these two groups. The stripe patter does not correspond to any grouping structure.

Morphological variation was drawn along canonical axes to describe in which respect populations differs (Figure 14, right of the plot)

On LD1, ordination is more or less the same than for the whole set, except that differences that are explained are a bit different. (the humero-pectoral sulcus is more oblique for the high scores (Central plain populations), and more perpendicular to the symmetry axis for the lowest scores (Northeastern populations).

On LD2, variation is more subtile and oppose shorter humeral and more pronounced anal notch for higher scores by comparison to longer humeral and smaller anal notch for lower scores.

3.3.4.6 *Male plastron*

There are 155 males identified in the data set. On the lda plot for males, two groups can be identified, turtles identified with the stripe pattern on the head do not form any grouping structure (Figure 15).

Morphological variation was drawn along canonical axes to describe in which respect populations differed (Figure 3.15, right of the plot).

LD1 (axis that discriminate Northeastern populations from the central plain) describe is more or less the same shape variation than the general analysis considering males and females.

LD2, display more subtile variation, involving the relative length of the pectoral scute, and it does not seems that this axis discriminate well between populations.

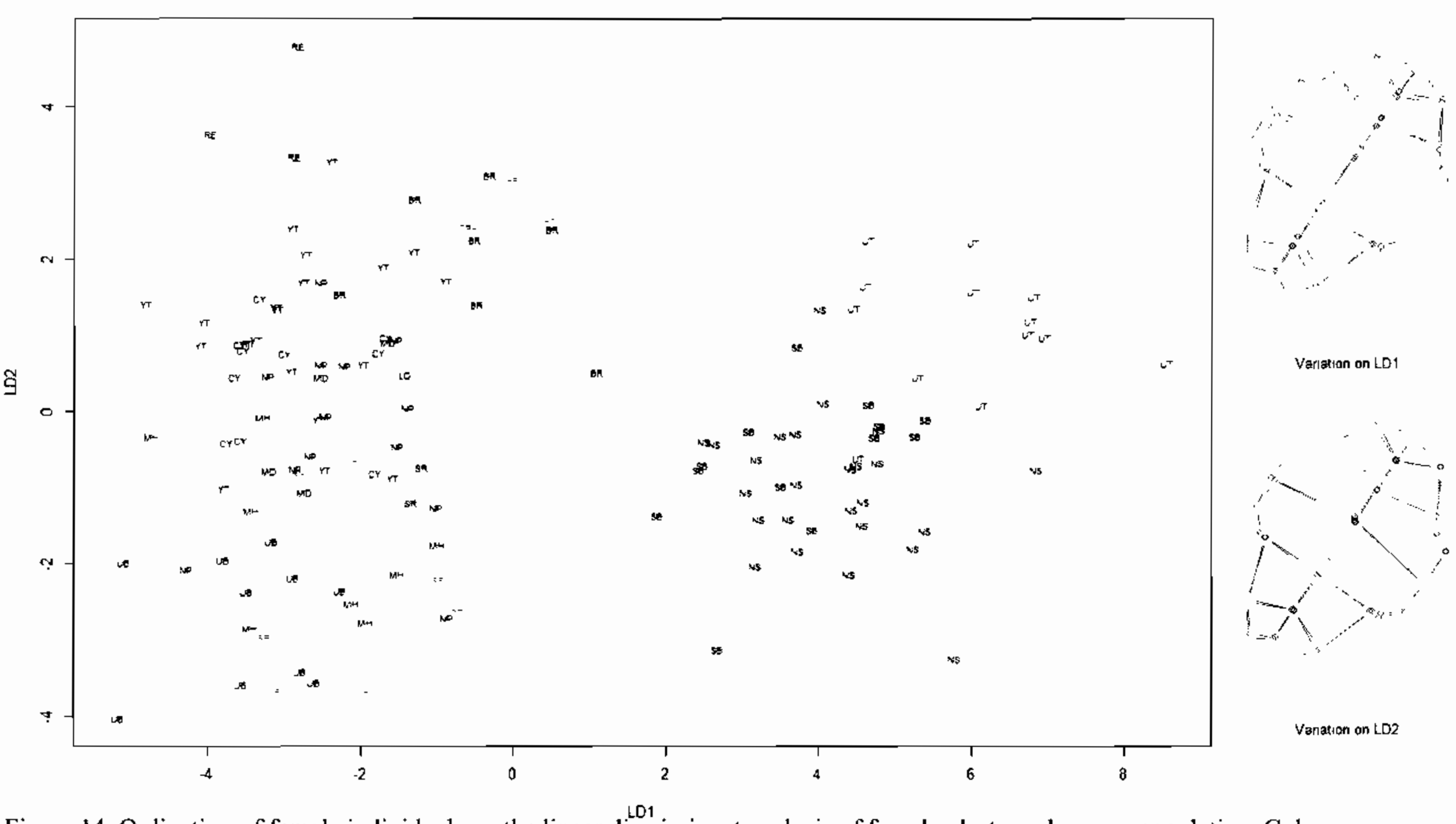


Figure 14 Ordination of female individuals on the linear discriminant analysis of female plastron shape on population. Colors indicate strip pattern: black, *macrocepala*; red, *sutrijuga* in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

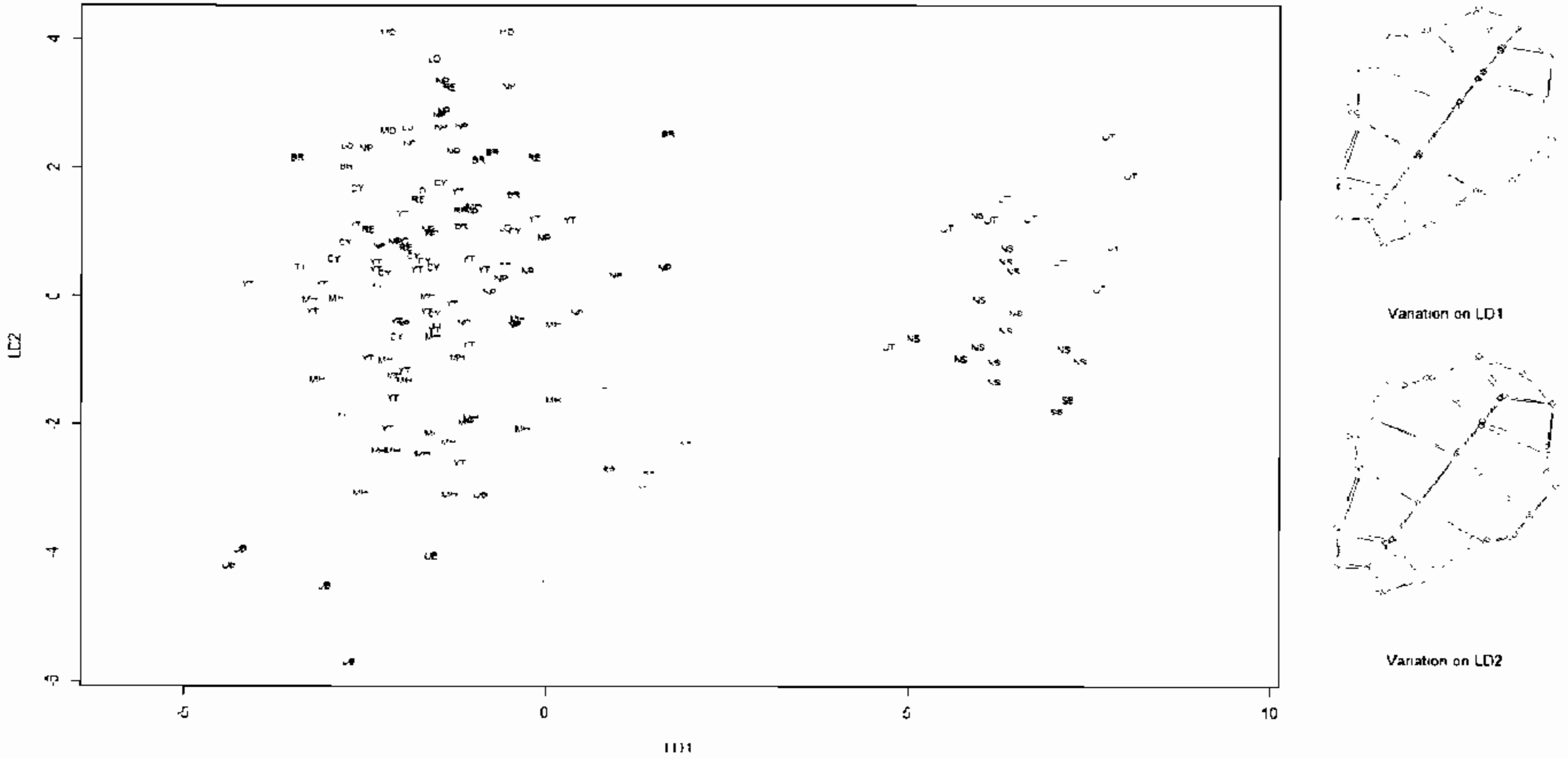


Figure 15 Ordination of male individuals on the linear discriminant analysis of male plastron shape on population. Colors indicate strip pattern: black, *macrocepala*; red, *sutrijuga* in following localities, BR, Buriram; CY, Chaiyaphum; LO, Loei; MD, Mukdahan: MH, Maha Sarakham; NP, Nakhon Phanom; NS, Nakhon Sawan; RE, Roi Et; SB, Singburi; SR, Surin; UB, Ubon Ratchathani; UT, Uthai Thani; YT, Yasothon. Patterns of variation on LD1 and LD2 are presented on the right side of the plot, purple corresponding to maximal scores, green to minimal ones.

3.4 Conclusion and discussion

There are differences in carapace shape between *Malayemys* populations and sexes. These differences do not seems correlated with head stripe pattern suggesting but discriminate between central and Northeastern population. The presence of both stripe patterns in the South of Northeastern Thailand is problematic, because this turtle are clearly united with the other population of Northeastern Thailand on the basis of the plastron and of the carapace shape variation. This study challenges what is known about the distribution of the supposed species in Northeastern Thailand, an area that has been particularly poorly sampled by museum and for which one had no other option that to extrapolate based on the work on Brophy (2004). If Brophy is right, *M. macrocephala* range should be extended to the North of Northeastern Thailand (also in Aowphol, 2010), and *M. subtrijuga* should be restricted to the southern part of Northeastern Thailand. This would also mean that differentiating species on the basis of the carapace shape would be difficult and that recognizing species in the fossil record would be impossible.

If groups match carapace major differences, *M. subtrijuga* only should be found in Northeastern Thailand; this would also indicate that we could recognize both species on the basis of the osteology and that fossil species could be identified.

Plastral shape variation follows the same pattern than carapace shape variation, and is also different from head stripe pattern. Moreover, when considering males and females together, the position of specimen identified as *M. subtrijuga* because of stripe pattern together with turtle identified as *M. macrocephala* furthermore suggests that strip head color pattern does not easily explain plastral variation. Instead, it suggest that the color patterns have maybe lower precision for defining *Malayemys* species by comparison to morphometrics and carapace and plastron scute conformation.

This method could be also applied to the systematic problem of closer taxa such as *Cylemys*; for which, by contrast species has been re-established on the basis of molecular character (Fritz *et al.*, 2008).

CHAPTER 4

ILLUSTRATION OF LIVING TRIONYCHID POSTCRANIAL MATERIAL IN THAILAND AND ADJACENT TERRITORIES

4.1 General introduction

Soft-shell turtles belong to the family Trionychidae Gray, 1825. They are all freshwater. They are distinguished from other turtles by their flat shell (carapace and plastron) covered with a smooth skin, and they lack epidermal scutes (Meylan, 1987). The trionychid turtle carapace is made of nuchal, neurals and costals; but the suprapygal, pygal, and peripheral plates are absent in nearly all species except the living *Lissemys,* in which incomplete peripheral plates are present in the posterior part of the carapace. The plastron of trionychids is reduced and pointed processes are present between the plates instead of sutures except between hyo-hypoplastron. The carapace and plastron are attached by ligaments. The family of Trionychidae includes thirty one extant species (Turtle taxonomy working group, 2011). The living trionychid turtles are distributed in Africa, North America, Indo-Australian archipelago, and Asia including Thailand. The fossil record shows that this group was also present in South America and Europe (Mustoe and Girouard, 2001).

In Thailand, five native species of living trionychids are present: *Amyda cartilaginea* (Boddaert, 1770), *Chitra chitra* (Nutaphand, 1986), *Chitra vandijki* (McCord & Pritchard, 2003), *Dogania subplana* (Geoffroy, 1809) and *Pelochelys cantorii* Gray, 1864. There is also at least one introduced species, *Pelodiscus sinensis* (Stuart *et al.*, 2001). The skeletal anatomy of living Thai trionychid turtles has been partially reported in literature. In adjacent territories, *Nilssonia* (*Nilssonia formosa* (Gray, 1869)), and *Lissemys (Liseemys scutata* (Peters, 1868)) are known in Myanmar, *Rafetus* (*Rafetus swinhoei (*Gray, 1873)) and *Palea* (*Palea steindachneri*) are known in Vietnam. Recently Praschag *et al.* (2007), proposed that *Nilssonia* and *Aspideretes* are in fact a same genus, a position that I follow here too. Because these genera could possibly occur in the fossil record; when material was available, they will also be described and pictured in this study.

In the following, a literature overview concerning the skeletal anatomy of these soft-shell turtles (Thailand and adjacent territories) is provided, followed by an illustration and description, and concluded by an anatomical key.

4.2 Literature overview

Our knowledge on the osteology of these turtles, seems very incomplete since the work by the herpetologists generally focus on the external aspect. Description of Southeast Asia trionychid species and illustrations are provided in Smith, 1931. He provided some illustrations shell drawings of *Amyda cartilaginea* (figures 18 and 19), *Lissemys punctata* (figures 40 and 41) and skulls for *Pelochelys* (*Pelochelys bibroni*) (Figure 37), *Nilssonia hurum* (Figure 54), *Chitra indica* (Figure 28), *Nilssonia gangetica* (Figures 48 and 49). He also provided illustrations of a juvenile individual of *Trionyx hurum* (*Nilssonia hurum*) (see Figure 51). Nutaphand (1979) provided some illustrations of skulls of *Amyda cartilagenea* (Figure 21) and *Pelochelys cantorii* (Figure 36) and drawing of axis, atlas and pelvic of *Pelochelys cantorii* (Figure 35). The external morphology of *Amyda cartilagenea* (figures 16 and 17), *Chitra chitra* (Figure 24), *Dogania subplana* (Figure 31) and *Pelochelys cantorii* (Figure 33) are also provided. Meylan (1987) described the phylogenetic relationships within trionychids with the help of skeletal characters, he also presented shell drawing of *Lissemys punctata Dogania subplana*, *Chitra chitra, Trionyx hurum* (*Nilssonia hurum*), *Trionyx sinensis* (*Pelodiscus sinensis*). Illustrations are displayed in figures 27, 30, 38, 42, 43, 52 for shells, figures 44, 45, 53 for skeletons and figures 22, 23, 29, 37, 39, 46, 55 for skulls . Pritchard *et al.* (2009) showed that the ornamentation structure of the carapace surface of trionychid turtles can be used for recognizing species among which he gave some description for *Chitra indica*, *Amyda cartilagenea*, *Dogania subplana*, and *Pelochelys cantorii*. The images of them are presented in figures 20, 25, 26, 32, 34 More recently, Le *et al.* (2010) proposed a new species of *Rafetus*, *R. vietnamensis* from Northern Vietnam based on morphology and DNA analysis. Then Farkas, Le, & Nguyen (2011) reviewed the description of *R. vietnamensis* and found that this species was not different from *R. swinhoei*. *Rafetus leloii* is invalid too according to Farkas and Webb, 2003. The images of these taxa are shown in figures 56, 60. *Rafetus* is better known in the Anatolian peninsula and Taskavak (1999) described the cranial morphology of *Rafetus euphraticus* (Daudin, 1801). The skull morphology is presented here in figures 57-59.

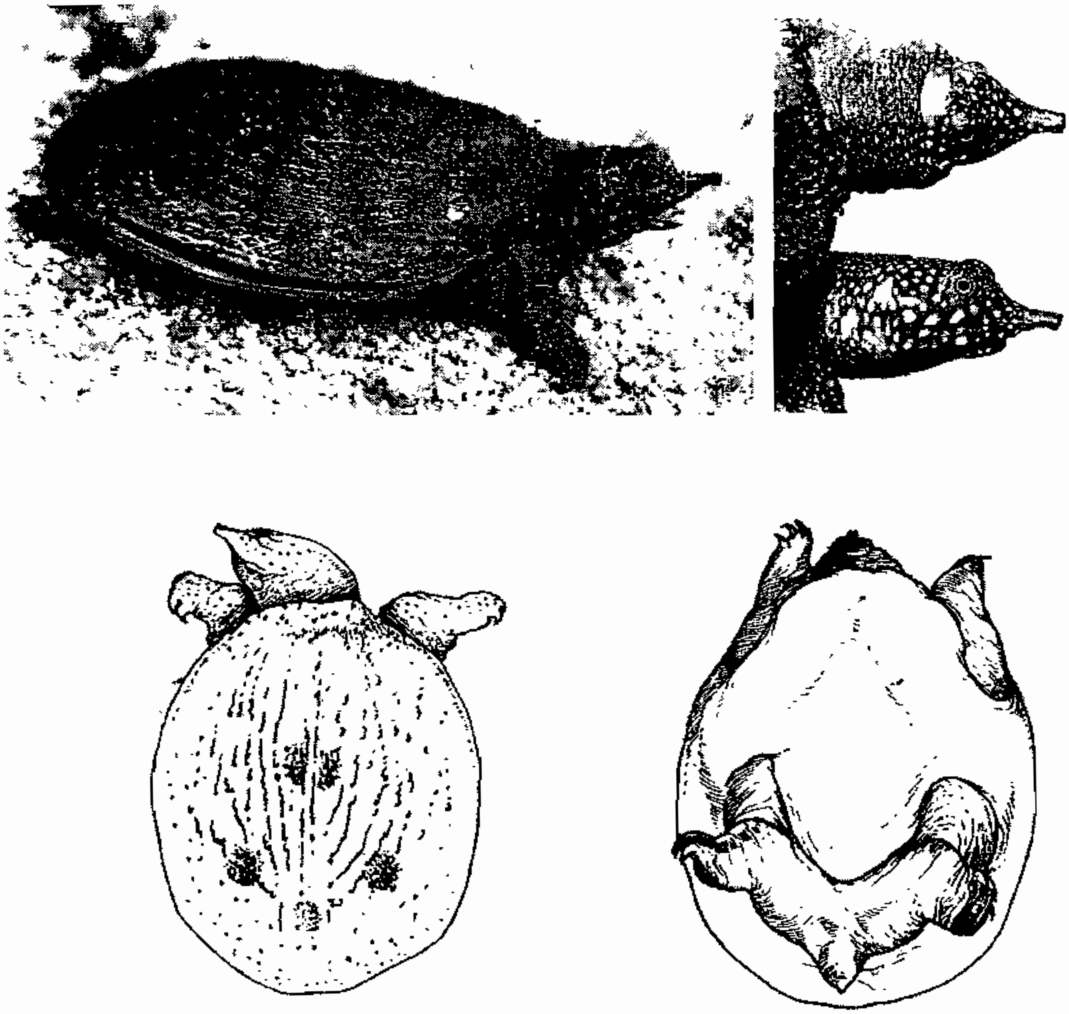


Figure 16 *Amyda cartilagenea* in lateral (upper left), dorsal (lower left) and ventral (lower right) views and its head (upper right) (Nutaphand, 1979, p 198,199, Fig. 143-145).

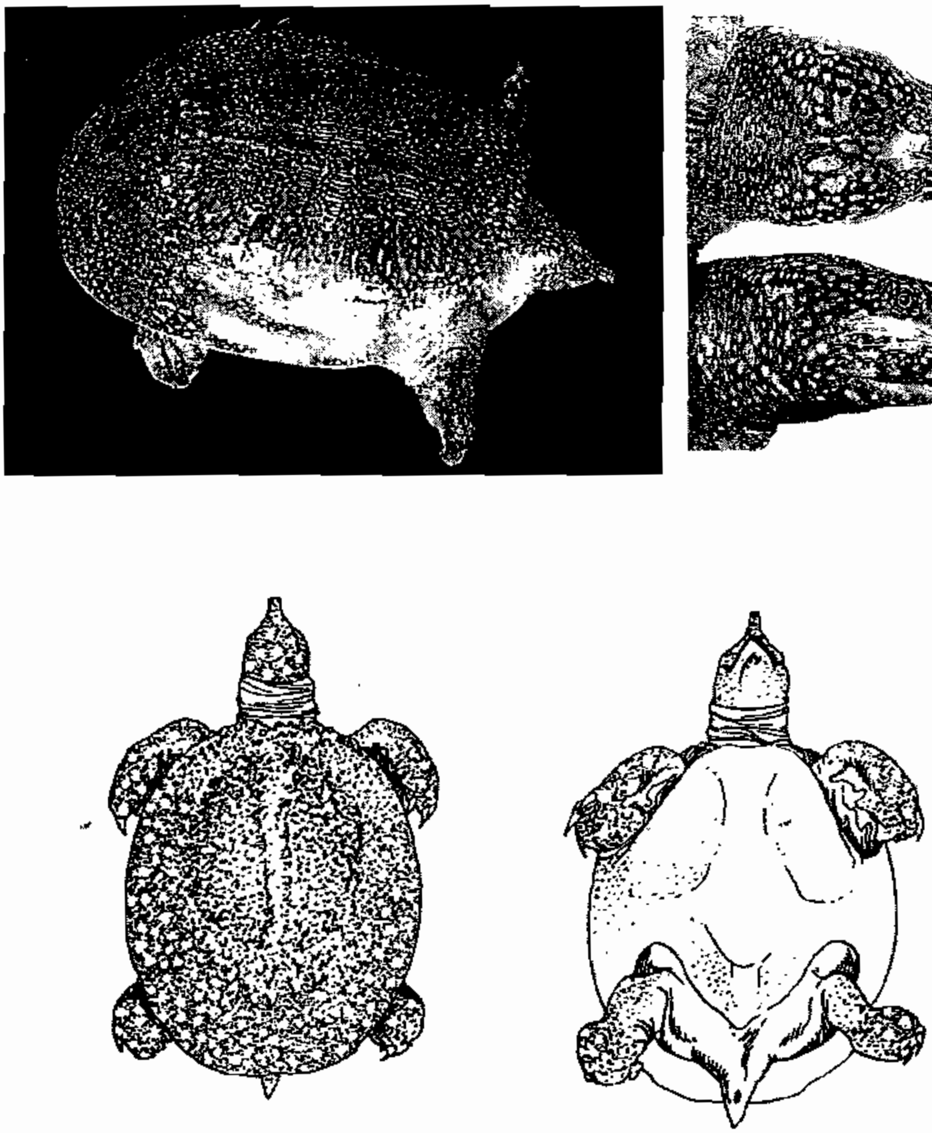


Figure 17 *Amyda cartilagenea* in lateral (upper left), dorsal (lower left) and ventral (lower right) views and its head (upper right) (Nutaphand, 1979, p 200, 201, Fig. 146-148).

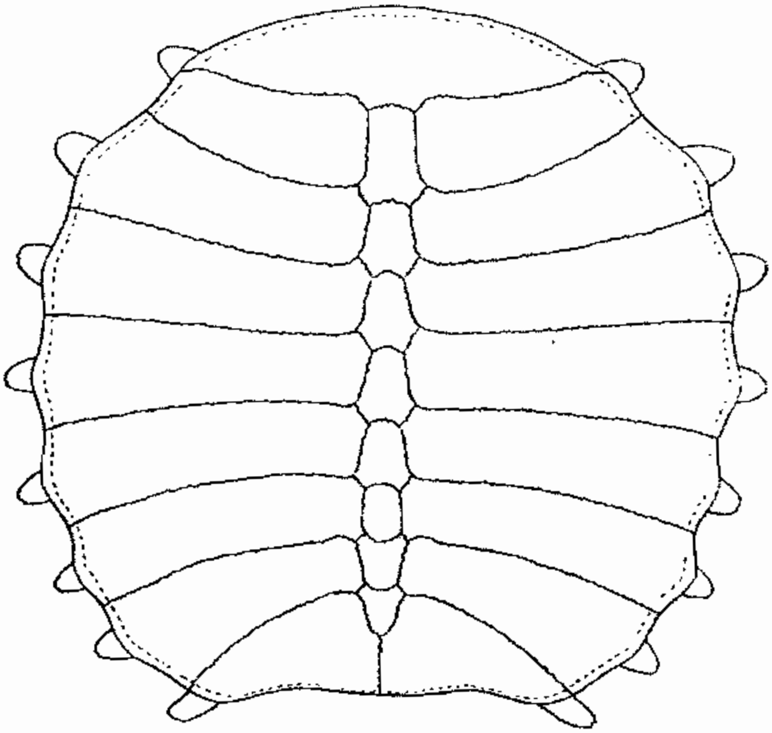


Figure 18 The carapace *Amyda cartilagenea* in dorsal view (*Trionyx cartilagineus* in Smith, 1931, p 150, Fig. 31).

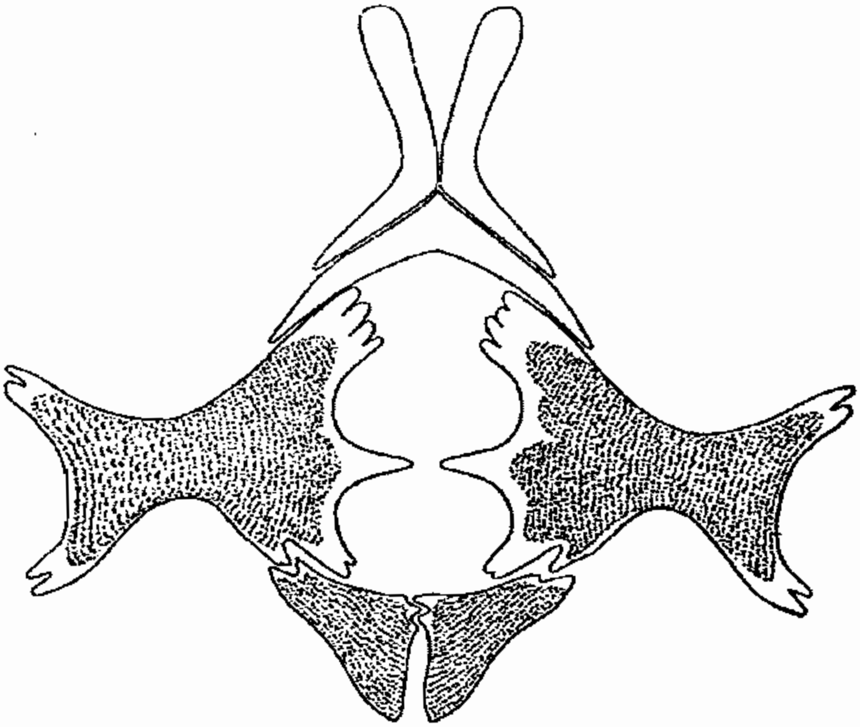


Figure 19 The plastron of *Amyda cartilagenea* in ventral view (*Trionyx cartilageneus in* Smith, 1931, p 151, Fig. 32).

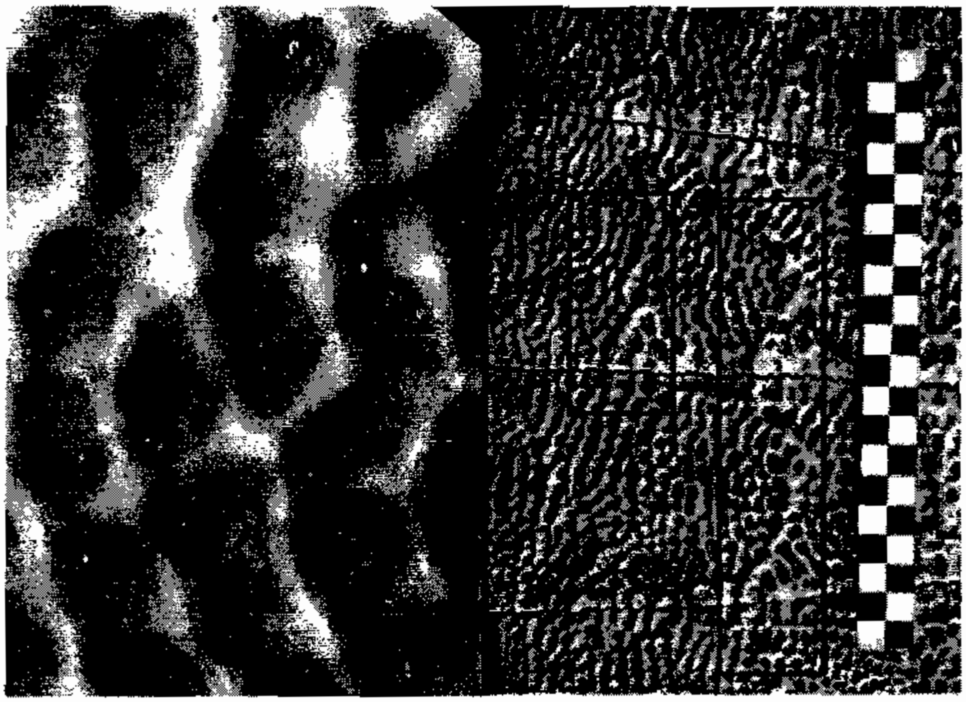


Figure 20 Dorsal view of *Amyda cartilagenea* surface; 10x magnification (left) and longitudinal ridge along the costal (right) (Pritchard *et al.*, 2009, p 541, Fig. 8).

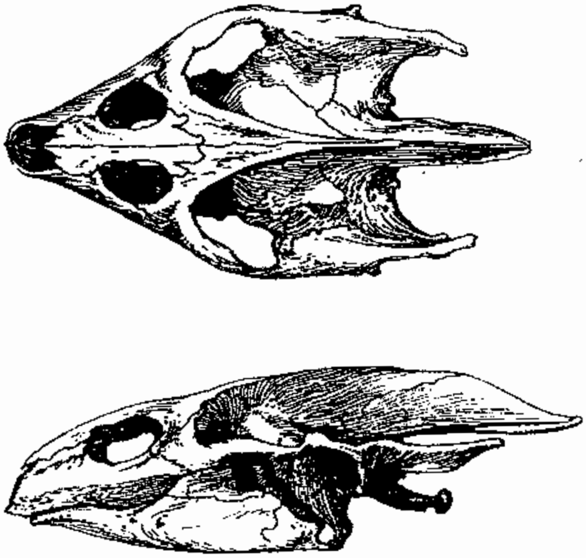


Figure 21 Skull of *Amyda cartilagenea* in dorsal (top) and lateral (bottom) views; (Nutaphand, 1979, p 69, Fig. 53).

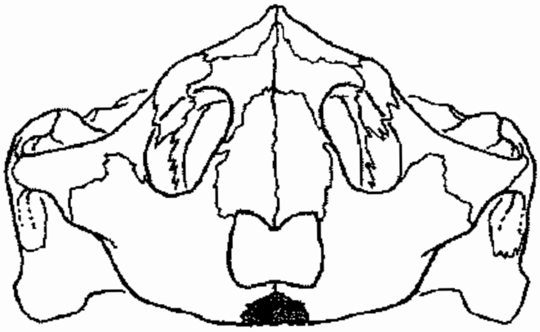


Figure 22 Skull of trionychid turtle in frontal view; *Trionyx cartilageneus* (RH 1129), recently *Amyda cartilagenea*, (Meylan, 1987, p 31, Fig. 9, A).

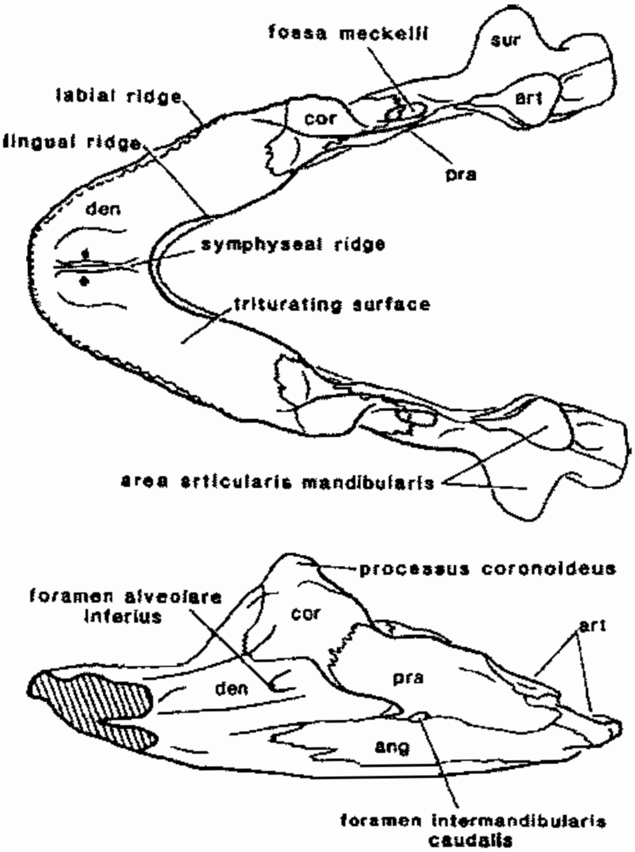


Figure 23 Lower jaw of *Amyda cartilagenea* in dorsal (top) and medial (bottom) views; (RH 129), (*Trionyx cartilagineus* in Meylan, 1987, p 39, Fig. 17).

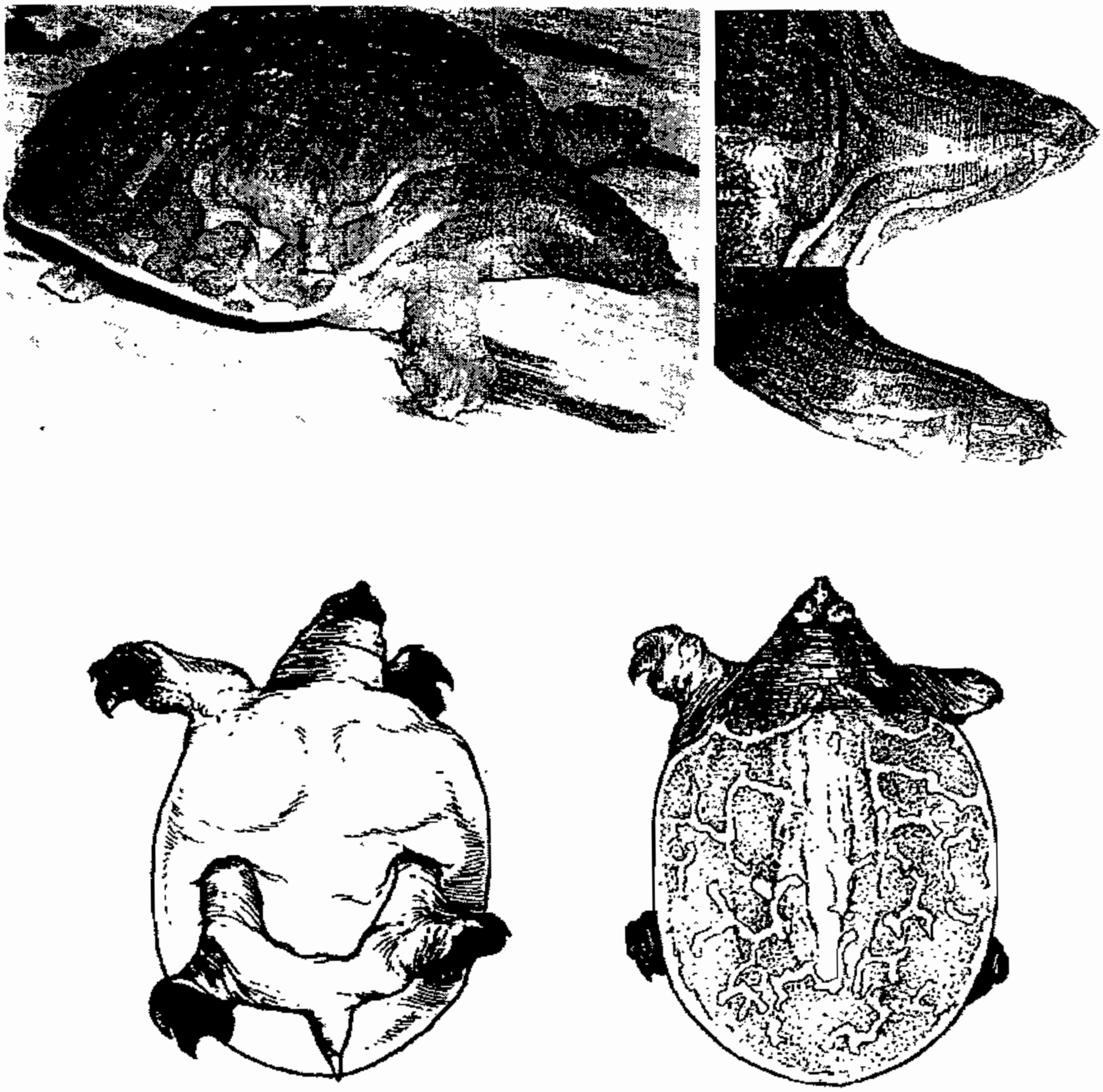


Figure 24 *Chitra chitra* in lateral (upper left), ventral (lower left) and dorsal (lower right) views and its head (upper right) (Nutaphand, 1979, p 186, 187; Fig. 134-136).

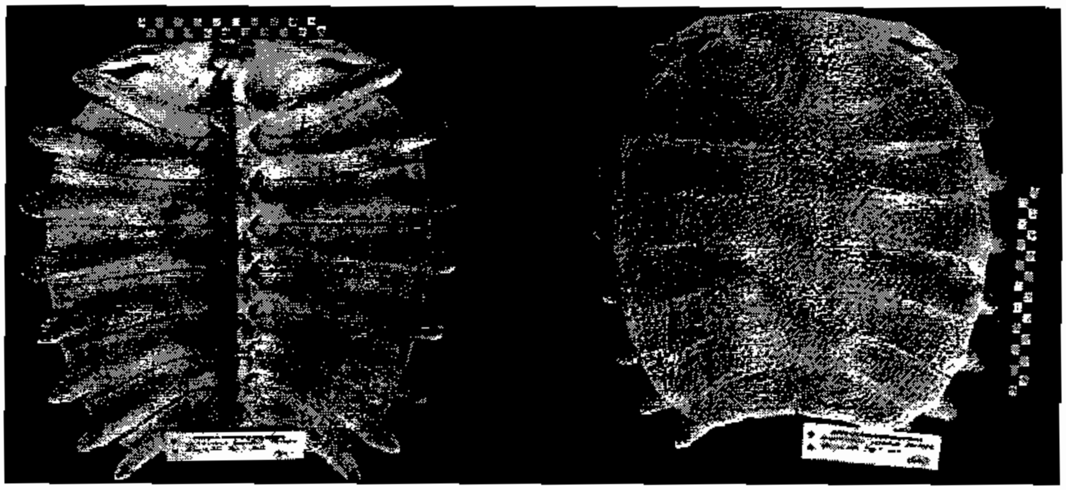


Figure 25 *Chitra indica* in visceral (left) and dorsal (right) views (Pritchard *et al.*, 2009, p 540, Fig. 7).

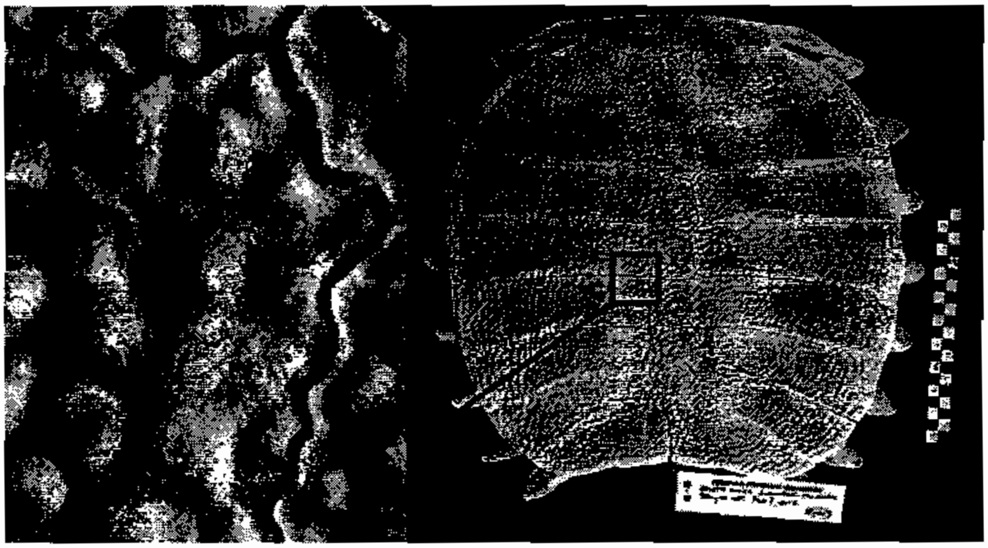


Figure 26 Dorsal view of *Chitra indica* carapace (right); an example of surface pattern close to the costal-neural contact in 10x magnification (left) (Pritchard *et al.*, 2009, p 543, Fig. 10).

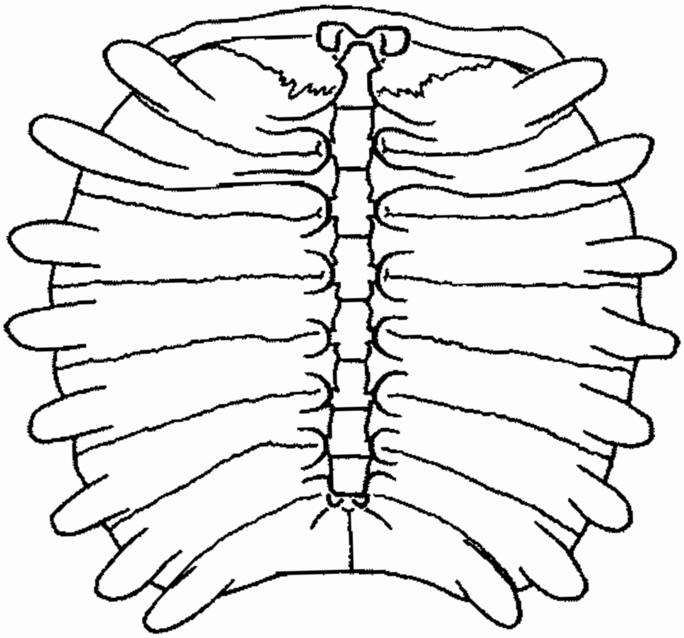


Figure 27 The carapace of *Chitra indica* (MCZ 29487) in visceral view (Meylan, 1987, p 18, Fig. 6, D).

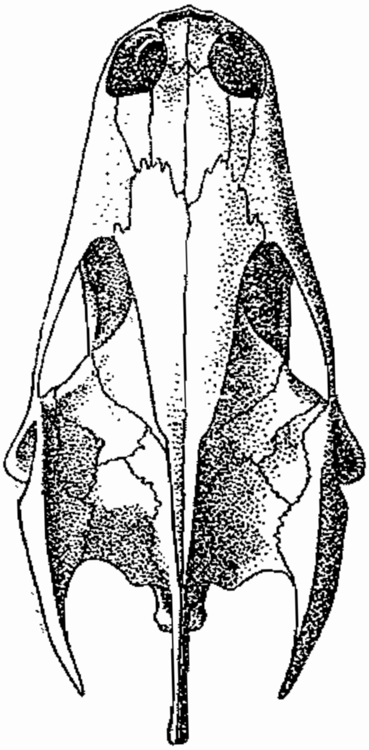


Figure 28 Skulls of *Chitra indica* in dorsal views (Smith, 1931, p 163, Fig.37).

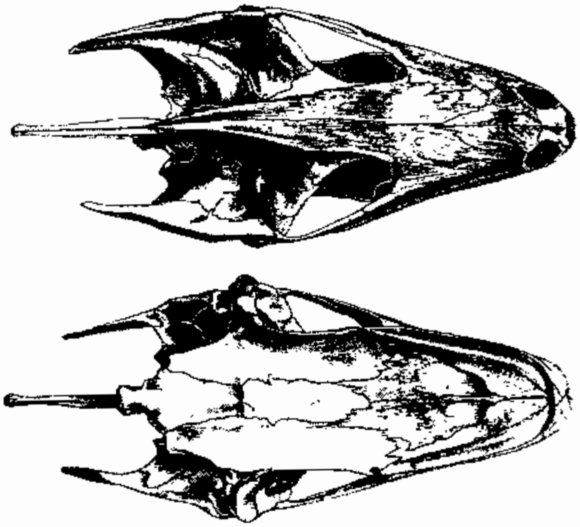


Figure 29 Skull of *Chitra indica* in dorsal (top) and palatine (bottom) views (Meylan, 1987, p 33,41, Fig. 11,15, middle).

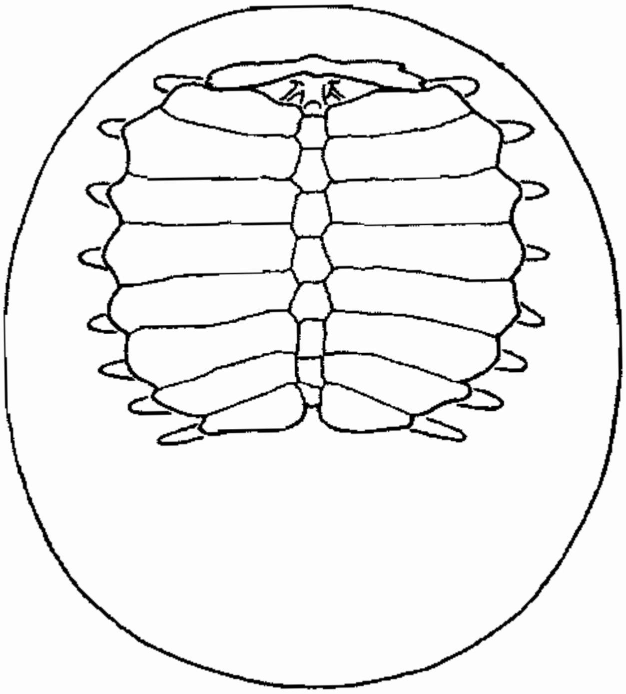


Figure 30 The carapace of *Dogania subplana* (MNHNP unnumbered, holotype, with details from BMNH 53.5.38) in dorsal view, (*Trionyx subplanus* in Meylan, 1987, p 16, Fig. 4, B).

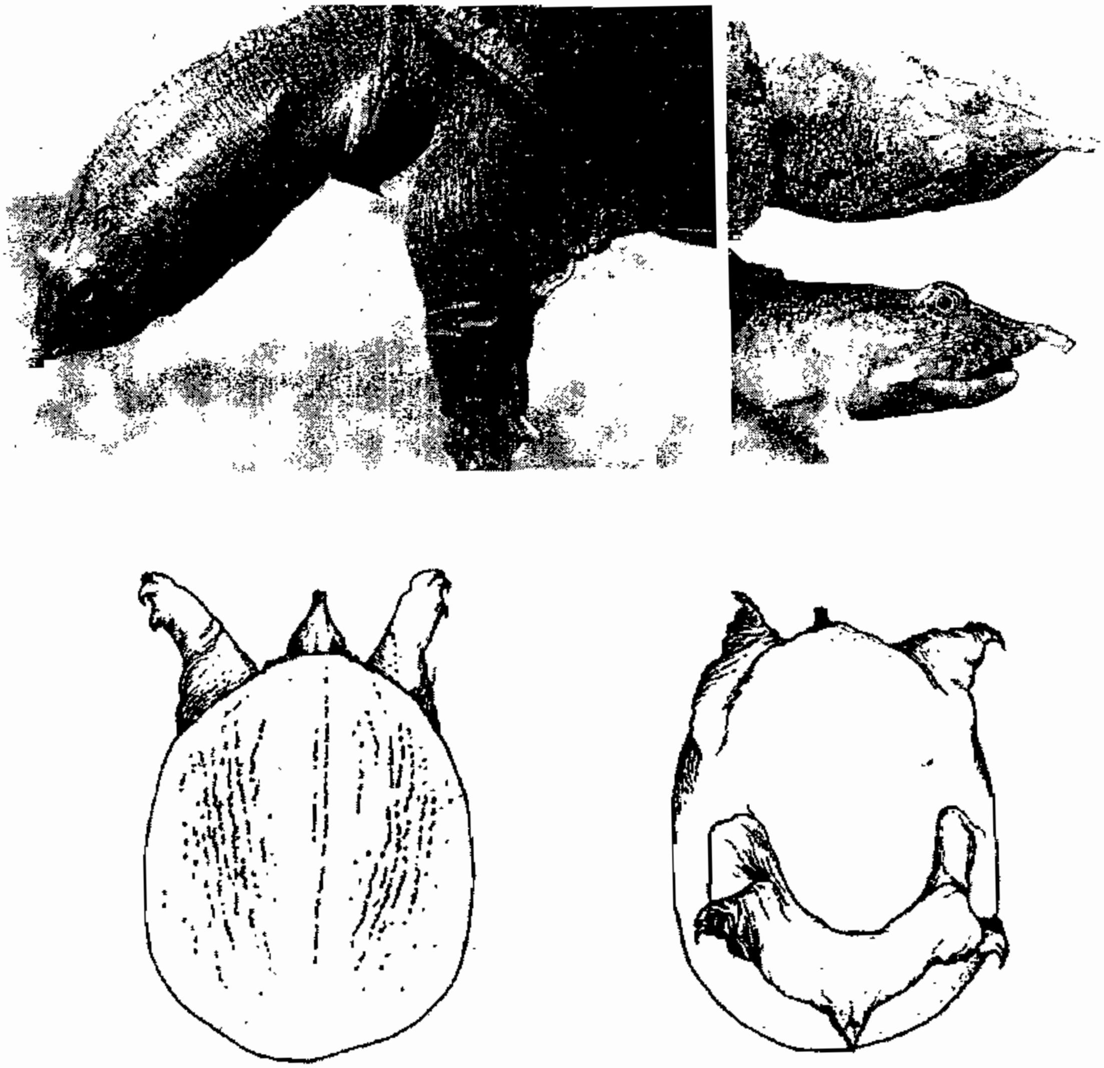


Figure 31 *Dogania subplana* in lateral (upper left), dorsal (lower left) and ventral (lower right) views and its head (upper right) (Nutaphand, 1979, p 194, 195, Fig. 140-142)

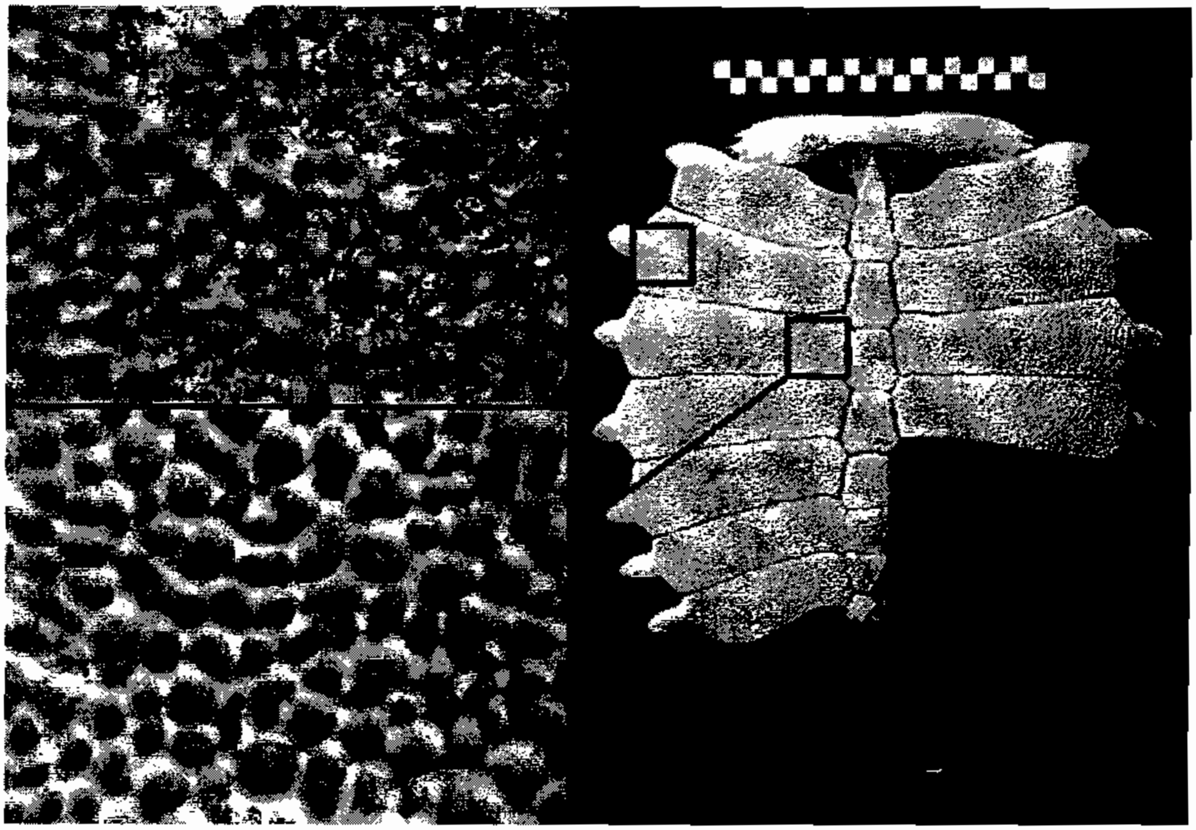


Figure 32 Dorsal view of *Dogania subplana* carapace (right); example of patterning close to the medial end of costal (lower left) and an example of more open, rounded protuberances near lateral margin (upper left) (Pritchard *et al.*, 2009, p 542).

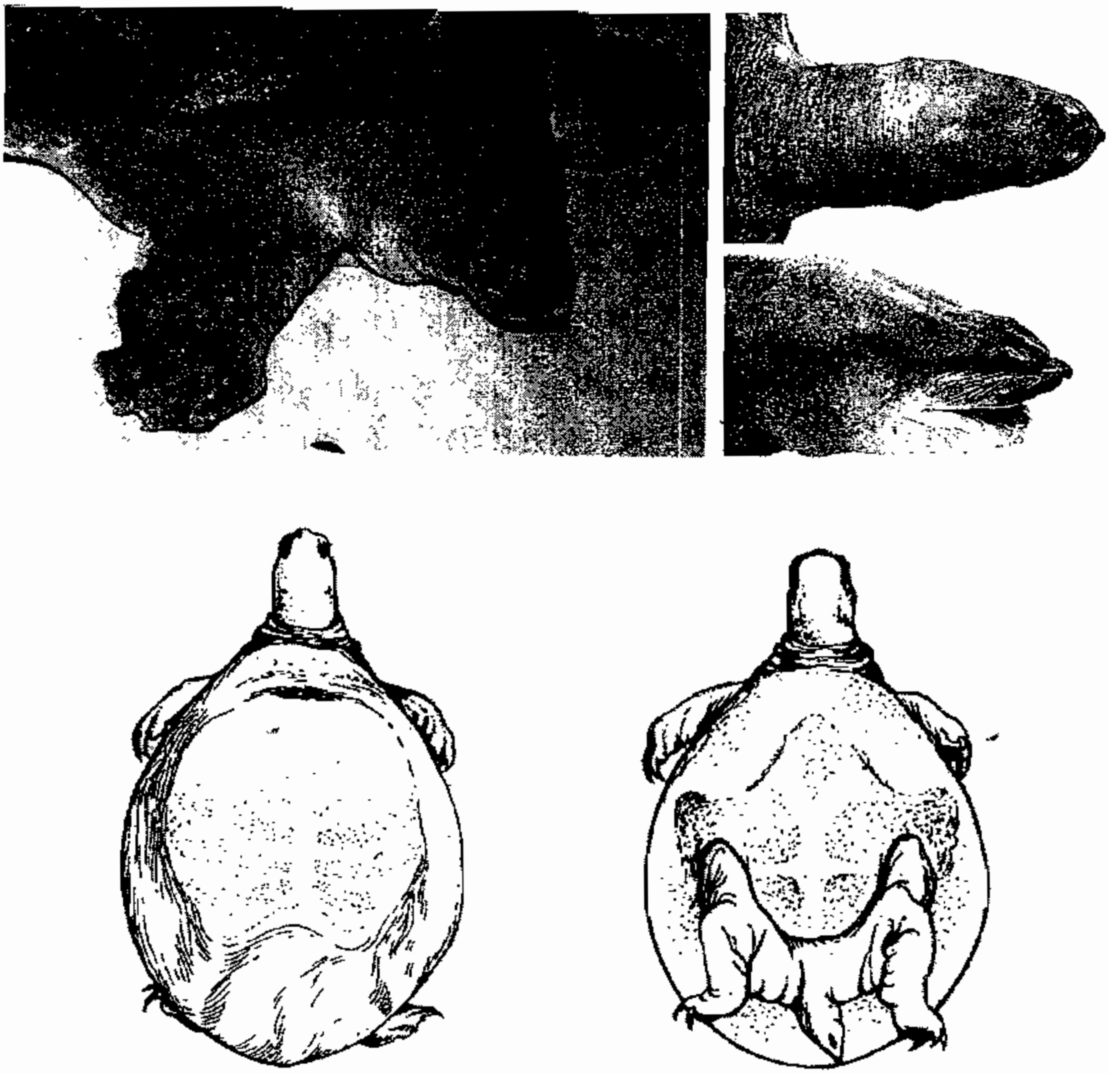


Figure 33 *Pelochelys cantorii* in lateral (upper left), dorsal (lower left) and ventral (lower right) views and its head (upper right) (Nutaphand, 1979, p 190, 191, Fig. 137-139).

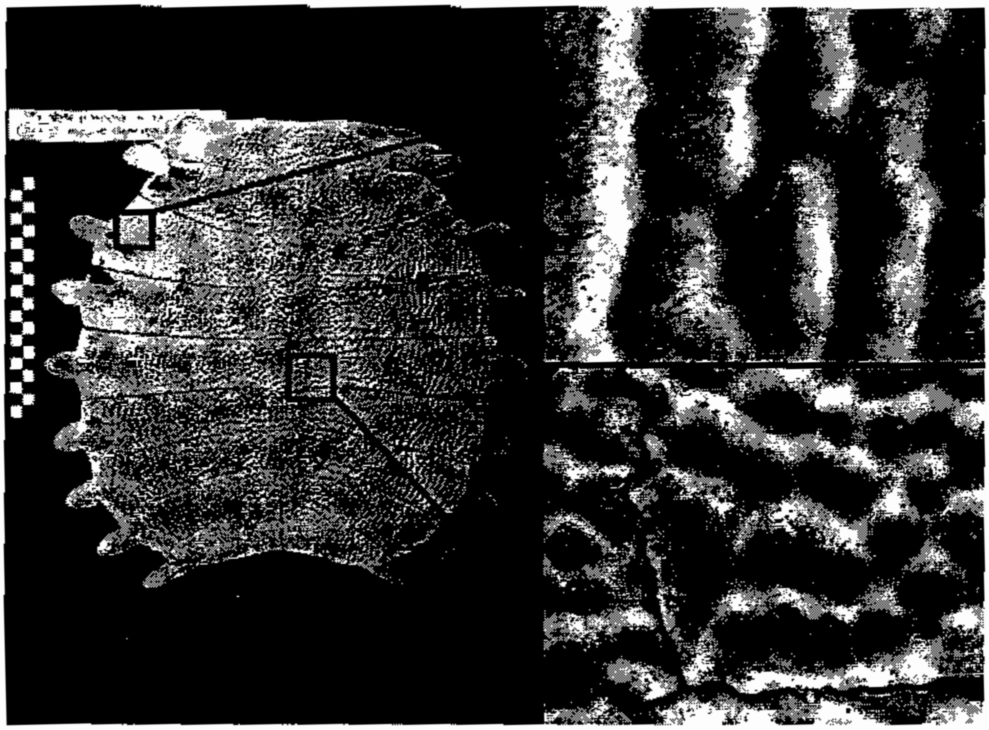


Figure 34 Dorsal view of *Pelochelys cantorii* carapace (left); an example of surface pattern close to the costal-neural contact in 10x magnification (lower right) and an example of surface pattern close to lateral margin of the costal in 10x magnification (upper right) (Pritchard *et al.*, 2009, p 544, Fig. 11).

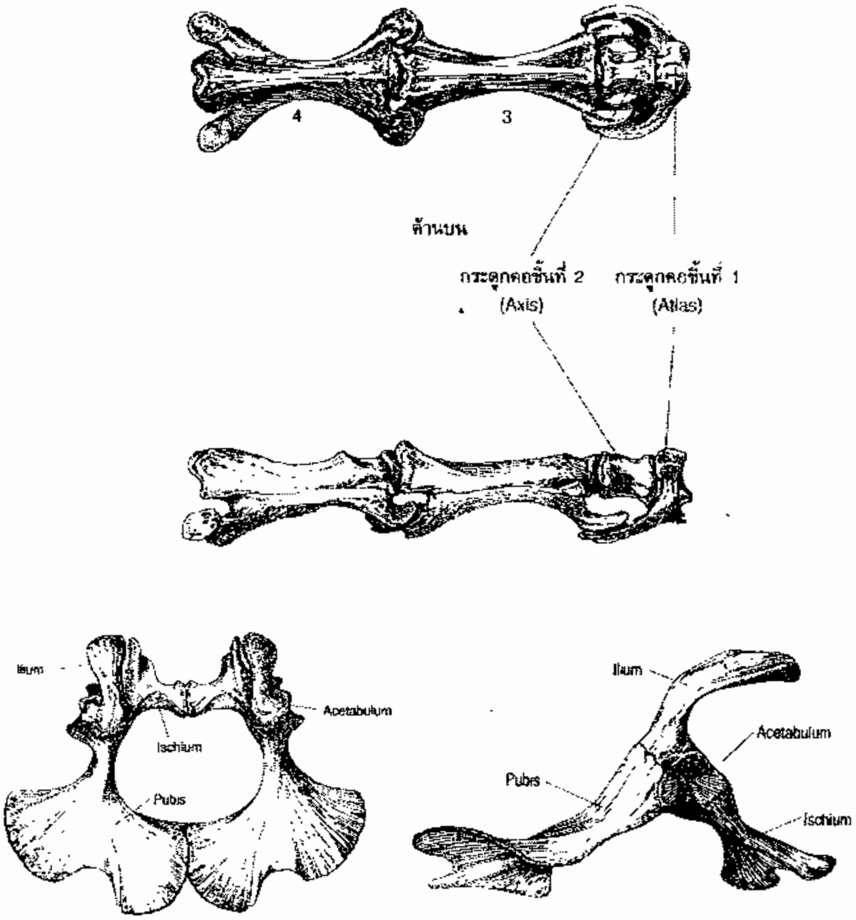


Figure 35 *Pelochelys cantorii*; axis and atlas in dorsal and lateral views (top), pelvic girdle in anterior (left bottom) and lateral (right bottom) views (Nutaphand, 1979, p 71-73, Fig. 55,56,57).

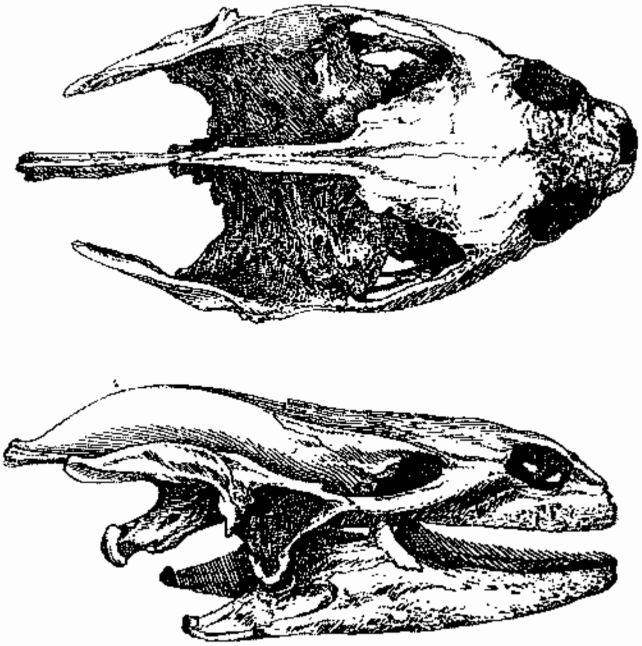


Figure 36 Skull of *Pelochelys cantorii* in dorsal (top) and lateral (bottom) views; (Nutaphand, 1979, p 70, Fig. 54).

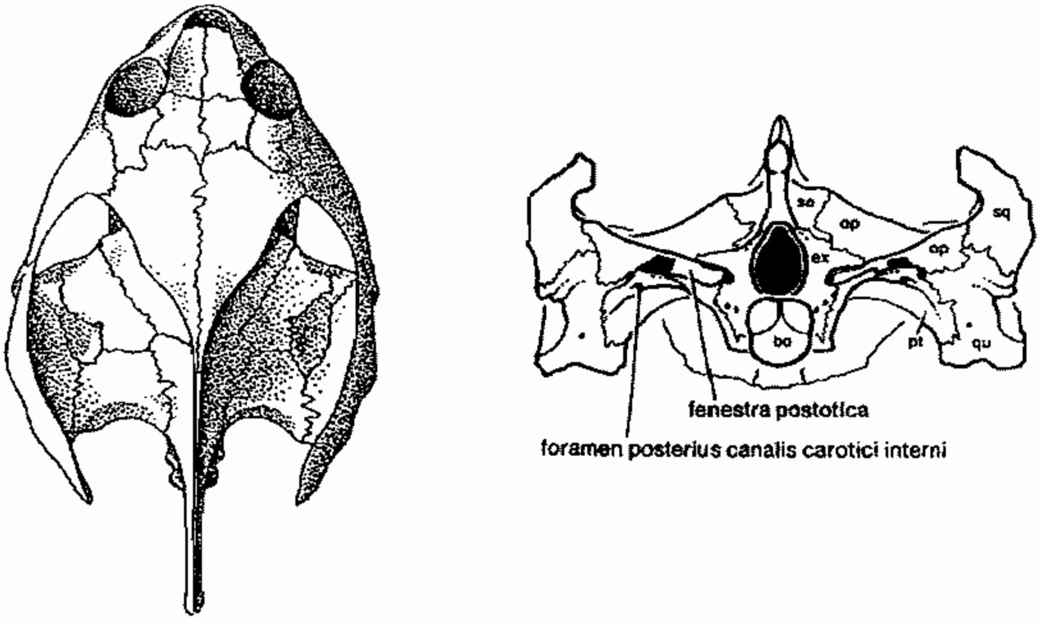


Figure 37 Skull of *Pelochelys bibroni* in dorsal (left) (Smith, 1931, p 161, Fig.36) and in posterior (right) views (Meylan, 1987, p 39, Fig. 14, D).

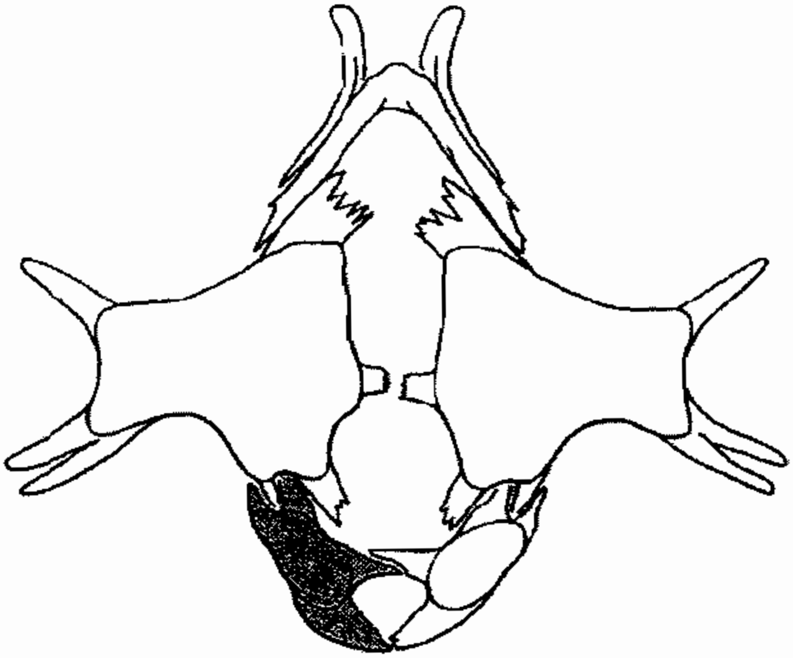


Figure 38 Plastron of *Pelodiscus sinensis* in ventral views (*Trionyx sinensis* in Meylan, 1987, p 24, Fig. 8, C).

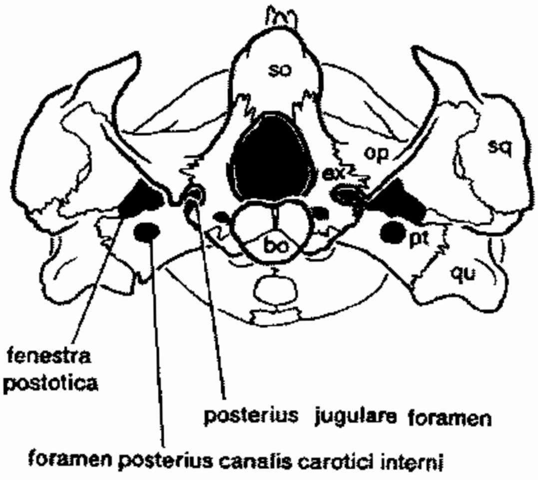


Figure 39 Skull of *Pelodiscus sinensis* (UF H 2406) in posterior views (Meylan, 1987, p 39, Fig. 14, E).

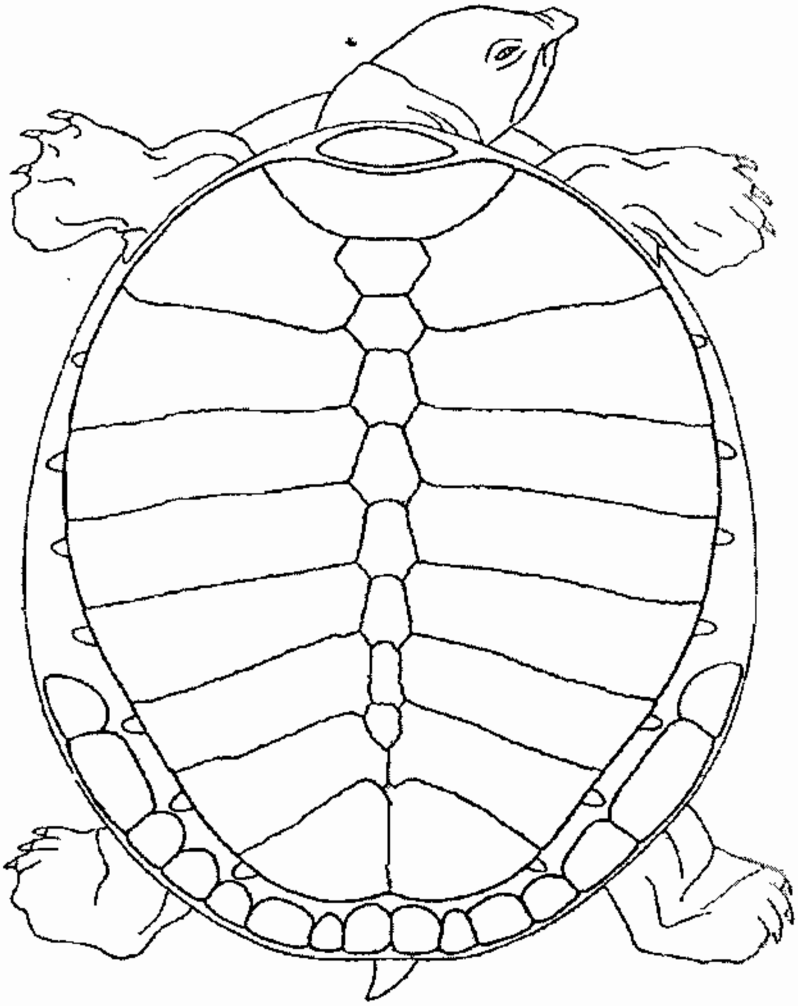


Figure 40 *Lissemys scutata*, in dorsal view (*Lissemys punctata scutata* in Smith, 1931, p 155, Fig. 34).

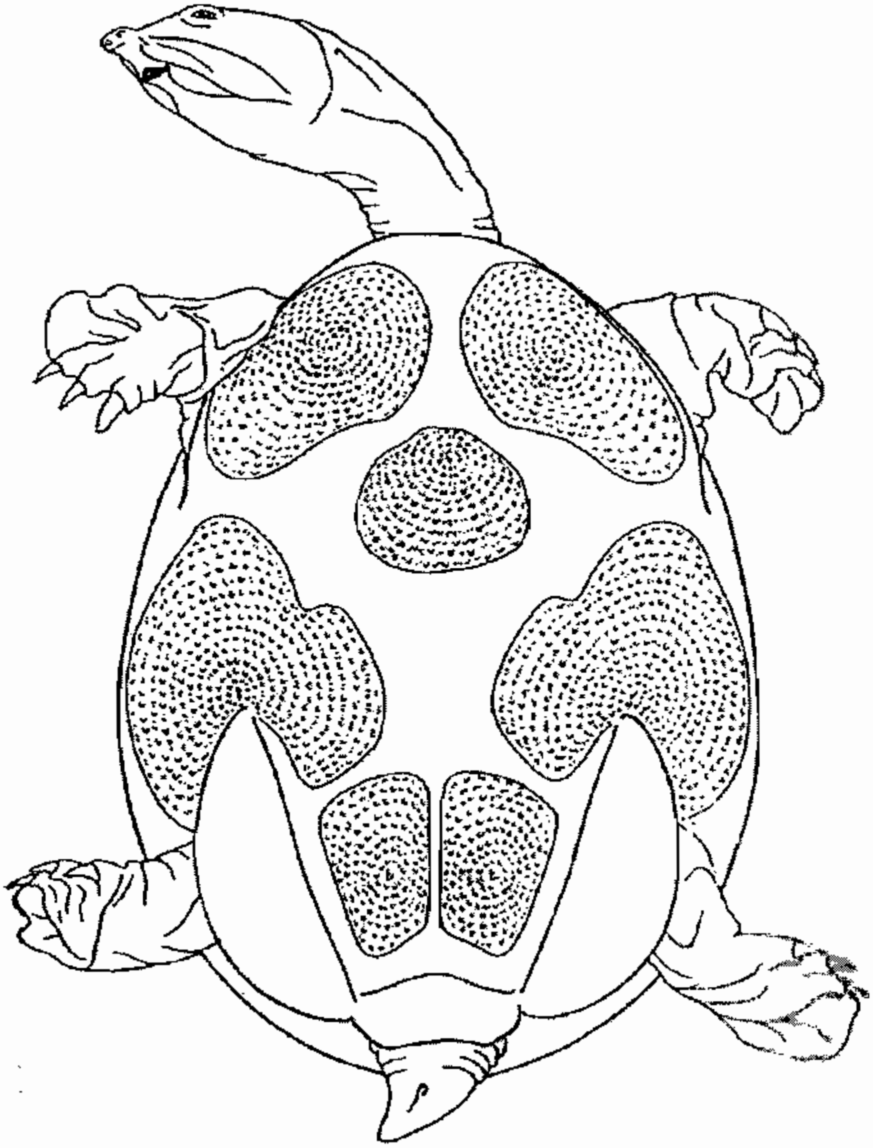


Figure 41 *Lissemys scutata*, in ventral view (*Lissemys punctata scutata* in Smith, 1931, p 156, Fig. 35).

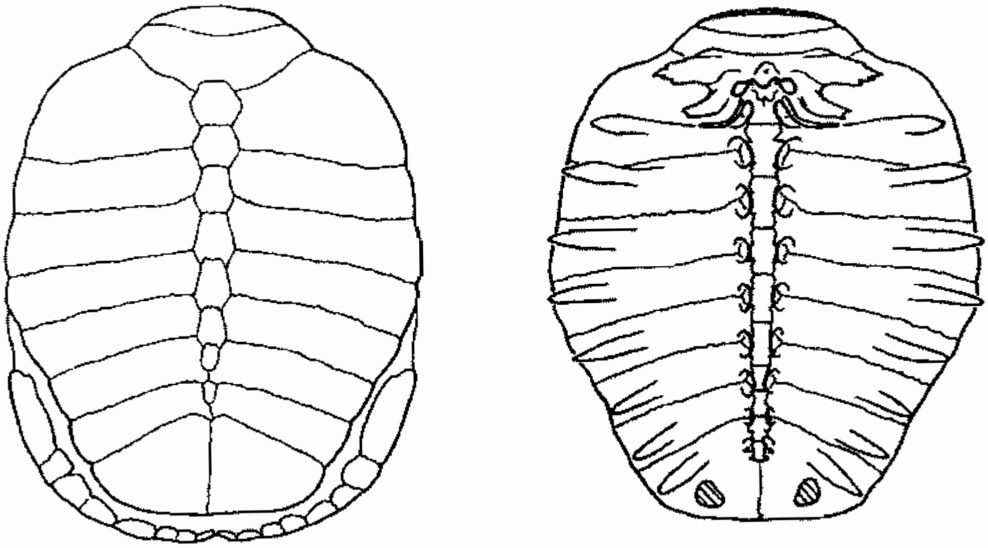


Figure 42 The carapace of two *Lissemys punctata* (UF 56017) in dorsal (left) and visceral (right) views (Meylan, 1987, p 16, Fig. 4, A; p 18, Fig.6, B).

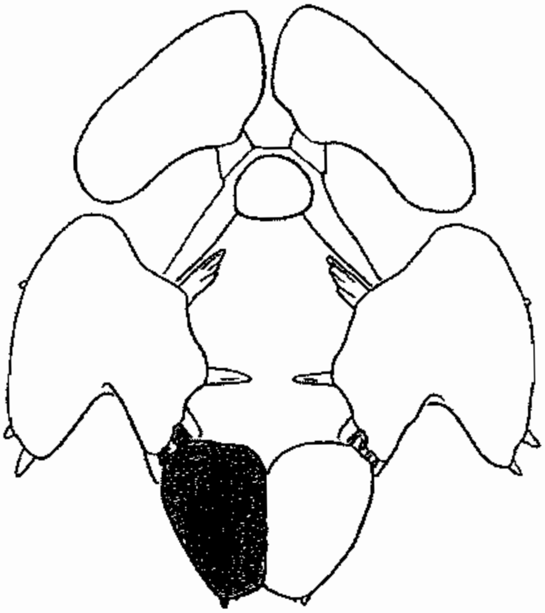


Figure 43 The plastron of *Lissemys punctata* (UF 56017) in ventral view (Meylan, 1987, p 24, Fig. 8, B).

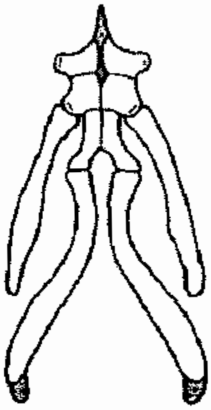


Figure 44 Hyoids of *Lissemys punctata* in dorsal view (Meylan, 1987, p 49, Fig. 18, B).

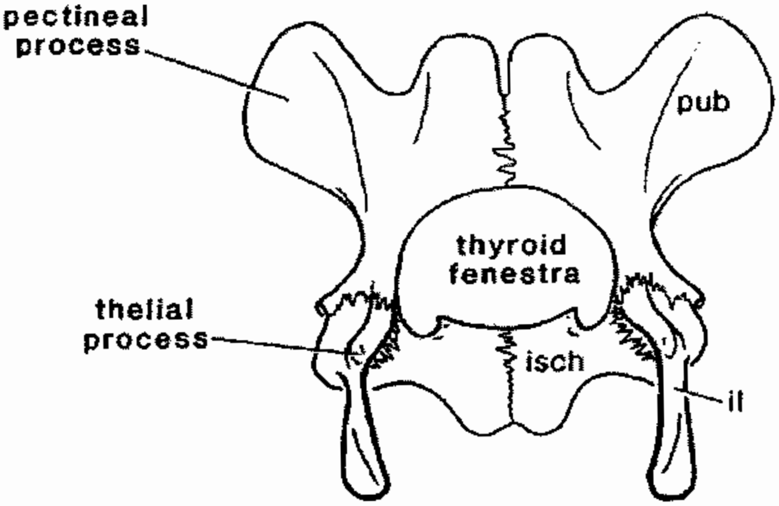


Figure 45 Pelvis of *Lissemys punctata* (UF 56017) in dorsal view (Meylan, 1987, p 52, Fig. 21, E).

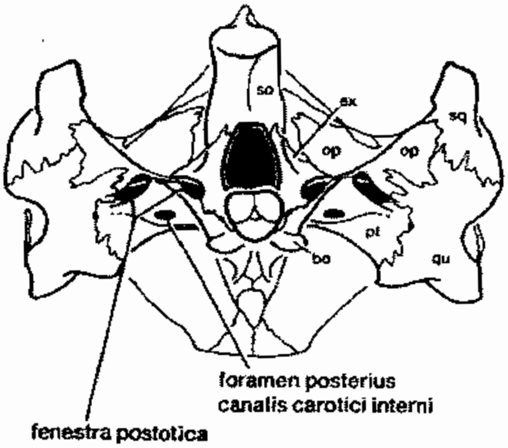


Figure 46 Skull of *Lissemys punctata* (NMNH 61094) in posterior view (Meylan, 1987, p 39, Fig. 14, F).

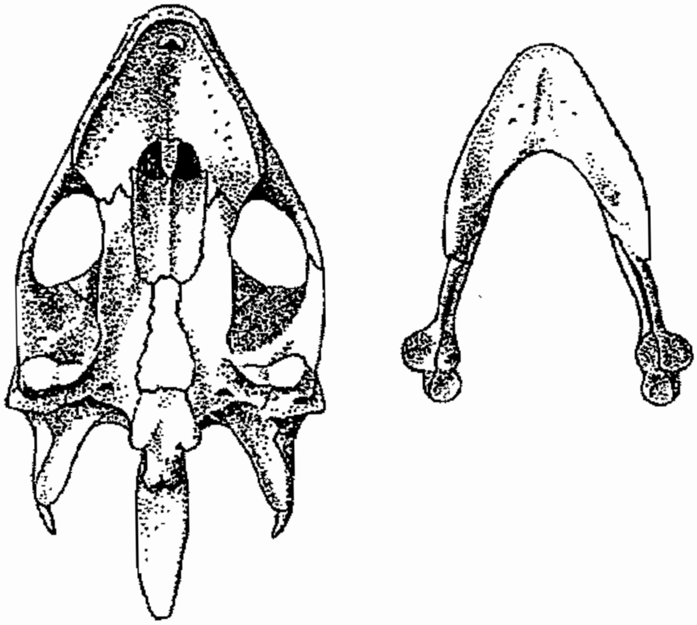


Figure 47 Skull of *Nilssonia hurum*; in palatine view (left) and lower jaw in dorsal view (right) (*Trionyx hurum* in Smith, 1931, p 71, Fig. 39).

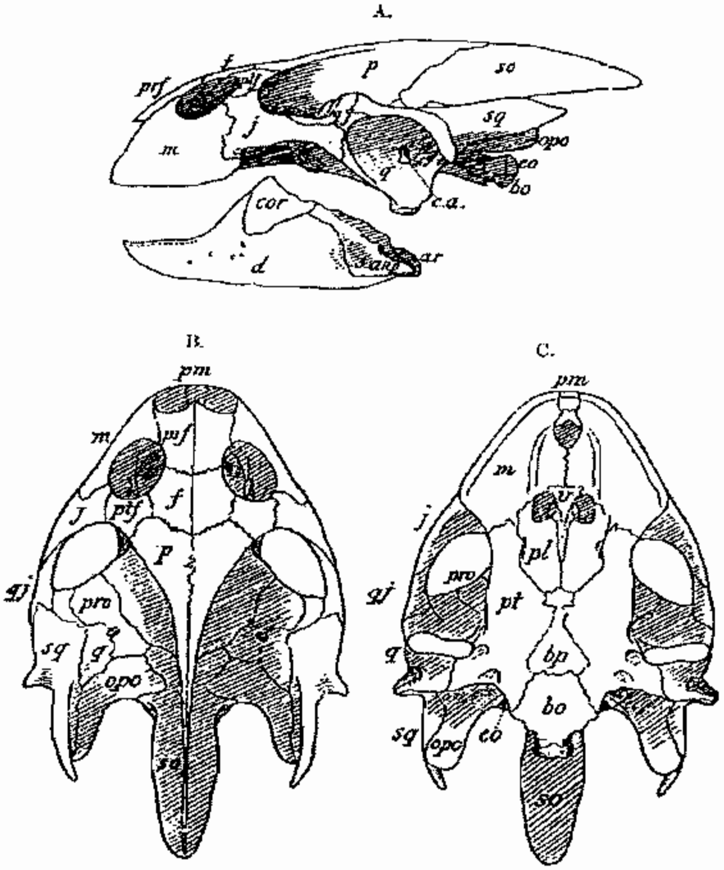


Figure 48 Skull of *Nilssonia gangetica* in lateral (A), dorsal (B) and ventral (C) views (*Trionyx gangeticus* in Smith, 1931, p 149, Fig. 30).

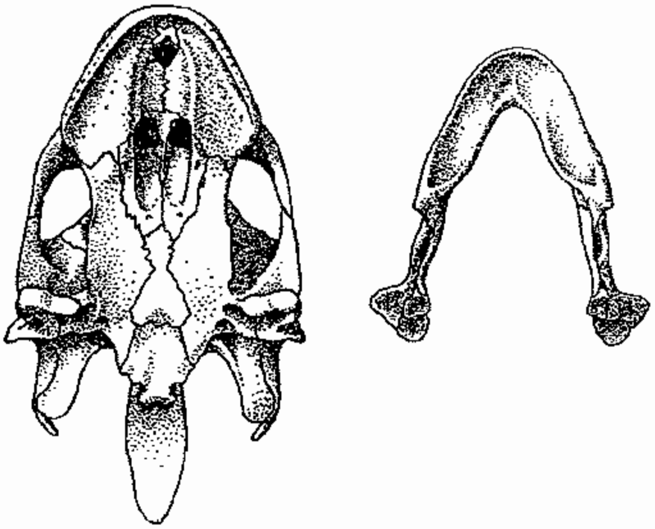
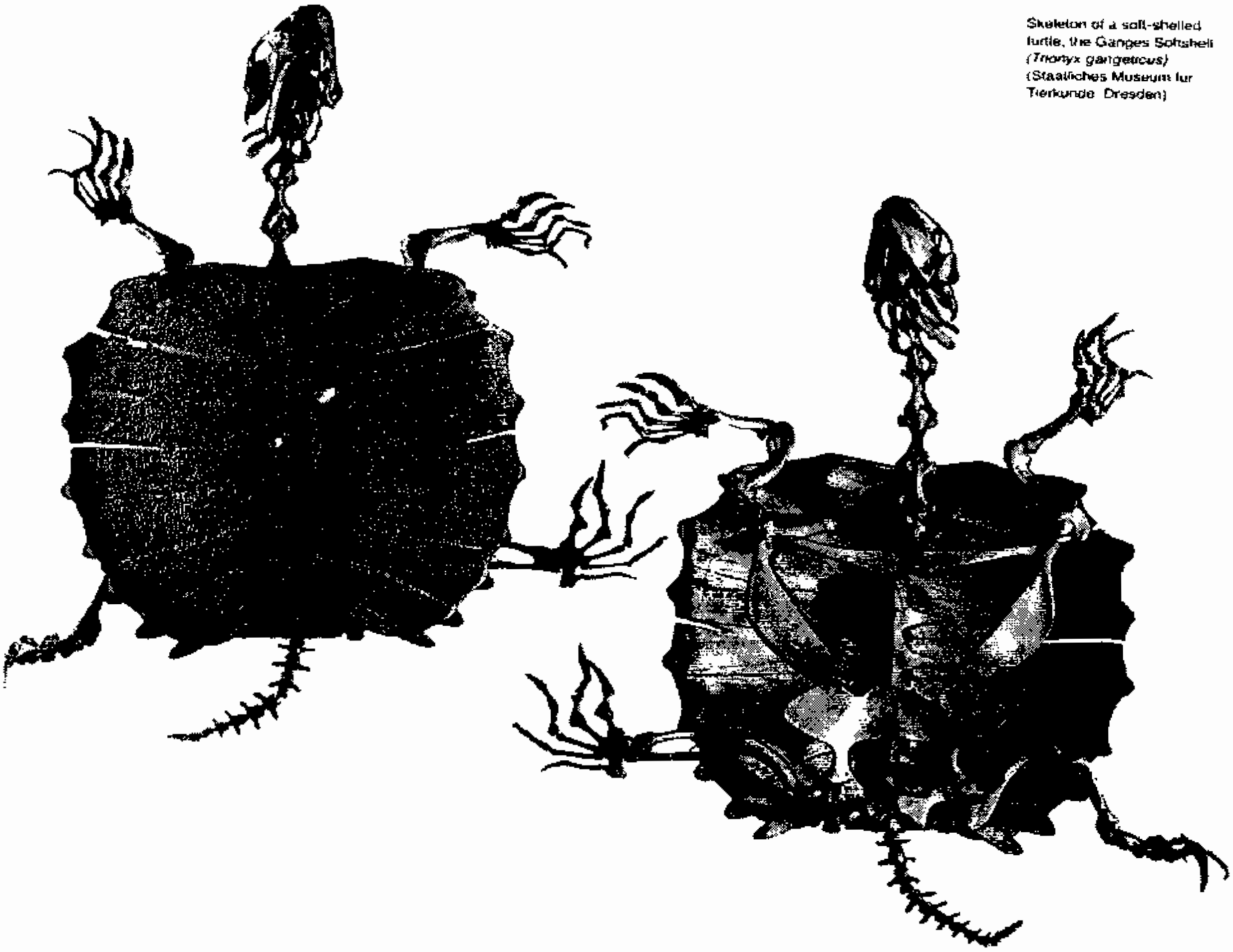


Figure 49 Skull of *Nilssonia gangetica* ; skull table in palatine view (left) and lower jaw in dorsal view (right) (*Trionyx gangeticus* in Smith, 1931, p 168, Fig. 38).



Skeleton of a soft-shelled
turtle, the Ganges Softshell
(Trionyx gangeticus)
(Staatliches Museum fur
Tierkunde Dresden)

Figure 50 *Nilssonia gangetica* (*Trionyx gangeticus*) (obst, 1986)

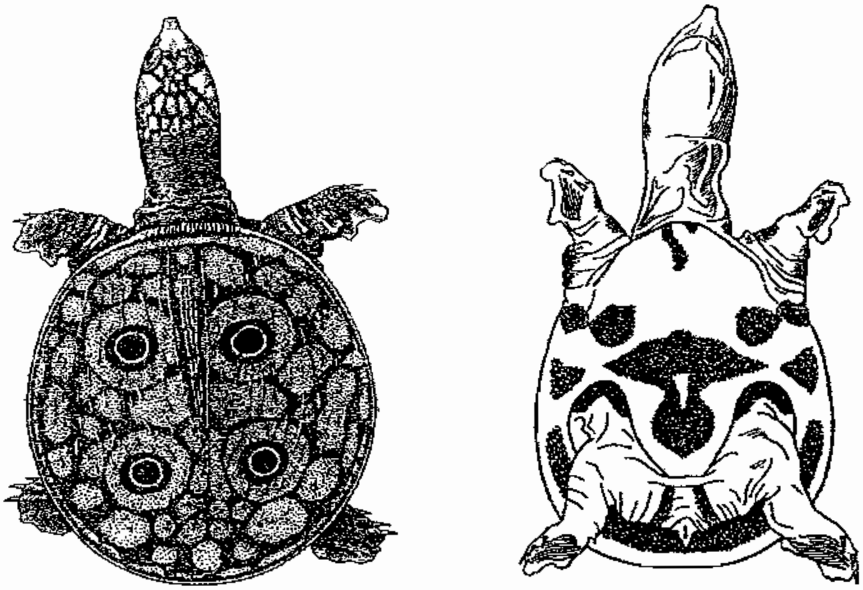


Figure 51 Juvenile individual of *Nilssonia hurum* in dorsal view (*Trionyx hurum* in Smith, 1931, p 172, Fig. 40) and *Pelodiscus sinensis* in ventral view (*Trionyx sinensis* in Smith, 1931, p 177, Fig. 41).

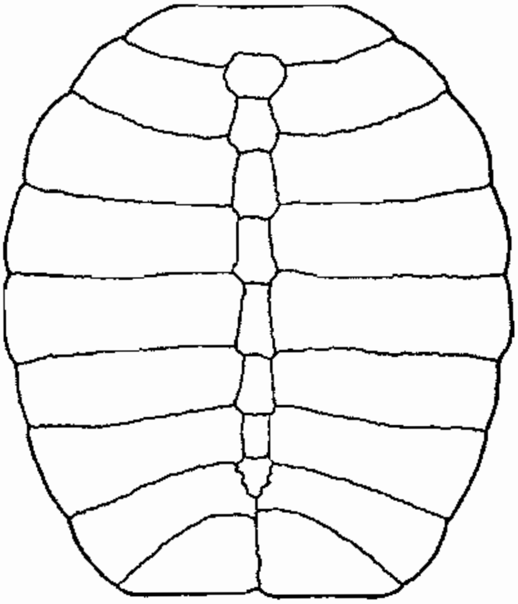


Figure 52 Carapace of *Nilssonia hurum* (BMNH 86.8.22.2), recently in dorsal view (*Trionyx hurum* in Meylan, 1987, p 17, Fig. 5, B).

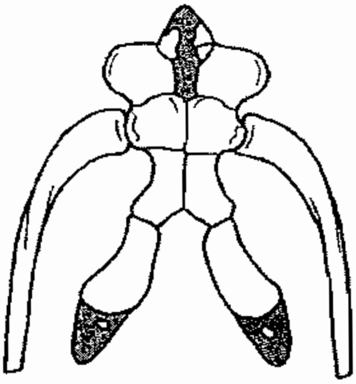


Figure 53 Hyoids of *Nilssonia hurum* in dorsal view (*Trionyx hurum* in Meylan, 1987, p 49, Fig. 18, C).

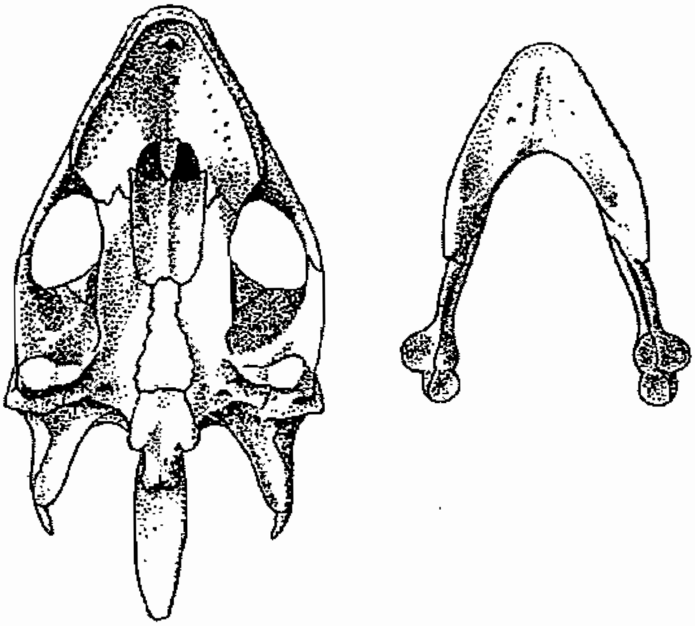


Figure 54 Skull of *Nilssonia hurum*; skull in palatine view (left) and lower jaw in dorsal view (right) (*Trionyx hurum* in Smith, 1931, p 71, Fig. 39).

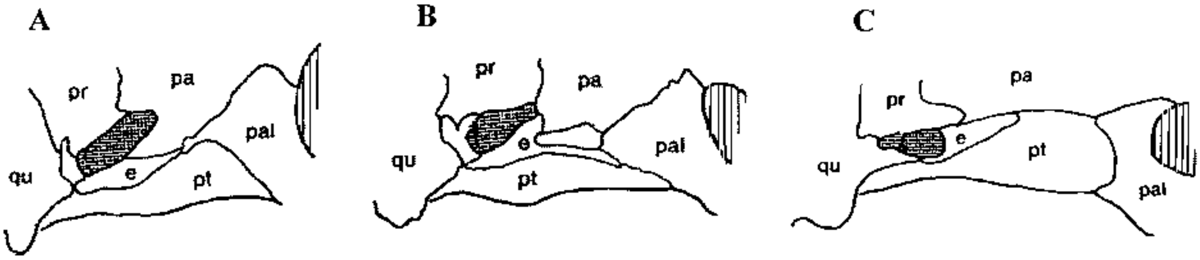


Figure 55 The trigeminal region of two trionychid turtles exhibiting contacts of the skull elements around the formamen nervi and participation by the palatine in the lateral wall of the braincase; (A) *Lissemys punctata* (UF 56017), (B) *Nilssonia hurum* (*Trionyx hurum*) (BMNH 86.8.16.2), (C) *Chitra indica* (IRSNB 3295) (Meylan, 1987, p 36, Fig. 13, D,F).

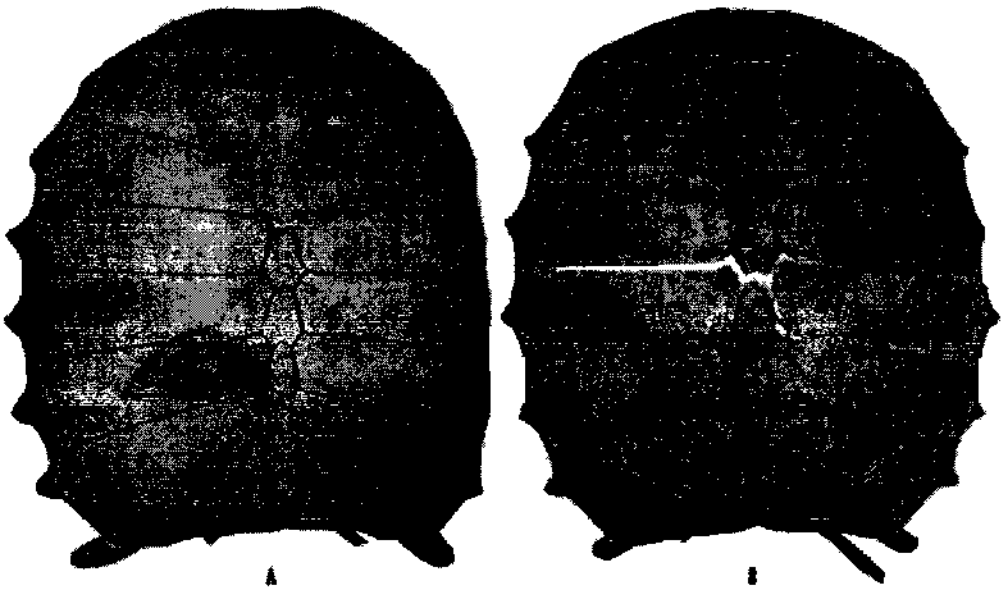


Figure 56 Shell of *Rafetus vietnamensis* Le et al., 2010 in dorsal view; (A) holotype and (B) VNUHT 91 from Ma River, Thanh Hoa Province (Farkas, Le, & Nguyen 2011, p 68, Fig. 4).

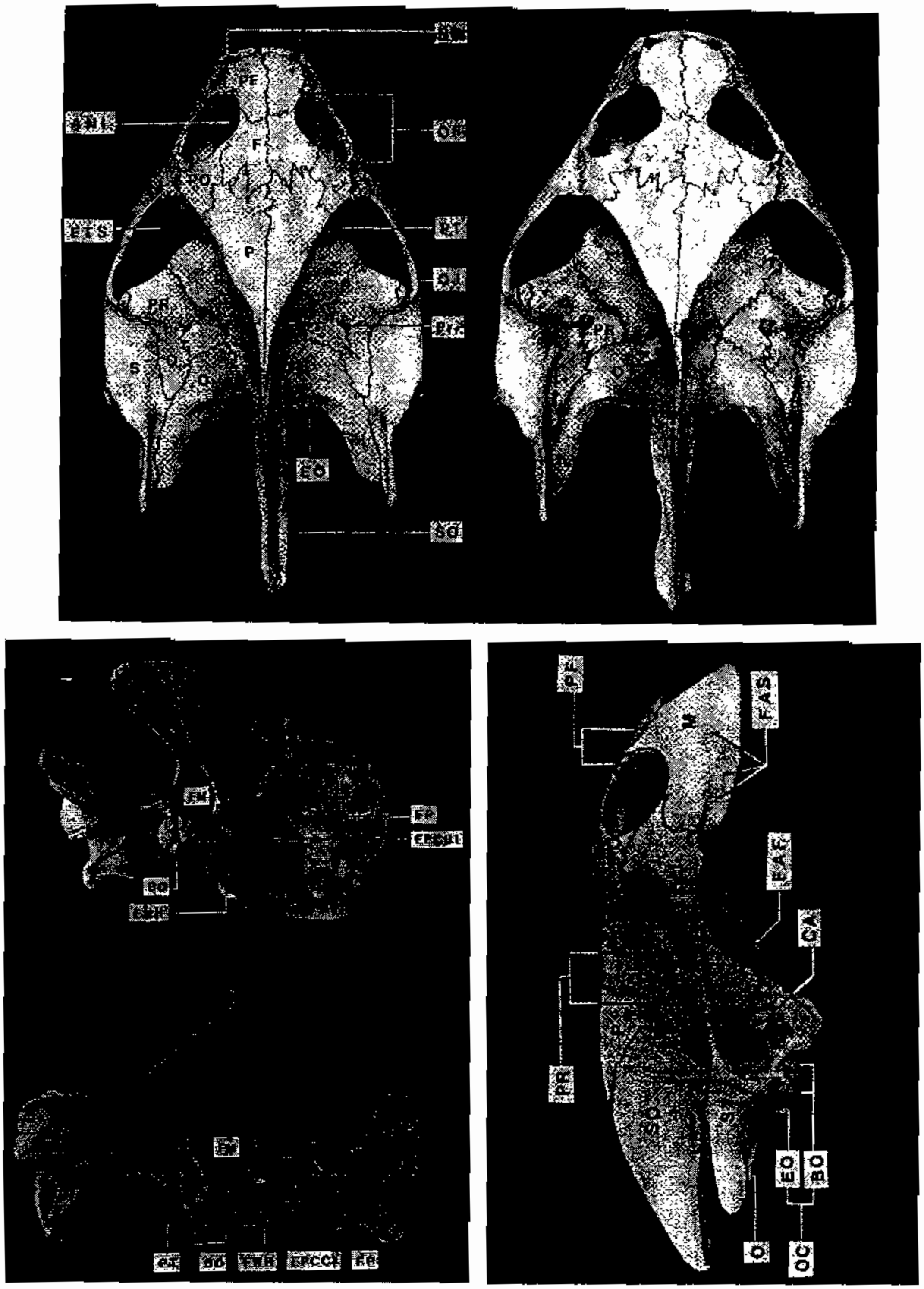


Figure 57 Skull of *Rafetus euphraticus* in dorsal (top; ZDEU-30/989-1 and ZDEU-29/989-2), lateral (right bottom; ZDEU-30/989-1), posterolateroventral (left upper, bottom; ZDEU-25/989-2) and posterior (left lower, bottom; ZDEU-29/989-2) views (Taskavak, 1999, p 40, 43,48, Fig. 2,4,7).

Figure 58 Skull of *Rafetus euphraticus* in ventral view; Top, ZDEU-30/989-1 and ZDEU-67/990-4; bottom, ZDEU-25/989-3 and ZDEU-25/989-5 (Taskavak, 1999, p 45, Fig. 6).

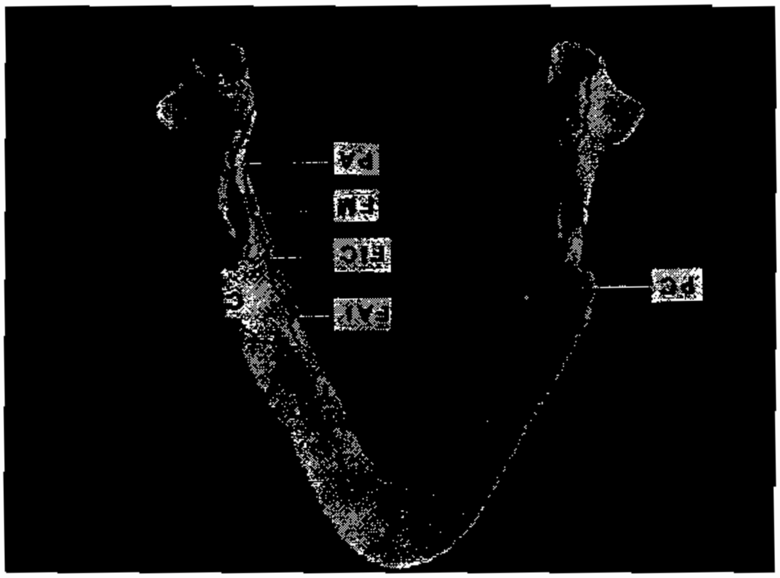


Figure 59 Lower jaw of *Rafetus euphraticus* in dorsal view (ZDEU-67/990-4) (Taskavak, 1999, p 51, Fig. 8).

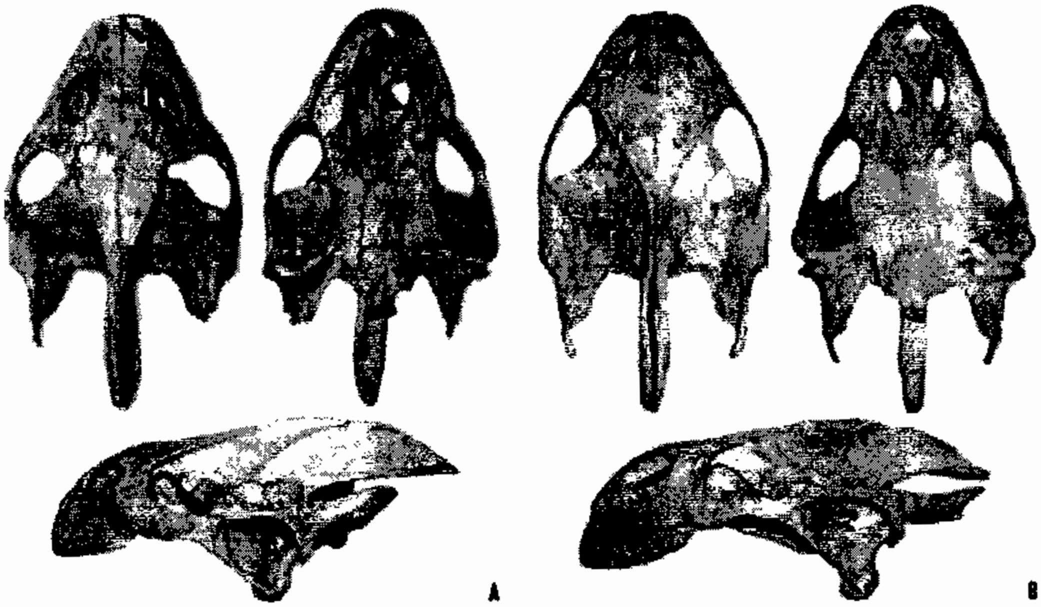


Figure 60 Skull of *Rafetus*; in dorsal (top; 1,3), palatine (top;2,4) and lateral (bottom) views; (Farkas, Le, & Nguyen 2011, p 68, Fig. 3).

4.3 Objective of this study

Despite of these scattered publication, there is still a lack of detailed information about the osteology of shell characters, which are often found in fossils. A detailed description of the living trionychid turtle shells in Thailand and from neighbor countries such as *Lissemys scutata* (Bonnaterre, 1789), *Aspideretes, Nilssonia* and *Rafetus* will constitute a useful tool for describing and diagnosing the fossil and sub-fossil turtle record in Thailand.

4.4 Methods

Trionychid turtles were photographed for carapace and plastron. Drawings, when necessary are also provided. A short description of the carapace and plastron anatomy was provided, and a key was established to identify skeleton of living specimens on the base of their osteology.

4.5 Anatomy of soft-shell turtle carapace

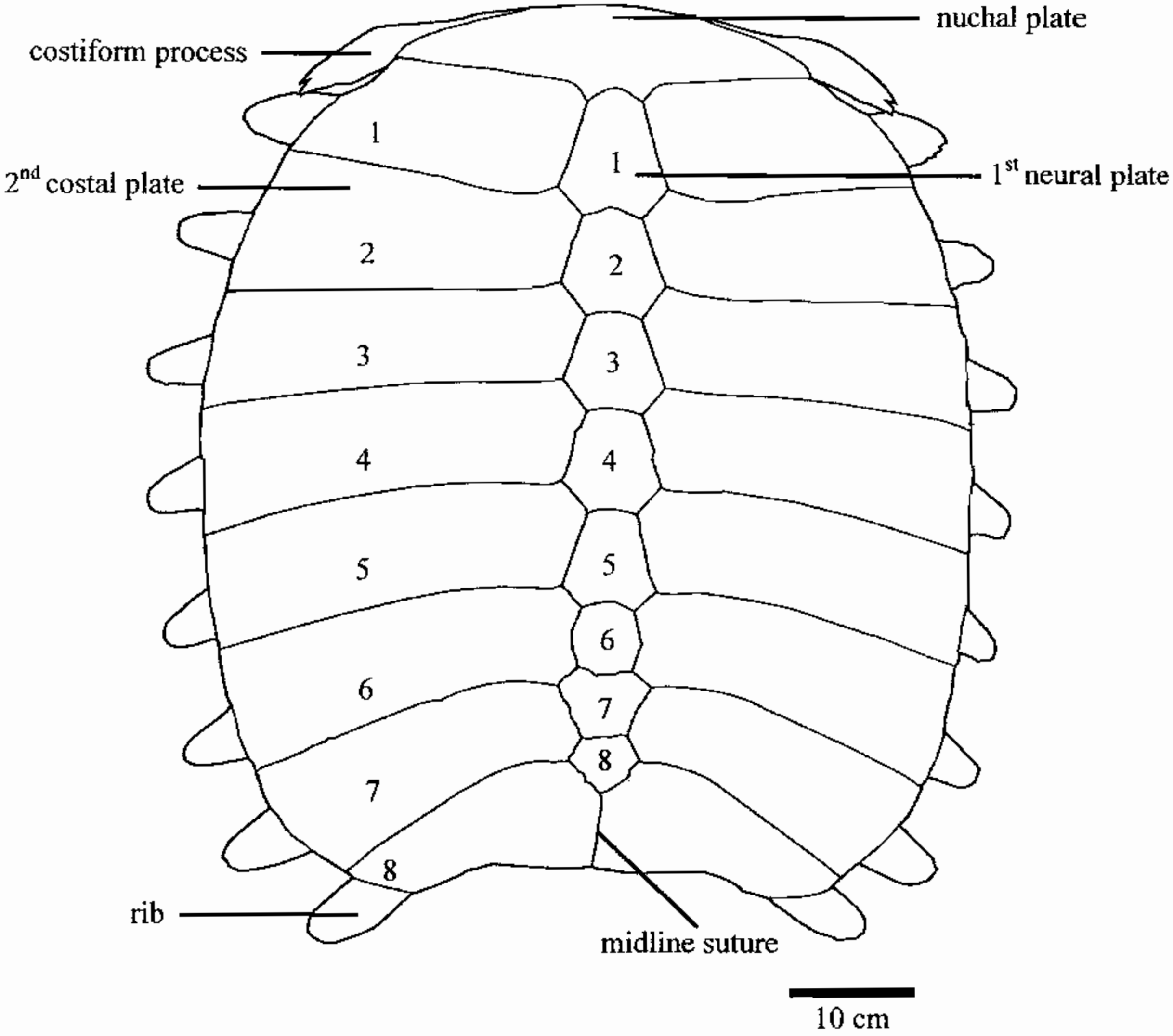


Figure 61 Terminology used for the soft-shell carapace anatomy. The representative specimen is *Chitra chitra* from collection of Chulalongkorn University, Bangkok, Thailand.

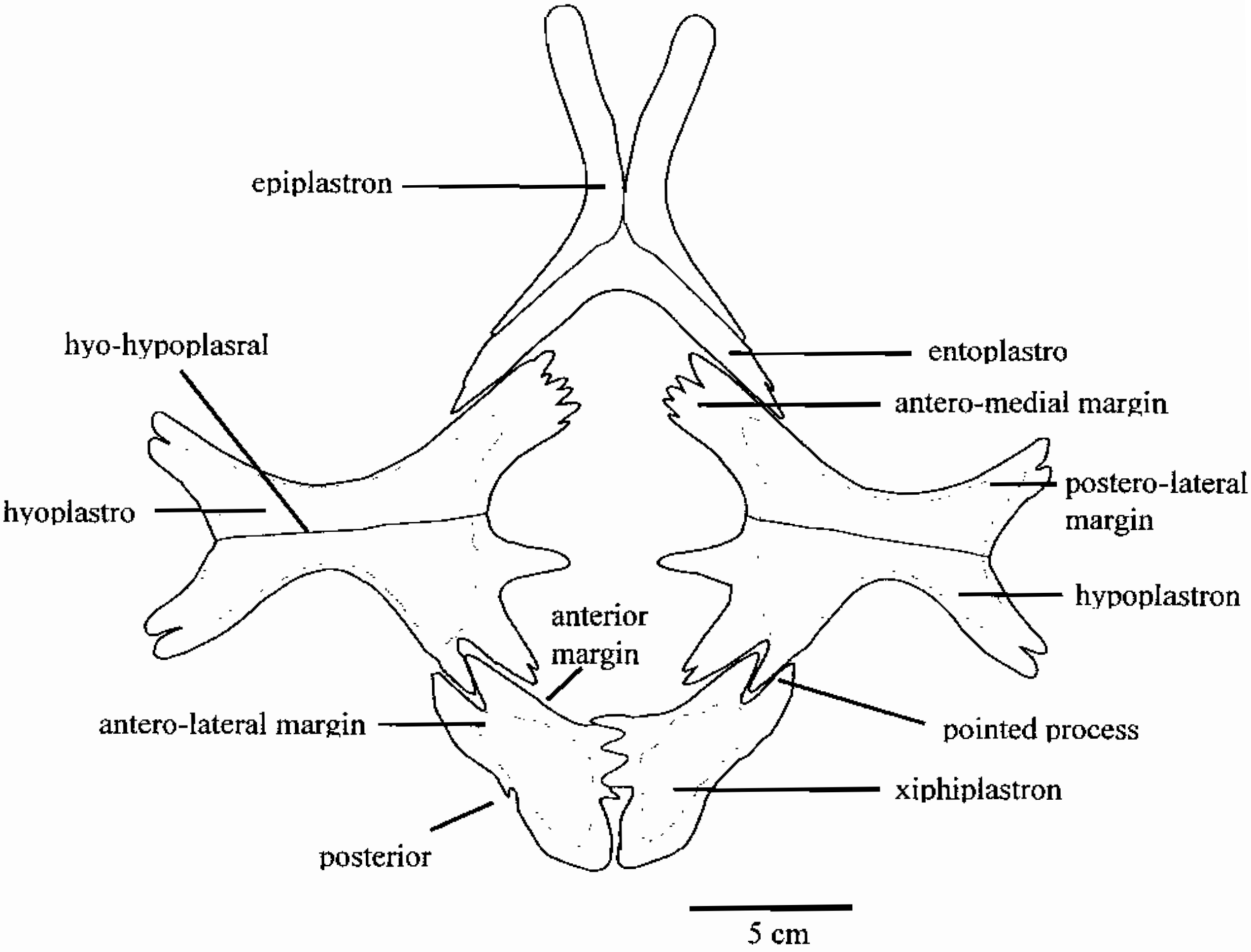


Figure 62 Terminology used for the soft-shell plastron anatomy. The representative specimen is *Amyda cartilagenea* from collection of Chulalongkorn University, Bangkok, Thailand.

4.6 Pictorial key of living trionychid turtle shells in Thailand and neighbor countries

4.6.1 *Amyda cartilaginea* (Boddaert, 1770) (Figure 63-65)

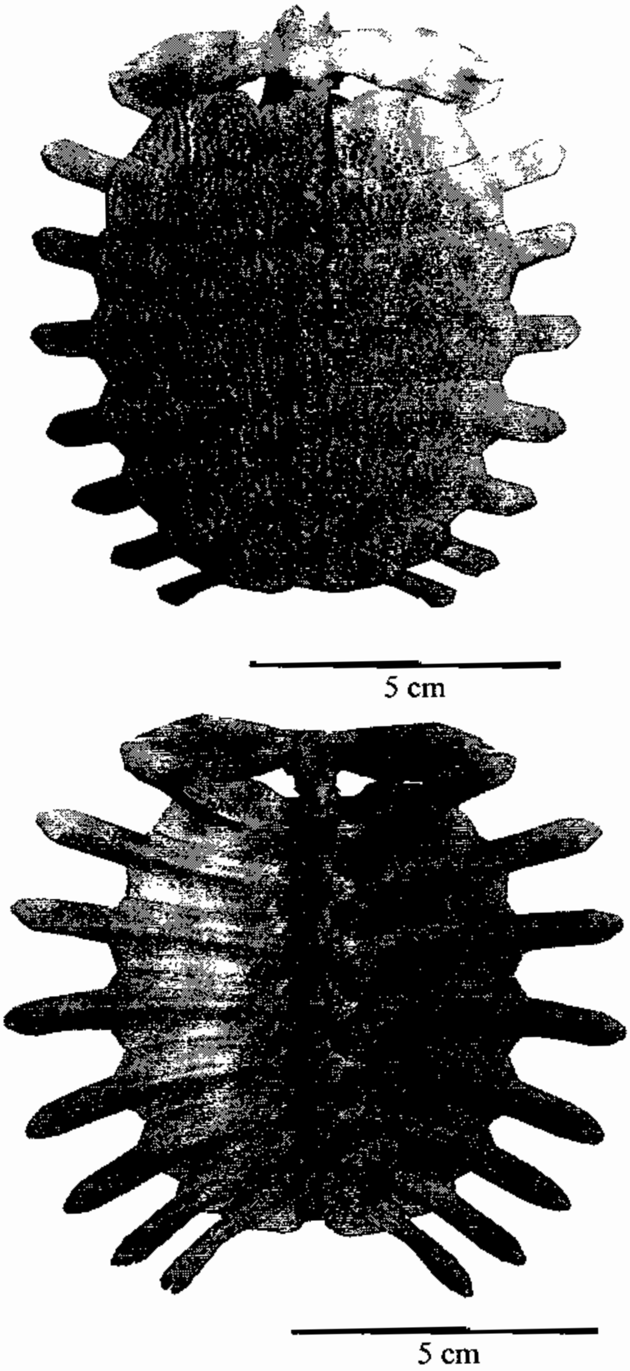


Figure 63 Juvenile individual of *Amyda cartilagenea* carapace (CUMZ(R) 1994-6-10-1) in dorsal view (above) and visceral view (bottom).

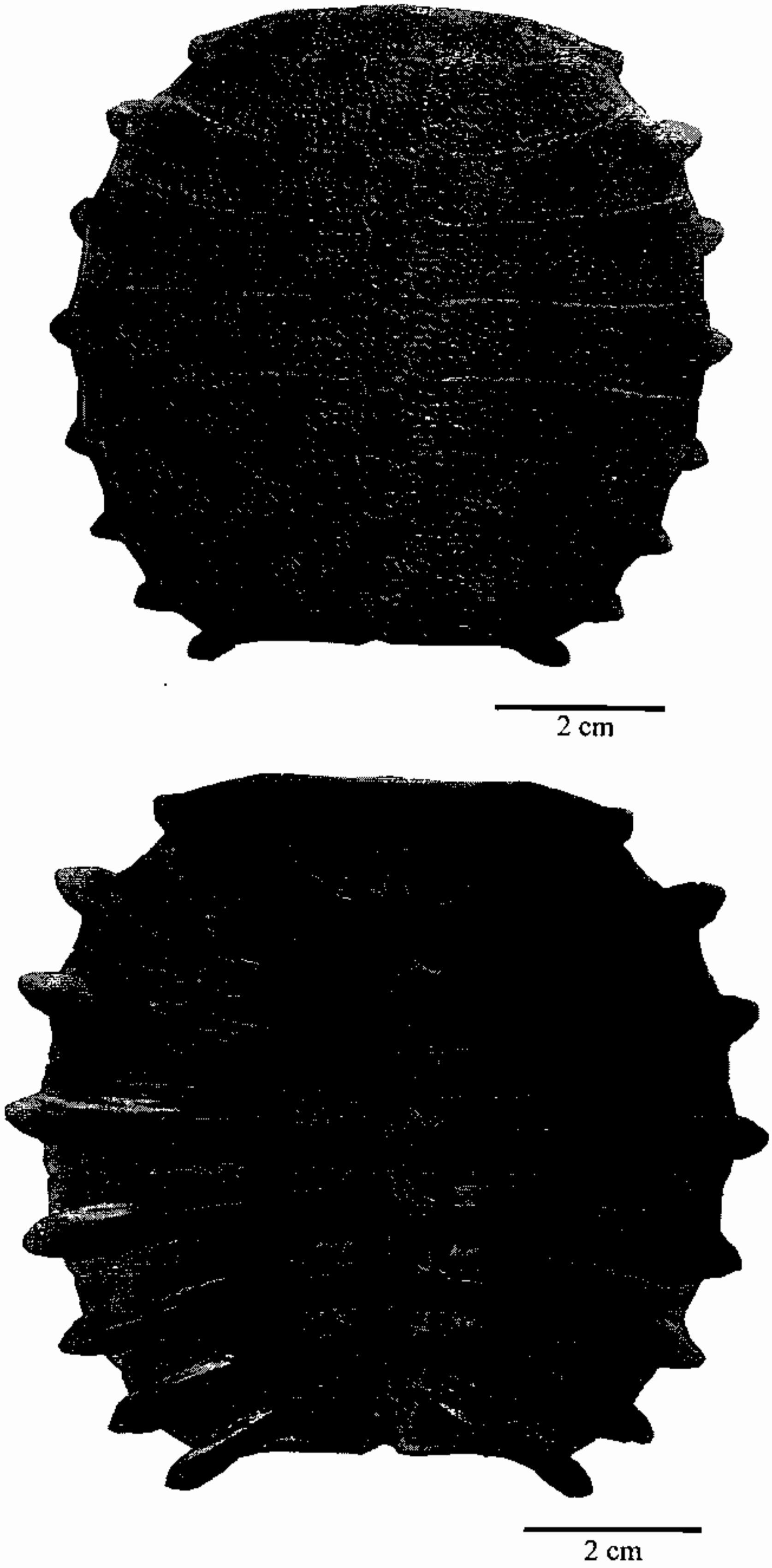


Figure 64 Adult individual of *Amyda cartilagenea* carapace (CUMZ(R) 1994-3-4, 3) in dorsal view (above) and visceral view (bottom). (Photo: Teppei Sonoda).

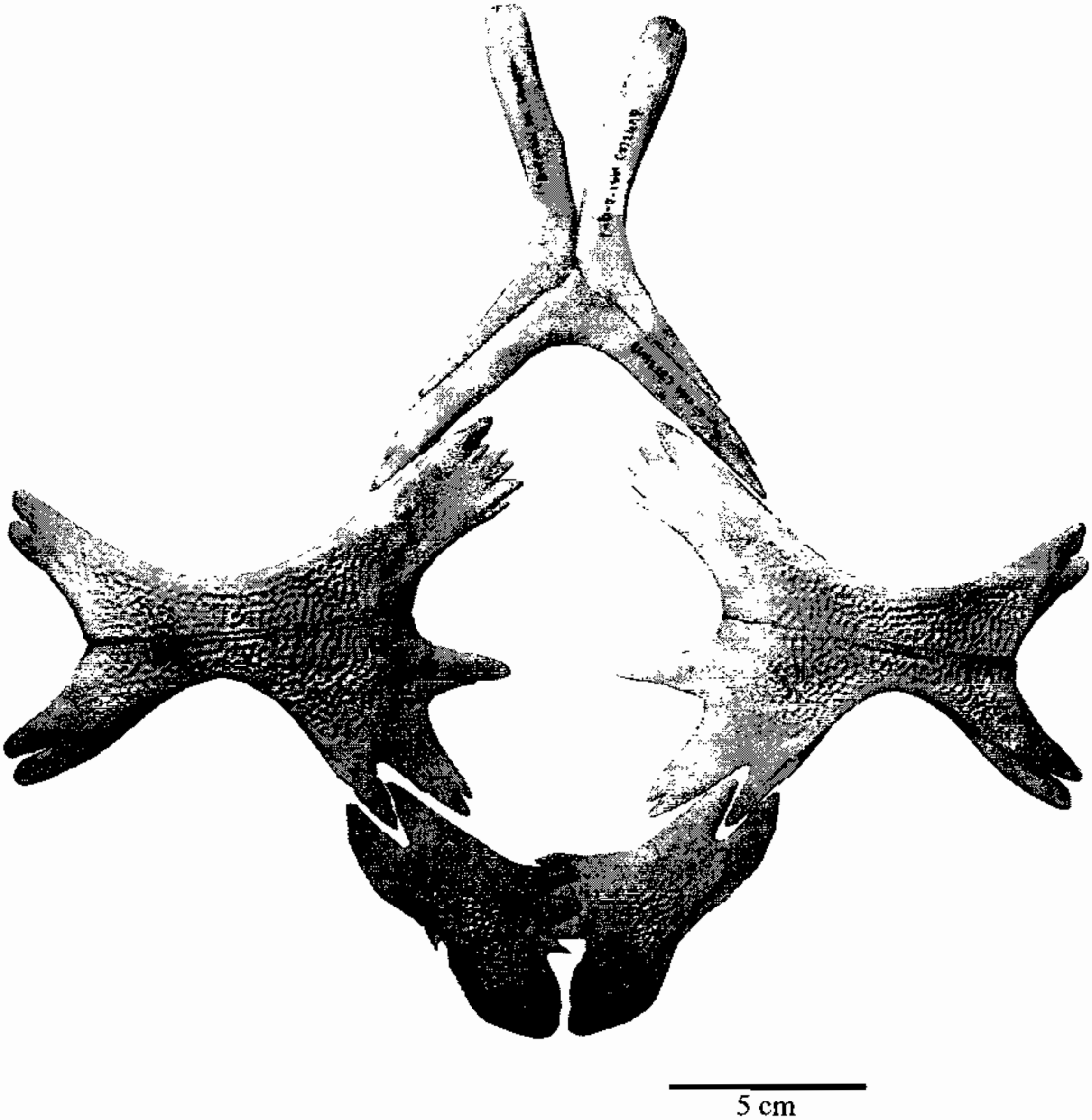


Figure 65 Adult individual of *Amyda cartilagenea* plastron (CUMZ(R) 1994-3-4, 3) in ventral view.

4.6.2 *Chitra chitra* (Nutaphand, 1986) (Figure 66-69)

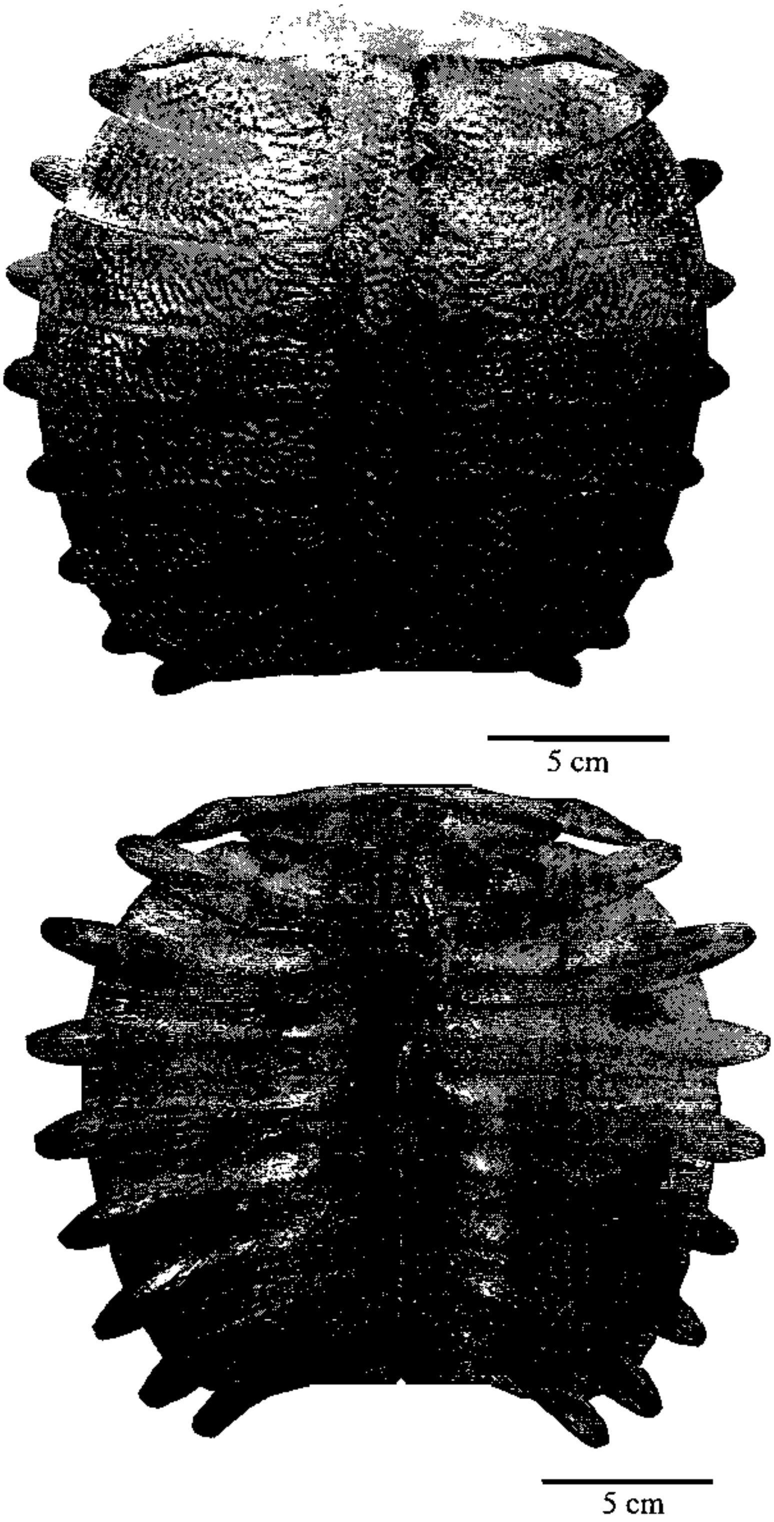


Figure 4.66 Juvenile individual of *Chitra chitra* carapace (CUMZ(R) unnumbered) in dorsal view (above) and visceral view (bottom).

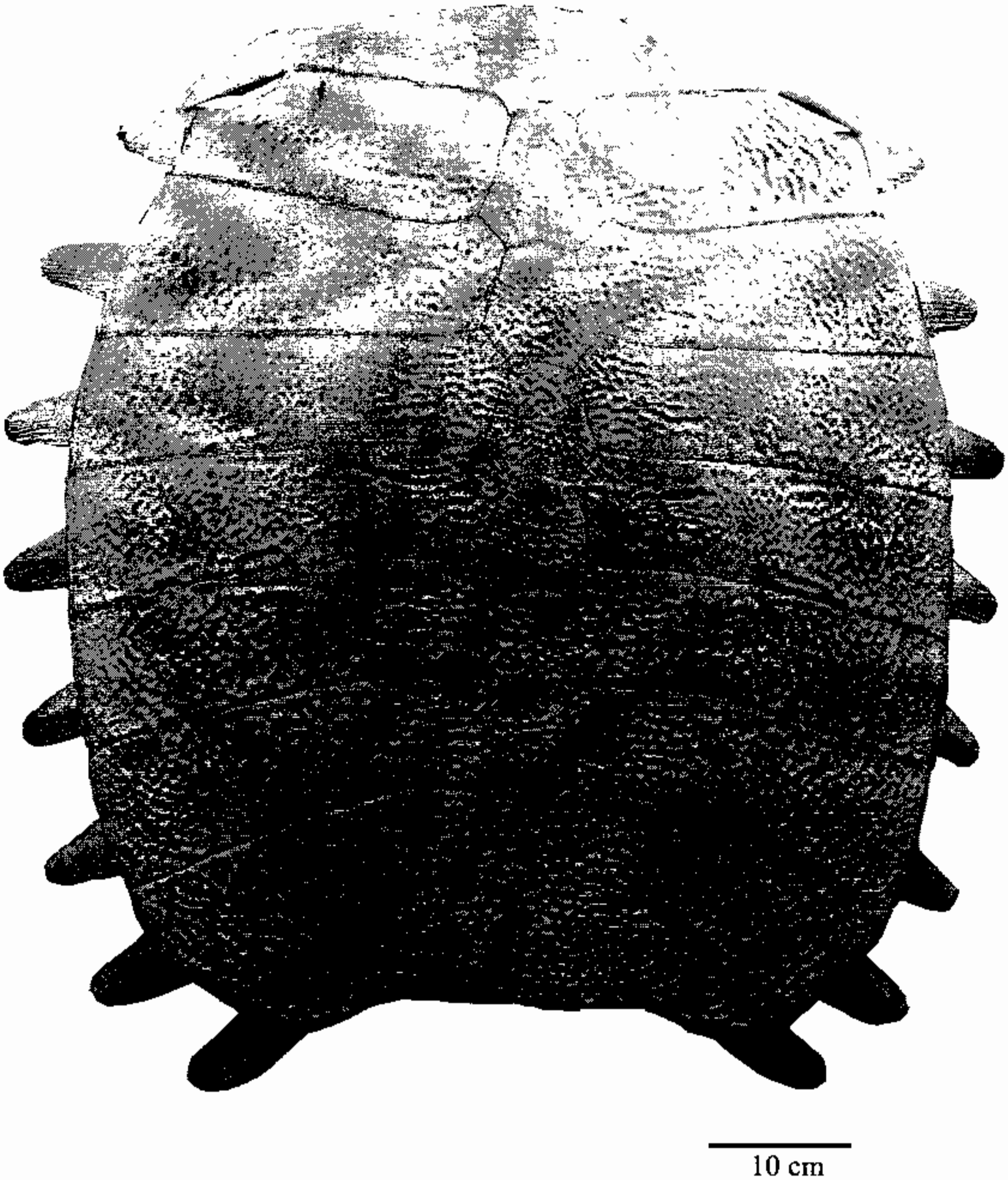


Figure 67 Adult individual of *Chitra chitra* carapace (CUMZ-R-T156) in dorsal view.

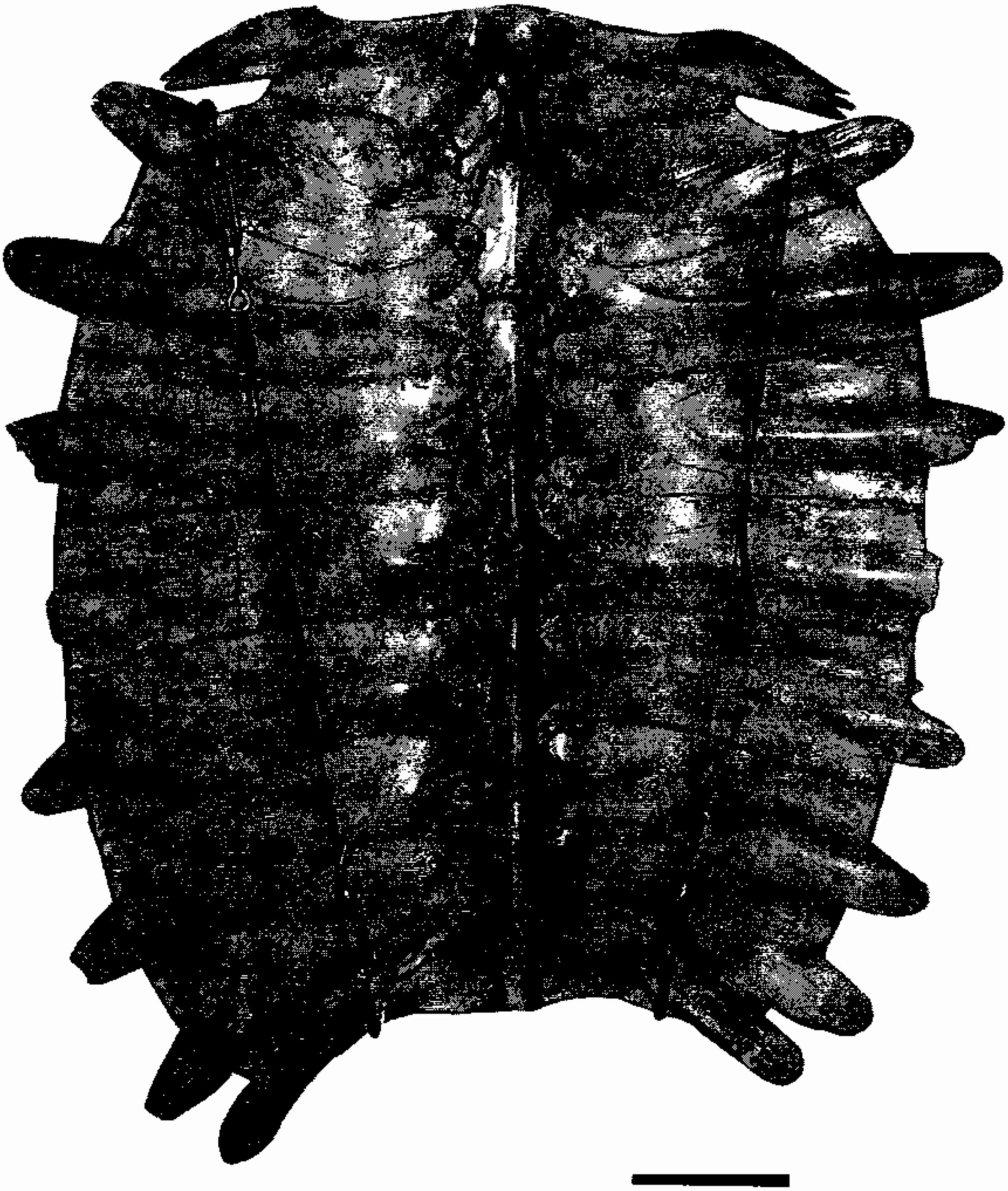


Figure 68 Adult individual of *Chitra chitra* carapace (CUMZ-R-T157) in visceral view. Scale bar equal 10 cm.

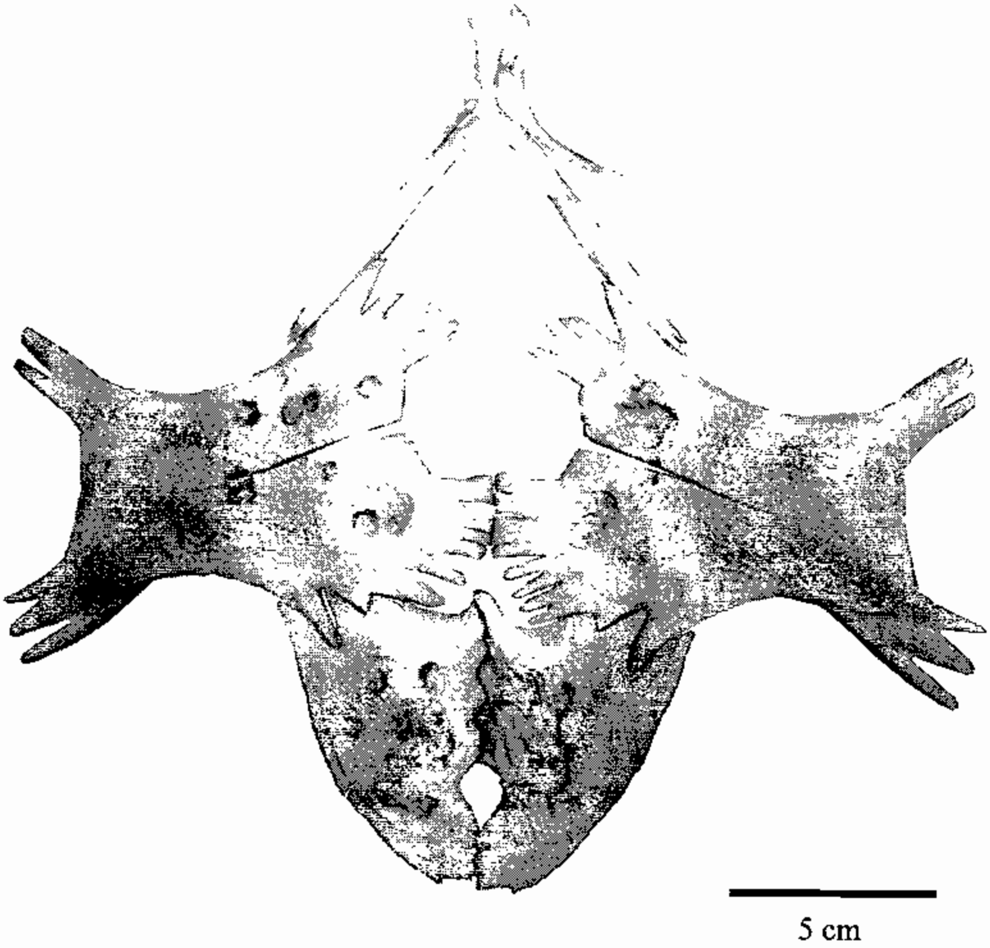


Figure 69 *Chitra chitra* plastron (CUMZ-R-T138) in ventral view.

4.6.3 *Dogania subplana* (Geoffroy, 1809) (Figure 70-73)

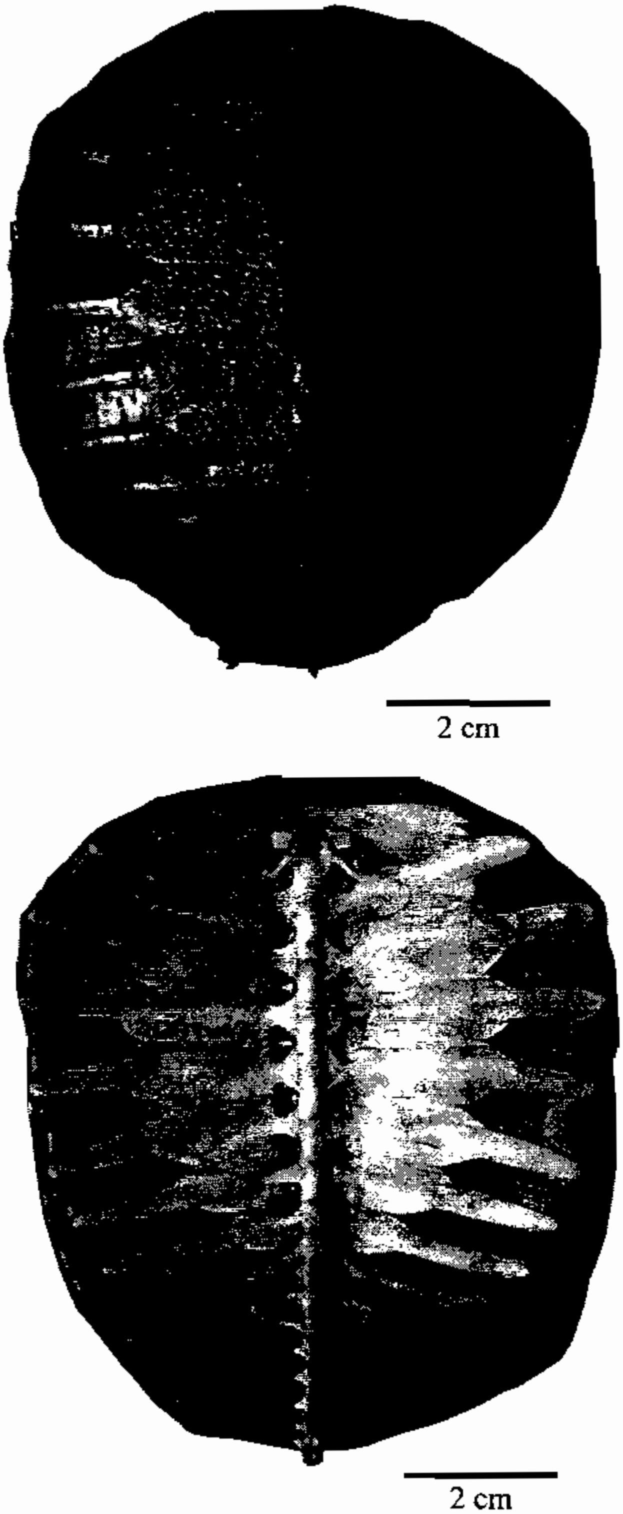


Figure 70 Juvenile individual of *Dogania subplana* carapace (CUMZ(R) 1993-5-18, 1) in dorsal view (above) and visceral view (bottom).

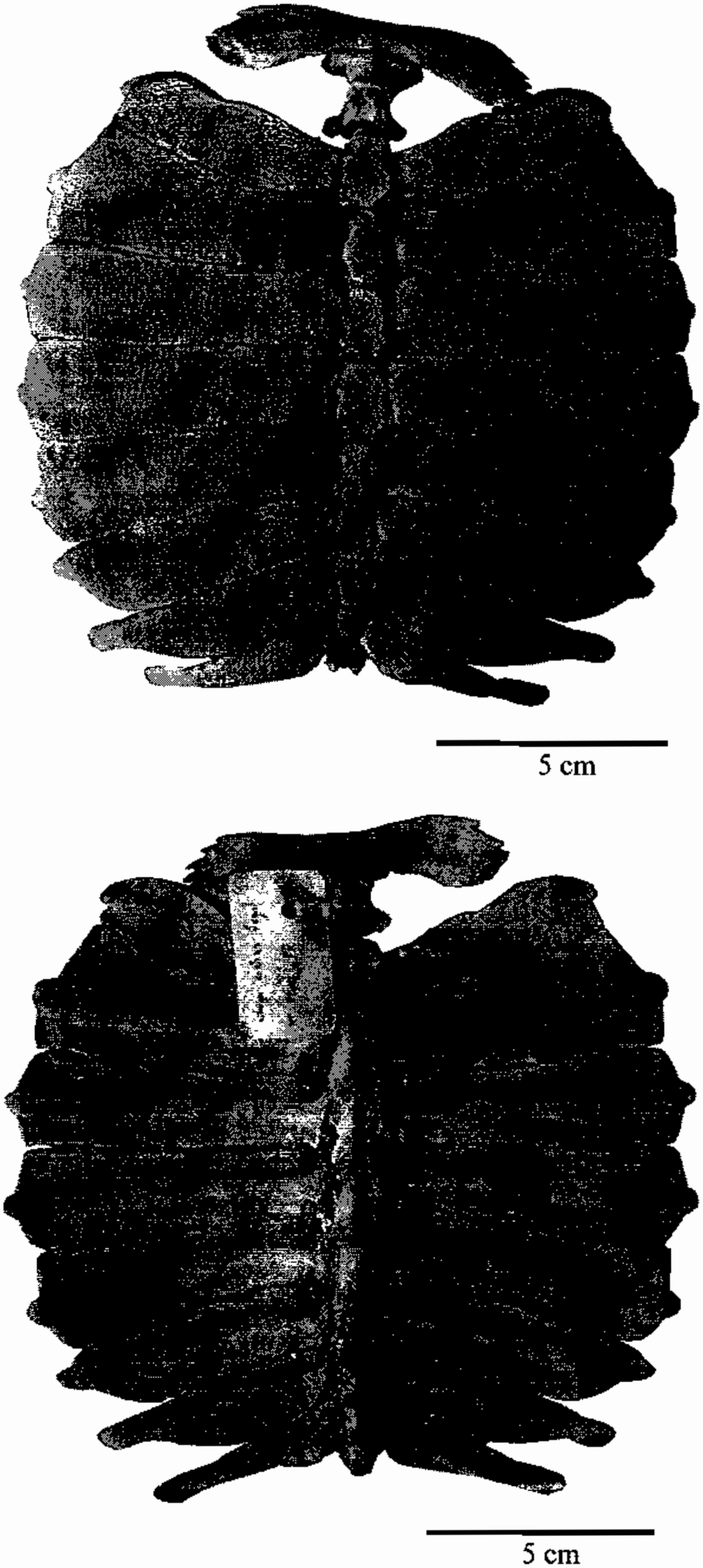


Figure 71 Adult individual of *Dogania subplana* carapace (CUMZ(R) 1997-3-10, (1)) in dorsal view (above) and visceral view (bottom).

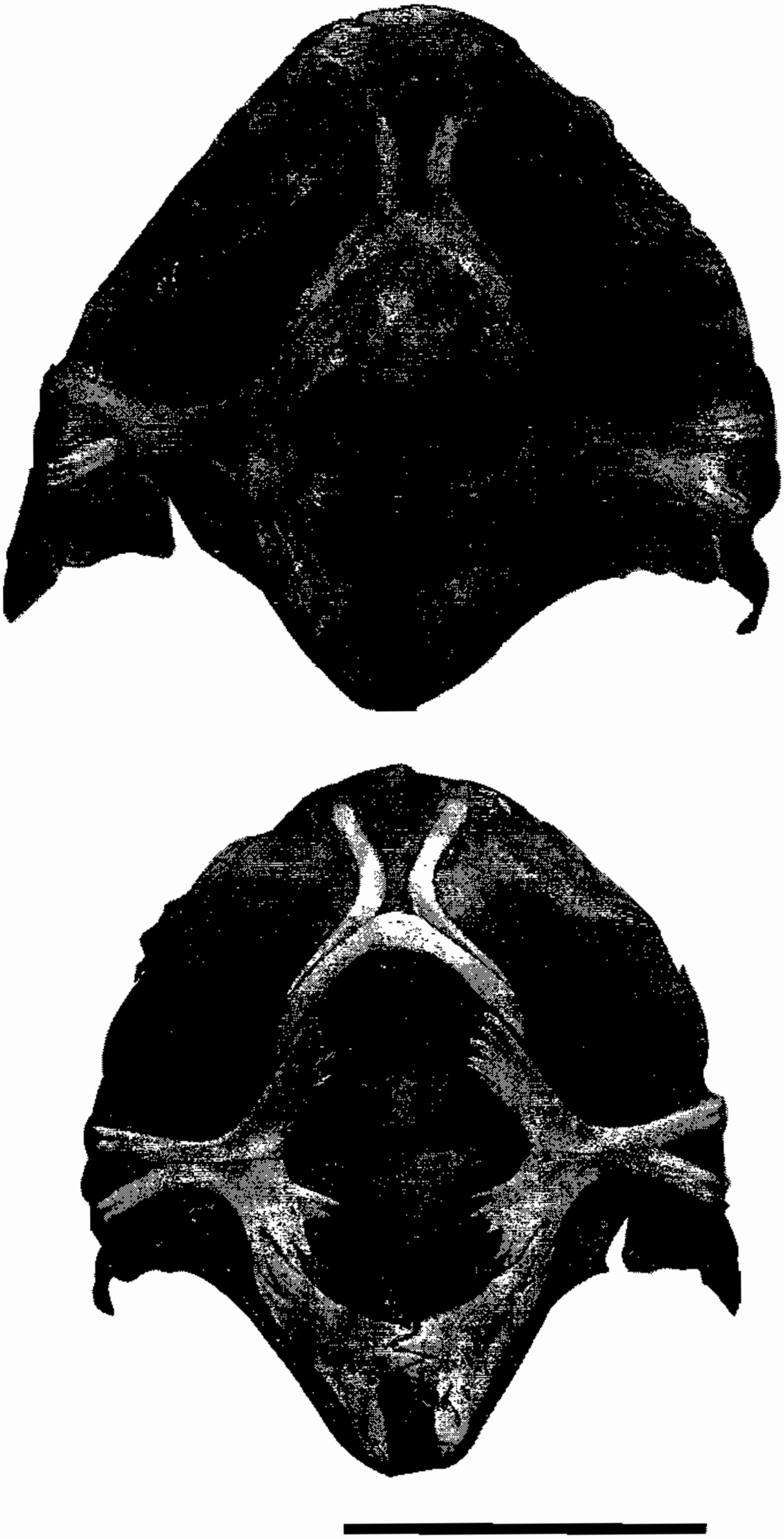


Figure 72 Juvenile individual of *Dogania subplana* plastron in ventral (upper) and visceral (lower) views. (Photo: Haiyan Tong)

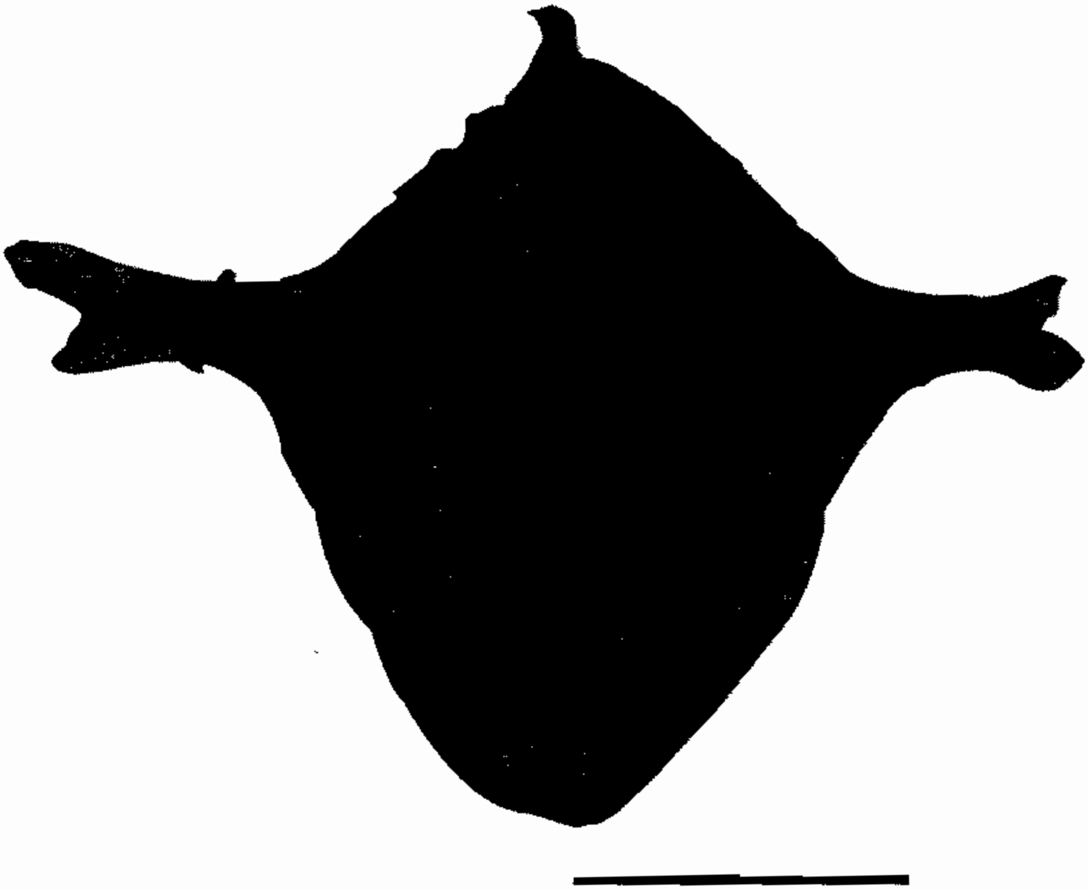


Figure 73 Adult individual of *Dogania subplana* plastron (CUMZ(R) 1992-4-14, 3) in visceral view.

4.6.4 Pelochelys cantorii Gray, 1864 (Figure 74-77)

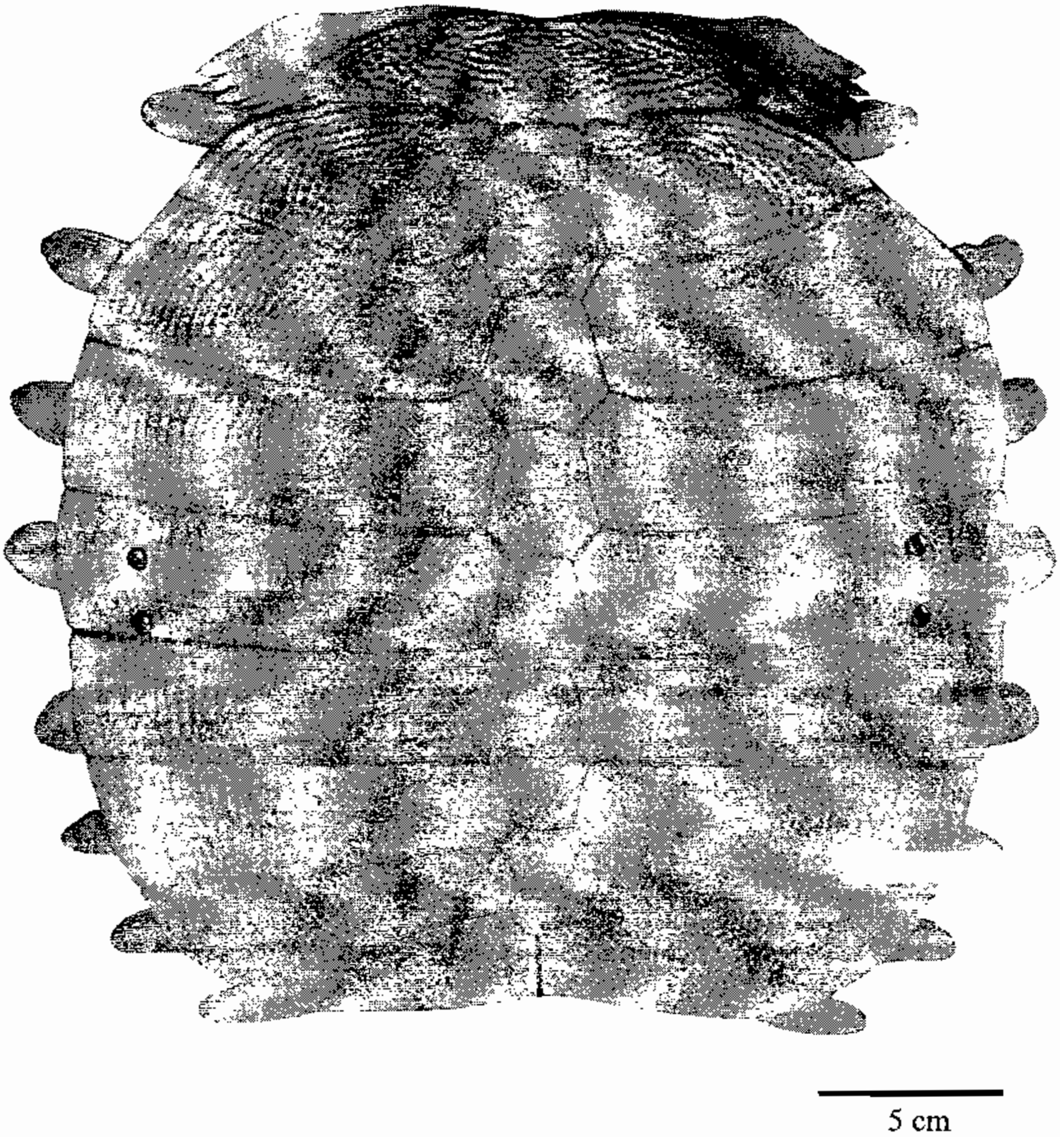


Figure 74 Adult individual of *Pelochelys cantorii* carapace (CUMZ-R- T120) in dorsal view.

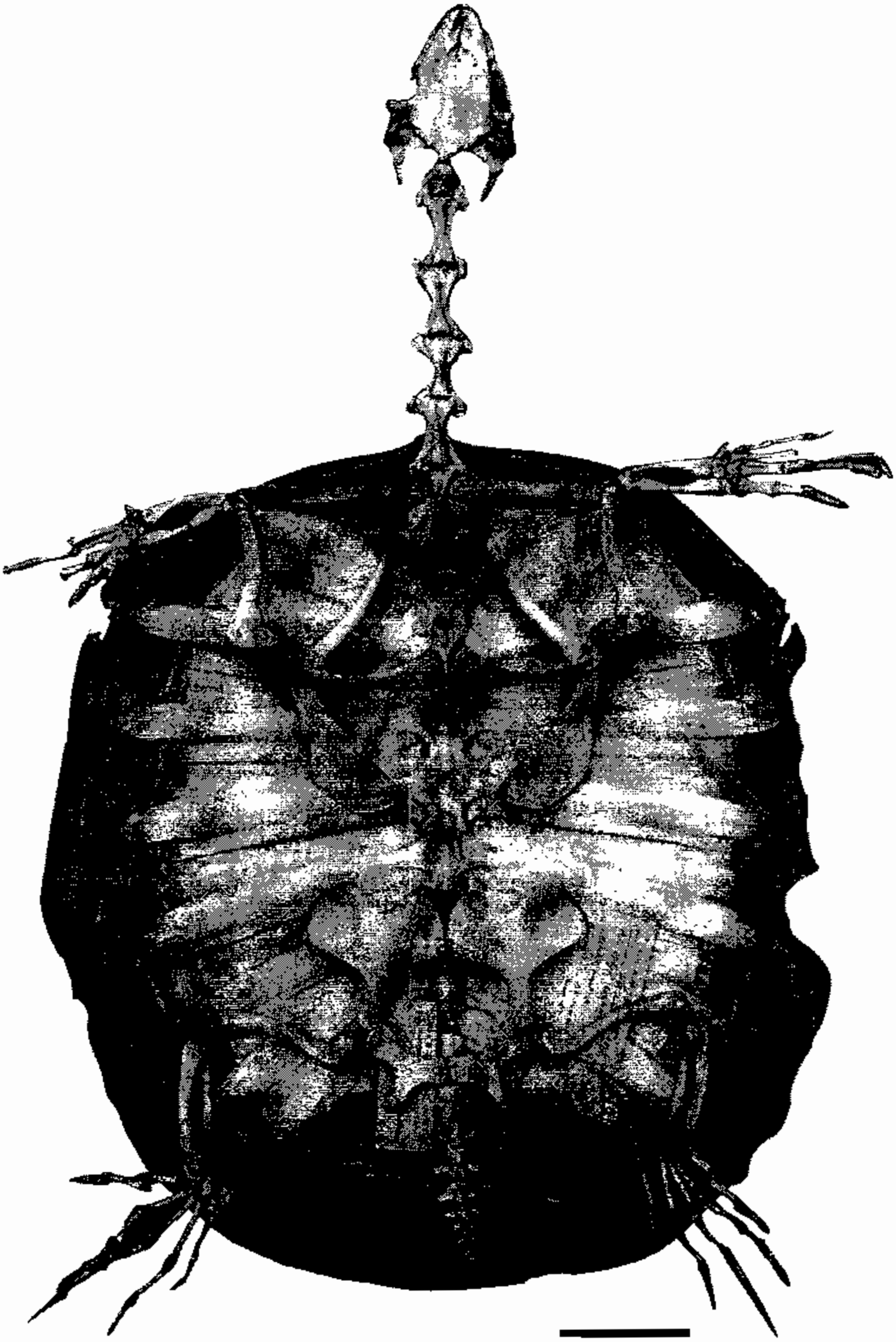


Figure 75 Adult individual of *Pelochelys cantorii* carapace (1857) in visceral view. Scale bar equals 5 cm. (Photo: Haiyan Tong)

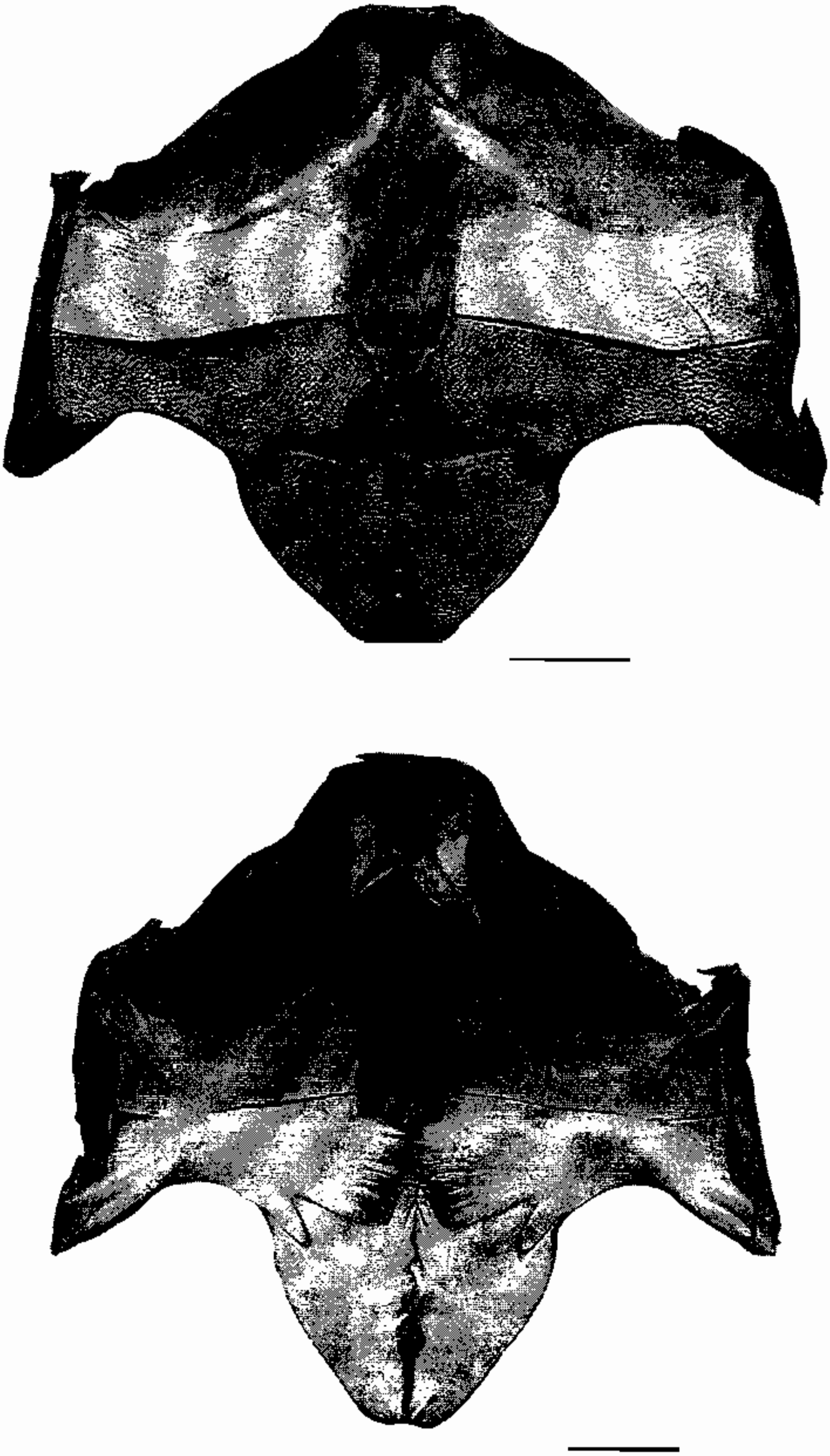


Figure 76 Adult individual of *Pelochelys cantorii* plastron (1857) in visceral view. Scale bars equal 5 cm. (Photo: Haiyan Tong)

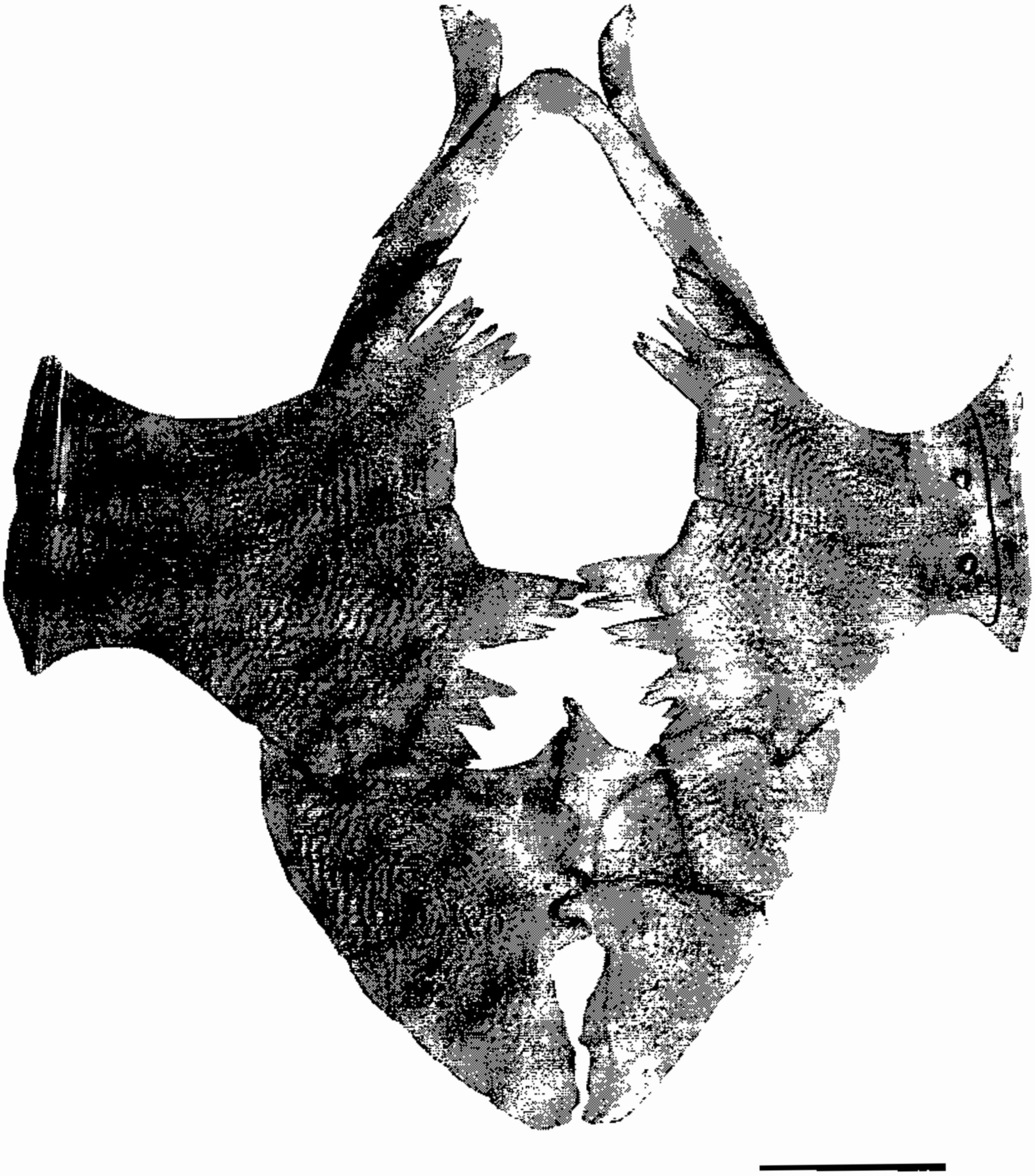


Figure 77 *Pelochelys cantorii* plastron (CUMZ-R-T120) in ventral view. Scale bars equal 5 cm.

4.6.5 *Lissemys scutata* (Bonnaterre, 1789) (Figure 78-82)

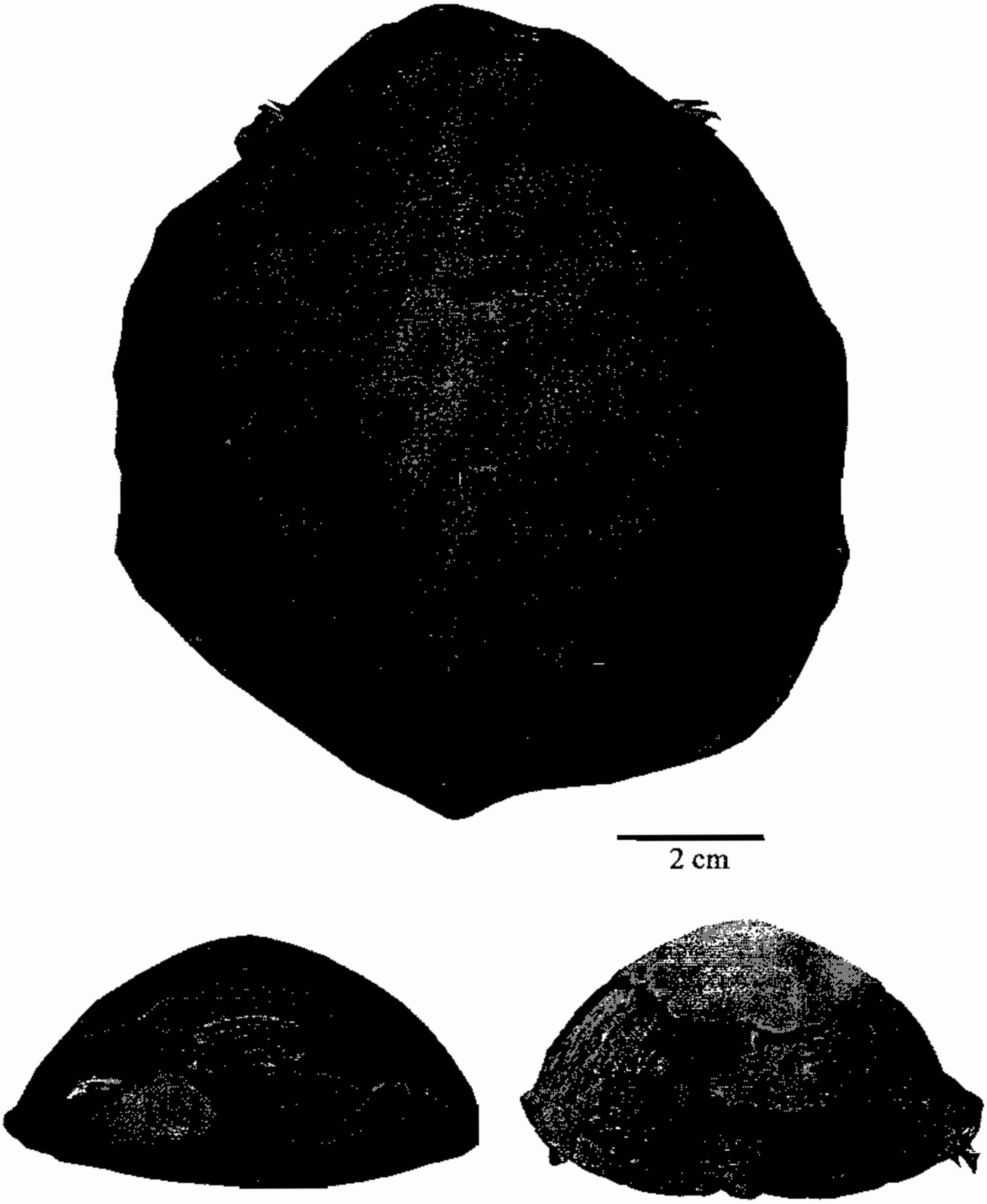


Figure 78 Juvenile individual of *Lissemys scutata* carapace (CUMZ-R-T154) in dorsal (above), anterior (left bottom) and posterior (right bottom) views. Scale bar equals 2 cm.

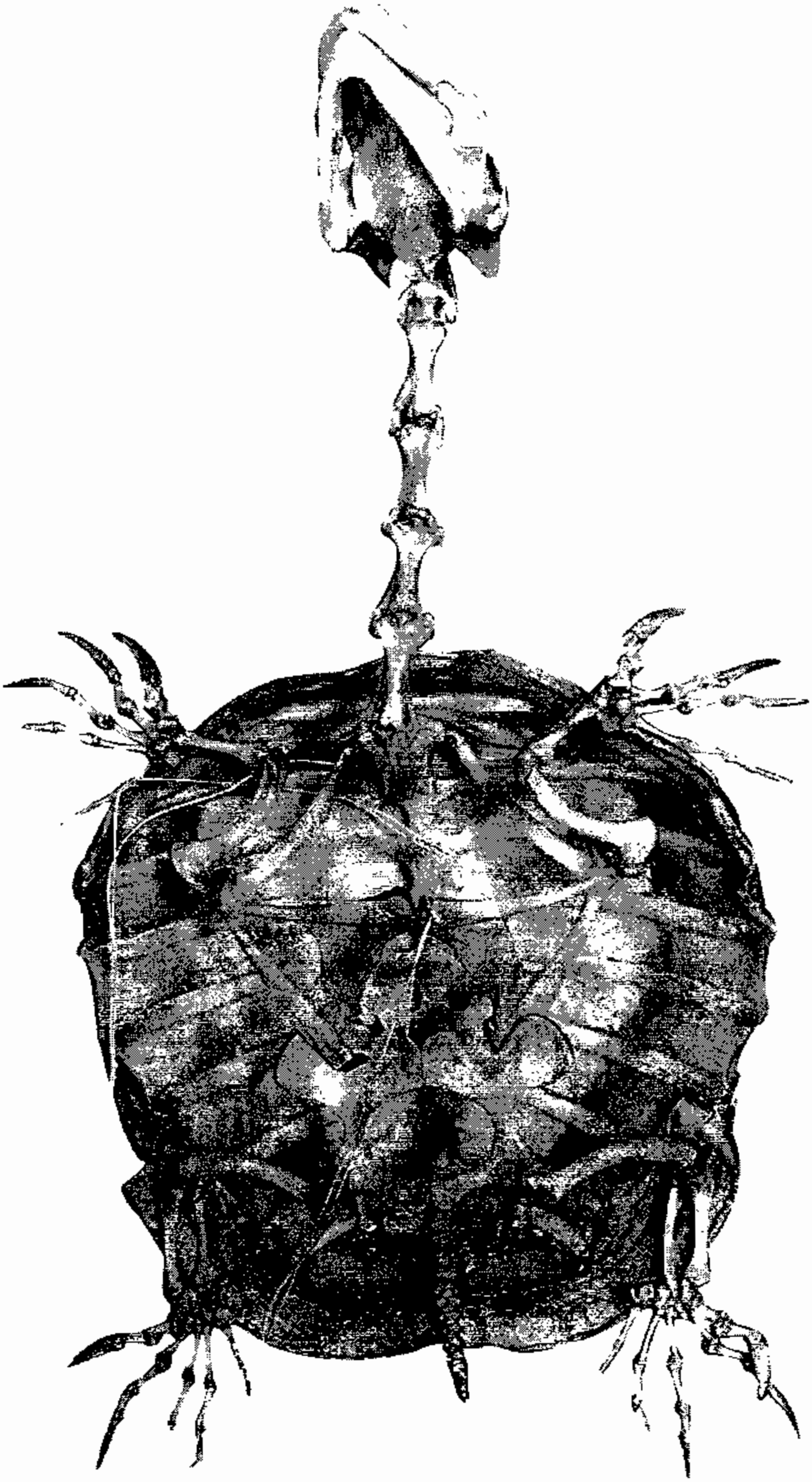


Figure 79 Juvenile individual of *Lissemys scutata* carapace (1872) in visceral view. (Photo: Haiyan Tong)

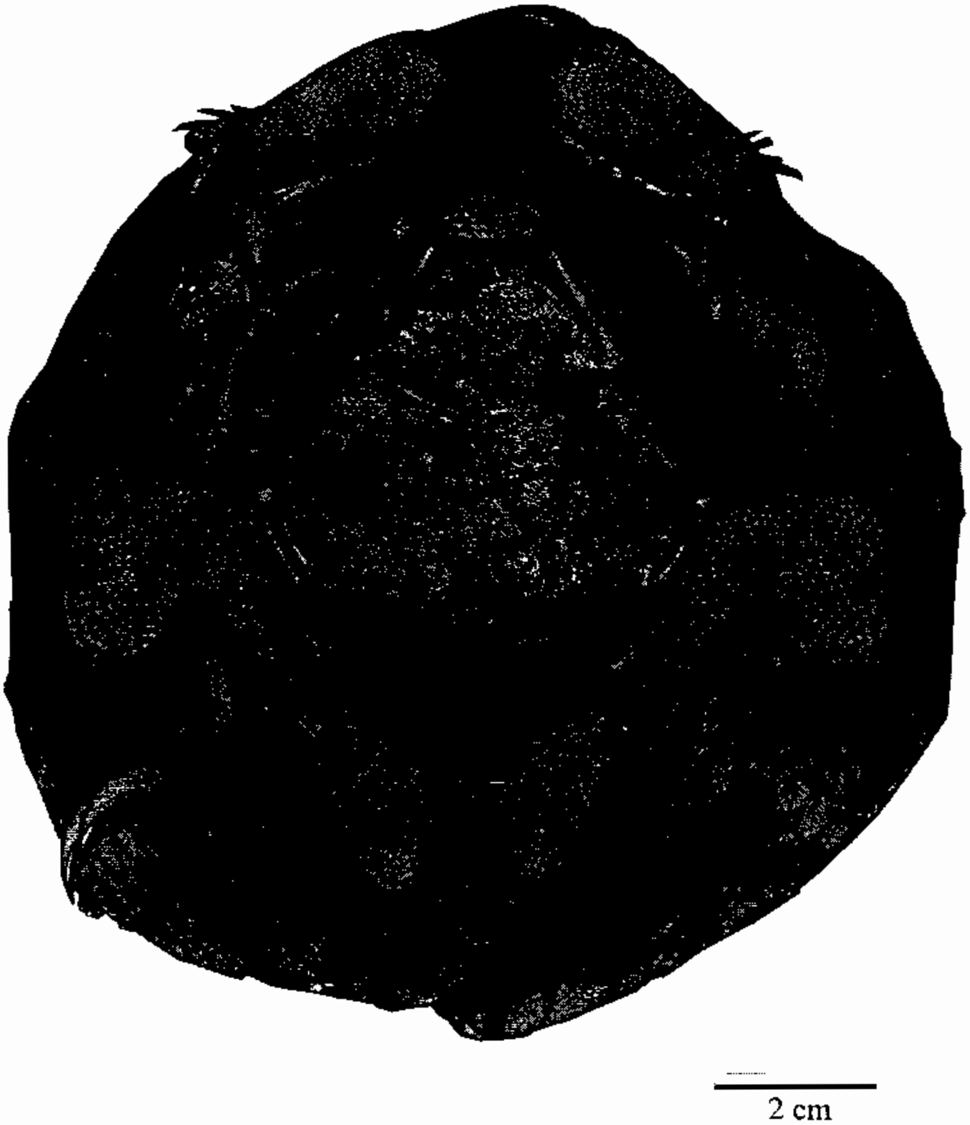


Figure 80 Juvenile individual of *Lissemys scutata* plastron (CUMZ-R-T154) in ventral view.

Figure 81 Juvenile individual of *Lissemys scutata* plastron (1872) in ventral (upper) and visceral (lower) views. Scale bars equal 5 cm. (photo: Haiyan Tong)

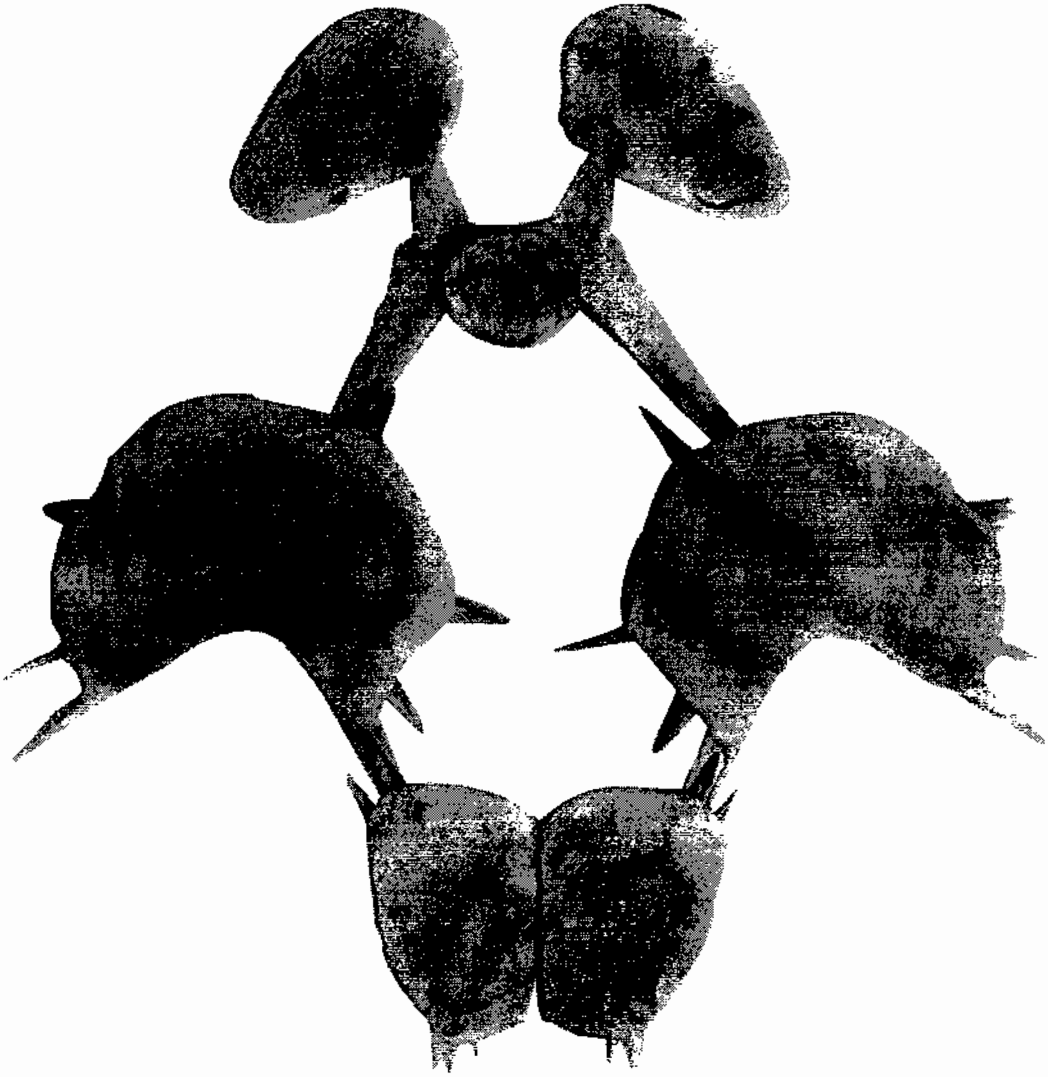


Figure 82 Adult individual of *Lissemys punctata* plastron in ventral view. (Photo: Haiyan Tong)

4.6.6 *Pelodiscus sinensis* Wiegmann, 1835 (Figure 83-86)

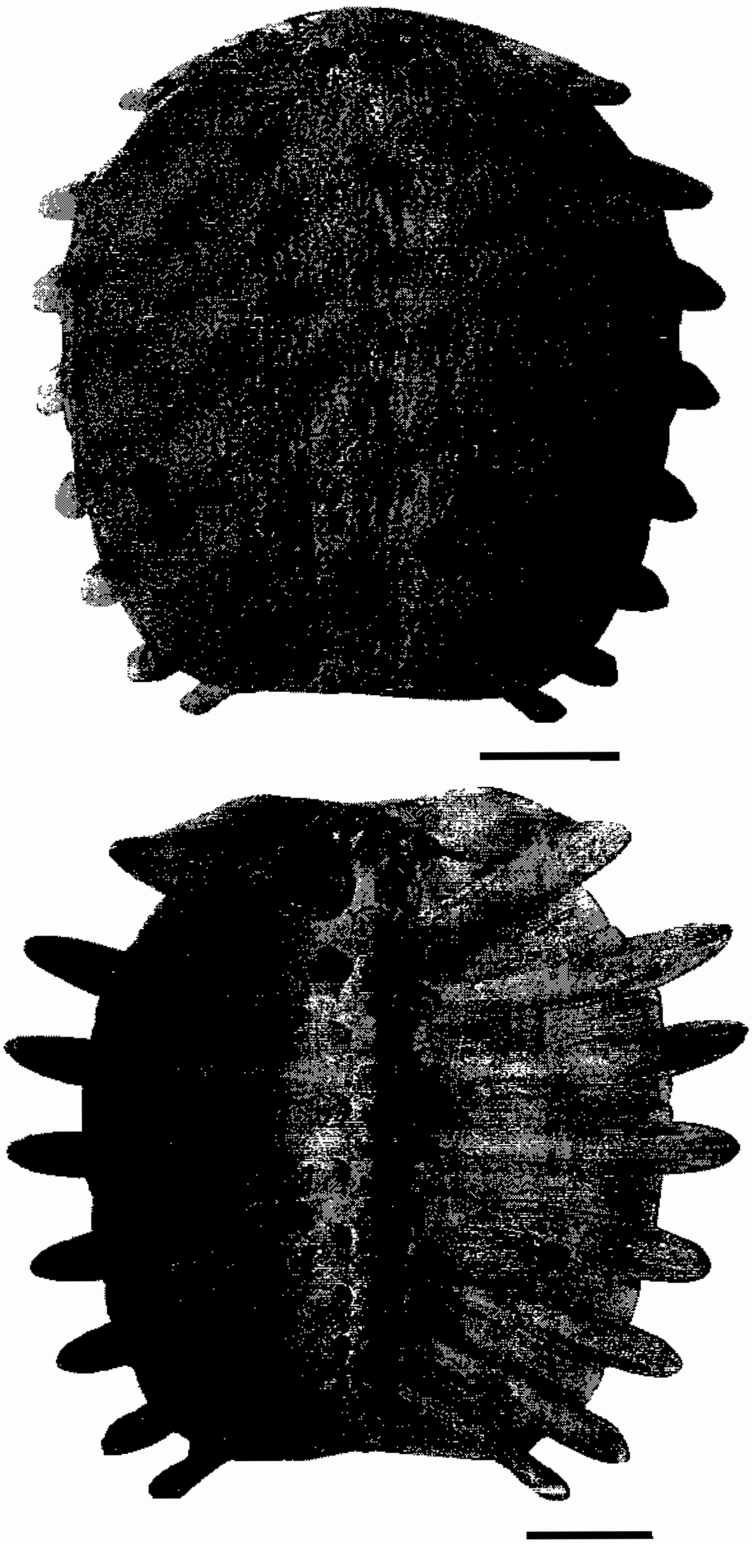


Figure 83 Juvenile individual of *Pelodiscus sinensis* carapace in dorsal view (above) and visceral view (bottom). Scale bar equals 2 cm. (Photo: Haiyan Tong)

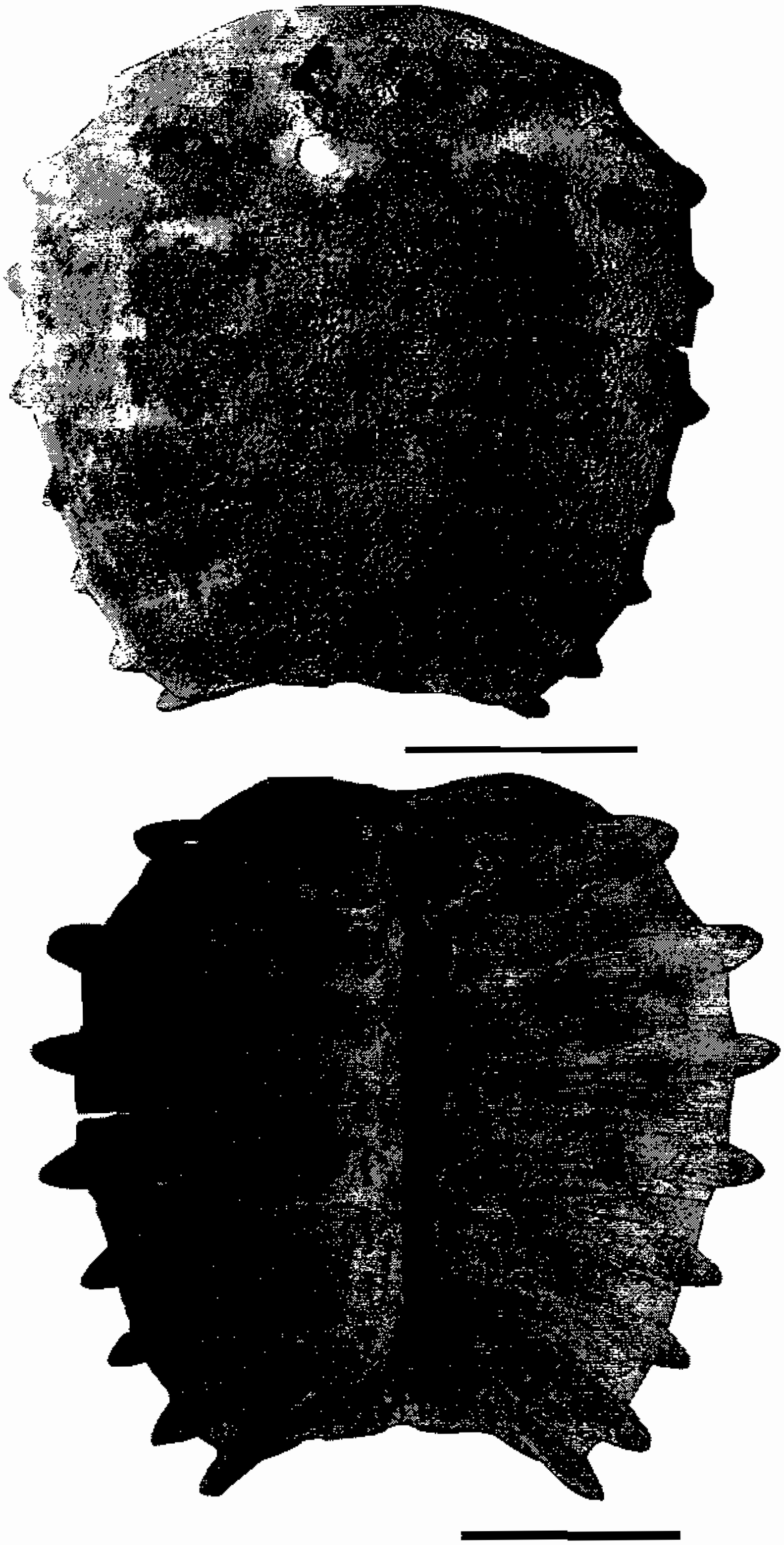


Figure 84 Adult individual of *Pelodiscus sinensis* carapace (537) in dorsal view (above) and visceral view (bottom). Scale bar equals 5 cm. (Photo: Haiyan Tong)

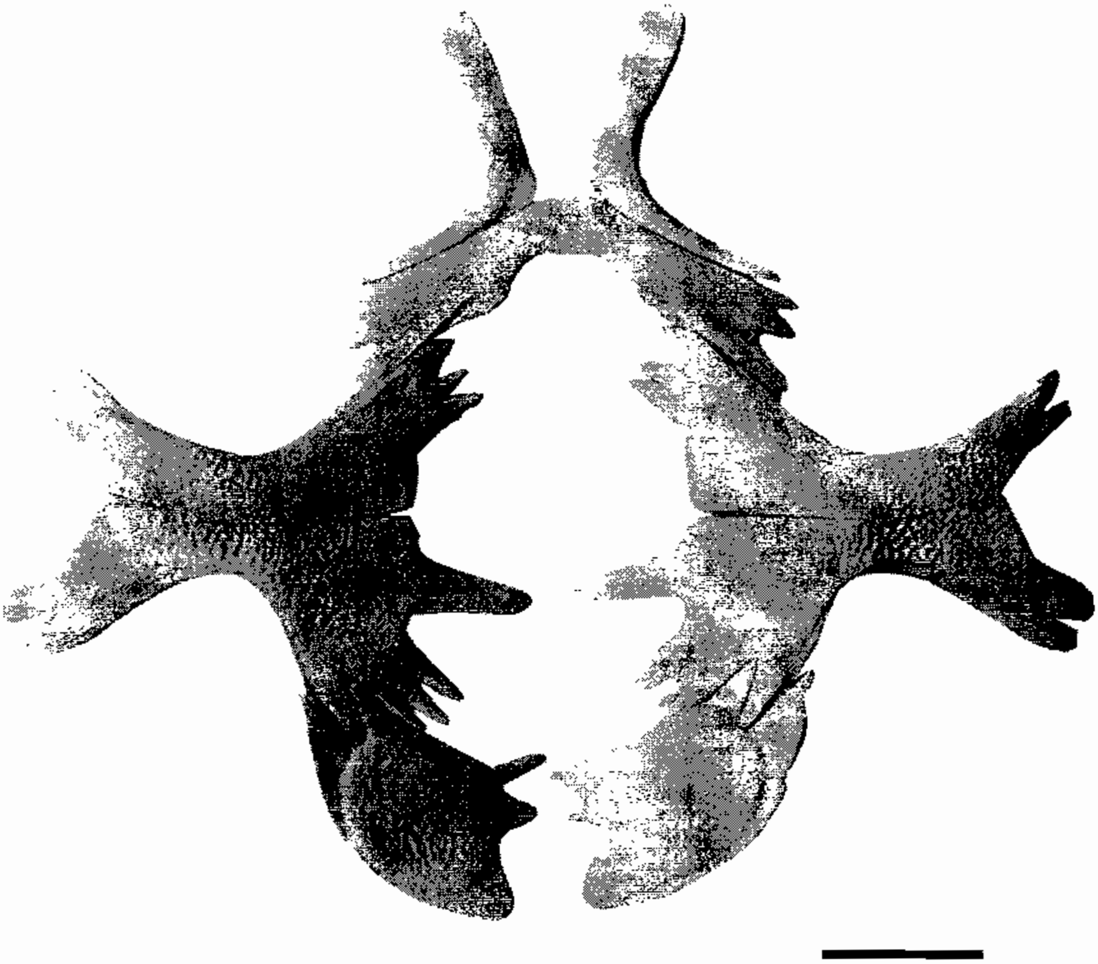


Figure 85 Juvenile individual of *Pelodiscus sinensis* plastron in ventral view. Scale bar equals 2 cm. (Photo: Haiyan Tong)

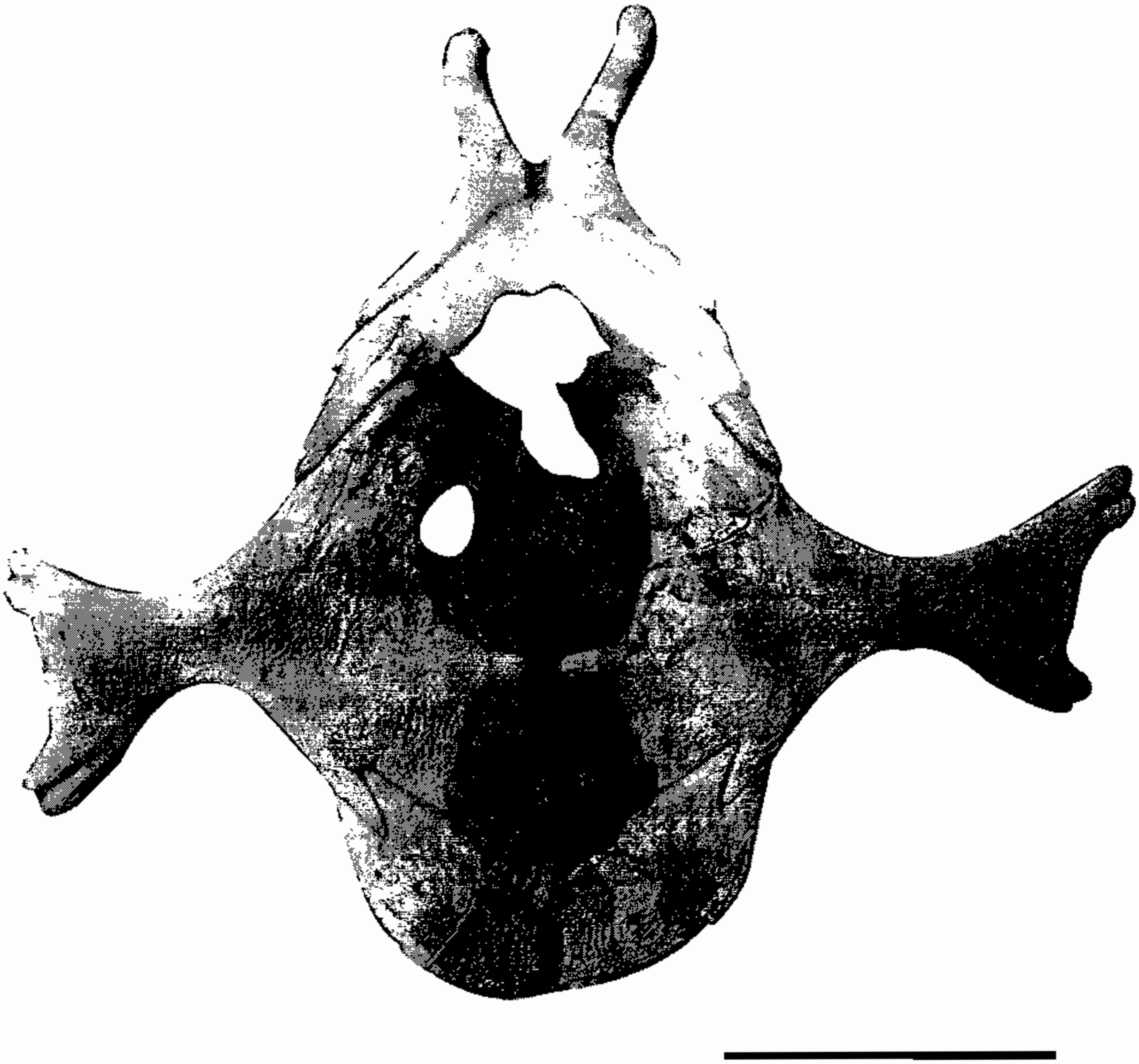


Figure 86 Adult individual of *Pelodiscus sinensis* plastron in ventral view. Scale bar equals 5 cm. (Photo: Haiyan Tong)

4.6.7 *Nilssonia formosa* (Gray, 1869) (Figure 87-88)

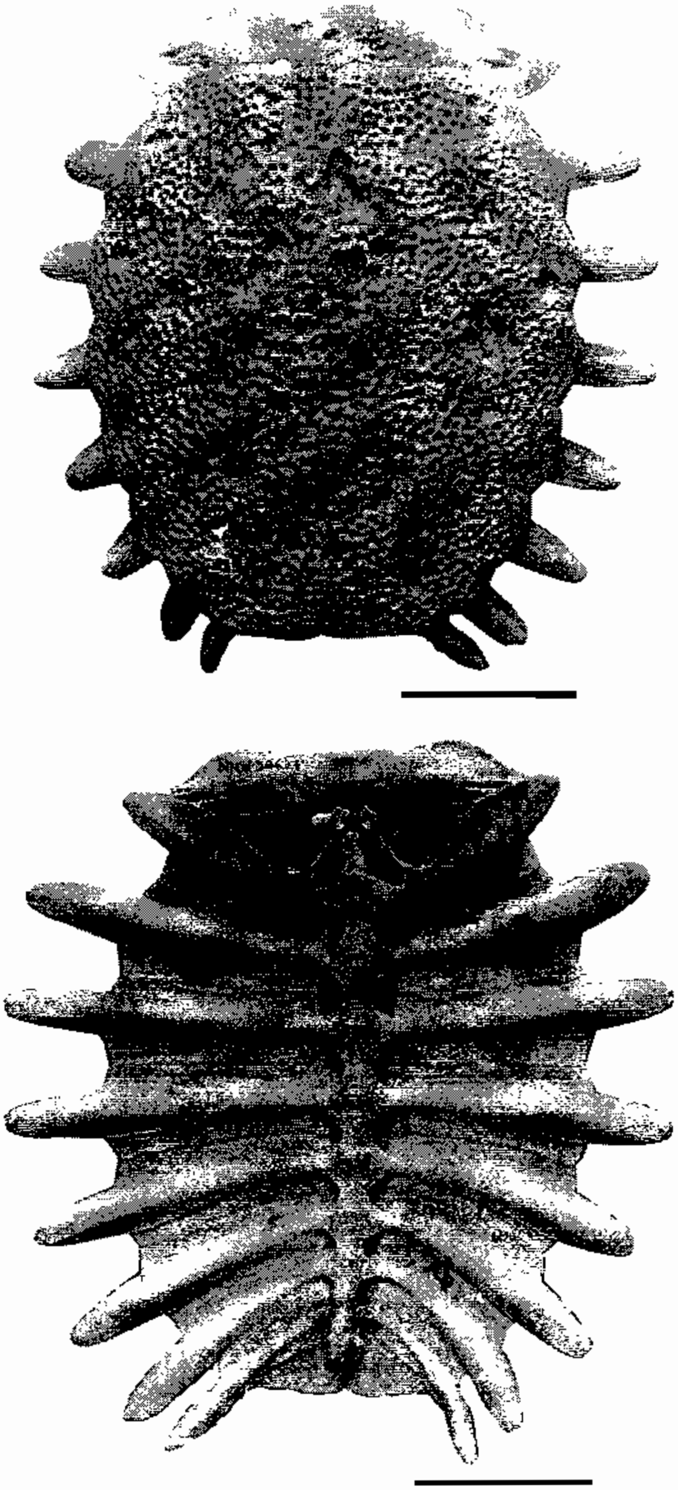


Figure 87 Juvenile individual of *Nilssonia formosa* carapace (NMW 3861) in dorsal view (above) and visceral view (bottom). Scale bars equal 5 cm. (Photo: Haiyan Tong)

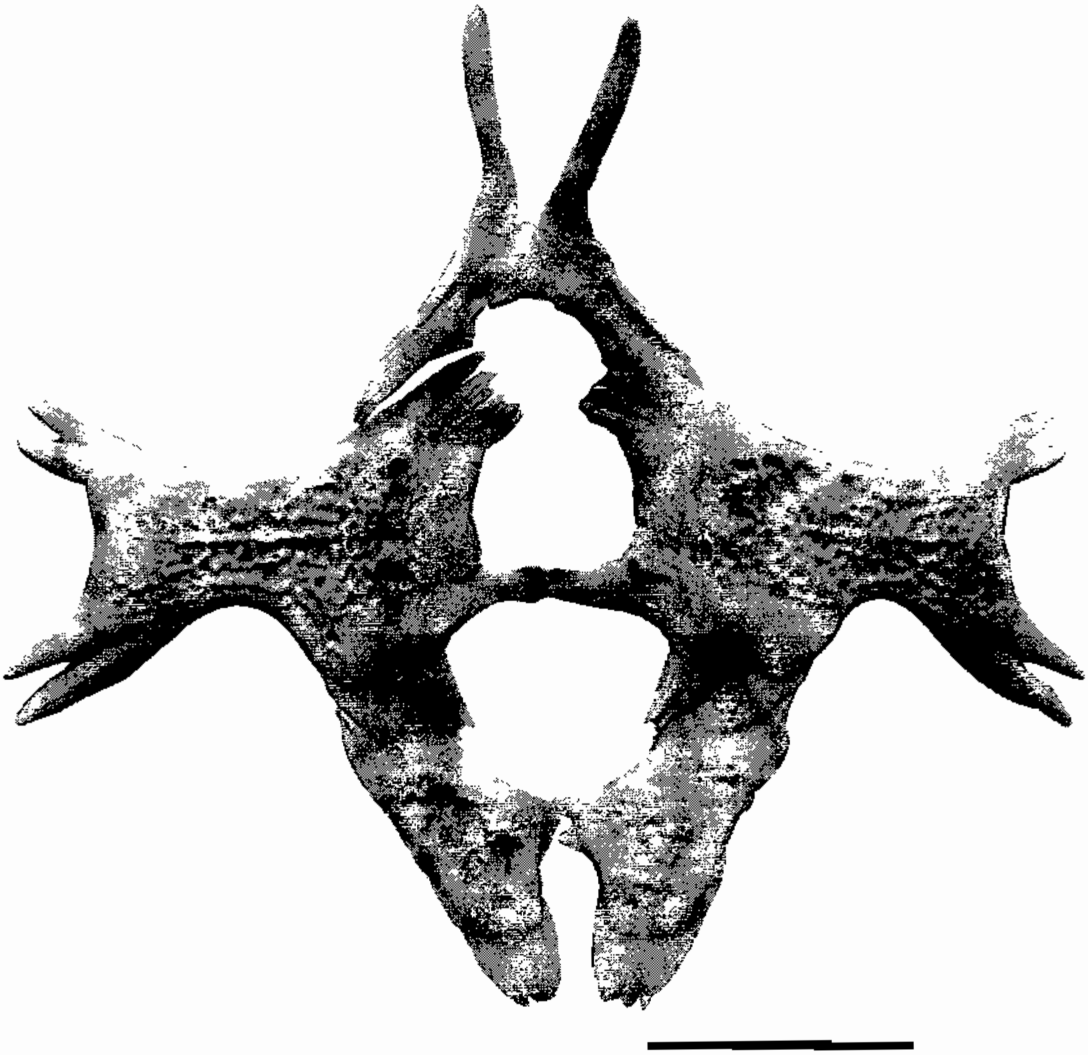


Figure 88 Juvenile individual of *Nilssonia formosa* plastron (NMW 3861) in ventral view. Scale bars equal 5 cm. (Photo: Haiyan Tong)

4.6.8 *Nilssonia hurum* (Gray, 1831) (Figure 89-91)

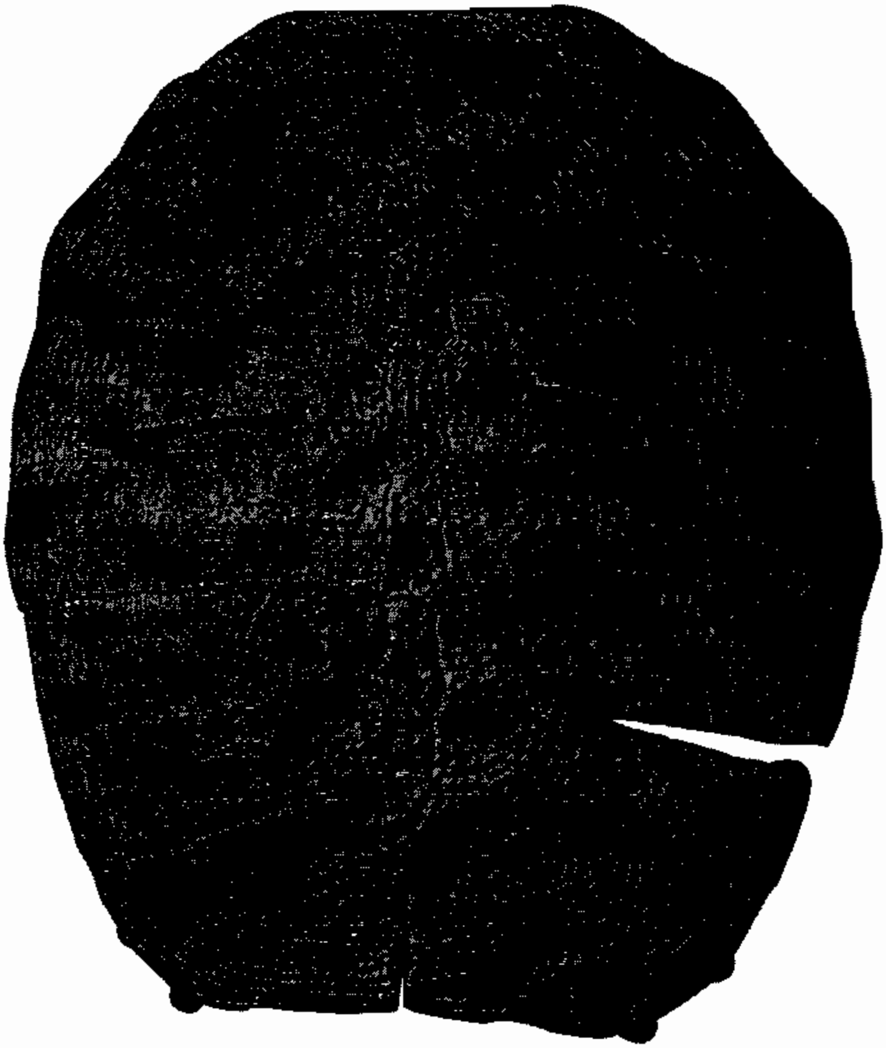


Figure 89 Adult individual of *Nilssonia hurum* carapace (BMNH 86.8.26.2) in dorsal view. (Photo: Walter Joyce)

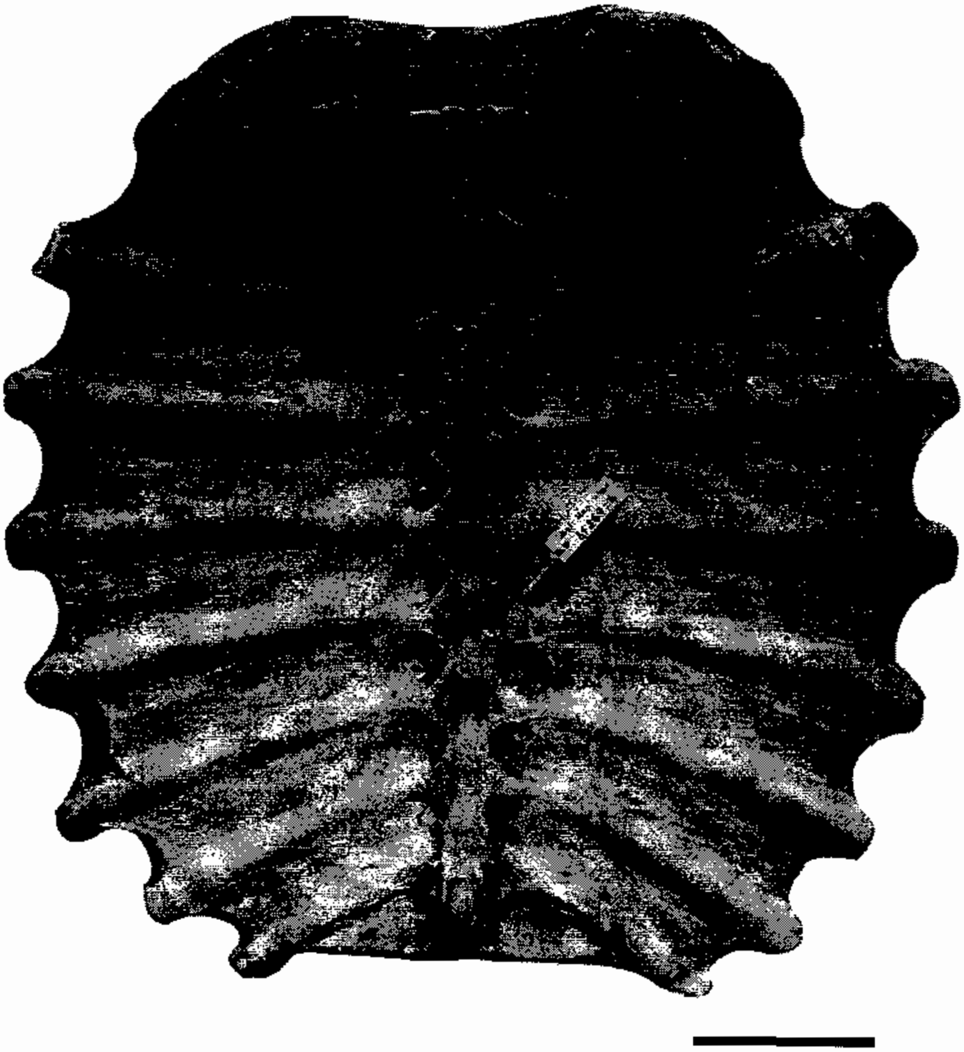


Figure 90 Adult individual of *Nilssonia hurum* carapace (NMW31269.3) in visceral view. Scale bar equals 5 cm. (Photo: Haiyan Tong)

Figure 91 Adult individual of *Nilssonia hurum* plastron (BMNH 86.8.26.2) in ventral view. (Photo: Walter Joyce)

4.6.9 *Rafetus euphraticus* Daudin, 1802 (Figure 92-96)

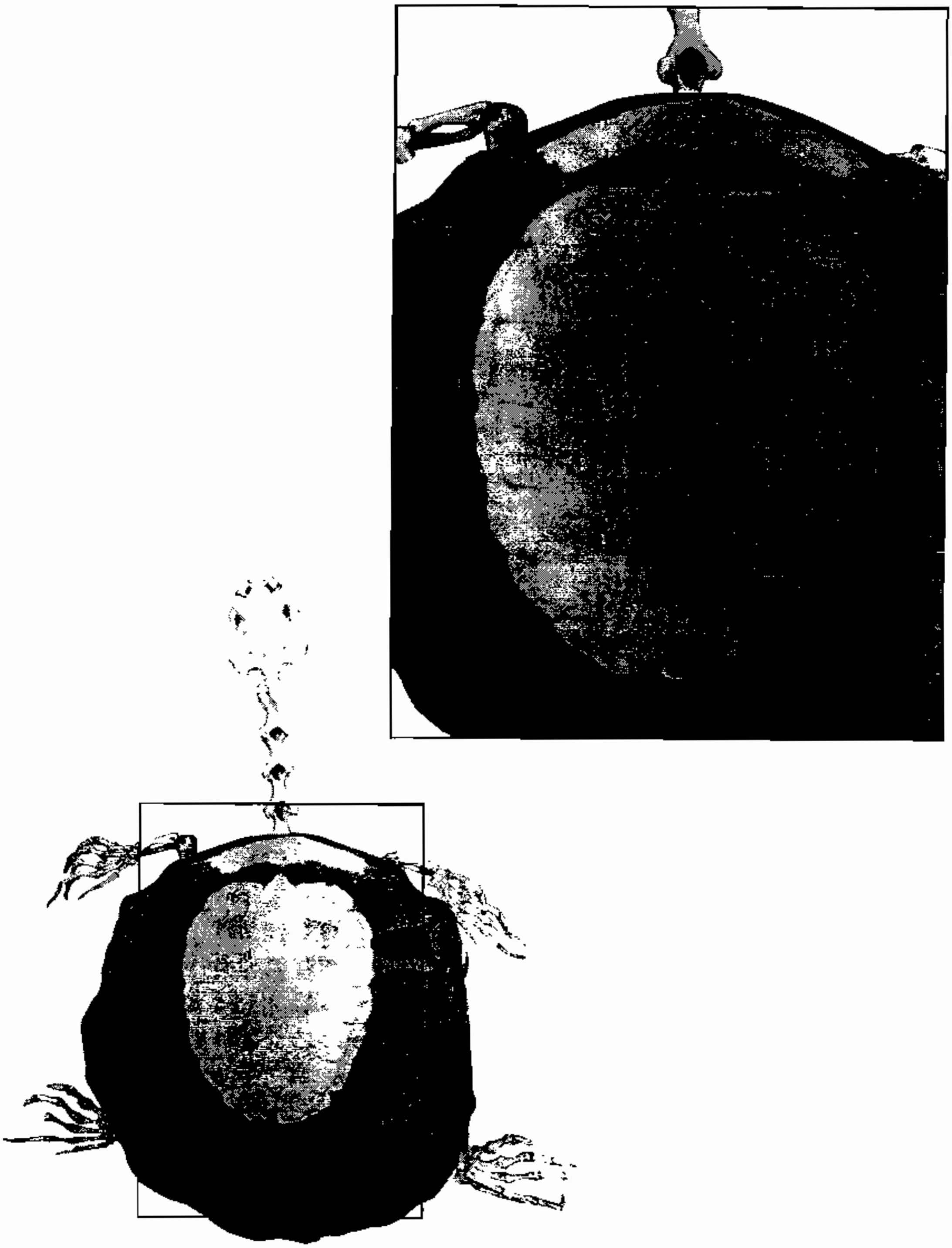


Figure 92 Juvenile individual of *Rafetus euphraticus* carapace (NMW 1861) in dorsal view. (Photo: Haiyan Tong)

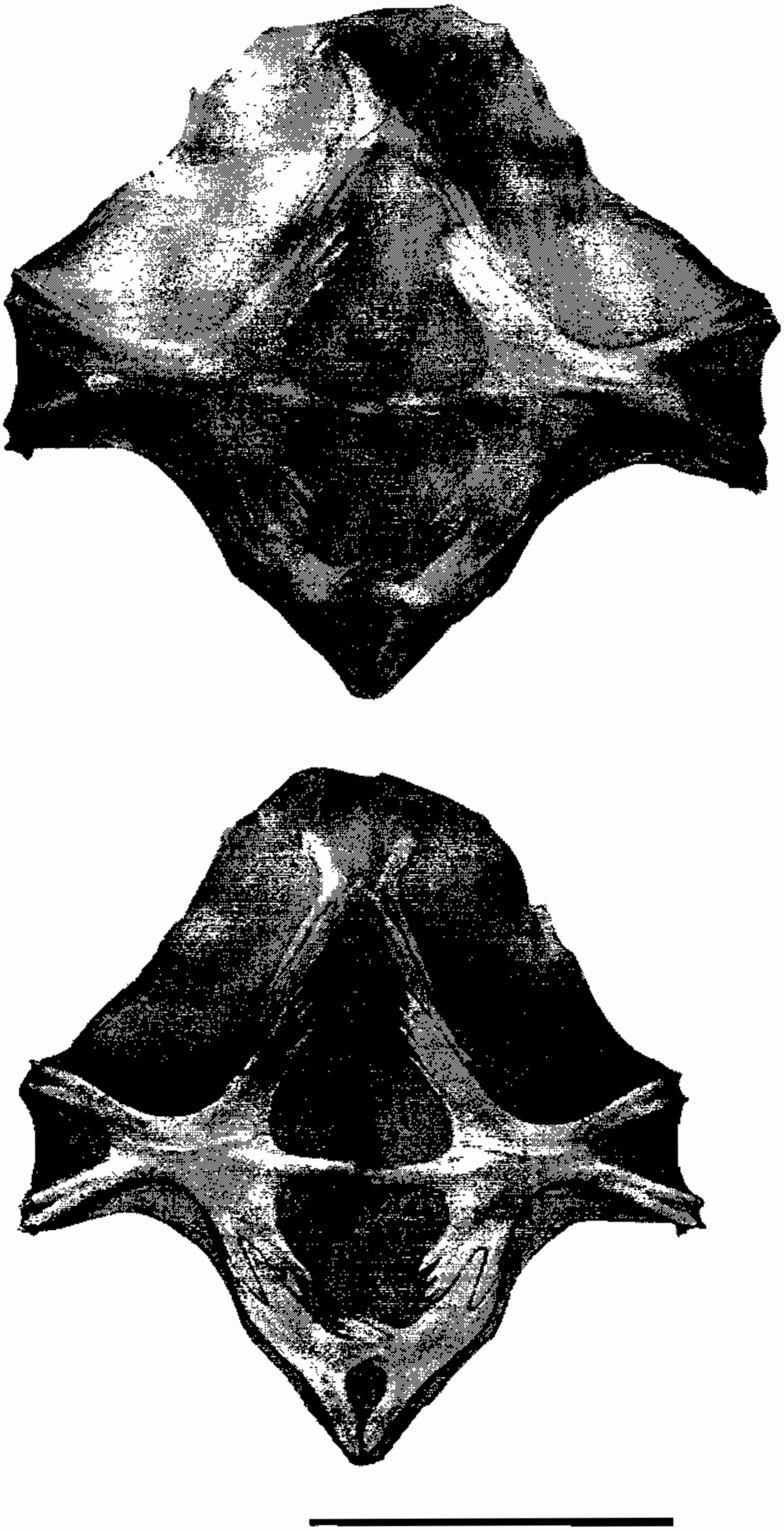


Figure 93 Juvenile individual of *Rafetus euphraticus* plastron (NMW 1861) in ventral (upper) and visceral (lower) views. (Photo: Haiyan Tong)

Figure 94 Adult individual of *Rafetus euphraticus* carapace (1450) in dorsal view. Scale bare 5 cm. (Photo: Haiyan Tong)

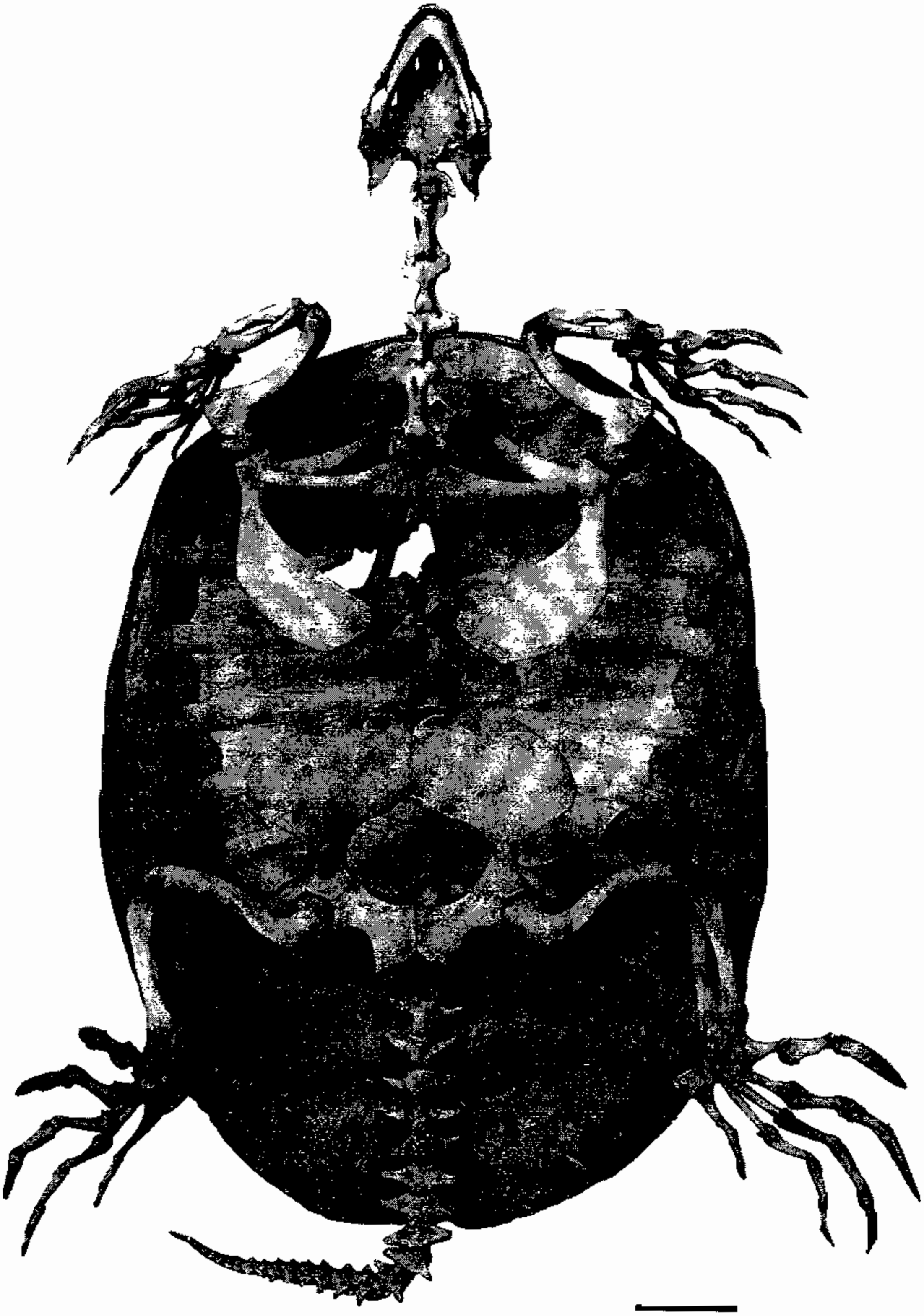


Figure 95 Adult individual of *Rafetus euphraticus* carapace (NMW 1856) in visceral view. Scale bare 5 cm. (Photo: Haiyan Tong)

Figure 96 Adult individual of *Rafetus euphraticus* plastron (1450) in ventral view. Scale bare 5 cm. (Photo: Haiyan Tong)

4.6.10 *Rafetus swinhoei* (Gray, 1873) (Figure 97)

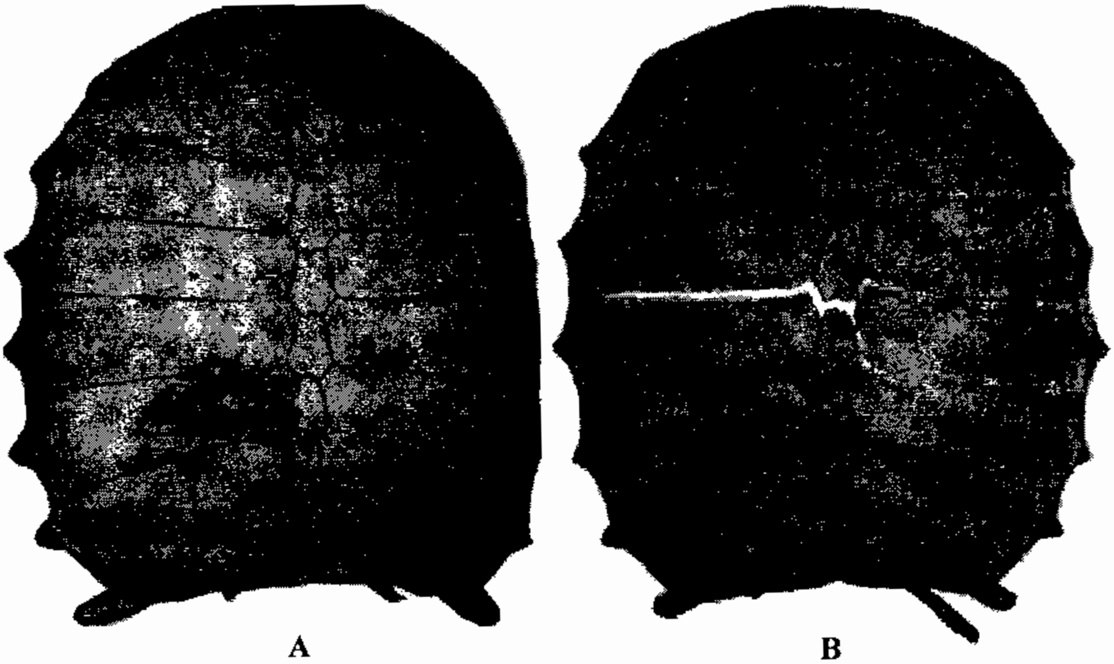


Figure 97 Shell of *Rafetus vietnamensis* Le *et al.*, 2010 (recently *R. swinhoei*) in dorsal view; (A) holotype and (B) VNUHT 91 from Ma River, Thanh Hoa Province (Farkas, Le, & Nguyen 2011, p 68, Fig. 4).

4.7 Description of living trionychid turtle shells in Thailand and adjacent countries

4.7.1 *Amyda cartilaginea* (Boddaert, 1770) (Figure 63-65)

Examined specimens: CUMZ(R) 1994-6-10-1; CUMZ(R) 1992-2-5, 23(1); CUMZ(R) 1994-3-18, 5; CUMZ(R) 1994-3-4, 2(1); CUMZ(R) 1991-4-9, 1; CUMZ(R) 1994-12-29 (8); CUMZ(R) 1995-9-3(1); CUMZ(R) 1994-3-4, 3; CUMZ(R) 1993-2-18, 2; CUMZ(R) 1994-3-30, 1(1); CUMZ(R) 1994-3-4, 1(1); CUMZ(R) 1992-4-21, 2; CUMZ(R) 1992-6-18(2)

Carapace (Figure 63-65)

1. *General*

The alive carapace length can reach up to 83 cm (Stuart *et al.*, 2001). There is no peripheral plate. The carapace disc is longer than wide in juveniles but as long as wide or a bit longer in adults. The suprascapular fontanelles between the nuchal and first pair of costals are present in juveniles, but disappear in adult individuals. These fontanelles have an oval, eye liked shape. The ornamentation on the carapace is pitted and vermiculated. Most of pits are present on neural and medial parts of costal plates while laterally these pits tends to disappear and the aspect of the ornamentation becomes more vermiculated. The pits are irregular in size and shape. They are rather shallow. There are several longitudinal ridges along the carapace which are more distinct in juveniles. These ridges is thought to be a characteristic of this species (Pritchard *et al.*, 2009). In the posterior part of carapace, oblique ridges can be observed. A continuous midline carina runs along all neural plates. Pit density is high in the middle costal plates in the anterior part of carapace. There are about 12 pits from anterior and posterior margin of the fourth costal at the medial end.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width on length ratio of the nuchal is greater than 4 in adult. The anterior border of nuchal is convex forming a semi-circular shape and the posterior margin is straight in adults while it is concave between fontanelles in juveniles. Lateral extremities of the nuchal plate are slightly expanded. The costiform process overlies on the dorsal rib of the first costal plate both in juveniles and adults. It is expanded in several small minor processes in juveniles (Figure 63); while in adults, the costiform process is short and slightly expanded (Figure

64). In visceral view, the plate is smooth. The anterior edge of the first body vertebra reaches the posterior edge of the nuchal.

2.2 Neurals: There are eight neural plates. Only one neural plate contacts the first pair of costal plates. The anterior margin of the first neural plate is straight. The first neural is longer than other neurals. The shape of the first to fourth neurals is hexagonal with short posterolateral sides. The fifth to sixth neurals display variable shapes. The seventh neural is hexagonal with short anterolateral side. The eighth neural is hexagonal with short anterolateral sides in juvenile and it is reduced with a pentagonal in shape in adults. The more common neural formula is 6 < 6 < 6< 6< 5 5 6 > 5(6>). The neural carina is wide and runs from the second to the eighth neural plate.

2.3 Costals: There are eight pairs of costal plates. The medial end of the first and eighth costals is longer than its lateral end. The eighth pair of costals is in contact at the midline except in juveniles where the eight neural plates reaches the posterior end of the carapace. The free margin of the eighth costal plate form the posterior margin of the carapace. The free rib ends are expanded, they are elongated in juveniles and become short in adults. The orientation of rib ends, the first to the third costals goes forward, and the fifth to eighth are directed posteriorly.

3. *Variations*

3.1 Ontogenetic Variations

1. The suprascapular fontanelles are present in juveniles but absent in adults.

2. The eighth neural is reduced in adults, allowing the eighth pair of costal plates to meet in the midline while in juveniles, the eight neural is longer and fully separate the last pair of costal plates.

3. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

1. The fourth to sixth neurals can be hexagonal with short posterolateral sides or oval or pentagonal in shape.

Plastron (Figure 65)

1. *General*

The plastron consists of nine reduced plates loosely connected one to another, except hyo-hypolastral connection. Fontanelles are present. Ornamentation of the plastron is principally pitted. There are rare vermiculations located on the anteromedial side of the hyo-hypoplastral callosity.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped and thin. Epiplastra are broad anteriorly and slender posteriorly. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape and is thin. It is also concave posteriorly. The entoplastron is long and become sharp at the end. It articulates slightly with the anteromedial margin of the hyoplastron. The callosity, when present, has a smooth, unornamented surface for the examined specimens.

2.3 Hyo-hypoplastra: Hyo-hypoplastra are sutured and have distinct dermal ossification (forming callosities). The hyo-hypoplastral suture is visible. The medial side of hyoplastron is shorter than hypoplastron. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a laterally a semi-circular shape (at the level of the hyoplastron), while the posterior part has triangular shape (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in four to five short pointed processes. At the level of the inguinal and axillary buttresses, the hyoplastron is slightly longer than the hypoplastron. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) consists in a single pointed and long process, the posteriormost one is subdivided into relatively small two pointed process, while between the anteriormost process and the posteriormost process, the process is longer and bifurcates in two or three small processes at its medial end. The two main posterior processes of the hypoplastron articulates with the anterior pointed process of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra have more or less a triangular shape. The posterior margin of each xiphiplastron is slightly concave posteriorly, while the anterior margin is slightly concave anteriorly. The xiphiplastra articulate medially with three interdigited pointed processes.

3. *Variations*

-

4.7.2 *Chitra chitra* (Nutaphand, 1986) (Figure 66-69)

Examined specimens: CUMZ(R) one unnumbered individual, CUMZ-R-T127, CUMZ-R-T155, CUMZ-R-T156, CUMZ-R-T157, CUMZ-R-T158, CUMZ-R-T159, CUMZ-R-T160, CUMZ-R-T161

Carapace (Figure 66-68)

1. *General*

The carapace length can reach up to 140 cm (McCord and Pritchard, 2002). There is no peripheral plate. The carapace is flat. The carapace disc is clearly longer than wide in adults. The fontanelles between nuchal and first costal pairs are absent. The ornamentation on the carapace consists in more or less radiating patterns of elongated pits at the contact between neurals and costals that replace the more regular pits. The pits present a certain degree of variation in size and shape on costal. There is no clear vermiculation and they are never anteroposterior except in juveniles. There are about 13 pits from posterior and anterior margin of the four costal at medial end.

2. *Plates*

2.1 Nuchal: The nuchal is narrow, wider than long. The width/length ratio of the nuchal is greater than 5 times in adults. The anterior border of the nuchal is convex forming semi-circular shape. Its posterior margin is nearly straight. It is convex only in the middle of the plate where it articulates with the anterior rim of the first neural. Lateral extremities of nuchal plate are not expanded. The costiform processes, close to posterior margin of the nuchal are elongated and taper to the lateral end. These costiform processes overly on the free rib ends of the 1st costal plates both in juveniles and adults. In visceral view, a strong crest is present along the anterior margin of nuchal. The anterior margin of the first body vertebra is situated at the level of the anterior part of the nuchal plate.

2.2 Neurals: There are eighth neural plates. The neural plates of *Chitra chitra* are relatively wider than in *Amyda cartilagenea*. The first neural plate contacts both the first costals and second costals. The anterior margin of the first neural plate is convex anteriorly. The first to fourth neural plates are hexagonal with short posterolateral sides. The fifth and sixth neural plates can show some variation in being hexagonal with short posterolateral sides or oval in shape for the fifth, and hexagonal with short anterolateral side or oval in shape for the sixth. The seventh neural plate is hexagonal with short anterolateral side. The eighth neural is reduced and pentagonal in shape. The neural formula is 6< 6< 6< 6< 4 6> 6> 5 or 6< 6< 6< 6< 6< 4 6> 5.

2.3 Costals: There are eight pairs of costal plates. The medial end of the first costal is longer than its lateral end. The eighth costals contact on each other at the midline. The anterior part of the lateral end of the first costal plate is concave while the lateral ends of other costal plates are rather straight except for the seventh and eighth costal ends that are slightly curved. The lateral ends of the seventh and eighth costal plates are in contact. The free rib ends are visible outside of costal disc. They are elongated in juveniles and become short in adults. In visceral view, on the second costal plate, a distinct rib crest is present at the medial part to middle costal plate (see Figure 68) which is similar to *Pelochelys cantorii*. The rib process under costal plates are oriented posteriorly from the third to the eight costal plates. The eight costal plates form the posterior margin of the carapace. The posterior part of the carapace at the level of the eighth costal plate can be straight or can show a small emargination.

3. *Variations*

3.1 Ontogenetic Variations

1. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

1. The neural number is variable from seventh to eighth plates.
2. The reversion of shorter sides on neural is on the fifth or on the sixth neural plates.

Plastron (Figure 69)

1. *General*

The plastron consists of nine reduced plates and loosely connected one to another, except hyo-hypolastral connection. Fontanelles are present. There is no vermiculation on callosities. The pits are present on xiphiplastral callosities and on hyo-hypoplastral one, they are, however, smaller on xiphiplastral callosities.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped, thin, and short. They is relatively smaller and shorter when compared with *Amyda cartilagenea*. Epiplastra are wider anteriorly and slender posteriorly. The epiplastra articulate medially with anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape. It is thin and elongated. Its posterior part is concave posteriorly. Lateral parts of the entoplastron are long and taper to a sharp end. The entoplastron articulates slightly with the anteromedial margin of the hyoplastron. The surface of the entoplastron is not ornamented (no pitted callosity).

2.3 Hyo-hypoplastra: Hyo-hypoplastra articulate broadly and have distinct dermal ossification (forming callosities). The hyo-hypoplastral suture is present. The medial side of hyoplastron is longer than the medial side of the hypoplastron. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a well developed hexagonal shape in a large individual, (at the level of the hyoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in five to six short pointed processes. The relative length between the inguinal and axillary notches is longer by comparison to other species including *Amyda cartilargenea*, *Dogania subplana*, *Pelodiscus sinensis*, *Nilssonia formosa* and *Rafetus euphraticus* and these notches are consequently not as strong as in others except *Pelochelys cantorii*, *Nilssonia hurum* and *Lissemys punctata*. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends three pointed processes with rounded ends. Medially, the hypoplastra send multifurcated processes. The anteriormost (at midlength of the hypoplastron) is subdivided in five straight and short processes, the posteriormost one is subdivided in three pointed processes, while between the anteriormost process and the posteriormost process, there is a longer process that multifurcates in four or five small processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed process of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are more or less triangular in shape. The anterior margin of each xiphiplastra is straight while its posterior is slightly convex posteriorly. The xiphiplastron articulate medially with four interdigited pointed processes.

3. *Variations*

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4.7.3 *Dogania subplana* (Geoffroy, 1809) (Figure 70-73)

Examined specimens: CUMZ(R) 1993-5-18-1; CUMZ(R) 1993-5-18-2; CUMZ(R) 1997-3-10(1); CUMZ(R) 1992-4-14,3; CUMZ(R) three unnumbered individuals; Meylan, 1987: 16, NMW 1870, NMW 1871

Carapace (Figure 70-71)

1. *General*

The carapace length reaches up 25 cm (Smith, 1931). There is no peripheral plate. The carapace is flat, longer than wide. Large suprascapular fontanelles remains in adults (Figure 71). The ornamentation on the carapace consists of small regular pits. These pits are polygonal in shape and deep. The density of pits on the plates is high. There are about 50 pits from anterior and posterior margin of the four costal at medial end. There is nearly no vermiculation except on the contact between costal plates. There is no longitudinal ridges on the carapace.

2. *Plates*

2.1 Nuchal: The nuchal is very short, much wider than long. The width/length ratio of the nuchal is greater than 6 times in adults. The anterior border of nuchal is rather straight in both juveniles and adults. Its the posterior margin is convex anteriorly. Lateral extremities of nuchal plate are expanded. The costiform process are shorter than the nuchal plate but slightly expanded at the margin. The visceral surface of the plate is rather smooth. The anterior end of the first body vertebra is located at the level of the posterior margin of the nuchal.

2.2 Neurals: There are eight neural plates. The first neural plate contacts the first and the second costals. The neural plates are relatively narrower than in *Chitra chitra*. The anterior margin of the first neural plate is straight. The first neural plate is shorter than the second one or nearly the same size. The first to fifth neural plates are hexagonal with short posterolateral sides. The shape of sixth to eighth plates are variable. These plates can be hexagonal with short posterolateral sides or oval or hexagonal with short anterolateral sides or present an asymmetric shape.

2.3 Costals: There are eight pairs of costal plates. The lateral end of the second costal is longer than others. The anterior margin of the first costal plate is concave posteriorly forming a large suprascapular fontanelle with the nuchal except in juvenile, it is straight (see Figure 70). The anterior margin of the first costal plate in other trionychids is straight. The ribs in visceral view are flat. The medial end of the eighth costal plate is the shortest. The eighth costal plates are small and are not contacting each others. The posterior lateral end of the seventh costal plate does not contact the eighth costal plates. The free rib ends are expanded. They are elongated in juveniles and become short in adults. The rib end on the first costal plate extends out of the costal plate in the anterior part. The free rib end of the eight costal plate is longer than the others. The rib processes under costal plates are oriented posteriorly from the third to the eighth costal plates. The eight costal plates form the posterior margin of the carapace. The posterior part of the carapace at the level of the eighth costal plate has a deep emargination between the costals because they are not contact.

3. *Variations*

3.1 Ontogenetic Variations

1. The fontanelles in juveniles are much more developed than in adults

2. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

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Plastron (Figure 72-73)

1. *General*

The plastron consists of nine reduced plates, loosely connected one to another, except hyo-hypolastral connection. Fontanelles are present. Ornamentation of plastron is finely pitted and vermiculated on the callosities of hyoplastra, hypoplastra and xiphiplastra.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped and thin. They are similar in shape to *Amyda cartilagenea* but of smaller size. Epiplastra are wider anteriorly and slender posteriorly. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape. It is thin. Its posterior part is concave posteriorly. Lateral parts of the entoplastron are short and tapers to a sharp end. They articulate slightly with the anteromedial margin of the hyoplastron. The surface of the callosity is smooth.

2.3 Hyo-hypoplastra: Hyo-hypoplastra have a long and visible suture and have distinct dermal ossification (forming callosities). The medial side of hyoplastron is shorter than the medial side of the hypoplastron. Medially, a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a laterally oval shape (at the level of the hyoplastron), while the posterior part is shorter (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in five short pointed processes. At the level of the inguinal and axillary buttresses, the hyoplastron is more longer than the hypoplastron. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) is made of two pointed and long processes, the posteriormost is divided in two pointed processes, while between the anteriormost process and the posteriormost process, a longer process is present and trifurcates in three processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed processes of the xiphiplastron. The ends of the anteriormost of the hypoplastron processes are pointed and are not as straight as in *Chitra chitra*.

2.4 Xiphiplastra: The xiphiplastra are more or less triangular in shape. The dermal ossification is rather large and slender. The anterior margin of each xiphiplastron is concave anteriorly while its posterior is slightly concave posteriorly. The xiphiplastra articulate medially with two interdigited pointed processes.

3. *Variations*

3.1 Ontogenetic Variations

1. The posteromedial margins of the xiphiplastra contact at the midline in adults while they do not contact in juveniles.

3.2 Intraspecific Variations

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4.7.4 *Pelochelys cantorii* Gray, 1864 (Figure 74-77)

Examined specimens: CUMZ-R-T120, NMW 1857

Carapace (Figure 74-75)

1. *General*

The carapace length can reach up to 60 cm (Smith, 1931). There is no peripheral plate. The carapace is flat and longer than wide. The ornamentation on the carapace is pitted and vermiculated. The pits are present on neurals and most costal plates. The pits have polygonal shapes and are shallow. Their size is more or less regular. Vermiculations are present only in the lateral part on costals at and start at about 2/5 of their width. There is no longitudinal vertical ridges on the carapace. There are about 25 pits from anterior and posterior margin of the four costal at the medial end.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width/length ratio of the nuchal is greater than 4 times in adults. The anterior margin of the nuchal is convex anteriorly whereas its posterior margin is rather straight. Lateral extremities of nuchal plate are expanded. The costiform process are well expanded at the posterior margin in several coarsely pointed processes.

2.2 Neurals: There are eight neural plates. The first neural plate contacts the first and second costal plates. The neural plates are rather wide and similar in this respect with *Chitra chitra*. The anterior margin of the first neural plate is straight.

The first neural plate is longer than the second one. At least the first to fourth neural plates are hexagonal with short posterolateral sides. The fifth is oval in shape. The sixth to seventh neural plates are hexagonal with short anterolateral sides. The eighth neural is reduced and pentagonal. The neural formula is 6< 6< 6< 6< 4 6> 6> 5.

2.3 Costals: There are eight pairs of costal plates. The medial part of the second costal plate is longer than the medial part of the first costal plate. The eighth pair of costals are in contact in the midline. The eighth costal plate is very wide but it is rather short, it forms the posterior end of the carapace. The ribs in visceral view are flat. The medial part of the seventh costal plate is the shortest. The lateral ends of the seventh and eighth costal plates are in contact each other. The orientation of rib process from the first to the third costals goes forward, and are later perpendicular to the body axis, even at the level of the eight costal plate.

3. *Variations*

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Plastron (Figure 76-77)

1. *General*

The plastron consists of nine plates. Fontanelles are present. Ornamentation of plastron is coarsely pitted and vermiculated on the callosities present on the hyoplastra, hypoplastra and xiphiplastra.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped and thin. Epiplastra are short and wide anteriorly while their posterior part is slender and pointed at the tip. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape and is a thin bone. Its posterior part is deeply concave posteriorly. Lateral parts of the entoplastron are elongated and taper to a sharp end. They articulate with the anteromedial margin of the hyoplastra. The callosity surface is smooth.

2.3 Hyo-hypoplastra: Hyo-hypoplastra have a long visible suture and have distinct dermal ossification (forming callosities). The medial side of hyoplastron is shorter than the medial side of the hypoplastron. The length between axillary and inguinal notches is very short. Medially, a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a large hexagonal shape (at the level of the hyoplastron), while the posterior part is elongated (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in four to six short pointed processes. At the level of the inguinal and axillary buttresses, the hyoplastron is slightly longer than the hypoplastron. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra sends three main processes. The anteriormost one (at midlength of the hypoplastron) is subdivived in three or more pointed and long processes, the posteriormost one bifurcatess in two elongated and pointed processes, while between the anteriormost process and the posteriormost process, the process is longer and bifurcates into four or more small processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed process of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are more or less triangular in shape. They are longer than wide. The anterior margin of each xiphiplastron is rather straight while its posterior is slightly convex posteriorly. The xiphiplastra articulate medially with at least four interdigited pointed processes.

3. Variations

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4.7.5 *Lissemys scutata* (Bonnaterre, 1789) (Figure 78-82)

Examined specimens: CUMZ-R- T154; CUMZ(R) one unnumbered individual, NMW 1872

Carapace (Figure 78-79)

1. *General*

The carapace length can reach up 23 cm (Smith, 1931). The carapace disc is longer than wide, with the lateral margins convergent backward. The ornamentation on the carapace is distinct from other trionychid and consist of fine granulations. There is no longitudinal ridges on the carapace. Peripheral plates are present in posterior part of carapace. These peripheral plates are not connected to the ribs.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width/length ratio of the nuchal is greater than 4 times in adults. The anterior margin of the nuchal is slightly concave anteriorly and its posterior margin is convex posteriorly. Lateral process of nuchal plate are absent. The costiform process is very short. It does not reach the free rib in the first costal plate. A prenuchal plate is present. In visceral view, the position of anterior end of the first body vertebra is at the level of the prenuchal plate anteriorly.

2.2 Neurals: There are seven or eight neural plates. Two neural plates are between the first pair of costal plates. The anterior margin of the first neural plate is convex anteriorly and wider than others. The shape of the second to sixth neural plates is hexagonal with short posterolateral sides. The seventh neural plate is oval in shape. The eighth neural is reduced pentagonal in shape. The neural formula is 4 6< 6< 6< 6< 6< 4 5.

2.3 Costals: There are eight pairs of costal plates. The first costal is longer than other costal plates. The lateral end of the first costal plate is longer than its medial end. The ribs in visceral view are flat. The seventh and eighth costal pairs are in contact at the midline. The distal ends of the seventh and eighth costal plates are in contact each other. The ribs are very slender by compared with other trionychid species. The first to the eighth costals are directed posteriorly. There is no depression for ilia on the eighth costal plates.

3. *Variations*

3.1 Ontogenetic Variations

1. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

1. Seven to eight neural plates can be present.

Plastron (Figure 80-82)

1. *General*

The plastron consists of nine plates that are reduced in size and loosely connected one to another. Ornamentation of plastron is finely granulated on the callosities of the epiplastra, entoplastron, hyoplastra, hypoplastra and xiphiplastra.

2. *Plates*

2.1 Epiplastra: The epiplastra are oval in shape with wide anteromedial part. A pointed process is present posteromedially and articulates medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape but the dermal ossification covering it is rounded. The ornamentation consists in fine granulations.

2.3 Hyo-hypoplastra: The hyoplastron and hypoplastron are fused. The anterior part of hyo-hypoplastron is convex anteriorly. Medially, a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a triangular shape (at the level of the hyoplastron), while the posterior part has a square shape (at the level of the hypoplastron). The hyoplastron sends antero-medially a long and pointed process. Laterally and posteriorly, the hypoplastron sends two pointed processes. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) one consists in a single pointed and long process, the posteriormost is divided into two relatively small pointed process, while between the anteriormost process and the posteriormost process, the process is longer and trifurcates into three pointed processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed process of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are more or less tetragonal in shape. The anterior and posterior margins of each xiphiplastron are slightly convex anteriorly and posteriorly respectively. The xiphiplastra articulate medially with a fine suture, and do not display angular processes like in other trionychid species.

3. *Variations*

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4.7.6 *Pelodiscus sinensis* Wiegmann, 1835 (Figure 83-86)

Examined specimens: CUMZ(R) 1997-5-24-(1); NMW 1865, NMW 1866, NMW 1868, NMW 1869, 537; 556; 2 unnumbered

Carapace (Figure 83-84)

1. *General*

The carapace disc is longer than wide in juveniles but as long as wide or a bit longer in adults. There is no peripheral plate. The suprascapular fontanelles between the nuchal and first pair of costals are present in juveniles, but absent in adult individuals. The shape of fontanelles is oval in shape. The ornamentation on the carapace is pitted. The pits are rather small, shallow and irregular in size and shape. The wall of the pits are quite thick. There is no clear neural keel as in *Amyda cartilagenea.* There are some irregular vertical ridges. There are about 22 pits from anterior and posterior margin of the four costal at medial end. There is no clear vermiculation.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width/length ratio of the nuchal is greater than 7 times in adults. The anterior border of nuchal is convex forming semi-circular shape and its posterior margin is straight in adults while its posterior margin is concave between fontanelles in juveniles. Lateral extremities of the nuchal plate are slightly expanded. The costiform process overlies on the dorsal rib in the first costal plate both in juveniles and adults. It is expanded in a small minor processes in juvenile (Figure 83) and reduced in adults where it is short and slightly expanded. In visceral view, the plate is smooth. The anterior edge of the first body vertebra reaches the posterior edge of the nuchal.

2.2 Neurals: There are seven or eight neural plates. The first neural plate contacts the first and second costal plates. The anterior margin of the first neural plate is straight. The first neural is longer than other neurals. The shape of the first to fourth neurals is hexagonal with short posterolateral sides. The fifth to seventh neural plates display variations in shape, and can be hexagonal with short posterolateral sides or tetragonal or asymmetric shape. The eighth neural is pentagonal in shape.

2.3 Costals: There are eight pairs of costal plates. The eighth pair of costals is in contact at the midline both in juveniles and adults. The free rib ends are expanded, which are elongated in juveniles and become short in adults. The posterior margin of the carapace is convex and formed by the eight costal plates. The ribs in visceral view are flat. The orientation of rib process from the first to the fourth costals goes forward, and are then perpendicular to the body axis, even at the level of the eight costal plate.

3. *Variations*

3.1 Ontogenetic Variations

1. The suprascapular fontanelles are present in juveniles but absent in adults.

2. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

1. The number of neural plates can be seven or eight.

2. The fifth to seventh neurals show variation in shape which can be hexagonal with short posterolateral sides or oval or regular shape or asymmetric shape.

Plastron (Figure 85-86)

1. *General*

The plastron consists of nine reduced plates and loosely connected one to another, except hyo-hypolastral connection. Fontanelles are present. Ornamentation of plastron is pitted on the callosities of hyoplastra, hypoplastra and xiphiplastra and a vermiculated pattern is present for some close to the margins of the bones.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped. Epiplastra are broad anteriorly and slender posteriorly. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape. The entoplastron is rather short and its lateral margin is wider than in other trionychids. The lateral sides of the entoplastron are longer than other species and subdivided at their end in small processes. The entoplastron is concave posteriorly. It articulates slightly with the anteromedial margin of hyoplastron dermal ossification.

2.3 Hyo-hypoplastra: Hyo-hypoplastra have a long suture and have a distinct dermal ossification (forming callosities). The medial side of hyoplastron is longer than the medial side of the hypoplastron. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a triangular shape (at the level of the hyoplastron), while the posterior part has an oval shape (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in three short pointed processes. At the level of the inguinal and axillary buttresses, the hyoplastron is slightly longer than the hypoplastron. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) consists in a single pointed and long process, the posteriormost one is divided at its end by two small pointed process, while between the anteriormost and the posteriormost processes, the process is longer and multifurcates into four or more small processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed processes of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are more oval than triangular in shape in juveniles and also in adults. The anterior margin is slightly concave anteriorly. The posterior margin of each xiphiplastron is convex posteriorly. The xiphiplastra articulate medially with two interdigited pointed processes.

3. *Variations*

3.1 Ontogenetic Variations

1. The suprascapular fontanelles are present in juveniles but absent in adults.

2. The free rib ends are elongated in juveniles but short in adults.

3. The posterior end of entoplastron is expanded in juveniles and tapers to sharp in adults.

3.2 Intraspecific Variations

1. The fifth to seventh neurals can be hexagonal with short posterolateral sides or oval or asymmetric shape.

4.7.7 *Nilssonia formosa* (Gray, 1869) (Figure 87-88)

Examined specimens: NMW 3861

Carapace (Figure 87)

1. *General*

The carapace length can reach up to 20 cm (Meylan, 1987). There is no peripheral plate. The carapace is longer than wide. The ornamentation on the carapace is coarsely pitted. These pits are rounded and show some variation in size. They are rather deep. The wall of the pits are thick. The density of the pits is lower on neurals and medial end of costals. There are about 9 pits from anterior and posterior margin of the four costal at medial end. There is no clear vermiculation.

2. *Plates*

2.1 Nuchal: The nuchal is slightly wider than long. The width/lenght ratio of the nuchal is greater than 5 times. The anterior margin of nuchal is convex anteriorly whereas its posterior margin is rather straight. Lateral extremities of nuchal plate are expanded. The costiform process are expanded at the lateral and posterior margins. The posterior end of the costiform process lies on the free rib end of the first costal plate.

2.2 Neurals: There are eight neural plates. The first neural plate contacts the first and second costal plates. The neural plates are slender. The anterior margin of the first neural plate is straight. The first neural plate is longer than the second one. The first to fifth neural plates are hexagonal with short posterolateral sides. The sixth is oval in shape. The seventh neural plate is hexagonal with short anterolateral sides. The eighth neural is reduced and pentagonal in shape. The neural formula is 6< 6< 6< 6< 6< 4 6> 5.

2.3 Costals: There are eight pairs of costal plates. The medial part of the second costal plate is shorter than the medial part of the first costal plate. The eighth pair of costals are in contact in the midline. The ribs in visceral view are flat. The medial part of the seventh costal plate is the shortest. The lateral ends of the seventh and eighth costal plates are in contact each other. The posterior margin of the carapace is formed by the eighth costal plates. It is rather straight. The free rib ends are expanded. The orientation of rib processes from the first to the third costals goes forward, and the fourth to eighth are directed posteriorly.

Plastron (Figure 88)

1. *General*

The plastron consists of nine plates. The fontanelles are present. The ornamentation of the plastron is coarsely pitted and vermiculated on the callosities of hyoplastra, hypoplastra and xiphiplastra.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped and thin. Epiplastra are elongated and slightly wide anteriorly while their posterior part is slender and tapers to a pointed end posteriorly. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape. Its posterior part is deeply concave posteriorly. Lateral parts of the entoplastron is elongated and tapers to a sharp end. It articulates with the anteromedial margin of the hyoplastron. The callosity surface is smooth.

2.3 Hyo-hypoplastra: Hyo-hypoplastra have a long contact and have distinct dermal ossification (forming callosities). The hyo-hypoplastral suture is ankylosed and therefore these bones are fused. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a laterally oval shape (at the level of the hyoplastron) and the posterior part has also an oval shape (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in four to six short pointed processes. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost one (at midlength of the hypoplastron) consists in a single pointed and long process, the posteriormost one is divided at its end in two relatively small pointed process, while between the anteriormost and the posteriormost processes, the process is longer and bifurcates or trifurcates in two to three small processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed processes of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are more or less triangular in shape. The dermal ossification is elongated. The anterior margin of each xiphiplastron is slightly concave anteriorly while its posterior is rather straight. The xiphiplastra articulate medially with two short interdigited processes.

4.7.8 *Nilssonia hurum* (Gray, 1831) (Figure 89-91)

Examined specimens: BMNH 86.8.26.2, NMW 31269.1, NMW 31269.2, NMW 31269.3, NMW 31269.4, NMW 31269.5, NMW 31269.6, NMW 31269.7, NMW 31269.8

Carapace (Figure 89-90)

1. *General*

The carapace is longer than wide. There is no peripheral plate. The ornamentation on the carapace is pitted and vermiculated. The pits are irregular in shape and show variation in size. They are rather shallow. These pits are present on neurals and on the medial end of costals. The vermiculation pattern is present on the lateral end costal plates. There are about 12 pits from the anterior to the posterior margin of the four costal at its medial end. There is no longitudinal vertical ridges on the carapace.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width/length ratio of the nuchal is greater than 3 times in adult. The anterior margin of nuchal is rather straight and its posterior margin is rather straight except the area which articulates with the neural plate and which is convex anteriorly. Lateral process of nuchal plate contact with costal laterally. The costiform process are slightly expanded at the end of posterior margins.

2.2 Neurals: There are eight neural plates. There are two neural plates between a pair of costal plates. The neural plates are longer than wide. The anterior margin of the first neural plate is convex anteriorly. The first neural plate is short and oval in shape. It is wider than other neurals. The second to sixth neural plates are hexagonal with short posterolateral sides. The seventh is oval in shape. The eighth neural is reduced and pentagonal in shape. The neural formula is 4 6< 6< 6< 6< 6< 4 5>.

2.3 Costals: There are eight pairs of costal plates. The medial part of the second costal plate is shorter than the medial part of the first costal plate. The eighth costals contact in the midline. The ribs in visceral view are flat. The medial part of the seventh costal plate is the shortest. The lateral ends of the seventh and eighth costal plates are in contact each other. The midline contact between eight costal plates is rather long by comparison with other species. The free rib ends are expanded. They become short in adult. The orientation of rib process from the first to the third costals goes forward, and the fourth to eighth are directed posteriorly.

3. *Variations*

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Plastron (Figure 91)

1. *General*

The plastron consists of nine plates. The fontanelles are present and are narrow compared with *Amyda cartilagenea*. Ornamentation of plastron is finely pitted on the callosities of hyoplastra, hypoplastra and xiphiplastra and vermiculations are present on the edges of these bones.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped. Epiplastra are elongated and slightly wide anteriorly while their posterior part is slender and tapers to a pointed end posteriorly. Their anterior parts are shorter than their posterior parts. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape. Its posterior part is deeply concave posteriorly. Lateral parts of the entoplastron are elongated and display slightly expanded ends. The entoplastron articulates posteriorly with the anteromedial margin of the hyoplastron. The surface of the callosity is smooth.

2.3 Hyo-hypoplastra: Hyo-hypoplastra articulate along a long visible suture and have distinct dermal ossification (forming callosities). The medial side of the hyoplastron is longer than the medial side of the hypoplastron. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The medial processes of the hyo-hypoplastron are very short which allow to observe a nearly continuous plastral fontanelle (see Figure 91). The hyoplastron sends antero-medially a long process that is subdivided at the end in two short pointed processes. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) is divided into two shorted processes, the posteriormost one bifurcates into two relatively small and pointed process, while between the anteriormost process and the posteriormost process, the process is shorter and bifurcates or trifurcates into two or three short processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed process of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra are triangular in shape. The anterior margin of each xiphiplastron is convex anteriorly and the posterior margin is convex posteriorly. The xiphiplastra articulate medially with two interdigited rounded processes.

3. *Variations*

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4.7.9 *Rafetus euphraticus* Daudin, 1802 (Figure 92-96)

Examined specimens: 1450, NMW 1856, NMW 1861, and NMW 1862

Carapace (Figure 92, 94-95)

1. *General*

The carapace disc is longer than wide. There is no peripheral plate. The suprascapular fontanelles between the nuchal and first pair of costals are present in juveniles and become smaller in adults. These fontanelles are more or less circular shape. The ornamentation on the carapace is pitted and vermiculated. The pits are irregular shape and display variation in size. They are rather shallow. The pits are present on neurals and on the medial part of costals. The vermiculation pattern is present in the lateral end of costal plates. The density of the pits is high on the middle of the plates. There are about 25 pits from the anterior to the posterior margins of the four costal at its medial end.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width/length of the nuchal is greater than 2 in adults. The anterior border of the nuchal is convex forming a semi-circular shape and the posterior margin is straight except in the area of fontanelles where it shows a concavity. Lateral extremities of nuchal plate are slightly expanded. The costiform process overlies on the dorsal rib of the first costal plate both in juveniles and adults. In visceral view, the plate is smooth. The anterior edge of the first body vertebra reaches the posterior edge of the nuchal.

2.2 Neurals: There are seven neural plates. Only one neural plate contacts the first pair of costal plates. The anterior margin of the first neural plate is convex anteriorly. The first neural is wider than other neurals. The shape of the first to third neurals is hexagonal with short posterolateral sides. The fourth neural displays a variable shape that can be hexagonal with short anterolateral sides or hexanogal with short posterolateral sides. The fifth and sixth neurals are hexagonal with short anterolateral sides. The seventh neural is reduced and pentagonal in shape. The neural formula is 6< 6< 6< 6<(>), 6>, 6>, 5>.

2.3 Costals: There are eight pairs of costal plates. The eighth costals are reduced. The medial end of the first is longer than its lateral end. The second to the eight costal are longer laterally than medially. The first two costals are laterally projected forward while the fifth to the eight costal are projected backwards. The seventh and eighth pair of costals are in contact at the midline in both juveniles and adults. The free rib ends are expanded, they are elongated in juveniles and become short in adults. The posterior margin of the carapace is formed by the seventh and eighth costal plates.

3. *Variations*

3.1 Ontogenetic Variations

1. The suprascapular fontanelles are present, large with an oval shape in juveniles but become more circular in adults.

2. The free rib ends are elongated in juveniles but short in adults.

3.2 Intraspecific Variations

1. The fourth neural plate can be hexagonal with short posterolateral sides or hexagonal with short anterolateral sides.

Plastron (Figure 93,96)

1. *General*

The plastron consists of nine reduced plates loosely connected one to another, except the hyo-hypolastral connection. Three fontanelles are present: between entoplastron and hyohypoplastron, hypoplastron and xiphiplastron and between xiphiplastron. Ornamentation of plastron is vermiculated on the callosities of hyoplastra and hypoplastra.

2. *Plates*

2.1 Epiplastra: The epiplastra are J-shaped and thin. Epiplastra are broad anteriorly and slender posteriorly. The epiplastra articulate medially with the anterolateral margin of the entoplastron.

2.2 Entoplastron: The entoplastron has a boomerang shape and is rather thin. It is deeply concave posteriorly. The entoplastron is long and tapers to a sharp end. It articulates medially with the anteromedial margin of the hyoplastron. The callosity, when present, has a smooth, unornamented surface .

2.3 Hyo-hypoplastra: Hyo-hypoplastra articulate broadly along a long visible suture and have distinct dermal ossification (forming callosities). The medial margin of hyoplastron is shorter than the medial margin of the hypoplastron. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has an oval shape (at the level of the hyoplastron), while the posterior part has a semi-circular shape (at the level of the hypoplastron). The hyoplastron sends antero-medially a long process that is subdivided at the end in four short pointed processes. At the level of the inguinal and axillary buttresses, the hyoplastron is slightly longer than the hypoplastron. The lateral margin of each hypoplastron is smaller than the medial margin. Laterally and posteriorly, the hypoplastron sends two pointed processes with rounded ends. Medially, the hypoplastra send three main processes. The anteriormost (at midlength of the hypoplastron) consists in a single pointed and long process, the posteriormost one is divided into two relatively small pointed processes, while between the anteriormost and the posteriormost processes, the process is longer and multifurcates into three or four small processes at its medial end. The two main posterior processes of the hypoplastron articulate with the anterior pointed processes of the xiphiplastron.

2.4 Xiphiplastra: The xiphiplastra have more or less a triangular shape. The posterior margin of each xiphiplastron is rather straight, while the anterior margin is slightly concave anteriorly. The xiphiplastra articulate medially with three interdigited pointed processes.

3. *Variations*

-

4.7.10 *Rafetus swinhoei* (Gray, 1873) (Figure 97)

Examined specimens: Farkas *et al.*, 2011 (p 68, Fig. 4)

Carapace (Figure 97)

1. *General*

The carapace disc is longer than wide in juveniles in adults. There is no peripheral plate. There is no fontanelles in adults. The ornamentation of the shell are not clear observed from the figure.

2. *Plates*

2.1 Nuchal: The nuchal is wider than long. The width on length ratio of the nuchal is greater than 2 in adults. The anterior border of nuchal is convex forming a semi-circular shape and the posterior margin is rather straight. Lateral extremities of the nuchal plate are no expanded. The costiform process overlies on the dorsal rib of the first costal plate.

2.2 Neurals: There are seven or eight neural plates. Only one neural plate contacts the first pair of costal plates. The anterior margin of the first neural plate is straight or convex anteriorly. The first neural is longer than other neurals. The shape of the first to fourth neurals is hexagonal with short posterolateral sides. The fifth to sixth neurals show variable shapes (see Figure 97). The seventh neural is reduced with a pentagonal in shape in adults. The eighth neural is more reduced or absent.

2.3 Costals: There are eight pairs of costal plates. The eighth costals are reduced. The medial end of the first and eighth costals is longer than its lateral end. The six pair of costals is in contact neural plates. The medial ends of the seventh and eight costals contact at the midline. The free margin of the seventh and eighth costal plates form the posterior margin of the carapace. The seventh costal plate reach the lateral side of carapace and the posterior part.

3. *Variations*

3.1 Ontogenetic Variations

-

3.2 Intraspecific Variations

1. The anterior margin of the first neural is straight or convex anteriorly.
2. Number of neural is seventh or eighth.
3. The fifth neural can be oval or asymmetric in shape.
4. The sixth neural can be hexagonal with short posterolateral sides or asymmetric in shapes
5. The shortest at the medial end of costal can be seventh or eighth costals.
6. Lateral end of the seventh costal plates reach the lateral side of carapace or only posterior part.

4.8 Comparison and conclusion

4.8.1 Comparison

Ten species of trionychid turtles were compared for the carapace morphology and nine species for the plastron morphology (except *Rafetus swinhoei*). They include *Amyda cartilagenea*, *Chitra chitra*, *Dogania subplana*, *Pelochelys cantorii*, *Pelodiscus sinensis*, *Lissemys scutata*, *Nilssonia formosa*, *Nilssonia hurum*, *Rafetus euphraticus* and *R. swinhoei*. 24 characters differ between species and are listed below. These characters consist of:

1) presence of prenuchal

2) shape of the anterior margin of nuchal

3) presence of a strong crest along the anterior border of the inner surface of nuchal

4) shape of costiform process

5) presence of suprascapular fontanelles in adults

6) number of neural contacting the first pair of costals

7) neural size

8) anterior margin of first neural

9) first neural plate sutured with nuchal

10) lateral end of first costal plate narrower or longer than medial end

11) lateral end of the seventh and eight costals contacting each other

12) lateral end of the eighth costal plate narrower or longer than medial end

13) presence of a continuous midline ridge along neurals

14) presence of rib crest on second costal in visceral view

15) shortest medial end of costal

16) length of the midline contact between eight costal plates

17) reduced the eighth costal

18) longitudinal ridges on carapace

19) presence of elongated pits near the suture between neurals and costals forming a radiating pattern

20) presence of well marked vermiculation on the lateral end of costals in adults

21) presence of fine granulation ornamentation

22) approximative number of pits on the fourth costal at medial end

23) orientation of rib ends

24) presence of peripherals

A comparative table for the carapace is provided in Table 4.1

For the plastron, 14 characters allowed me to recognize the different species and are listed below:

1) epiplastron shape

2) anterior process of epiplastron

3) posterior process of entoplastron

4) entoplastron shape

5) presence of hyo-hypoplastral suture

6) at the level of the inguinal and axillary buttresses, the hyoplastron is longer or shorter than the hypoplastron

7) number and size of processes in the anterior most of hypoplastron at the medial end

8) the morphology of the end of processes in the anterior most of hypoplastron at the medial end

9) lateral ends of hyo-hypoplastron callosities

10) medial length of xiphiplastra longer or shorter the midline length of hyoplastron in adults

11) xiphiplastra contact

12) anterior margin of xiphiplastra

13) posterior margin of xiphiplastra

14) ornamentation

A comparative table for the plastron is provided in Table 4.2.

Table 4.1 Comparative morphology of carapace characters in *Amyda cartilagenea*, *Chitra chitra*, *Dogania subplana*, *Pelochelys cantorii*, *Pelodiscus sinensis*, *Lissemys scutata*, *Nilssonia formosa*, *Nilssonia hurum*, *Rafetus euphraticus* and *Rafetus swinhoei*.

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
presence of prenuchal	no	no	no	no	yes	no	no	no	no	no
shape of anterior margin of nuchal	convex anteriorly	convex anteriorly	convex anteriorly	convex anteriorly	rather straight	convex anteriorly	rather straight	rather straight	convex anteriorly	convex anteriorly
presence of a strong crest along the anterior border of the inner surface of nuchal	no	yes	no	yes	no	no	no	no	no	no
shape of costiform process	slightly expanded	elongated and pointed	expanded	expanded	no expanded	slightly expanded	expanded	no expanded	no expanded	no expanded
presence of suprascapular fontanelles in adults	no	no	yes	no	no	no	no	no	yes	no

Table 4.1 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
number of neural contacting the first pair of costals	one	one	one	one	two	one	one	two	one	one
neural size	narrow	wide	narrow	wide	narrow	narrow	narrow	narrow	narrow	narrow
anterior margin of first neural	straight	convex anteriorly	straight	straight	convex anteriorly	straight	straight	straight	convex anteriorly	straight or anteriorly
Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
first neural plate suture with nuchal	yes	yes	no	yes	yes	yes	yes	yes	yes	yes

Table 4.1 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
lateral end of first costal plate narrower or longer than medial end	narrower	longer	longer	narrower	longer	narrower	narrower	longer	narrower	narrower
lateral end of the seventh and eight costals contacting	yes	yes	no	yes	yes	yes	yes	yes	yes	yes
lateral end of the eighth costal plate narrower or longer than medial end	narrower	narrower	narrower	narrower	-	narrower	narrower	narrower	longer	longer
presence of a continuous midline ridge along neurals	yes	no	no	no	no	no	no	no	no	no

Table 4.1 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
presence of rib crest on second costal in visceral view	no	yes	no	yes	no	no	no	no	no	no
Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
shortest medial end of costal	seventh	seventh	eighth	seventh	seventh	seventh	seventh	seventh	eighth	eighth or seventh
length of the midline contact between eight costal plates	short	long	-	long	short	short	long	very long	very short	short
reduced the eighth costal	no	no	no	no	yes	no	no	no	yes	yes
longitudinal ridges along the carapace	yes	no	no	no	no	yes	no	no	no	no

Table 4.1 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
presence of elongated pits near the suture between neurals and costals forming a radiating pattern	no	yes	no	no	no	no	no	no	no	no
presence of well marked vermiculation on the lateral end of costals in adults	no	no	no	yes	no	no	no	yes	no	-
presence of fine granulation ornamentation	no	no	no	no	yes	no	no	no	no	no

Table 4.1 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*	*Rafetus swinhoei*
approximative number of pits on the fourth costal at medial end	12	13	50	25	-	22	9	12	25	-
orientation of rib ends	the first to the third costals goes forward, and the fifth to eighth are directed posteriorly	the first to the second costals goes forward, and the third to eighth are directed posteriorly	oriented posteriorly from the third to the eighth costal plates	the first to the third costals goes forward, and are later perpendicular to the body axis	The first to the eighth costals are directed posteriorly	the first to the third costals goes forward, and the fourth to eighth are directed posteriorly	the first to the third costals goes forward, and the fourth to eighth are directed posteriorly	the first to the third costals goes forward, and the fourth to eighth are directed posteriorly	first two costals are laterally projected forward while the fifth to the eight costal are projected backwards	-
presence of peripherals	no	no	no	no	yes	no	no	no	no	no

Table 4.2 Comparative morphology for plastral characters in *Amyda cartilagenea*, *Chitra chitra*, *Dogania subplana*, *Pelochelys cantorii*, *Pelodiscus sinensis*, *Lissemys scutata*, *Nilssonia formosa*, *Nilssonia hurum* and *Rafetus euphraticus*.

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*
epiplastron shape	J shape	J shape	J shape	J shape	Oval shape	J shape	J shape	J shape	J shape
anterior process of epiplastron	elongated	elongated	elongated	short	rounded	elongated	elongated	elongated	short
Posterior process of entoplastron	elongated and pointed	elongated and pointed	elongated and pointed	elongated and pointed	rounded	short and expanded	elongated and pointed	elongated and pointed	elongated and pointed
entoplastron shape	boomerang	boomerang	boomerang	boomerang	oval - round	boomerang	boomerang	boomerang	boomerang
presence of hyo-hypoplastral suture	yes	yes	yes	yes	no	yes	yes	yes	yes
at the level of the inguinal and axillary buttresses, the hyoplastron is longer or shorter than the hypoplastron	longer	slightly longer	slightly shorter	slightly longer	-	longer	more or less equal	longer	more or less equal

Table 4.2 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*
number and size of process in the anteriormost of hypoplastron at the medial end	a large single process	elongated multifurcated processes	multifurcated processes	elongated multifurcated processes	a large single process	a large single process	a large single process	very short multifurcated processes	a large single process
the length of hyo-hypoplastron in medial part	short	long	very short	long	long	short	long	long	long
the end of process in the anterior most of hypoplastron at the medial end	pointed	straight	pointed	pointed	pointed	pointed	pointed	pointed	pointed

Table 4.2 (continued)

Character/species	*Amyda cartilagenea*	*Chitra chitra*	*Dogania subplana*	*Pelochelys cantorii*	*Lissemys scutata*	*Pelodiscus sinensis*	*Nilssonia formosa*	*Nilssonia hurum*	*Rafetus euphraticus*
lateral ends of hyo-hypoplastron callosities	dispart	no	dispart	no	dispart	no	no	no	no
medial length of xiphiplastron longer or shorter midline length of hyoplastron in adult	longer	longer	shorter	longer	longer	shorter	longer	longer	shorter
xiphiplastra contact	Pointed process	Pointed process	Pointed process	Pointed process	suture	Pointed process	Pointed process	Pointed process	Pointed process
anterior margin of xiphiplastra	concave anteriorly	straight	concave anteriorly	rather straight	convex anteriorly	concave anteriorly	concave anteriorly	convex anteriorly	concave anteriorly
posterior margin of xiphiplastra	concave posteriorly	convex posteriorly	slightly concave posteriorly	slightly convex posteriorly	Slightly convex posteriorly	convex posteriorly	rather straight	convex posteriorly	rather straight
ornamentation	rather pitted and rare vermiculated	pitted and no vermiculated	finely pitted and vermiculated	coarsely pitted and vermiculated	finely granulated	rather pitted and some vermiculated	coarsely pitted and vermiculated	finely pitted and some vermiculated	vermiculated

Key for living trionychid turtle carapace in Thailand and neighbor countries

1a presence of prenuchal
presence of peripherals
The first to eighth costal are directed to posterior
fine granulated ornamentation..*Lissemys scutata*

2a absence of prenuchal
absence of peripherals
the first to eighth costal are not directed to posterior
no fine granulated ornamentation...b

1b first neural not suture with nuchal in adults
lateral ends of the seventh and eighth costal not contact
approximately, ≥ 50 pits on the fourth costal at medial end....*Dogania subplana*

2b first neural suture with nuchal in adults
lateral ends of the seventh and eighth costal in contact
approximately, < 50 pits on the fourth costal at medial end...............................c

1c costiform process slightly expanded
presence of longitudinal ridges along the carapace...d

2c costiform process expanded or elongated or no expanded
absence of longitudinal ridges along the carapace..e

1d presence of a continuous midline ridge along neurals
approximately, < 20 pits on the fourth costal at medial end
....*Amyda cartilagenea*

2d absence of a continuous midline ridge along neurals
approximately, > 20 pits on the fourth costal at medial end
....*Pelodiscus sinensis*

1e presence of a strong crest along the anterior border
of the inner surface of nuchal
wide neural plates...f

2e absence of a strong crest along the anterior border
of the inner surface of nuchal
narrow neural plates...g

1f costiform process elongated and pointed
anterior margin of the first neural convex anteriorly
presence of elongated pits near the suture between
neurals and costals forming a radiating pattern
approximately, < 20 pits on the fourth costal at medial end
....*Chitra chitra*

2f costiform process expanded
anterior margin of the first neural straight
presence of well marked vermiculation on the lateral end
of costals in adults
approximately, > 20 pits on the fourth costal at medial end
....*Pelochelys cantorii*

1g anterior margin of nuchal convex anteriorly
lateral end of the eighth costal plate longer than medial end
length of the midline contact between eight costal plates very short
eight costal reduced
....h

2g anterior margin of nuchal rather straight
lateral end of the eighth costal plate narrower than medial end
length of the midline contact between eight costal plates long
eight costal not reduced
....i

1h presence suprascapular fontanelles in adults.........................*Rafetus euphraticus*

2h absence suprascapular fontanelles in adults..............................*Rafetus swinhoei*

1i costiform process not expanded
two neurals contacting the first pair of costals
lateral end of first costal plate longer than medial end
presence of well marked vermiculation on the lateral end
of costals in adults... *Nilssonia hurum*

2i costiform process expanded
one neurals contacting the first pair of costals
lateral end of first costal plate narrower than medial end
absence of well marked vermiculation on the lateral end
of costals in adults..*Nilssonia formosa*

Key for living trionychid turtle plastron in Thailand and neighbor countries

1a oval shaped epiplastron
rounded anterior process of epiplastron
rounded posterior process of entoplastron
oval shaped entoplastron
hyo-hypoplastron suture fused
suture contact between xiphiplastra
finely granulated ornamentation..*Lissemys scutata*

2a J shaped epiplastron
short and elongated anterior process of epiplastron
not rounded posterior process of entoplastron
boomerang shaped entoplastron
presence of hyo-hypoplastron suture
pointed process contact between xiphiplastra
not granulated ornamentation...b

1b at the level of the inguinal and axillary buttresses,
the hyoplastron is slightly longer than the hypoplastron
elongated multifurcated process in the anterior most of
hypoplastron at the medial end
anterior margin of xiphiplastra straight..c

2b at the level of the inguinal and axillary buttresses,
the hyoplastron is not slightly longer than the hypoplastron
no elongated multifurcated process in the anterior most of
hypoplastron at the medial end
anterior margin of xiphiplastra convex or concave...d

1c elongated anterior process of epiplastron
the end of process in the anterior most of
hypoplastron at the medial end straight
pitted ornamentation..*Chitra chitra*

2c short anterior process of epiplastron
the end of process in the anterior most of
hypoplastron at the medial end pointed
coarsely pitted and vermiculated ornamentation...................*Pelochelys cantorii*

1d at the level of the inguinal and axillary buttresses,
the hyoplastron is shorter than the hypoplastron
the length of hyo-hypoplastron in medial part very short........*Dogania subplana*

2d at the level of the inguinal and axillary buttresses,
the hyoplastron is equal or longer than the hypoplastron
the length of hyo-hypoplastron in medial part shorter or long...........................e

1e lateral ends of hyo-hypoplastron callosities dispart
the length of hyo-hypoplastron in medial part is short.......................................f

2e lateral ends of hyo-hypoplastron callosities not dispart
the length of hyo-hypoplastron in medial part is long..g

1f elongated and pointed posterior process of entoplastron
medial length of xiphiplastron longer than midline
length of hyoplastron in adult...*Amyda cartilagenea*

2f short and expanded posterior process of entoplastron
medial length of xiphiplastron longer than midline
length of hyoplastron in adult...*Pelodiscus sinensis*

1g at the level of the inguinal and axillary buttresses,
the hyoplastron is longer than the hypoplastron
very short multifurcated process in the anterior most of
hypoplastron at the medial end
posterior margin of xiphiplastron convex posteriorly............ *Nilssonia hurum*

2g at the level of the inguinal and axillary buttresses,
the hyoplastron is more or less equal the hypoplastron
a large single process in the anterior most of
hypoplastron at the medial end
posterior margin of xiphiplastron rather straight..h
1h elongated anterior process of epiplastron................................*Nilssonia formosa*
2h short anterior process of epiplastron.....................................*Rafetus euphraticus*

4.8.2 Conclusion

Despite of intraspecific and ontogenetic variation, all living trionychids from Thailand and adjacent territories can be distinguished from each other, based on carapace morphology, ornamentation and plastral morphology. The key and comparison tables can help for identifying fossils. The description can also help to know whether the fossil material differ from living ones. Finally, the key can help at identifying skeleton in recent time (archeological purpose or zoological and conservation purposes)

In the future, it would be interesting to add information concerning the appendicular and axial skeleton for these different species. It would also be interesting to have information concerning the plastron shape in *Rafetus swinhoei* rather than *Rafetus euphraticus,* also this species became one of the rarest trionychid turtles. It would be also necessary to gather information on *Palea steindachneri*, because this species can be found not far from Thailand in Laos, China and Vietnam.

CHAPTER 5

DESCRIPTION OF FOSSIL AND SUB-FOSSIL MATERIALS OF TURTLES FROM THAILAND

The study starts first with oldest fossil remains and follows in time until archaeological times. It should be reminded that not all the sites of Thailand have been investigated for this study. This is particularly true for archaelogical localities, where just a sample of localities were analyzed.

5.1 Miocene turtles in Thailand

5.1.1 Turtles from Ban Na Sai, Lamphun Province

Locality (Thasod, 2007):

Ban Na Sai locality is situated Li District, Lumphun Province. This locality belongs to Na Sai sub-basin which is one of the four basins of Li Basin. The Li Basin includes the Ban Pa Kha, Ban Pu, Mae long and Ban Na Sai sub-basin.

Na Sai sub-basin correspond to a large area of the southern Li basin. The uppermost sequence of this sub-basin consists in light gray mudstones, shales, sandstones and conglomeratic sandstones. This sequence contains fossils of fishes, mastodontids, suids, rhinocerotids, and anthracotherids (Thasod, 2007). The underlying sequence consists in lignites that are interbedded with light gray to dark gray claystones, shales, and sandstones with some carbonaceous shale and conglomeratic sandstones. The fossils found in this sequence belong to mammals, turtles, crocodiles, gastropods, leaves and also fishes (Songtham *et al.*, 2003). The top of the uppermost sequence of the Ban Na Sai basin was eroded and subsequently covered by Quaternary and fluvial beds. The age of this locality is Middle Miocene based on the fossil mammals (DMR, 2001; Ducrocq *et al.*, 1994).

Three turtle taxa can be recognized from Ban Na Sai, Lumphun Province

Systematic paleontology

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Genus *Amyda* Geoffroy Saint-Hilaire, 1809

cf. *Amyda*

(Figure 98)

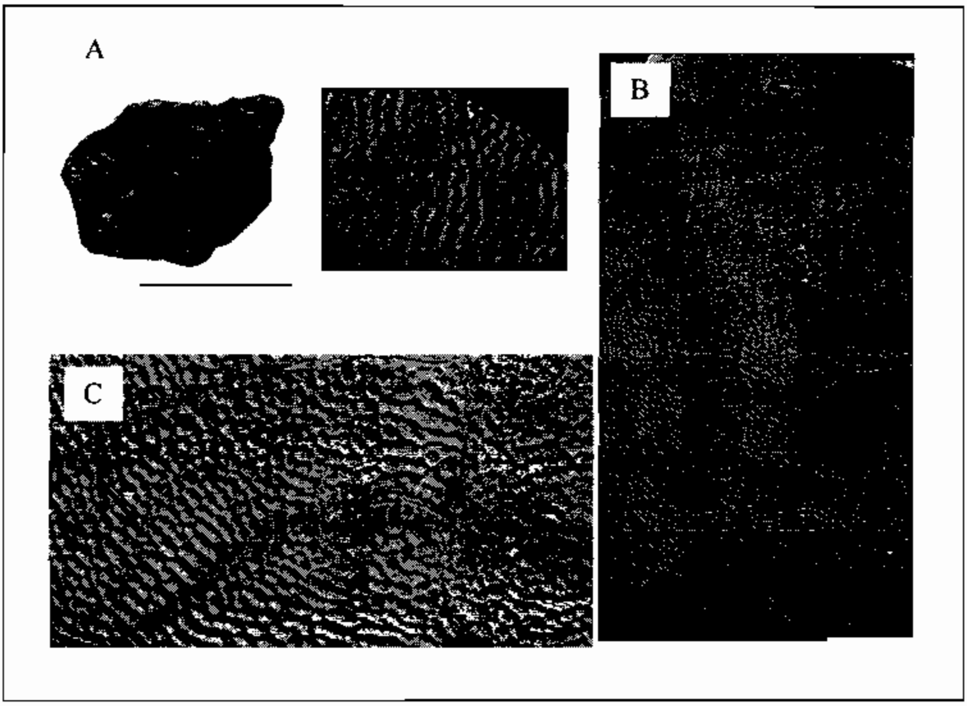

Figure 98 Isolated plates of cf. *Amyda* (A) from Na Sai, Lamphun Province (NS1, left and SM-unnumbered, right). Carapace of the living *Amyda cartilagenea* for comparative purposes (B); detail in the region of the seventh and eight costal plates where oblique ridges are indicated by black arrow. Scale bar equals 1 cm.

Material: Two costal fragments (NS1 and SM-unnumbered).

Description:

NS1 displays an ornamentation principally consisting of pits of random size, ridges and tubercules while SM-unnumbered displays an ornamentation consisting of ridges and vermiculations on its lateral side becoming series of tubercules at the medial end of costal and near the suture with the neural. The pits are shallow and the wall of the pits are thin. On the NS1 and SM-unnumbered, a clear oblique ridge is superimposed on the ornamentation (Figure 98).

Comparison and discussion:

The ornamentation is typical for the Trionychidae. The presence of ridges along carapace is characteristic of *Amyda cartilaginea* and *Pelodiscus sinensis* (see chapter IV). These two genus differ by the presence of a neural carina that is only present in *Amyda*. However, no neurals were found in Na Sai. The two species can be also identified on the basis of the thickness of the wall of the pits (thin in *Amyda* and thicker in *Pelodiscus*). Therefore, these material are tentatively identified as cf. *Amyda*. However, it should be reminded that tubercules are not present on the costal bones of *Amyda cartilaginea* and that these bones may belong to a different group than the living Southeast Asian trionychids.

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Family Trionychidae Gray, 1825
gen et sp indet.
(figures 99 and 100)

Material: costal plates (SHM-NS 22 and SHM-NS 24), costal plate and fragments (SHM-NS 116), left hypoplastron (SHM-NS 23), right hypoplastron (SHM-NS 115), xiphiplastron, (SHM-NS 114) , right hypoplastron (SHM-NS 115), xiphiplastron (SHM-NS 114) and costal plate and fragments (SHM-NS 116)

Description:

The SHM-NS 22 (Figure 99, B) specimen is probably a left fourth costal. The ornamentation is not well preserved but allows to see vermiculations on the lateral end of costal plate and some pits more medially. The medial end of this plate is missing. Its lateral end is straight and present a free rib end which is rather short and rounded. The SHM-NS 24 specimen is also a costal with its medial end preserved (Figure 99, C). It is probably the seventh costal because the lateral margin is rather long compared to medial end. The free rib end is present and is short and is rounded. The ornamentation is similar to SHM-NS 24. SHM-NS 116 is another large costal plate. Nearly all the edge of the plate are broken. The ornamentation is very fine and displays shallow vermiculations especially close to the lateral end of the plate (Figure 99, C).

SHM-NS 23 is an incomplete left hypoplastron, presenting only the anteromedial parts. A hyo-hypoplastral suture was present. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has a semi-circular shape (at the level of the hyoplastron). Medially, the hypoplastron SHM-NS 23 send two processes. The anteriormost (at midlength of the hypoplastron) one consists only in one straight and short process, and between the anteriormost process and the posteriormost processes, the process is longer and bifurcates in two processes at its medial end. The two main posterior processes of the hypoplastron probably articulated with the anterior pointed process of the xiphiplastron. The right hypoplastron (SHM-NS 115) (Figure 100, A) has a distinct and large dermal ossification (forming callosities). The hyo-hypoplastral suture is present. Medially a process of the hypoplastron delimitates two parts at the level of the plastral fontanelles. The anterior part has semi-circular shape (at the level of the hyoplastron). Medially, the the hypoplastron send several multifurcated processes. The anteriormost (at midlength of the hypoplastron) one consists in one short and wide process and between the anteriormost process and the posteriormost process, the process is longer and bifurcates in three small processes at its medial end. The two main posterior processes of the hypoplastron articulates with the anterior pointed process of the xiphiplastron. The xiphiplastron SHM-NS 114 (Figure 100, B) has its lateral margins damaged. The anterior and posterior margin of the xiphiplastron is straight.

Comparison and discussion:

These specimens can be recognized as belonging to Trionychidae Gray, 1825 because of the ornamentation, the absence of scute sulci and reduced plastron. All of them are isolated plates. In my opinion, two groups can be recognized in this sample based on the ornamentation and shape of hypoplastron.

The first group (1#) displays an ornamentation covered by vermiculations and pits consist of costal plates (SHM-NS 22 and SHM-NS 24) and left hypoplastron (SHM-NS 23). Compared with living Asian trionychid species, this condition is different from *Chitra chitra*, *Pelochelys cantorii*, *Pelodiscus sinensis*, *Rafetus* *euphraticus* and *Dogania subplana. Lissemys punctata* differs from this morphology because the hyo-hypoplastral suture is present in the fossil but fused in *Lissemys*. The specimen is also different from *Nillsonia hurum* in having very short hypoplastral processes. The morphology of the processes is similar to those of *Amyda cartilagenea*. However, there are different from *A. cartilagenea* in being shorter and wider. This probably suggest that this morphotype may belong to a new taxon.

The second morphology (2#) consists of plates with a finer ornamentation. It is represented by a right hypoplastron (SHM-NS 115), a xiphiplastron (SHM-NS 114) and costal plate and fragments (SHM-NS 116). This specimen differs from the first group in having a finer ornamentation and the presence of a medial process of hypoplastron between the anteriormost process and the posteriormost process that multifurcates in three small processes at its medial end. In addition, this specimen displays a more rounded hypoplastron in the medial part, and the lateromedial part of this hypoplastron callosity is convex laterally which is different from *Chitra chitra*, *Pelochelys cantorii*, *Pelodiscus sinensis, Rafetus euphraticus, Lissemys punctata*, *Aspideretes hurum,* and *Dogania subplana* provided in tronychids catalogue (chapter 4 of this work). This material probably belongs to one other taxa.

More complete material is needed to confirm the systematic composition of the trionychids from Na Sai.

Superfamily Testudinoidea Batsch, 1788

Family Geoemydidae Theobald, 1868

gen et sp indet.

(Figure 101)

Material: Nuchals (PRCCR 19, PRCCR 3), third and ninth peripheral plates (PRCCR 2, PRCCR10), pygal plate (NS2), entoplastrons (NS3, PRCCR6), right hyoplastron (PRCCR13, PRCCR15, PRCCR17) and right xiphiplastron (PRCCR1).

Description:

Most of material from this locality are isolated plates. It includes nuchals (PRCCR 19, PRCCR 3), third and ninth peripheral plates (PRCCR 2, PRCCR10), pygal plate (NS2), entoplastrons (NS3, PRCCR6), right hyoplastron (PRCCR13, PRCCR15, PRCCR17) and right xiphiplastron (PRCCR1).

PRCCR19 is a nearly complete nuchal, for which only the posterior part is broken (Figure 101, A). The plate is rather thick. The outline is pentagonal with a strong anterior emargination. The cervical scute is very narrow anteriorly, elongated and has a triangular shape. Its posterior part is concave posteriorly while its anterior part is slightly emarginated. The first vertebral sulcus is observable on the plate. The first vertebral plate is convex and narrow anteriorly. The pleuro-marginal sulcus is located posteriorly, and the first marginal should have been long. In visceral view, it is smooth. The lateral end of the plate is thicker than the anterior margin. The cervical sulcus impression is wider and more elongated in ventral view than the one in the dorsal view. Another nuchal (PRCCR3) is incomplete, having all its outline edge broken (Figure 101, B). Only the posterior right part of the cervical scute is preserved, indicating that this scute probably had an elongated triangular shape. The first vertebral scute impression can be observed on the right side of the plate. Its anterior part is convex whereas laterally, it is concave internally. In visceral view, the right side of the cervical is present indicating that this scute was wider in ventral view than in dorsal view. At the level of the anterior part of the vertebral in visceral view, the plate is thick and convex dorsally which is not similar to PRCCR 19 which is being gradually increasing thickness in sagital section (Figure 101, A3). The right third peripheral plate (PRCCR10) present a musk duct foramen (Figure 1014, C2). The plate is crossed by the pleuro-marginal sulcus on its dorsal side, and displays the sulcus between the third and fourth marginal scutes. The pleuro-marginal sulcus is relatively low by comparison to the costo-peripheral suture. PRCCR 2 is a right ninth peripheral plate (Figure 101, D). The plate is thick. Its posterior margin is serrated. The indentation is angular but the serration is rounded. The pleuro-marginal sulcus is restricted slightly below to the medial end of the plate. The pygal plate NS2 is small and wider than long (Figure 101, E). Its anterior part is rather straight while its posterior part exhibits a pygal notch. The middle of the plate is crossed by the marginal sulcus. There is no impression of the fifth vertebral sulcus on the pygal. There are two preserved entoplastrons. The entoplastron (NS3) is sub-rhombic shape (Figure 101, F). It is very small and thin. Its posterior part is intersected by the humero-pectoral sulcus. The humero-pectoral sulcus is oblique on this bone. The gulo-humeral sulcus crosses on the anterior end of the bone. The second entoplastron (PRCCR6) is rather thick and large and its complete right half is preserved (Figure 101, G). It is sub-rhombic shape. Its anterior part is well crossed by gulo-humeral sulcus and its posterior part is crossed by humero-pectoral sulcus. The right hyoplastron (PRCCR15) is nearly complete. It is a thick bone. The posterior part is broken while the anterior part is complete (Figure 101, H). Based on the suture outlines, the posterior end of the epiplastron is oblique. The entoplastron outline is large and convex laterally. The humero-pectoral sulcus was crossing the middle of the entoplastron. The right xiphiplastron surface does not display a good preservation and sulci are hardly visible. However, there is a lateral demarcation on its lateral side, that may have correspond to the ano-femoral sulcus. The suture between the xiphiplastron and the hypoplastron is oblique. The xiphiplastral process is elongated and rounded at the end. The anal notch is deep and wide with a triangular shape (Figure 101, I)

Comparison and discussion:

These plates can be referred to the family Geoemydidae Theobald, 1868 based on the presence of a musk duct foramen in the third peripheral plate, the pleuro-marginal sulcus restricted to peripheral plates, and the presence of a deep anal notch. The material correspond to several individuals which are represented by replicated plates and bones including nuchal and entoplastron. These material may have belong to at least two mixed taxa because two morphotypes can be recongnized on the basis of entoplastrons and nuchals. The first one entoplastral morphology is large with its anterior part longer than its posterior part. Its anterior part is crossed by gulo-humeral sulcus while its posterior part is crossed by humero-pectoral sulcus nearly in the middle plate. This kind of entoplastron can be found in living geoemydids such as *Cyclemys* complex, *Heosemys spinosa*, *H. annandalii* and *H. grandis*. The other entoplastral morphology is small, and displays a rhombic shape. Its anterior part is crossed by the gulo-humeral sulcus more anteriorly than the first morphotype while its posterior part is crossed by the humero-pectoral sulcus more posteriorly, close to the end of the plate. This morphology is similar to the living taxa *Malayemys* and *Melanochelys trijuga*. Two nuchal morphologies are found. One is emarginated covered with a narrow first vertebral scute the other is not, and covered by a wider first vertebral scute. The nuchal with an emarginated anterior margin and narrow vertebral scute is found in *Heosemys* *grandis*, *H. spinosa*, and *Cuora mouhotii*. Morphology of the described xiphiplastron clearly differs from *C. chiangmuanensis* from Chiang Muan locality by the presence of elongated xiphiplastron. Elongated xiphipastral process and oblique anal sulcus are found in *Malayemys* and *Siebenrockiella crassicollis*. The small pygal with wider than long and a small anal notch can be found in *Malayemys* and *Melanochelys trijuga*. The serrated ninth peripheral is found in several species including *Heosemys spinosa*, *Heosemys grandis*, *Notochelys platynota*, and *Cuora mouhotii*

Based on isolated plates, it is difficult to identify the fossil remains more precisely since material is represented by too few plates to provide reconstructions and associate plates together. However, they are probably have at least two species based on entoplastron morphology at least. In my opinion, pygal plate (NS2), entoplastron (NS3), and the right xiphiplastron (PRCCR1) probably belong to a small species which is similar to *Malayemys*. The nuchal (PRCCR 19), entoplastron (PRCCR6), peripheral plates (PRCCR 2, PRCCR10) and right hyoplastron (PRCCR13, PRCCR15, PRCCR17) are probably belonging to the second one which is similar to *Heosemys*. More complete material is needed to confirm the taxonomic composition of the locality.

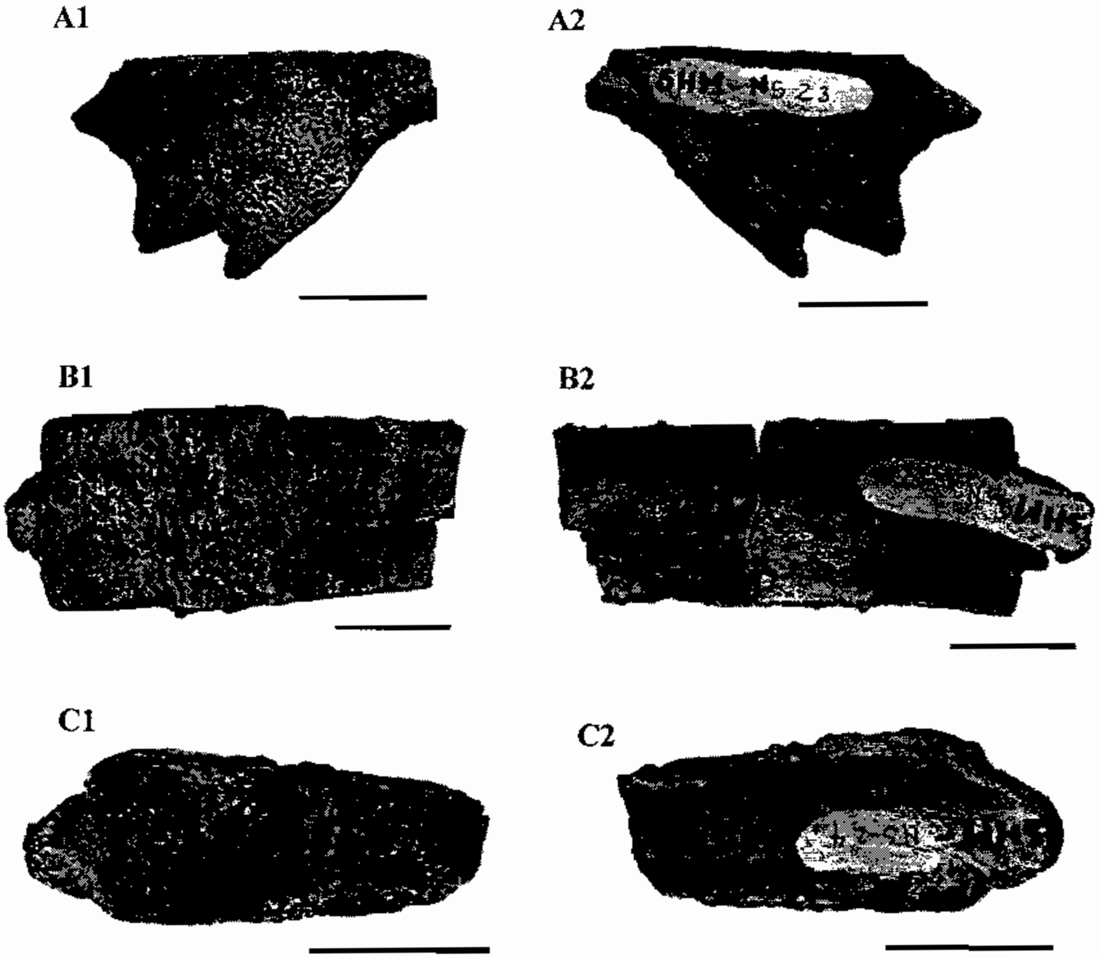

Figure 99 Isolated plates of Trionychidae (1#) from Ban Na Sai locality, Lamphun Province; left hypoplastron (A), costal plates (B and C) in outer (1) and inner (2) views. Scale bars equal 2 cm.

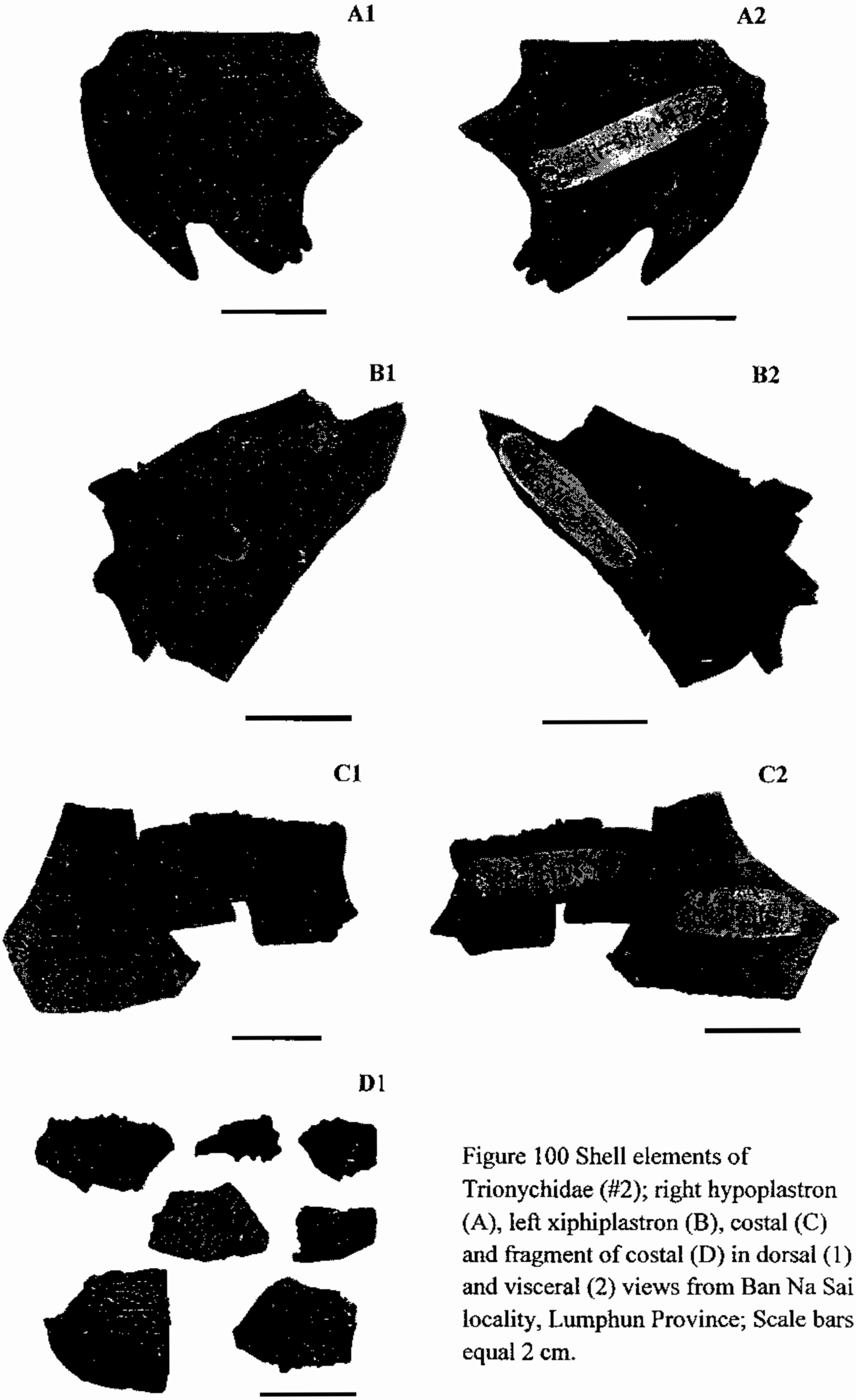

Figure 100 Shell elements of Trionychidae (#2); right hypoplastron (A), left xiphiplastron (B), costal (C) and fragment of costal (D) in dorsal (1) and visceral (2) views from Ban Na Sai locality, Lumphun Province; Scale bars equal 2 cm.

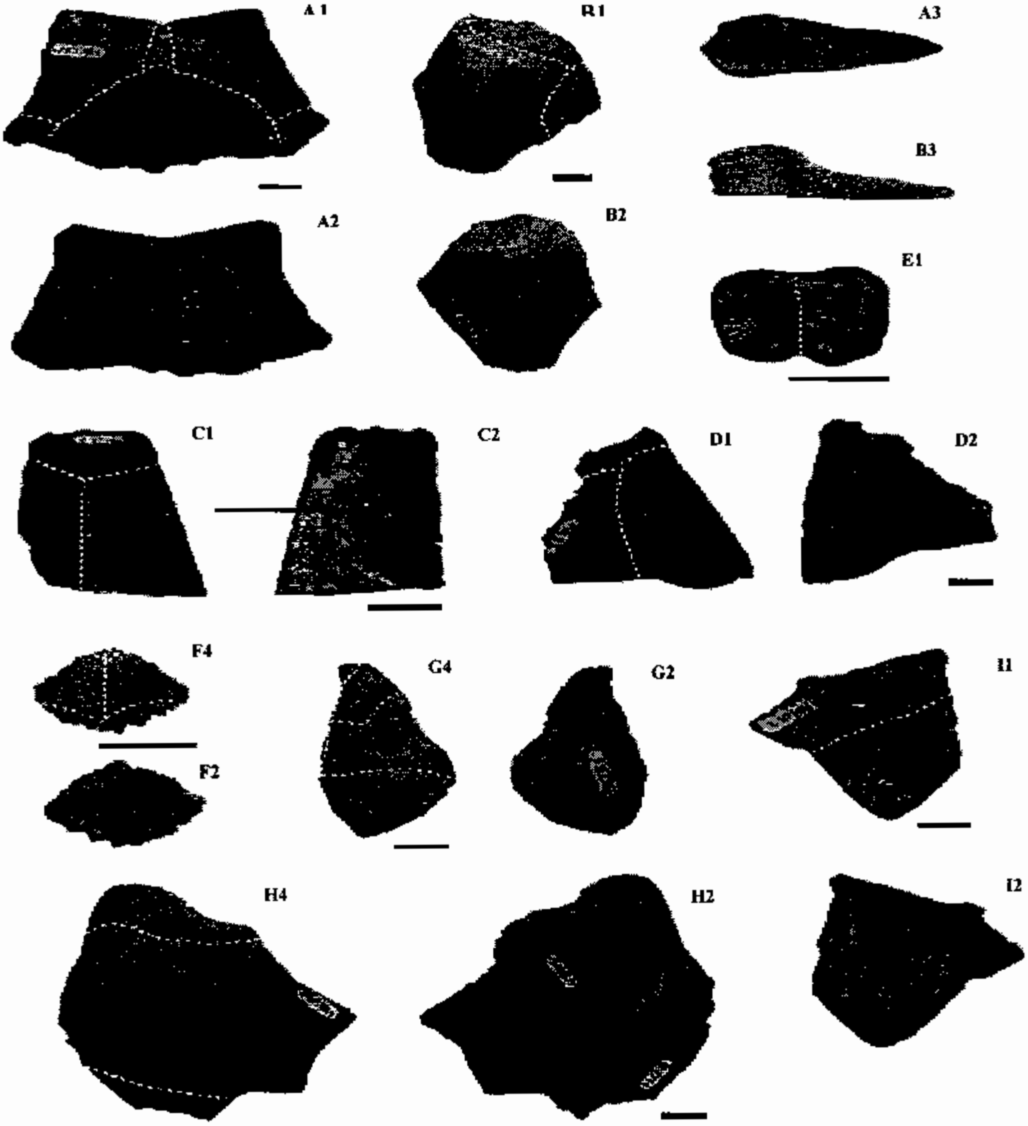

Figure 101 Isolated plates of the Miocene Geoemydidae, gen et sp. indet. from Ban Na Sai locality, Lamphun Province; **A**, nuchal (PRCCR 19); **B**, nuchal (PRCCR 3); **C,** third peripheral (PRCCR 2); **D**, ninth peripheral (PRCCR10); **E**, pygal (NS2); **F**, entoplastrons (NS3); **G**, entoplastron (PRCCR6); **H**, right hyoplastron (PRCCR13, PRCCR15, PRCCR17) and **I**, right xiphiplastron (PRCCR1) in dorsal (1)**,** visceral (2), lateral (3) and ventral (4) views. Scale bars for C and E equal 2 cm and for others equal 1 cm. White line dotting indicates sulci.

5.1.2 Turtles from Mae Moh, Lampang Province

Locality:

Mae Moh locality is the Mae Moh basin which is exploited by a lignite and coal mine. The locality is located in Mae Moh District, Lampang Province (Northern Thailand). It is a tertiary sedimentary basin, 16 kilometers long and 7 kilometers wide. It is the biggest lignite coal mine in Southeast Asia, and the fossil rocks excavated there are used for producing electricity (Thasod, 2007).

The Mae Moh basin has been divided into three formations including Huai King Fomation, Na Kham Formation and Huai Luang Formation ranging from old to young (DMR, 2001).

The Huai King Formation is composed of mudstones, siltstones, sandstones, conglomeratic sandstones, and conglomerates.

The Na Khaem Formation contains most of the coal formation in the basin. The sediment consists of semi-consolidated mudstone and five coal zones. It has yielded a variety of fossils, especially gastropods, ostracods, plants, and vertebrates including fishes, mammals, turtles and crocodiles.

The Huai Luang Formation is the uppermost formation and consists of semi-consolidated and unconsolidated strata. No macrofossils have been found, but there is abundant gypsum and pyrite and some roots and flame structures.

Paleomagnetic investigations in the Mae Moh basin of the lower third of the Na Khaem Formation and of the Huai Luang Formation indicate that the sequences correlate with the geomagnetic polarity from the C5ACn chron to C5An.2n chron of the geomagnetic time scale, which is between 13.5 and 12.2 million years ago. The ages of 12.5 and 12.8 million years ago can be extrapolated to the fossiliferous zones of the J-5, K-1, and K-2 coal beds according to Benammi *et al.*, 2002.

At least two turtle taxa can be recognized from this locality.

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Family Trionychidae Gray, 1825
Trionychidae nov. gen et sp.
(Figures 102-106)

Holotype: MM3 including nuchal (MM3-1), first costal plate (MM3-2), third, seventh and eighth cervical vertebrae (MM3-3, MM3-4, MM3-5), left humerus (MM3-6), femur (MM3-7), epiplastron (MM3-8), entoplastron (MM3-9)

paratype: two nearly complete carapaces (MM1 and MM2) preserved in visceral view, anterior left hyoplastron (MM4), hyo-hypoplastral bones (MM5-1, MM5-2) and right xiphiplastron (MM6), pectoral girdle (MM3-10)

Type locality: Mae Moh, Lampang Province

Stratigraphy: Middle Miocene

Diagnosis: Moderate carapace size (20-30 cm). The anterior margin of the nuchal is slightly emarginated; rib end present and expanded at the lateroanterior end of the first costal; suprascapular fontanelles present in adult; reduced eight neural; boomerang shaped entoplastron with rough ornamentation in the anteromedial part. Differ from all living genera by combination characters of shape of the first costal end with an extra rib end process and a boomerang shaped entoplastron with rough ornamentation in the anteromedial part, moderate size.

Description:

The carapace disc (MM1, MM2) is a bit longer than wide. The lateral extension of ribs are damaged and suprascapular fontanelles between the nuchal and the first pair of costals are present (Figure 103, 1). The fontanelles have a longer contact with the nuchal than with the costals. The anterior margin of fontanelles is also clearly observable on the posterior side of the isolated nuchal plate MM3 (Figure 104, A-B). Fontanelles are rounded in shape and are very close to the midline of the carapace. The ornamentation on the carapace is pitted medially and becomes vermiculated at the lateral end of costal. The pits are shallow and become more elongated t the contact between bones. The pit density is rather high. The ornamentation is better defined on nuchal and costal plates. There is no longitudinal ridges along the plates. No peripherals are preserved, and the end of costal bones suggest that they were absent. The nuchal is wider than long, with a width/length ratio greater than 5. The anterior margin of the nuchal is slightly emarginated. No strong crest along the anterior border of the visceral view of nuchal is present. The costiform process is expanded anteriorly and laterally (Figure 104, A-C). The position of anterior edge of the first body vertebra relative to nuchal plate is located at the posterior edge of the nuchal. There are two suprascapular fontanelles which are present in MM3-1, MM1 and MM2. There are eight neural plates. The shape of the first to third neurals is hexagonal with short posterolateral sides. The anterior side of the first neural plate is straight. The first neural is longer than other neurals. The fourth to seven neurals are variable in shape, which can be hexagonal with short posterolateral sides or oval. The eighth neural is pentagonal in shape. The neural formula is 6<6<6<6<4 6> 4 5 for MM1 and 6<6<6<6<6 4 5 ? for MM2.

There are eight pairs of costal plates. The medial end of the first costal is longer than other costals. The lateral end of the first costal is narrower than medial end. The rib end of the first costal plate is expanded from lateral end to anterolateral end of the first costal (see Figure 104, E). The second costal in visceral view does not display rib crest. The seventh or eighth pair of costals are in contact at the midline. The eighth costal is reduced. A depression is present on the visceral side of the eight costal for accommodating the upper end of the ilium (Figure 103). The first to third ribs go forward and the fourth to eighth are directed posteriorly laterally. The plastral bones consist of isolated bones (Figure 107). The ornamentation of the plastron is pitted and vermiculated on the hyoplastra, hypoplastron and xiphiplastron. This suggest that five callosities were present (two on hyo and hypoplastra, one entoplastron, two on xiphiplastra). The epiplastra is J-shaped and rather thin (Figure 5.10, B). The anterior projection of epiplastra is elongated and slightly expanded while the posterior part is more slender with the sharp end. The entoplastron is relatively large and has a boomerang shape. Its postero-lateral ends are long and have sharp margins at the tip. The anteromedial part of entoplastron is ornamented by a rough ornamentation on the middle part (Figure 107, A). The hyo-hypoplastral suture is present as seen in MM5

(Figure 107, D). The hyo-hypoplastra are preserved by two specimens including an incomplete left hypoplastron (MM4) and right hyo-hypoplastral bones (MM5). The hyoplastron sends antero-medially a long process that is subdivided at the end into four short pointed processes. The length of axillary notch is long. The medially, process ends of hypoplastron are missing. It is difficult to observe the medial process of hypoplastron at the anteromedially but the laterally and posteriorly processes of the hypoplastron probably sent multifurcated processes. The lateral margin of hyo-hypoplastron send a long process that the end is subdivided into two short pointed processes for each which are dispart allow to observe triangular outline. At the level of the inguinal and axillary buttresses, the hyoplastron is slightly longer than the hypoplastron.

Only one pointed posterior process of the hypoplastron is preserved for articulating with the anterior pointed process of the xiphiplastron.

A nearly complete of a right xiphiplastra (MM6) is preserved. The anterior margin of xiphiplastron is broken while its lateral margin is rather straight (Figure 107, E). The plate is rather thin and has more or less a triangular shape, it displays a well developed callosity (dermal ossification), and its posterior end is pointed. The xiphiplastron articulates medially with two short interdigited processes (Figure 107, E).

The third, seventh and eighth cervical vertebrae are preserved (Figure 105). The third cervical vertebra is elongated. Articular surfaces of prezygoapophyses are dorsal. Postzygoapophyses are relatively flat. The vacuity between the postzygoapophyses is deep V shaped while that of prezygoapophyses is rather short V shape. The anterior articular surface of centrum of the third cervical vertebra is nearly round and convex while the posterior one is deeply concave. This indicates that the third vertebra was opisthocoelous. The articular surface of the seventh cervical vertebra prezygoapophyses are expanded dorsoventrally. The postzygoapophyses are not preserved. The vacuity between the postzygoapophyses was certainly U shaped.
The eighth cervical vertebra (Figure 105, A) is extremely compressed dorsoventrally. The centrum of this vertebrae is probably opisthocoelous and is clearly convex anteriorly. The ventral margin is strongly concave at the midline whereas the posterior margin tapers to a rounded end. Postzygoapophyses are larger than prezygoapophyses. The articular surfaces of postzygoapophyses are deeply concave while

prezygoapophyses are clearly convex. The left pectoral girdle (MM) is preserved (Figure 108). It is composed of two bones, the coracoid and scapula with its acromion process. The end of these bones are missing. The coracoid is flat, thin and large. The anterior margin of the coracoid is thicker than the posterior one. Its anteromedial margin is slightly concave. The scapula is long and slender. Its medial part is rather flat. It is oval shape in cross-section. The glenoid fossa has been shifted a bit laterally because of deformation during preservation. It is directed anterolaterally and slightly compressed dorsoventrally.

A left humerus (MM3-6) and a femur (MM3-6) are present (Figure 106). The left humerus is short and thick. The caput and the anterior part of the humeral processes are missing. The medial process is relatively high. The lateral process is strongly damaged and its proportion and shape cannot be properly determined. The intertubular fossa is deep. The ectipicondylar is a deep and elongated groove (Figure 106, A3). The capitellum and trochlea are slightly oriented backward. The femur is slender and smaller than the humerus. The femoral head, trochanters and distal end of the femur are broken.

Comparison and discussion:

These specimens belong to the same taxa based on the thickness of the shell and ornamentation. They are assigned as Trionychidae Gray, 1825 because of the pitted and vermiculated ornamentation, no epidermal scute, absence of peripherals, reduced plastral bones, no suprapygal and pygal (Meylan, 1987). The shape of the eighth cervical vertebra is also typical for the group. According to the provided key for living Thai and territories trionychid species is used for identification, the trionychid specimens form Mae Moh can not be assigned to *Lissemys scutata* because of the absence of prenuchal, granulation pattern, peripherals and orientation of rib ends. This taxon also differs from *Lissemys scutata* as it has no oval shaped epiplastron, no rounded anterior process of epiplastron, no rounded posterior process of entoplastron, no oval shaped entoplastron, by the presence of a well visible suture between the hyo-hypoplastron suture, by the absence of suture contact between xiphiplastra and hypoplastron, and by the ornamentation that is pitted and not granulated. The fossil cannot be placed in *Dogania subplana* because of the nuchal contact with the first neural, and the lateral end of the seventh and eighth costal that are in contact and the difference in ornamentation. The absence longitudinal ridges along the carapace makes this taxon different from *Amyda cartilagenea* and *Pelodiscus sinensis*. The specimens has no rib crest on the second costal in visceral view and no strong crest along the anterior border of the inner surface of the nuchal, so it should be excluded from *Chitra* and *Pelochelys*. This taxon is different from *Nilssonia* because the anterior margin of the nuchal in *Nillsonia* is more straight, and the contact between the eighth costal plate is longer and the eight costal is not short in *Nillsonia*. The morphology of the eight and seven costals is more similar to *Rafetus* with a short midline contact between the eight costal plates that are reduced in width. It differs however from that genus and other trionychids by its emarginated nuchaland the extra expanding of rib end to latero-anterior end of the first costal. This morphology being only known in the living *Dogania subplana,* although it is not as marked in the fossil. In addition, this taxon has an elongated anterior process of epiplastron which is longer from *Pelochelys cantorii*, *Pelodiscus sinensis*, *Rafetus euphraticus*. It differs from *Amyda cartilagenea*, *Dogania subplana*, and *Nilssonia formosa* in having straight lateral margin of xiphiplastron while this margin is concave in these taxa; and it differs from from *Nilssonia hurum* where the margin is convex.

Finally, this fossil taxon also displays distinct characters from other living species in the boomerang shaped entoplastron with a rough ornamentation on its anteromedial part. The ornamentation on the entoplastron is present in *Lissemys scutata* but is granulated. However, the fossil does not display a clear callosity as in *L. scutata.* This fossil is placed tentatively into a new species and genus, because it exhibits several unique characters from other living taxa in both carapace and plastron. However, more comparison with more distant species and other fossil should be done to complete the taxonomic assessment of this material.

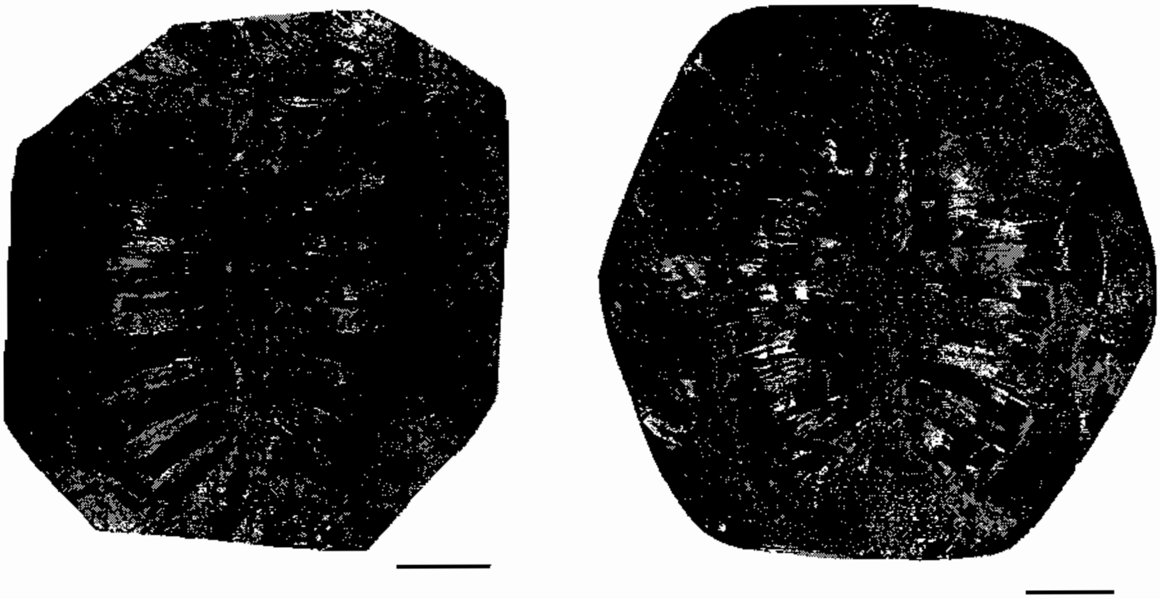

Figure 102 Carapaces of Trionychidae nov. gen et sp. in visceral view from Mae Moh locality, Lampang Province; MM 1(left) and MM 2 (right). Scale bars equal 5 cm.

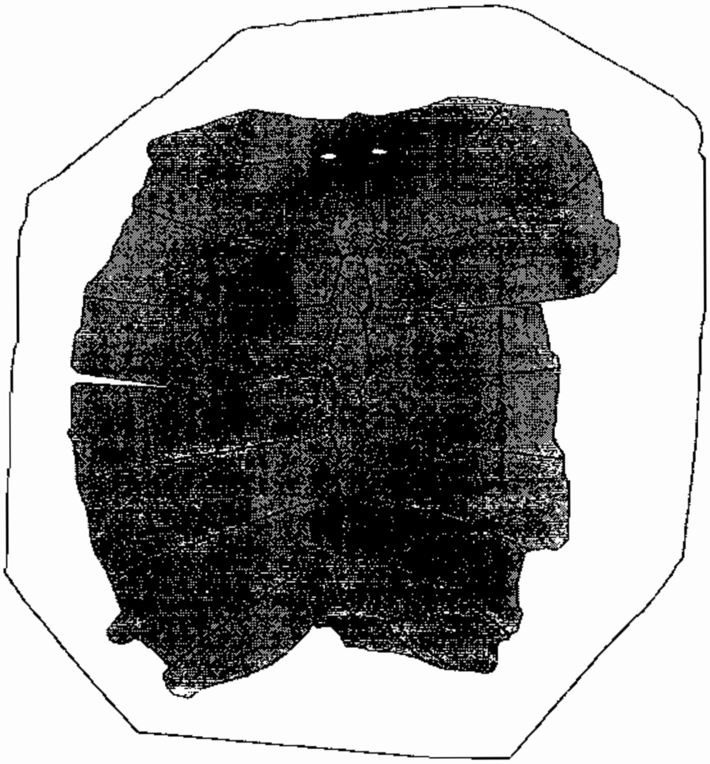

Figure 103 Carapace drawing of Trionychidae nov. gen et sp. (MM 1) in visceral view from Mae Moh locality, Lampang Province.

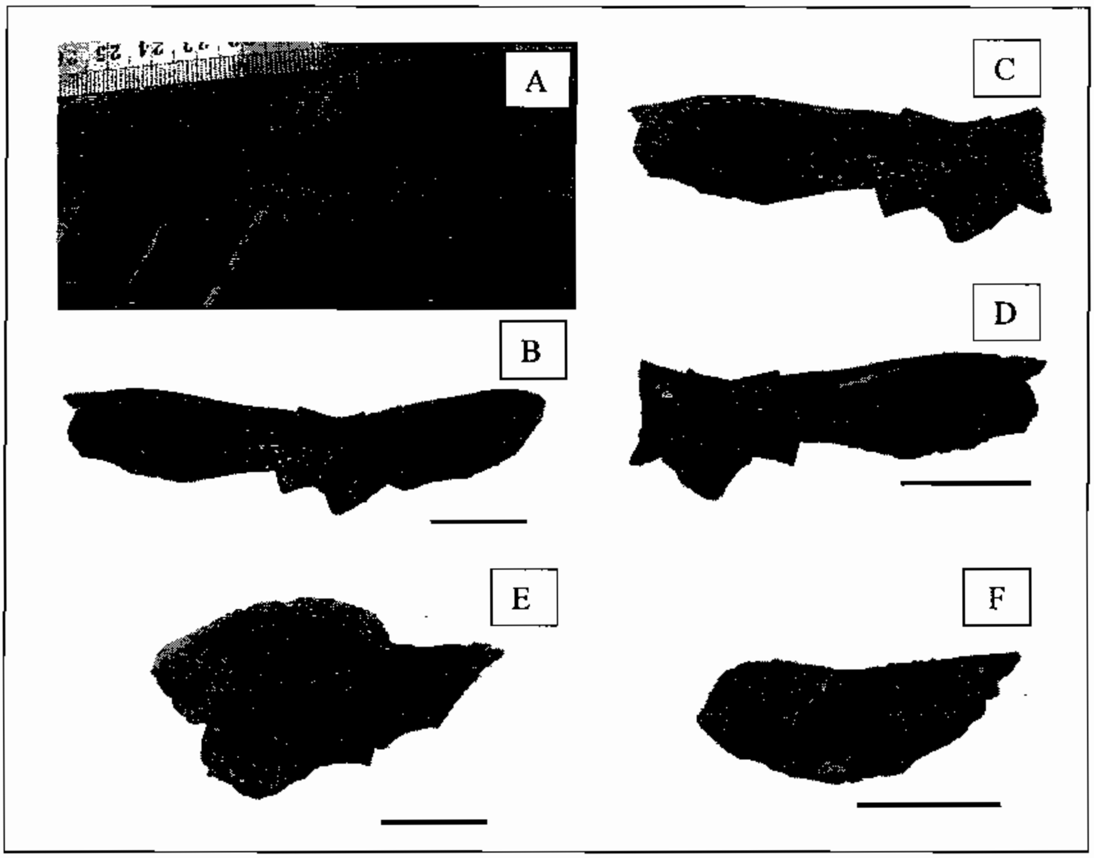

Figure 104 Anterior carapacial bones of Trionychidae nov. gen et sp. in dorsal view from Mae Moh locality, Lampang Province; left and right sides of nuchal bone with the right side still embedded in the sediment (A, B), left side of nuchal bone in dorsal view (C), left side of nuchal bone in visceral view (D), distal end of first left costal plate (E) and a part of the first costal plate (F); scale bars equal 2 cm.

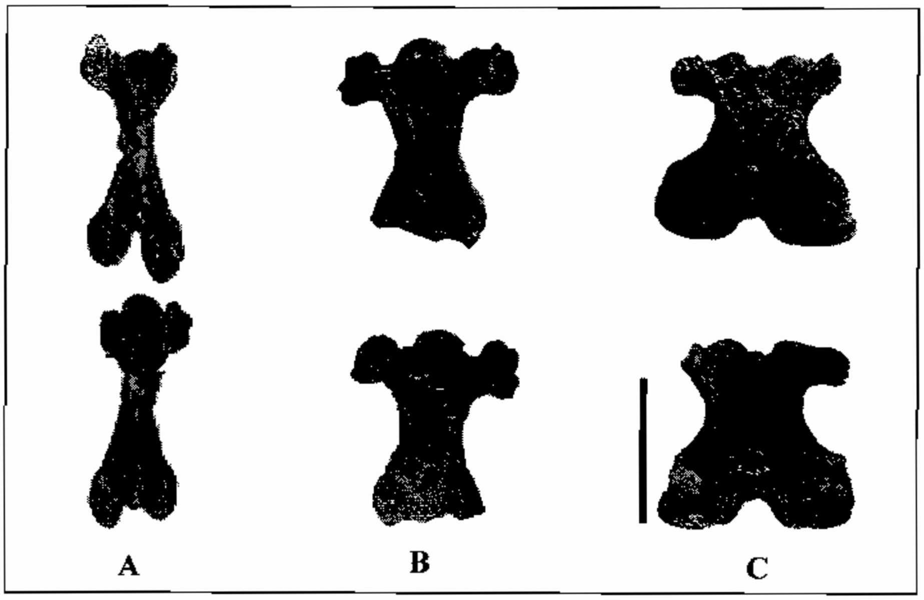

Figure 105 Cervical vertebrae of Trionychidae nov. gen et sp. from Mae Moh locality, Lampang Province; third cervical vertebra (A), seventh cervical vertebra (B) and the eighth cervical vertebra (C) vertebrae in dorsal (upper row) and ventral (lower row) views. Scale bar equals 2 cm.

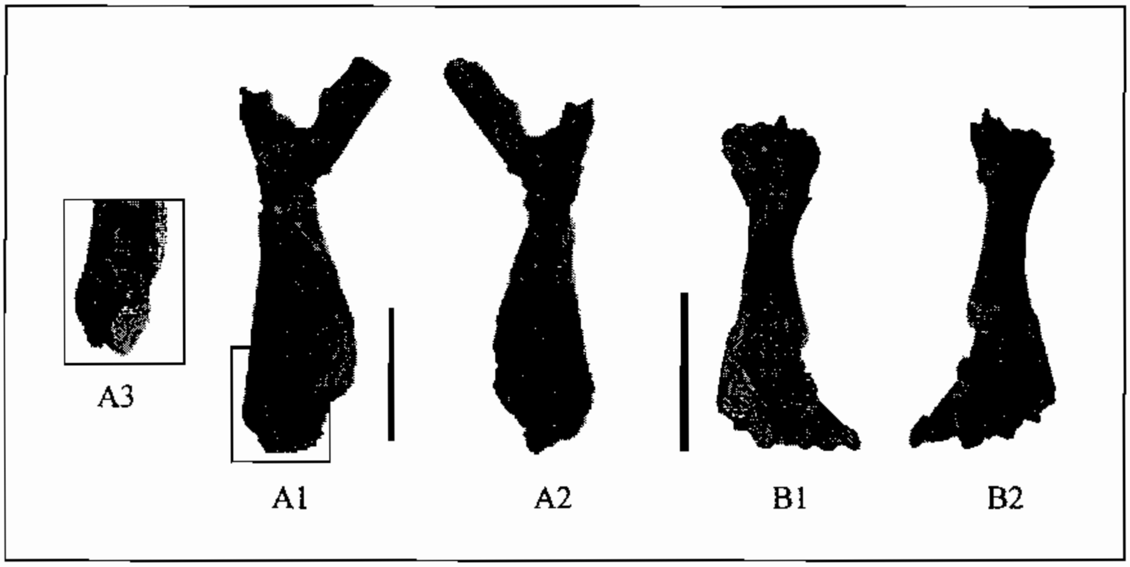

Figure 106 Limb bones of Trionychidae nov. gen et sp. from Mae Moh locality, Lampang Province; left humerus (A) and femur (B) in dorsal (1), ventral (2) and lateral (3) views. Scale bars equal 2 cm.

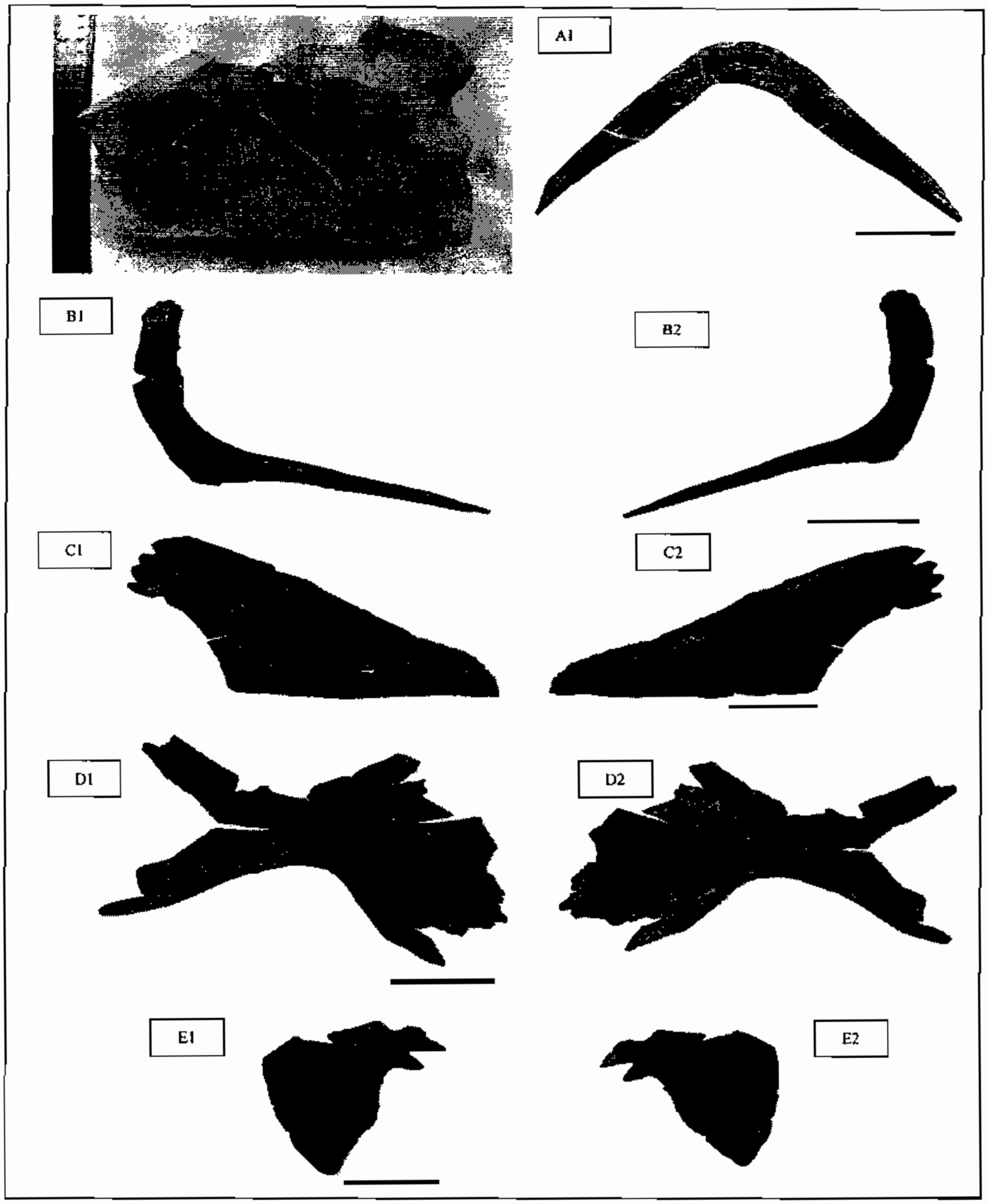

Figure 107 Plastral bones of Trionychidae nov. gen et sp. from Mae Moh, Lampang Province shown on a drawing of living *Amyda cartilagenea* plastron for displaying their position; left epiplastron (A), entoplastron (B), anterior left hyoplastron (C), hyo-hypoplastral bones (D) and right xiphiplastron (E). Scale bars are 2 cm.

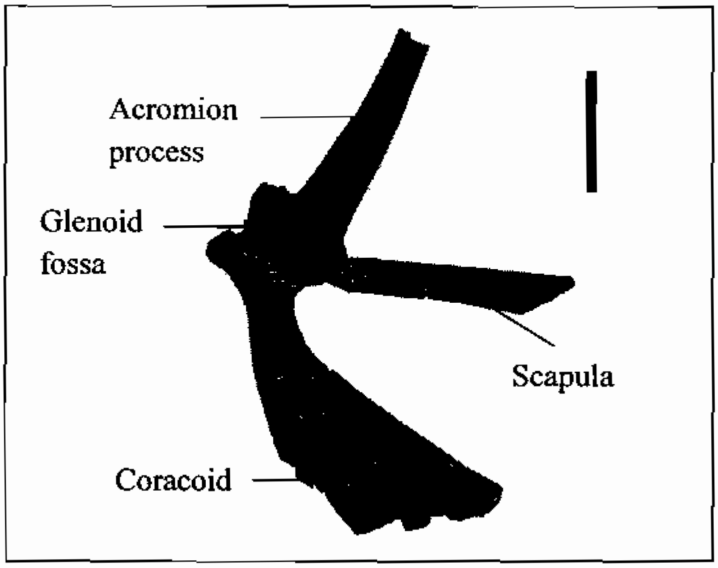

Figure 108 Left half of the pectoral girdle of Trionychidae nov. gen et sp. in dorsal view from Mae Moh, Lampang Province. Scale bar equals 2 cm.

Family Geoemydidae Theobald, 1868

gen et sp. indet.

(Figure 109)

Material: isolated plates (unnumbered)

Description and discussion:

There are several isolated plates displaying a smooth ornamentation in the locality (see Figure 109). Most of the plates are costal and peripheral plates. The pleuro-marginal sulcus restricted to peripheral is one typical character of Geoemydidae. However, there is no informative plate to help for a more precise classification. Therefore, this material is placed into Geoemydidae indet. although more material is needed to confirm this assertion.

Figure 109 Shell fragments of Geoemydidae gen et sp. indet. in dorsal view from Mae Moh, Lampang Province.

5.1.3 Turtles from Chiang Muan, Phayao Province

Locality:

Chiang Muan coal mine is located in the Chiang Muan Basin, Tambon Ban Sra, Chiang Muan District, Phayao Province, Northern Thailand. The tertiary sedimentary rocks of the Chiang Muan coal mine consist of alternating beds of conglomerates, sandstones, mudstones, claystones and coal, which yielded a rich vertebrate fauna. The paleomagnetic study and mammalian fossils indicates a late Middle Miocene to an early Late Miocene age for this sequence (about 11-12 Ma, Kunimatsu *et al.*, 2004; Pickford *et al.*, 2004; Silaratana *et al.*, 2004 or 9.8-13 Ma Suganuma *et al.*, 2006). The vertebrate assemblage from Chiang Muan mine includes fishes, crocodiles, birds, mammals, snakes and turtles (Silaratana *et al.*, 2004; Nakaya *et al.*, 2002).

At least three turtle taxa can be recognized from Chiang Muan locality, Phayao Province as following;

Superfamily Testudinoidea Batsch, 1788
Family Geoemydidae Theobald, 1868
Genus *Cuora* Gray, 1855
Cuora chiangmuanensis, sp. nov. (Naksri *et al.*, 2013)

The detail of this species is represented by a published online version as following (see Appendix VI).

This article is in press for publication in Geological Magazine Journal entitled "A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance"

Superfamily Testudinoidea Batsch, 1788 (fide Baur, 1893)
Family Geoemydidae Theobald, 1868
cf. Cuora chiangmuanensis
(Figure 111)

Material: nuchal plate (Cme-2)

Description:

An incomplete nuchal plate (Cme-2) has, its left side relatively well preserved (Figure 111, A). The plate is rather thin. The cervical scute is triangular in shape. The posterior part of cervical scute is convex anteriorly whereas its anterior margin is straight. The lateral side of the plate is not crossed by the pleuro-vertebral sulcus, indicating that the first vertebral was anteriorly wide. The sulcus of the cervical can also be seen on the visceral side of the nuchal and it is wider than long in dorsal view (Figure 111, A2).

Comparison and discussion:

The thin isolated nuchal plate is similar in shape and size to *Cuora chiangmuanensis* (Cme1/1). The latero-medial part of the nuchal plate not crossed by pleuro-vertebral sulcus which indicates a wide anterior part of the first vertebral scute, a morphology that is known in *Cuora chiangmuanensis* but also in in other geoemydid genera. The shape of the cervical is similar to *Cuora chiangmuanensis*. Because of the combination of these character and because of the presence of *Cuora chiangmuanensis* in the locality, this specimen is tentatively assigned to cf. *Cuora chiangmuanensis*.

Family Geoemydidae Theobald, 1868

gen et sp. indet.

(Figures 110)

Material: posterior part of carapace and plastron (Cme-9), neurals (Cme-3), right first costal plate (Cme-4), anterior peripheral plates (Cme-5), third peripheral plate (Cme-6), and left xiphiplastron (Cme-8).

The material is kept in Chiang Muan Mine Museum, Phayao Province, Thailand.

Description:

An articulated posterior part of carapace and plastron (Cme-9) is dorsoventrally crushed (Figure 110). It consists of the posterior half of the carapace with containing neurals from the fifth neural to the first supprapygal plates, the fourth to eight costals plates, hypoplastra, and part of the right ninth to eleventh peripherals. The posterior part of the fifth neural contact both fourth and fifth costal scutes and has short posterolateral sides. The shape of this neural should have been octagonal or hexagonal. The sixth neural has a tetragonal shape. It is posteriorly crossed by the sulcus between the third and fourth vertebral scutes. The seventh and eighth neurals are hexagonal with short antero-lateral sides. The eighth neural is crossed by the fifth vertebral sulcus at the posterior edge of the plate. The first suprapygal contacts the eighth neural and the eighth costals. Its posterior part is broken. It was probably tetragonal in shape, and was longer than wide. The fourth, sixth, and eighth costals are crossed by pleural sulci. The proximal part of the eight costals is rather rounded. The pleuro-marginal sulcus is restricted to peripheral plates. In ventral view, two hypoplastra can be recognized (Figure 5.13, A2, a2). The lateral and anterior and posterior margins of these bones are broken. The plastral buttress is crushed but d it can be seen that it connected with the posterolateral part of the fifth costal plate rather medially and part of the sixth costal

plate. The elongated lateral process of the hypoplastron suggests a relatively strong bony bridge. Some limb bones are embedded but cannot be clearly described. Two small neural plates (Cme-3) are also present. They probably belong to the seventh and eighth neural plates (Figure 110, B). They are slightly wider than long. Their shape are octagonal and hexagonal with short posterolateral sides in shape respectively. There is a central keel starting on the eighth neural plate. A first complete right costal plate (Cme-4) (Figure 111, C) rather thick and large, displays the impression of the vertebral sulcus in dorsal view. However, it can be seen that the vertebral sulcus was crossing the nuchal plate because it crosses the suture between the first costal and nuchal plates. The pleuro/vertebral sulcus was contacting the nuchal at the lateral side. On the visceral side, the scar for the contact with the axillary buttress is present and well developed. Specimen number (Cme-5) corresponds to thick articulated peripheral plates (Figure 111, D). It consists of the sixth to tenth peripherals in the left side. The pleuro-marginal sulcus is restricted to peripheral plates and placed far from the costo-peripheral suture; the marginals covering only two third of the dorsal side of peripheral plates. Cme-6 is a third right peripheral plate (Figure 111, E). The plate is rather thick and is mesio-laterally expanded. The pleuro-marginal sulcus can be seen on the upper part of plate as well as the sulcus between the third and fourth marginal scutes. In visceral view (Figure 111, E2), this plate exhibits a musk duck foramen. A nearly complete left xiphiplastron (Cme-8) is present. It is thick and its anterior part is broken while its posterior part displays a slightly elongated with rounded xiphiplastral process (Figure 112, B).
The anal is well developed; in the midline, it is not far behind the hypoxiphiplastral suture. The anal notch is deep and triangular in shape.

Comparison and discussion:

According to difference in size and bone thickness, these specimens belong to several individuals and maybe to different species. In all likelihood, they principally belong to Geoemydidae (pleuro-marginal sulcus impressed on peripheral, musk duct foramen in the third peripheral plate, presence of central keels, contact of the plastron with the sixth costal plate (Claude *et al.*, 2004).

Based on thickness of the plates, two groups can be defined. The thin bones consist of the posterior carapace and plastron (Cme-9), articulated anterior peripherals (Cme-5), neurals (Cme-3) and hypoplastra (Cme-7). Cme-9 differs from

Cuora chiangmuanensis and other *Cuora* in having plastral buttress sutured to the carapace and then belong to another species. The anterior peripherals (Cme-5) with a pleuro-marginal sulcus restricted to peripheral plates can allow to assign these specimen to Geoemydidae. In addition , the position of pleuro-marginal sulcus in these specimens is placed more laterally and is not straight as it is in *C. chiangmuanensis*.

The second ensemble corresponds to thicker plates and consists in a first costal plate (Cme-4), a third peripheral plate (Cme-6) and a left xiphiplastron (Cme-8). The position of the pleuro-vertebral sulcus on the first costal plate indicates that it was also present on the nuchal plate. This character differs from *Cuora chiangmuanensis* for which the nuchal plate is not crossed by the pleuro-vertebral sulcus. The third peripheral plate exhibits a musk duck foramen and the pleuro-marginal sulcus impressed on peripheral are synapomorphies of the family Geoemydidae (Claude and Tong, 2004). The suture on the plate contacting the plastral axillary buttress suggests that this geoemydid turtle had a strong bony bridge which is unlike *Cuora*. The shape of xiphiplastron process and anal notch differs from *C. chiangmuanensis* in being more elongated and rather pointed. The morphology of the xiphiplastron is also rare in geoemydids as it shows a well developed anal scute together with the well developped anal notch, this morphology can be found, however, in living genera like *Orlitia* and maybe also *Morenia*.

Testudinoidea indet.

(Figure 112)

Material: hypoplastra (Cme-7)

Description:

Two articulated hypoplastra (Cme-7) (see Figure 112, A) are rather small in size and wider than long. They are crossed by the abdomino-femoral sulcus posteriorly. The hypo-xiphiplastron suture is convex anteriorly based on the outline of the bones.

Comparison and discussion:

The hypoplastra are difficult to identifiy exactly at the family level because they can belong at least either to geoemydid or testudinid turtles. In geoemydid turtle, the latero-anteriorly part of hypoplastron is rather straight but its antero-lateral end is slightly curved. The antero-lateral end of hypoplastron of testudinid turtle is usually concave internally for contacting the sixth elongated peripheral, this be can seen clearly in *Manouria emys* and *M. impressa*. However, this specimen is only slightly concave, a condition that can be found in geoemydid and some testudinid as in *Indotestudo elongata*.

Besides this, *Cuora chiangmuanensis* differ from this hypoplastra by showing a wider lip on the visceral side.

According to this material there is certainly one other geoemydid turtle than *Cuora*, maybe two, in Chiang Muan site. They are, however, hardly identified at a finer taxonomic scale because the material is often disarticulated and far to be complete.

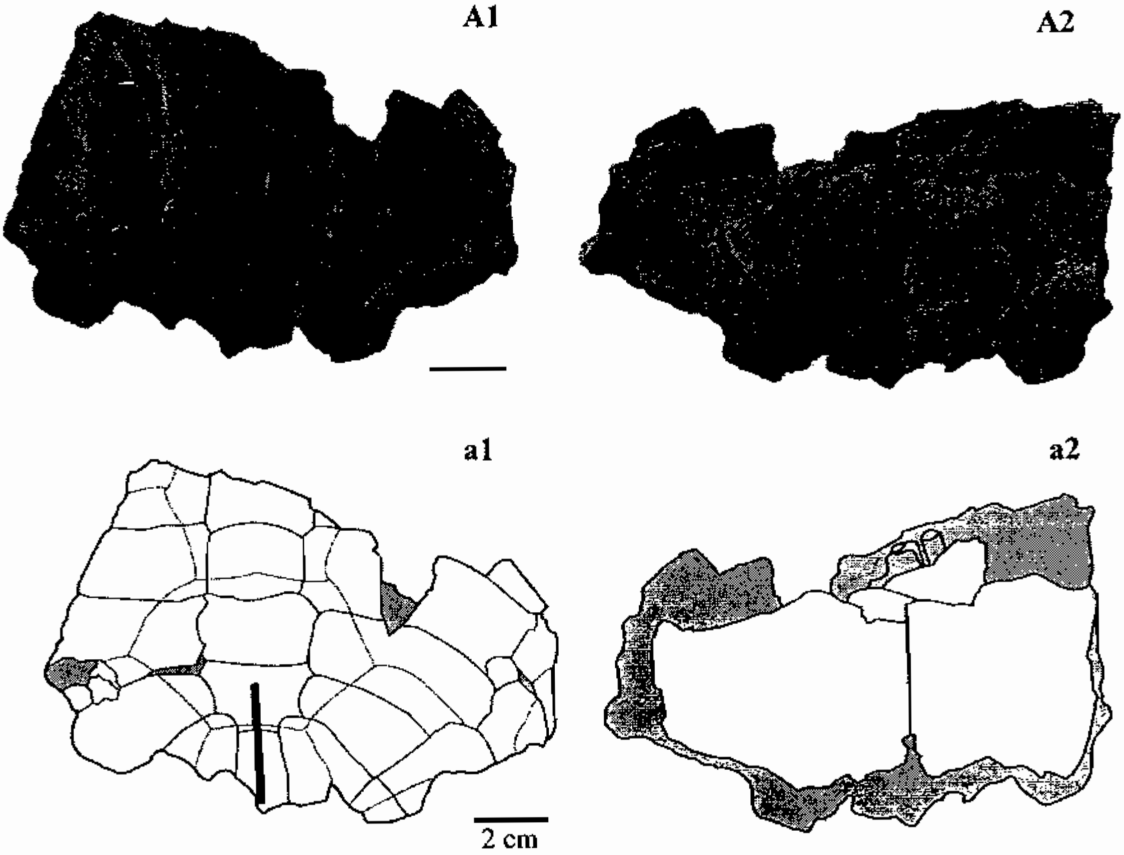

Figure 110 Geoemydid turtle from Chiang Muan, Phayao Province; articulated posterior part of carapace and plastron; photograph (**A, B**) and drawing (**a, b**) in dorsal (**1**) and ventral (**2**) views.

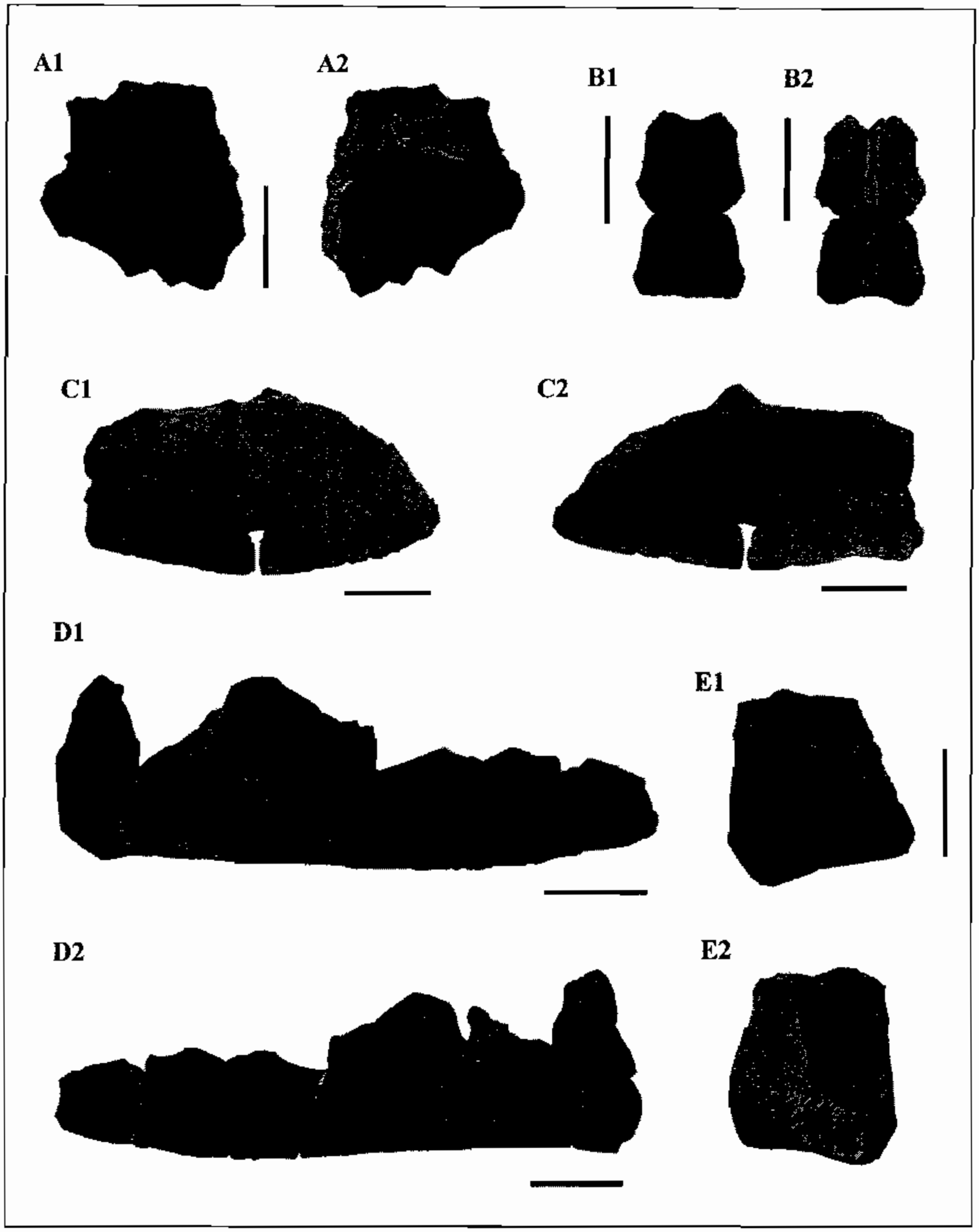

Figure 111 Geoemydid turtles from Chiang Muan, Phayao Province; nuchal plate of cf. *Cuora chiangmuanensis* (**A**), geoemydid neurals (**B**), right first costal (**C**), peripherals (**D**) and third peripheral (**E**) in dorsal (**1**) and visceral (**2**) views. Scale bars equal 2 cm.

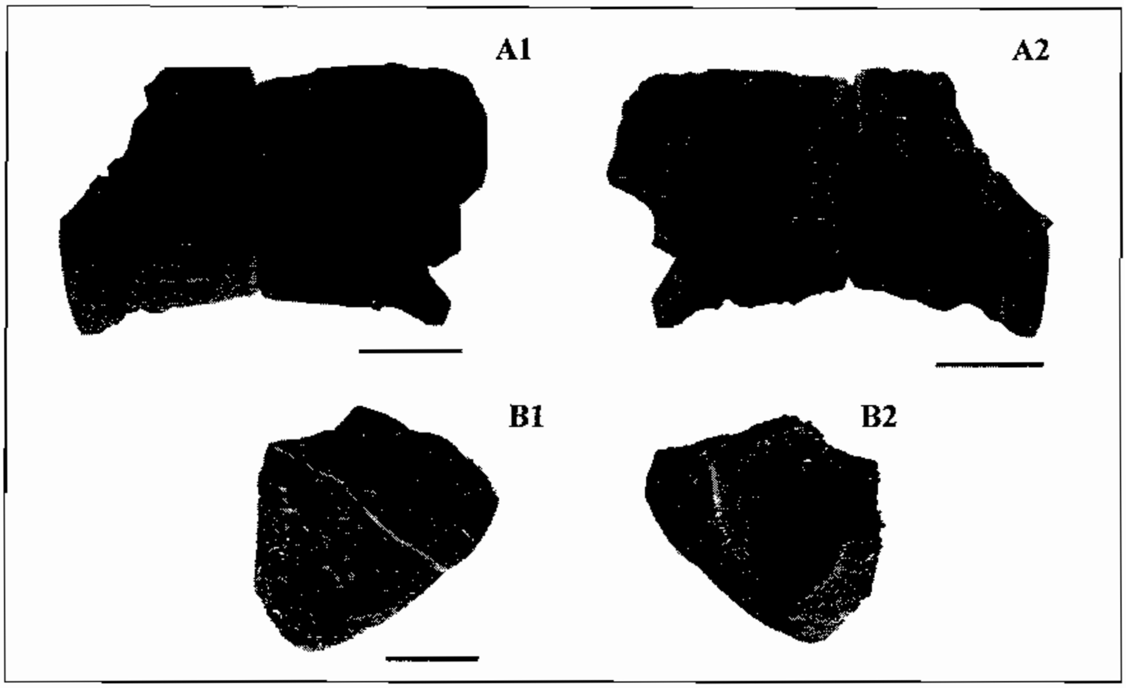

Figure 112 Plastron elements of turtles from Chiang Muan, Phayao Province; hypoplastron of Testudinoidea indet. (**A**) and left xiphiplastron of geoemydid (**B**) in ventral (**1**) and visceral (**2**) views. Scale bars are 2 cm.

5.2 Plio-Pleistocene turtles in Thailand

5.2.1 Turtles from NE Thailand

Fossil turtles Plio-Pleistocene from Northeastern Thailand have been reported in three localities consisting of Khok Sung, Tha Chang sandpits and Ban Si Liam, Nakhon Ratchasima Province (Tong *et al.*, 2006; Claude *et al.*, 2011). In Ban Si Liam locality only Testudinoidea indet. were identified, while the two other localities (Figure 113) presented richer turtle assemblages. Fossil turtles were found together with other reptiles, mammals, fishes and plants. These turtles belong to several taxa.

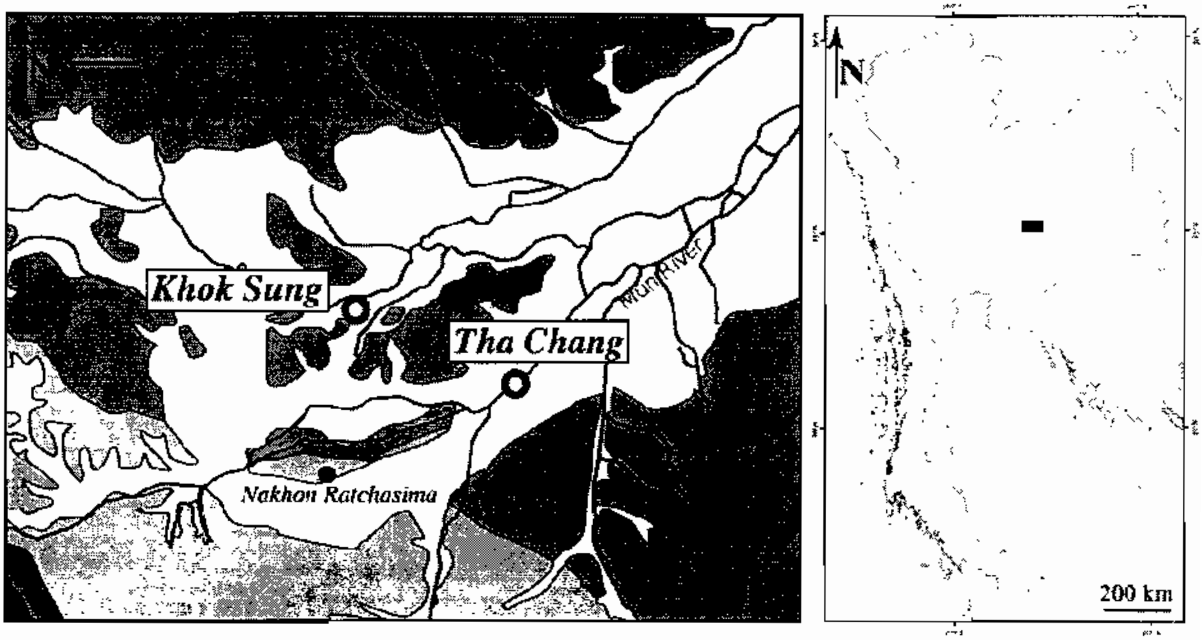

Figure 113 Map showing localities of Khok Sung and Tha Chang, Nakhon Ratchasima Province, northeastern Thailand (redrawn from Claude *et al.*, 2011).

5.2.1.1 Khok Sung, Muang District, Nakhon Ratchasima Province

Locality:

Khok Sung locality is located at Khok Sung village, Khok Sung Sub-district, Muang District, Nakhon Ratchasima Province, northeastern Thailand (Figure 113). This locality is a sand pit which was dig in the Paleo-Mun river bed. The quarry is 100 meters in length, 50 in width and 10-15 metres in depth. Sediments of the locality consists mainly of silts, sands, and gravels which indicate alluvial deposit. The stratigraphy of this locality is presented detail in Chaimanee *et al.*, 2005. The fossil layer was found at the 5 to 7 metres below the top of the quarry. The locality is recently flooded and one cannot access the fossil beds now.

A variety of vertebrate fossils have been found from this locality. Most of them belong to mammals including bovids, hyaena, *Stegodon* and cervids (Chaimanee *et al.*, 2005). Other vertebrates such as fishes, turtles, and gavial fossils also found (Claude *et al.*, 2011; Martin *et al.*, 2012). A part from these, fossil plants also found and studied by Grote, 2007. The material is kept in a local museum in Khok Sung village.

Based on mammals, the age of this locality is based on mammals is probably the Early Pleistocene. The presence of *Gavialis* cf. *benjawanicus* is in agreement with a late Pliocene to early Pleistocene age (Martin *et al.*, 2012)

Six taxa belonging to two turtle families were identified from Khok Sung locality were recognized in Claude *et al.* (2011). These taxa include the Geoemydidae: *Batagur* cf. *trivittata* (Duméril and Bibron, 1835), *Heosemys annandalii* (Boulenger, 1903), *Heosemys* cf. *grandis* (Gray, 1860), and *Malayemys* sp. and the Trionychidae: *Chitra* sp., and cf. *Amyda* sp. The description and discussion in detail is presented in see Appendix VII.

In addition to the material described in Claude *et al.*, 2011, some other material can be assigned to the same set of species and confirm the taxonomic assignation. Two other anterior plastral lobes of *Batagur* cf. *trivittata* (Duméril and Bibron, 1835) are known (see Figure 114). They are composed of epiplastra and entoplastron. The epiplastral lip is short, the gular is also short. The entoplastron is crossed only by the gulo-humeral sulcus anteriorly. The anterior plastral lobes are similar to DMR-KS0503-2446 in Claude *et al.*, 2011; plate 2, G. The dorsal view of carapace and ventral view of the plastron of *Batagur* cf. *trivittata* in Claude *et al.*, 2011; Plate 2, I is presented in Figure 115.

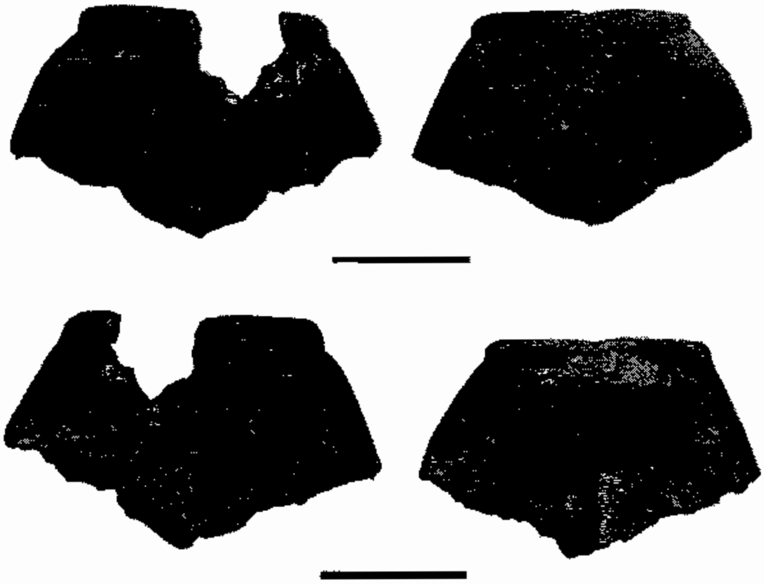

Figure 114 Additional material of *Batagur* cf. *trivittata*; two nearly complete anterior plastral lobes in ventral view (above) and visceral views (bottom) from the Early Pleistocene of Khok Sung locality, Muang District, Nakhon Ratchasima Province, northeastern Thailand. Scale bars equal 5 cm.

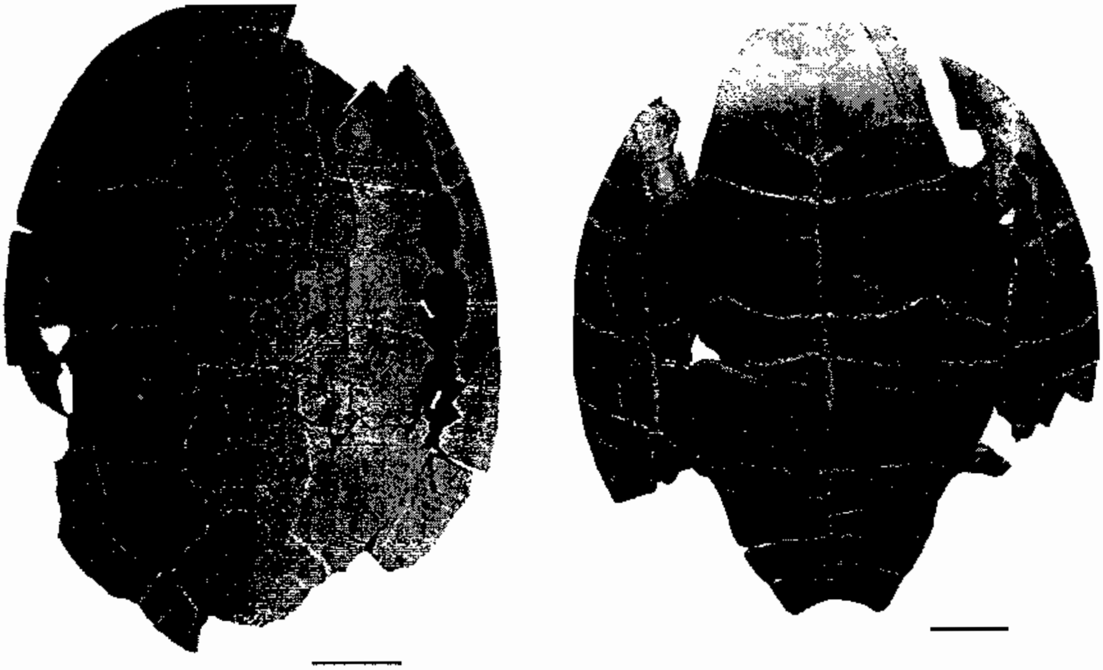

Figure 115 Nearly complete shell of *Batagur* cf. *trivittata* from the Early Pleistocene of Khok Sung locality, Muang District, Nakhon Ratchasima Province, northeastern Thailand: Carapace (left) and plastron (right). Scale bars equal 5 cm.

Some additional material of *Heosemys* cf. *grandis* consist in a complete plastron associated with nearly all the peripheral plates except the anterior part of right side (Figure 116). The anterior margin of carapace is smooth while its posterior part is slightly serrated. *H. annandalii* differs from this by its smooth posterior margin. *Heosemys depressa* and *H. spinosa* also differ from this species by displaying stronger serration on posterior and latereal margins. The plastron is elongated. It is concave ventrally which indicates that this individual was certainly a male. The posterior plastral lobe is longer than the anterior plastral lobe. The lateral of the posterior plastral lobe is straight. It differs from *H. spinosa* in having the lateral side of the posterior plastral lobe is rather curved. The posterior end of the entoplastron is blunt which is more similar to *Heosemys grandis* than others. In addition to this material, a nuchal plate of *Heosemys* cf. *grandis* is present and is illustrated in Figure 117.

Figure 116 Additional material of *Heosemys* cf. *grandis*; a complete plastron with peripheral plates from the Early Pleistocene of Khok Sung locality, Muang District, Nakhon Ratchasima Province, northeastern Thailand. Scale bars equal 5 cm.

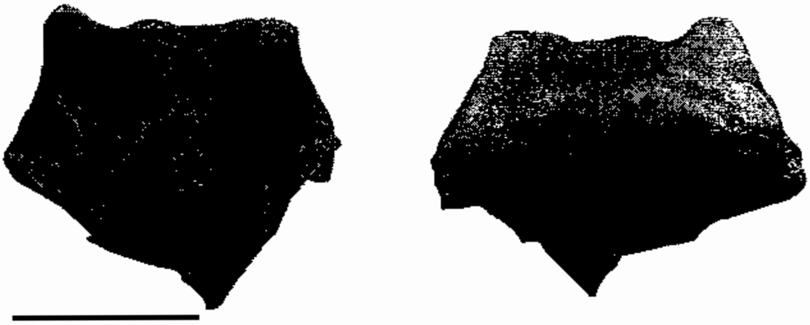

Figure 117 Nuchal plate of *Heosemys* cf. *grandis* in dorsal (left) and visceral views (right) from the Early Pleistocene of Khok Sung locality, Muang District, Nakhon Ratchasima Province, northeastern Thailand. Scale bars equal 5 cm.

5.2.1.2 Giant tortoises from Tha Chang, Nakhon Ratchasima

Locality:

Tha Chang locality consists of nine sandpits which had yielded fossil vertebrates especially mammals (Thasod, Jintasakul, & Ratanasthien, 2012). The sands, conglomerates, or mud composing the layers in which pits were dug were clearly deposited in a fluvial context. The sediments were accumulated and preserved around the present Mun River and overlie the Cretaceous Khok Kruat or Mahasarakham formations (Claude *et al.*, 2011). The pits were dug by water jets for the extracting the sands during mining and fossils were washed out from time to time and fell down at the base of the sand pits. Most of vertebrate remains are fragmentary material. They were mix together from several layers (see Claude *et al.,* 2011). The age of the sand pits is established based on the correlation of the mammal assemblages; ranging from the Middle or Late Miocene to the Pleistocene (Department of Mineral Resources, 2005; Hanta *et al.*, 2008). Most pits are now flooded. Giant tortoise material principally comes from the sand pit no 8 (Somsak sand pit) and the sand pit no 9 (Siam sand pit). The most spectacular material was a nearly complete shell with articulated carapace and plastron collected *in situ* by the Department of Mineral Resources (DMR) in June 2003. The specimen was found in situ in the Siam pit below conglomeratic levels in a sand layer, that was 13 meters below the surface. This layer belongs to the reducing subunit of the quarry (see Claude *et al.*, 2011).

Description and discussion: see detail in manuscript (Appendix VIII).

5.3 Holocene turtles in Thailand

5.3.1 Turtles from Khok Farang, Buriram Province

Locality:

Khok Farang locality is located at Koktaprom Village, Tajong Sub-district, Laharnsai District, Buriram Province. Archeologists from Phanomrung History Park started to excavate this locality in 2010. The age of the locality is about 2,500-1,500 years ago (Late Holocene, end of the Iron Age) (Pramjai, 2010). Two different layers are recognized in this locality according to archeological data from the preliminary report of Pramjai in 2010. In the upper layer, five human skeletons were found with antiques, decorations and animal bones. This layer probably corresponds to graves in a cemetery. A complete tortoise (object of that paper) was found close to the sepulture number 2 (Figure 118). In the second layers, antiques and scattered animal bones were found and shows indication of the ancient Khmer culture (Pramjai, pers. comm.).

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Genus *Indotestudo* Lindholm, 1929
Indotestudo enlongata Blyth, 1853
(figures 118-122)

Material: A complete shell, cervical vertebrae, pectoral girdle, limb bones and dentary (KF1).

Description:

The preserved shell is complete consisting of both carapace and plastron. Limb bones, cervical vertebrae and dentary were found within the shell (Figure 122). On the carapace, there is a natural pit between the distal parts of the fourth and fifth costal plates. This injury probably arrived during the lifespan of the animal, since the edge of the hole is round and there is no evidence of recent or archaeological damage. The anterior part of the nuchal plate presents a series of small pits distributed along the plate. It may probably be a trace of taphonomical decay during burial time.

Carapace (figures 119-121)

The carapace is convex and elongated and is slightly flattened in the vertebral region. There is no keel. The ornamentation on the carapace surface presents growth annuli. The carapace length is about 24 cm. The nuchal plate is hexagonal with narrow posterior part. There are eight neural plates. Overall, the neural pattern corresponds to alternative octagonal and tetragonal in shape. The first neural plate is oval in shape with the anterior part narrower than the posterior part. The second neural plate is octagonal in shape. The third neural plate is tetragonal. The fourth neural plate is octagonal. The fifth neural plate is tetragonal. The sixth to eighth neural plates are hexagonal with short antero-lateral sides. There are two suprapygal plates. The first one is hexagonal with short posterolateral sides. The second suprapygal is smaller than the first suprapygal. The anterior part of the second suprapygal is strongly convex anteriorly. Its posterior part is concave posteriorly. The pygal is large tetragonal and strongly in concave posteriorly. Its anterior part is wider than posterior part. The posterior end is straight. The pygal plate and posterior part of the eleventh peripheral plate are covered by a single large of supracaudal scute. The costal plates show alternative short and long proximal parts. The proximal part of the eighth costal plate is crossed by the vertebral and pleural sulci anteriorly. The anterior and posterior margins are slightly serrated. Lateral peripheral bones are rectangular.

The cervical scute is elongated and narrow. Its anterior part is concave posteriorly. There are five vertebral scutes. The first vertebral scute is small and longer than wide and pentagonal in shape. The second to fifth vertebral scutes are hexagonal and wider than long. The first pleural scute is as long as wide. It is in contact with the first to the fifth marginals. The second and the third pleural scutes are wider than long. The second to the fourth pleurals are rectangular in shape. The fourth pleural is about as wide as long. All marginal scutes are as long as peripheral plates. The pleuro-marginal sulcus and costo-peripheral suture are situated at the same level.

Plastron (figures 119, 121)

The plastron is elongated. It is concave ventrally. The anterior lobe is shorter than the posterior lobe. The lateral margin of the anterior lobe is rounded while the lateral margin of the posterior lobe is straight and slightly oblique until the end. The bridge is rather narrow and elongated.

The epiplastra are short. Their anterior parts are slightly projected anteriorly. Epiplastral lips are well developed. The entoplastron has a sub-rhombic shape. Its anterior end is intersected by the gulo-humeral sulcus and its posterior part is intersected by the humero-pectoral sulcus. The epi-hyoplastral suture is oriented anterolaterally. The hyoplastra are longer than the hypoplastra. The third to sixth peripheral plates contact the hyoplastra. The sixth to eighth peripheral plates contact the hypoplastra.

The xiphiplastra are rather elongated. The hypo-xiphiplastral suture is straight. The xiphiplastral processes are pointed. The anal notch is deep and triangular in shape. The buttresses are thin and elongated. The axillary buttress is connected to the distal part of the first costal plate and contacts the third peripheral and inguinal buttresses are connected to the distal parts of the fifth and sixth costal plates and contacts the seventh peripheral.

The gular scutes are narrow and reaching the anterior rim of the entoplastron. The humeral scutes are longer than pectoral scutes. The humero-pectoral sulcus is convex anteriorly. The midline contact of pectorals is shorter than the midline contact of humerals. The abdominal scutes are longer than the posterior plastral lobe of the plastron. The abdomino-femoral sulcus is slightly convex posteriorly. Femoral scutes are much longer than anal scutes. The abdominal scutes are the longest plastral scute while the anal scutes are the shortest plastral scute. The femoro-anal sulcus is straight and perpendicular to the axis of symmetry.

Beside of shell, part of dentary, scapular with acromion process, coracoid, ilium, scapula, acromion process, ischium, ulna, radius, humerus, femur, cervical vertebrae were also found within of the shell (Figure 122).

Comparison and discussion:

This specimen belongs Testudinoidea Batsch, 1788 on the basis of the contact of the buttresses with costals, the absence of inframarginal scales, the deep anal notch (Claude and Tong, 2004; Claude *et al*., 2007). Among this group, it is referred to modern Testudinidae Batsch, 1788 because of its dome liked shell, the absence of keel, the fact that pleuro-marginal sulcus and costo-peripheral suture run at the same level, because the neural pattern corresponds to alternative octagonal and tetragonal in shape and because costal bones are alternatively long and short along the neuro-costal suture and the costo-peripheral suture. In Southeast Asia, living testudinid turtles include *Indotestudo*, *Manuria emy*s, and *M. impressa*. *Manouria* differs from this specimen by a wider than long cervical scute, by the presence of a sulcus between the twelve marginal scutes, by the first suprapygal plate narrower than second suprapygal plate and by the entoplastron is not crossed by humero-pectoral sulcus. Apart from these, southeastern asian taxa as *Geochelone platynota* and *G. elegans* also differ from this specimen because, unlike them, the specimen displays a well developed cervical scute and a the flatter upper part of carapace. It is similar to *Indotestudo* by its elongated shell and its single supracaudal scute. This genus includes *Indotestudo elongata*, Blyth, 1853 *I. forstenii* (Schlegel and Müller, 1844) *I. travancorica* Boulenger, 1907. According to the *Indotestudo* key (Pritchard, 2000), *I. travancorica* differs from the described specimen here by the absence a cervical scute and the highest point of the carapace corresponds to the second vertebral scute (here located on the third or the fourth as for *I. elongata*). *Indotestudo forstenii* differs from this fossil specimen by the midline of humeral scute is much longer than pectoral scute. The turtle remains is therefore referred to *Indotestudo elongata* Blyth, 1853, on the basis of presence cervical scute and the midline of humeral scute that is shorter than the pectoral scute.

The size, the absence of fontanelles and the strong sutures indicate that the specimen is adult. The concave plastron and internally incurved pygal indicates that this specimen was a male *Indotestudo elongata* which is a land tortoise species. It is a common species which can be found everywhere in Thailand especially in hilly area.

The complete tortoise carapace contains many bones, several of them being still kept their original position, and it is not damaged. It indicates that the tortoise specimen was buried with flesh. Moreover, it was found together with a human sepulture. This shows that this specimen of *Indotestudo elongata* was buried at the same time with one of the humans graved in the cemetery. The specimen was certainly a gift for the defunct. In prehistoric times, such rituals associated with funeral are known since the Stone Age in Thailand at Tham Pra (11,000-8,500 years ago), Sai Yok Sub-district, Kanchanaburi Province (Pyopyo, 2012). Defunct were generally buried with a sleeping posture and food, equipment, decorations were also graved in order to help the defunct to travel and survive for their life after death.

The discovery of a complete *Indotestudo elongata* carapace in the cemetery implies that this species was probably used by humans for subsistence since it is still use as food resources in some Asian regions.

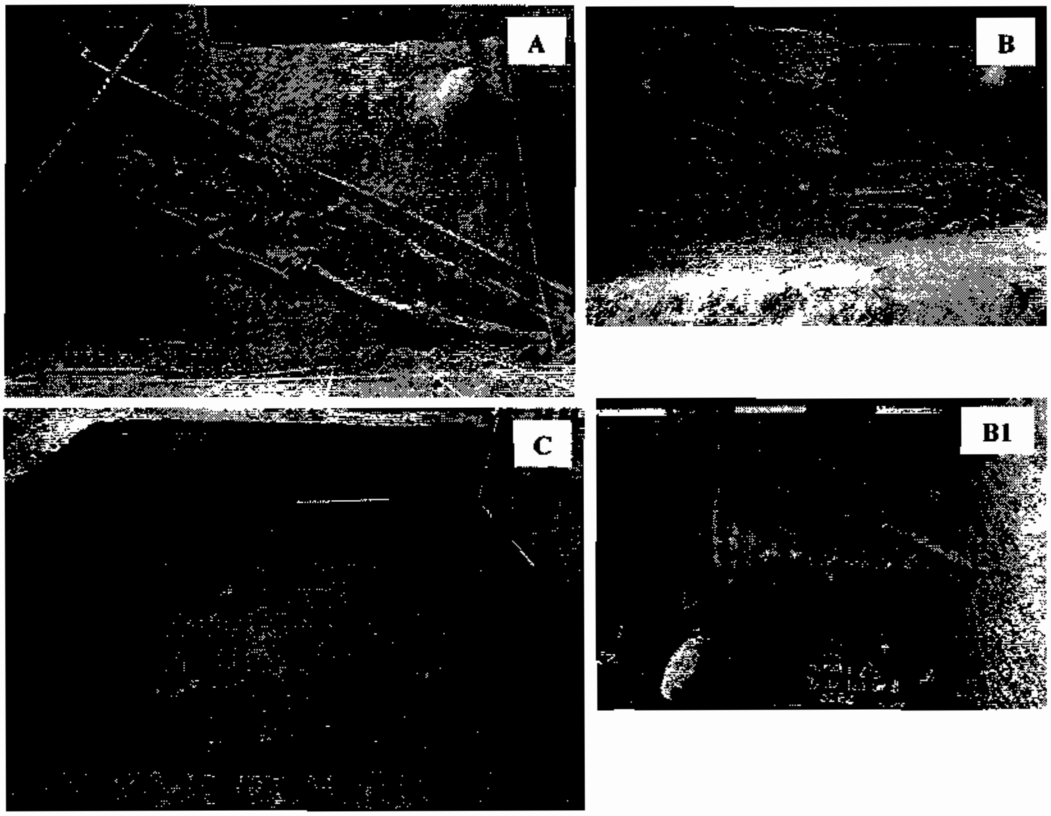

Figure 118 Archeological locality of Khok Farang, Buriram Province (Late Holocene in age). The in situ *Indotestudo elongata* specimen (KF1-1) found together with human skeleton at the grave number two (**A**), the grave number one present the human skeleton with antiques (**B, B1**), and animal bones from the grave number one (**C**).

Photographs: K. Pramjai.

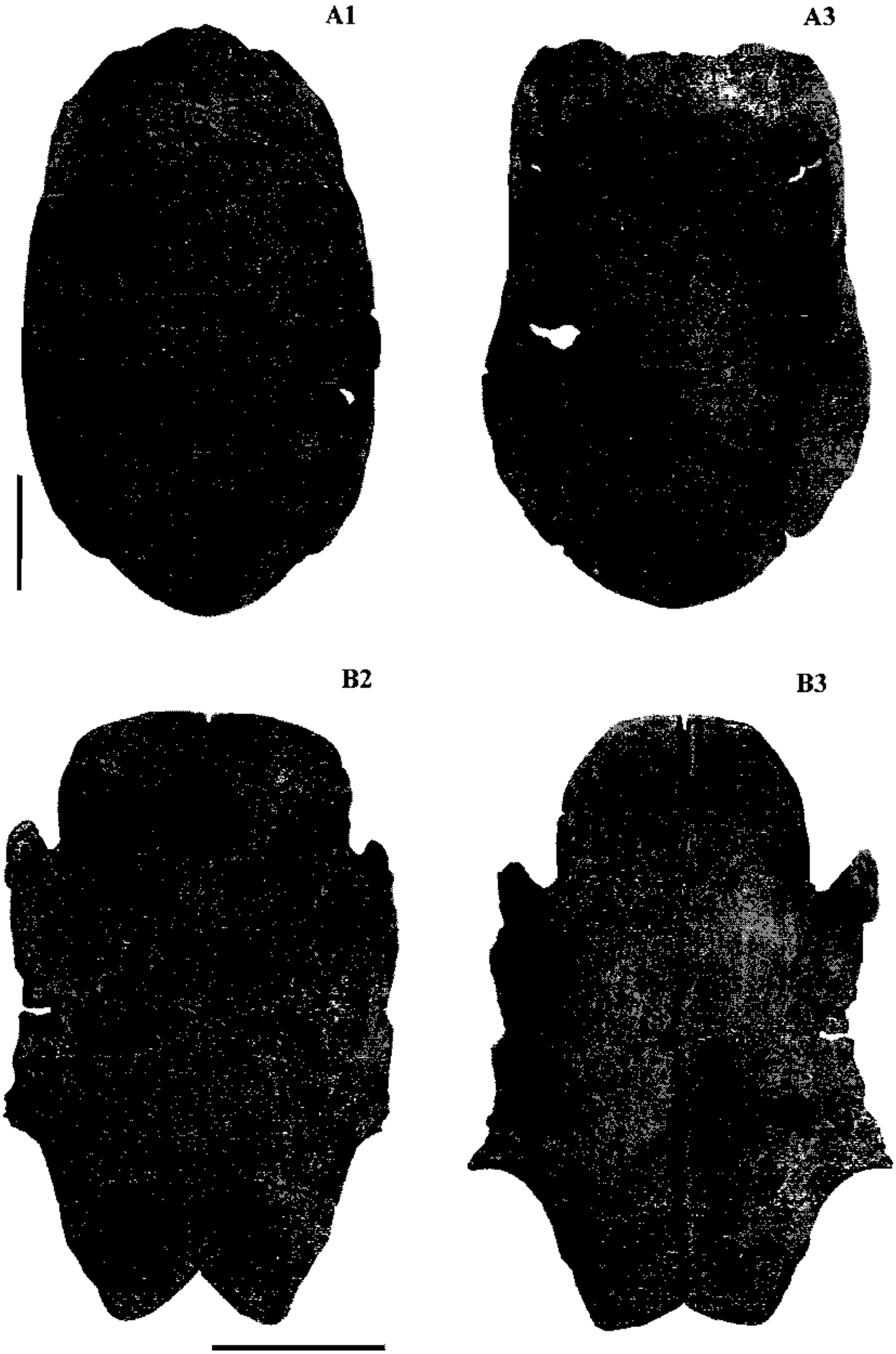

Figure 119 *Indotestudo elongata* (KF1-1) from Khok Farang, Buriram Province in the Holocene age; carapace (**A**), plastron (**B**) in dorsal (**1**), ventral (**2**) and visceral (**3**) views. Scale bars equal 5 cm.

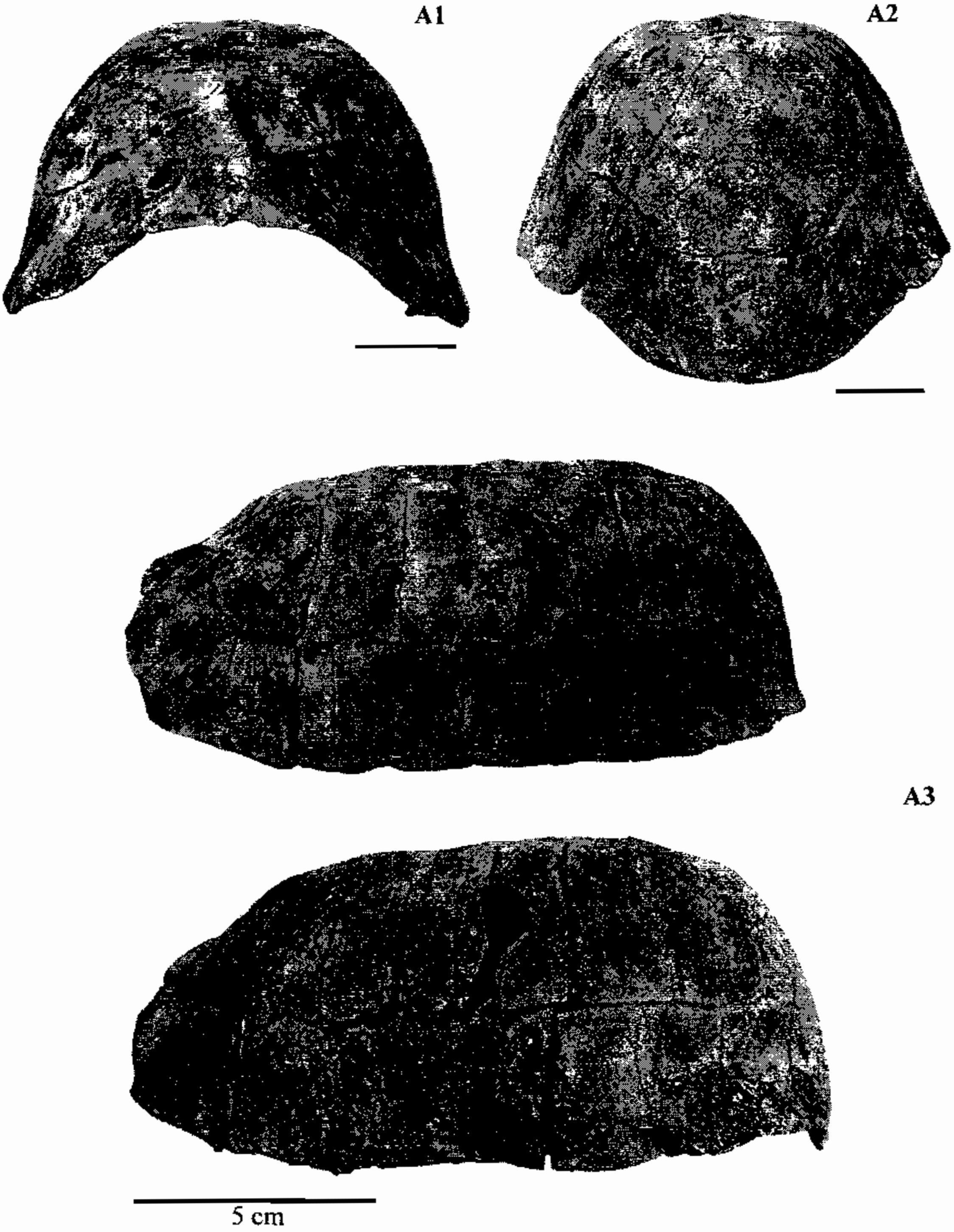

Figure 120 *Indotestudo elongata* (KF1-1) from Khok Farang, Buriram Province (Iron Age); carapace in anterior (**1**), posterior (**2**) and lateral (**3**) views. Scale bars equal 2 cm.

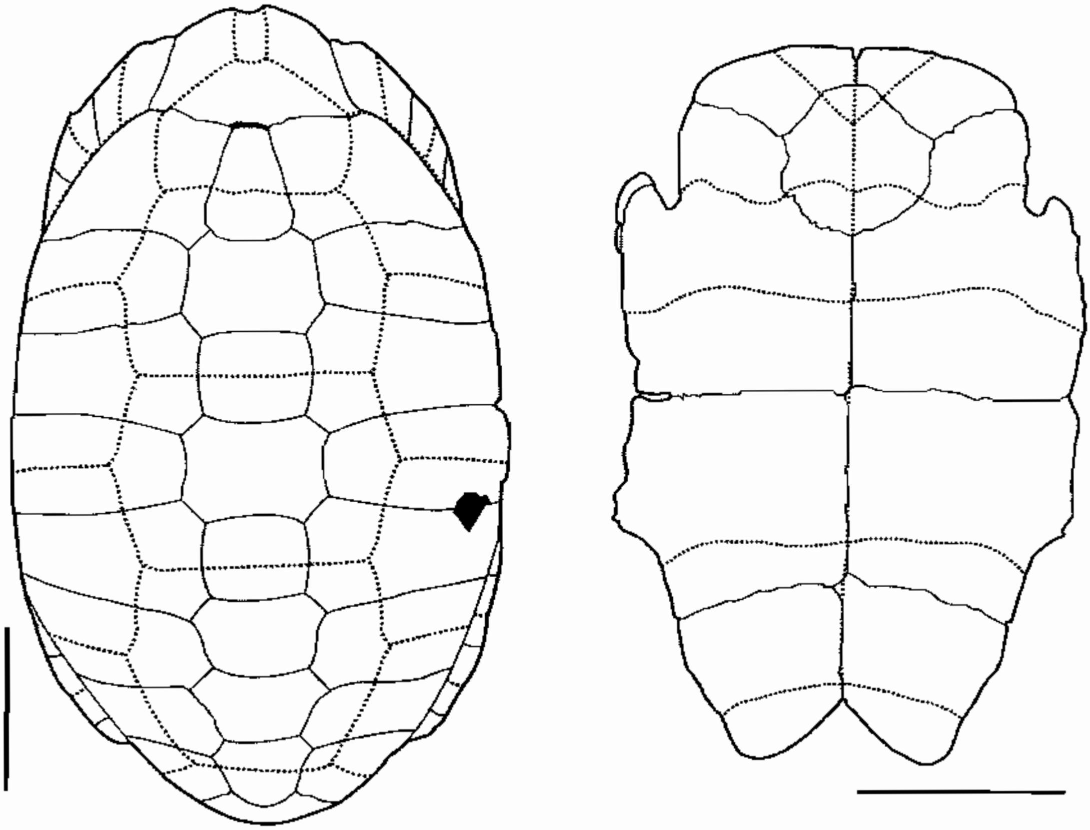

Figure 121 Drawing of *Indotestudo elongata* (KF1-1) from Khok Farang, Buriram Province in the Late Holocene (the end of the Iron Age); carapace in dorsal (A) and ventral (B) views. Scale bars equal 5 cm.

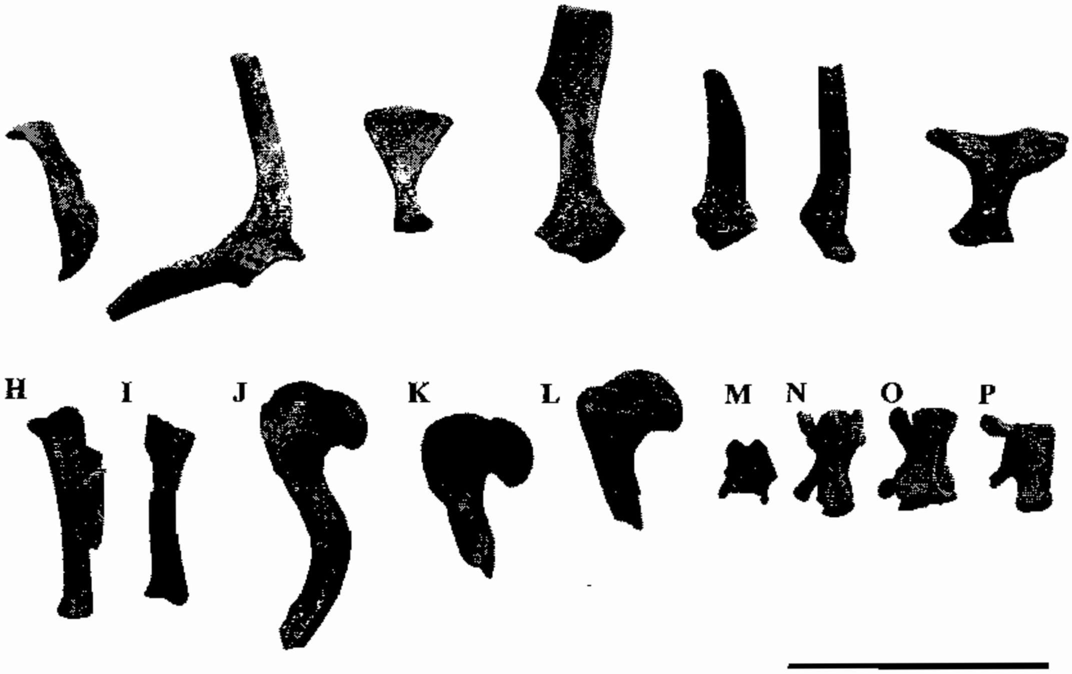

Figure 122 Bones within *Indotestudo elongata* shell from Khok Farang, Buriram Province (Iron Age); part of dentary (**A**), scapular with acromion process (**B**), coracoid (**C**), ilium (**D**), scapula (**E**), acromion process (**F**), ischium (**G**), ulna (**H**), radius (**I**), humerus (**J, K**), femur (**L**), axis (**M**) and cervical vertebrae (**N-P**). Scale bar equals 5 cm.

5.3.2 Turtles from Thammamongkol cave, Phetchaburi Province

Locality:

Thammamongkol cave is situated in Khao Yoi District, Phetchaburi Province. This cave is located as part of Koa E-go. Paladej Srisuk collected material from there in 2000. Several animal remains were found in this cave, most of them being mammals . Archeological remains such as pottery fragments found together with the vertebrate indicate a Holocene deposit. Sub-fossil remains from this locality consists of both fragments and articulated plates. These have been reported in Srisuk (2007), and are further described in the following.

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Genus *Indotestudo* Lindholm, 1929
Indotestudo enlongata Blyth, 1853
(Figure 123 and 124)

Material:

Nuchal plate (SHM-TTM unnumbered), neural plates associated with costal plates (SHM-TTM 138-2, SHM-TTM 138-3, SHM-TTM 138-5, costal plates (SHM-TTM 89, SHM-TTM 90, SHM-TTM 91, SHM-TTM 92, SHM-TTM 93, SHM-TTM 96, SHM-TTM 97, SHM-TTM 106, SHM-TTM 109, SHM-TTM 110, SHM-TTM 112, SHM-TTM 115, SHM-TTM 116, SHM-TTM 118, SHM-TTM 121, SHM-TTM 124, SHM-TTM 127, SHM-TTM 131, SHM-TTM 132, SHM-TTM 133, SHM-TTM 135, SHM-TTM 138-7, SHM-TTM 138-9, SHM-TTM 144, SHM-TTM 146, SHM-TTM 153, SHM-TTM 156, SHM-TTM157, SHM-TTM 158), suprapygal plate (SHM-TTM 94), peripheral plate (SHM-TTM 138-6, SHM-TTM unnumbered), pygal plate (SHM-TTM unnumbered) and plastron (SHM-TTM-x-11), entoplastron (SHM-TTM 88-11),

Description:

The isolated nuchal plate (SHM-TTM unnumbered) is nearly complete, it lacks the lateral margin of the left side (Figure 124, C1). It is hexagonal in shape. Its posterior part is much narrow than anterior part. The cervical scute is very narrow and elongated. The fourth and fifth neural plates (SHM-TTM 138) contacted with left and right side of the fourth and fifth costal plates (Figure 124). The fourth neural plate is octagonal in shape while the fifth neural plate is tetragonal in shape. The fifth one is crossed by the vertebral sulcus in the middle of the plate. The fourth costal plate is rounded in medial end. The medial end of costal is crossed by vertebral sulcus and crossed by pleural sulcus in the middle along the width of plate. Several preserved costal plates, mostly fragmented were found in this locality (Figure 123). They are rather thin and present growth annuli; furthermore they display alternatively long and narrow proximal and distal parts. The preserved articulated peripheral plates include the right side of the tenth and eleventh peripheral plates. The left side of associated peripheral plates are preserved from the sixth to eleventh peripheral plates. Bridge peripherals are short. The pygal plate (SHM-TTM unnumbered) is large (Figure 124 B1). Its anterior part is wider than its posterior part. The posterior end is straight. The pygal plate and posterior part of the eleventh peripheral plate are covered by a single large of supracaudal scute. The pleuro-marginal sulcus and costo-peripheral suture run at the same level.

The nearly complete plastron (SHM-TTM-x-11) lacks the right side of the epiplastron, the entoplastron and the distal end of the right xiphiplastral process. The plastron is elongated. The anterior lobe is shorter than the posterior lobe. The lateral margin of anterior lobe is rounded while the lateral margin of the posterior lobe is straight and slightly oblique until the end. The epiplastra is rather short. Their anterior parts are slightly projected anteriorly. The epiplastral lip is well developed. The outline of the entoplastron indicates it was sub-rhombic shape. Its anterior end is not crossed by the gulo-humeral sulcus while its posterior part was probably crossed by humero-pectoral sulcus. The isolated entoplastron (Figure 124, D2) is complete. It is sub-rhombic in shape. Its anterior part is crossed by the gulo-humeral sulcus anteriorly and its posterior part is crossed by the humero-pectoral sulcus, close to the middle plate. It is of larger size than the outline of the entoplastron of SHM-TTM-x-11. The epi-hyoplastral suture oriented anterolaterally. The hyoplastra are longer than hypoplastra. The xiphiplastra are rather elongated. Hypo-xiphiplastral suture is straight. The xiphiplastral process is pointed. The anal notch is deep and is triangular in shape.

The gular scutes are short. The humeral scutes are longer than pectoral scutes. The humero-pectoral sulcus was slightly convex anteriorly. The abdominal scutes are longer than the posterior plastral lobe of the plastron. The midline length of the humeral scute is shorter than the pectoral scute. The abdomino-femoral sulcus is slightly convex posteriorly. Femoral scutes are much longer than anal scutes. The abdominal scutes are the longest plastral scutes while the anal scutes are the shortest. The femoro-anal sulcus is straight and perpendicular to the axis of symmetry.

Comparison and discussion:

These material belong to Testudinidae by the presence of the absence of keel, the pleuro-marginal sulcus and costo-peripheral suture runing at the same level, the neural pattern corresponding to alternative octagonal and tetragonal in shape, abdominal scutes longer than posterior lobe. The material can be separated from *Manouria* by the shape of cervical scute which wider than long while longer than wide for this material. In *Geochelone*, the entoplastron is not crossed by the humero-pectoral sulcus whereas the material is crossed in the middle plate. These should be assigned to the *Indotestudo* genus by the presence of a large single supracaudal scute, octagonal and tetragonal shape neural pattern, a sub-rhombic entoplastron crossed by the humero-pectoral sulcus nearly in middle of the plate. This taxa differs from *I. travancorica* by the presence of a long and narrow cervical scute (a scute that is absent *I. travancorica)* (Pritchard, 2000). It is also differs from *I. forstenii* for which the midline length of the humeral scute is much longer than the pectoral scute (in this material, the midline length of humeral scute is shorter than pectoral scute). The material here is therefore referred to the species *Indotestudo enlongata* Blyth, 1853 based on the cervical scute shape and the midline length between humeral and pectoral ratio.

At least two individuals are present in this locality based on number and size of shell elements. The presence of this species in a cave can be considered as not normal because the habitat of this species correspond to hilly area. The presence can possibly be explained because humans brought them with them as food supply and were eating them in the caves. This is further suggested by the disarticulated nature of the specimens and the mix of disarticulated and scattered vertebrate remains in the cave. This indicates that in the past, people used *Indotestudo elongata* as food as people now eat this species in China.

Family Geoemydidae Theobald, 1868

Genus *Heosemys* Stejneger, 1902

Heosemys grandis (Gray, 1860)

(Figure 125)

Material: anterior part of carapace (SHM-TTM unnumbered), right epiplastron (SHM-TTM 88-10), hyoplastron (SHM-TTM 88-12), costal plates (SHM-TTM 88-3, SHM-TTM 103, SHM-TTM108, SHM-TTM 113)

Description:

The nuchal plate (SHM-TTM unnumbered) has a hexagonal shape with short posterolateral sides. It shows an anterior deep emargination. The lateral parts of the plate are covered by the pleuro-vertebral sulcus which indicate a lyre shaped first vertebral scute. The impressed cervical scute has a narrow triangular shape. Its posterior part is convex posteriorly. The anterior margin of the carapace is smooth. The first to third peripheral plates are preserved. The anterior edge of these peripherals is sharp. The first peripheral is crossed by the intermarginal sulcus in the middle. This sulcus is strongly curved laterally by comparison to the next intermarginal sulci. A musk duct foramen can be seen on the visceral view of the third peripheral plate. In visceral view, the marginal impression is hardly visible. The pleuro-marginal sulcus is placed below the costo-peripheral suture, about one/third of the peripheral plate length.

The epiplastron is short. Its anterior margin is straight. The epiplastral lip is thick and convex dorsally. The gulo-humeral sulcus is oblique to the midline suture. This sulcus contacts with the anterior end of the entoplastron. The hyoplastron is crossed by the humero-pectoral sulcus. The humero-pectoral sulcus is probably convex anteriorly and was crossing the middle of the entoplastron (Figure 125).

Comparison and discussion:

The presence of a musk duct foramen on the third peripheral plate and the inguinal buttress contacting the first costal bone indicates that this turtle belongs to Geoemydidae Theobald, 1868 within the superfamily Testudinoidea Batsch, 1788. According to the size of the plates, the material correspond to a large species. The entoplastron was crossed by both the gular and humero-pectoral sulcus. This association of character is found in the species *Melanochelys trijuga*, *Heosemys annandalei, H. depressa* and *H. grandis*. Large *Heosemys* differ from *Melanochelys* by having a stronger nuchal emargination, the anterior part of the first vertebral narrower, and the sulcus on the first peripheral strongly curved laterally. In addition, the humero-pectoral sulcus cross the entoplastron more anteriorly in *Heosemys* by comparison to *Melanochelys*. Large *Heosemys* species are known by *H. grandis*, *H. depressa* and *H. annandalei*. The described material differs mainly from *Heosemys annandalei* in visceral view of the nuchal plate by the absence a pair of ventral processes located in the middle portion of the plate. The fossil also can be excluded from *Heosemys depressa* by the shape of the sulcus on the first peripheral which is more strongly curved in the fossil. The material is more similar to *Heosemys grandis* (Gray, 1960) by the pleuro-marginal sulcus placed far from costo-peripheral suture, the marginal sulcus on the first peripheral plate curved strongly laterally. I therefore refer this material to that species.

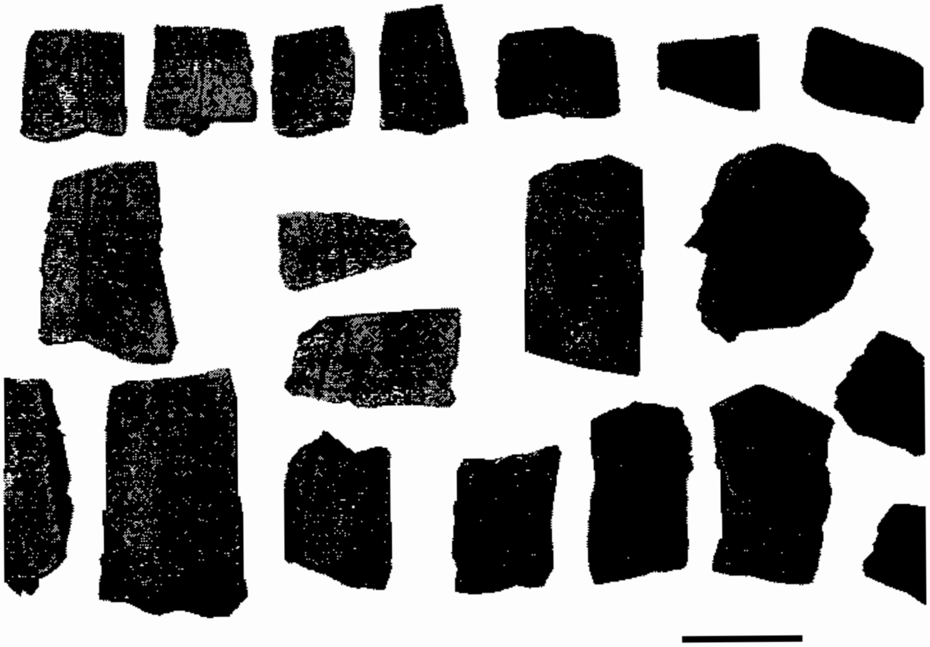

Figure 123 Isolated costal plates in dorsal view of *Indotestudo elongata* from Thammamongkol cave, Phetchaburi Province in the Holocene age. Scale bar equals 2 cm.

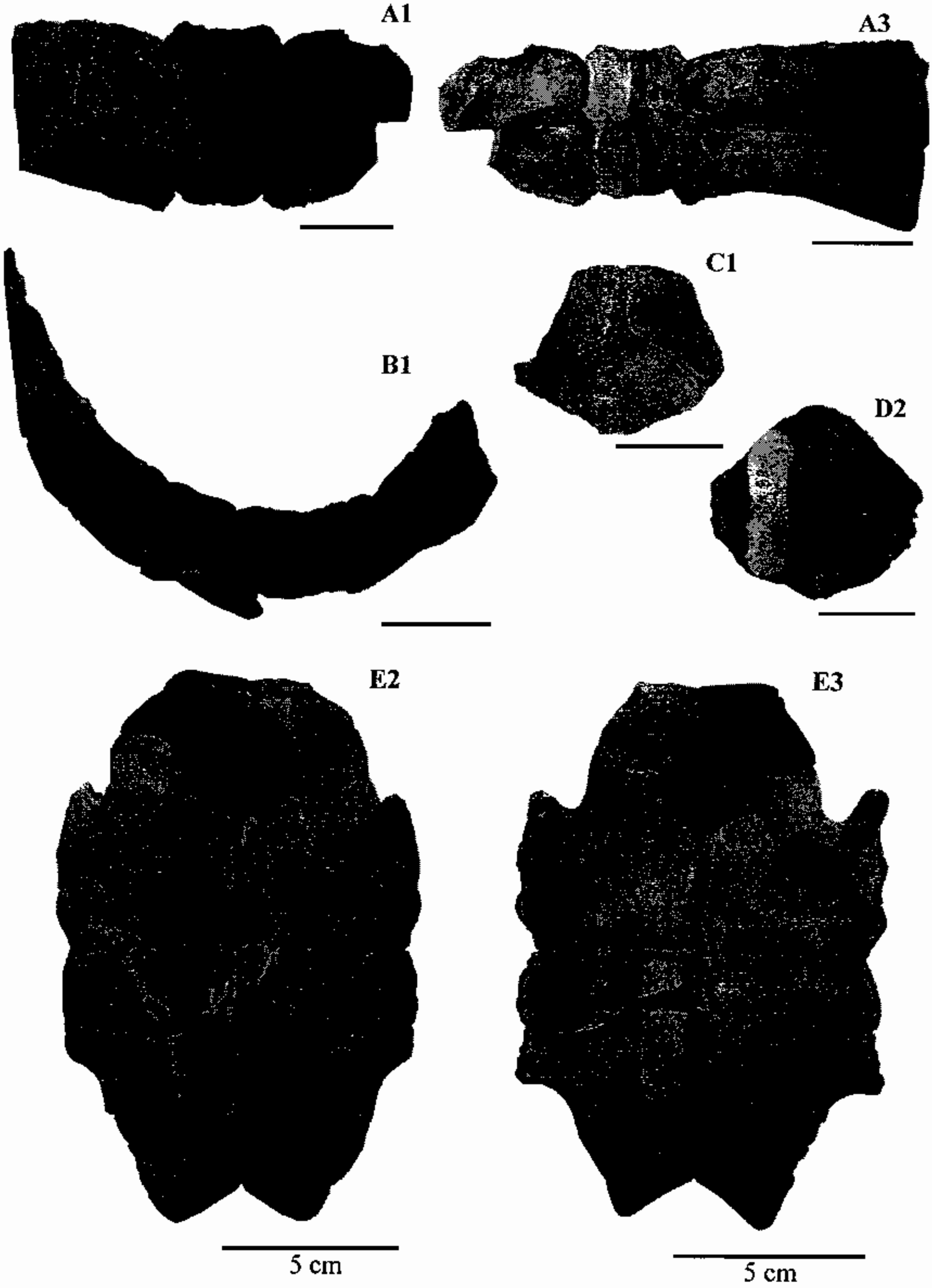

Figure 124 *Indotestudo elongata* specimens from Thammamongkol cave, Phetchaburi Province in the Holocene age; associated neurals and costals (**A**), associated posterior peripheral plates and pygal plate (**B**), nuchal plate (**C**), entoplastron (**D**) and plastron (**E**) in dorsal (**1**), ventral (**2**) and visceral (**3**) views. Scale bars equal 2 cm.

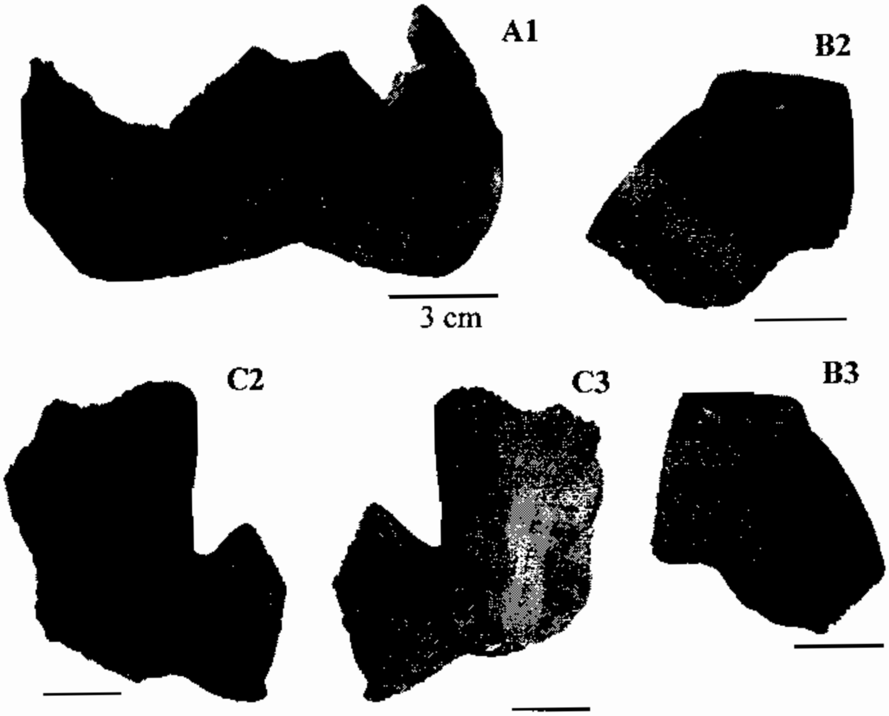

Figure 125 *Heosemys grandis* (Gray, 1960) specimens from Thammamongkol cave, Phetchaburi Province in the Holocene age; anterior part of carapace (**A**), right epiplastron (**B**) and left hyoplastron (**C**) in dorsal (**1**), ventral (**2**) and visceral (**3**) views. Scale bars equal 2 cm.

5.3.3 Turtles from Taling Tong, Sukhothai Province

Locality:

Taling Tong locality is situated in Srisatchanalai Sub-district, Srisatchanalai District, Sukothai Province. The sediment of this locality have been deposited by the Yom River. Paladej Srisuk collected the material in 1986. The material were found together at the base of a cliff surrounding the river bed and come from several layers. This locality was popular for finding gold in the river. Several archelological materials including ceramic, stone wear, and paleontological material including mammals, fishes, and turtle plates, were found.

Systematic paleontology

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Family Trionychidae Gray, 1825

Amyda cartilagenea (Boddaert, 1770)

(Figure 126)

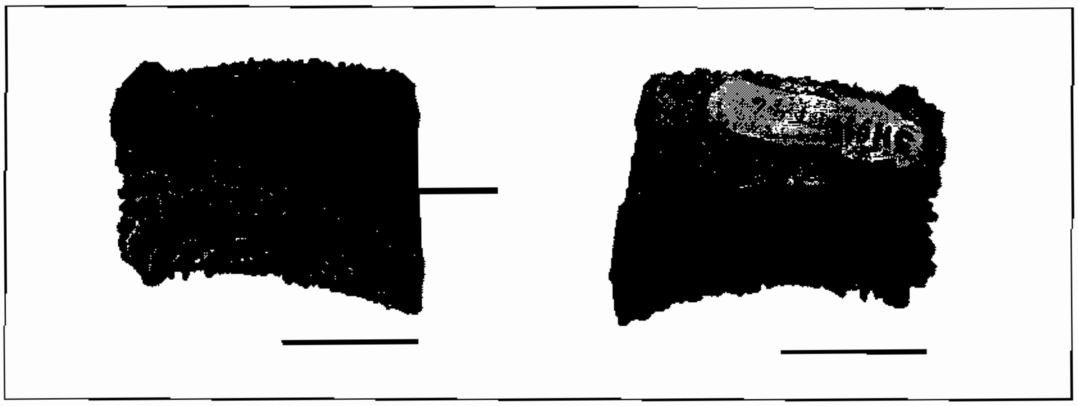

Figure 126 Proximal part of the sixth right costal plate of *Amyda cartilagenea* (SHM-TT46) from Taling Tong locality, Srisatchanalai Sub-district, Srisatchanalai District, Sukothai Province in dorsal (left) and visceral (right) views. Longitudinal ridge is indicated by black arrow. Scale bars equal 2 cm.

Material: Proximal part of the sixth right costal plate (SHM-TT46)

The specimen is kept in Palaeontological Research and Education Centre Collection, Mahasarakham University.

Description:

A single trionychid specimen (SHM-TT46) is collected from Taling Tong locality. It corresponds to the proximal part of a sixth right costal plate. The ornamentation consists of relatively coarse pits and vermiculations. The size of the pits is relatively large but displays an important variation. The number of the pitted at the medial end of this plate is about 16. Longitudinal ridges make also part of the ornamentation (see Figure 126).

Comparison and discussion:

The specimen is clearly referred to Trionychidae based on the pitted and vermiculated ornamentation. The coarse ornamentation with the presence of longitudinal ridges, as well as the rather large size of the specimen is a pattern found in the living *Amyda cartilagenea* (Boddaert, 1770). The present vertical ridges on the plate is a characteristic of this species (Pritchard et al., 2009). However, the present of vertical ridges on carapace also found in *Pelodiscus sinensis*. The number of the pitted at medial end is less than 20 and is also more similar to *Amyda cartilagenea* than it is of *Pelodiscus*. This material was found together with several kind of humann artefact. However, the mixed context, makes difficult to assess the relationship of this turtle with human activities; and in addition there is no any cutting mark on the plate.

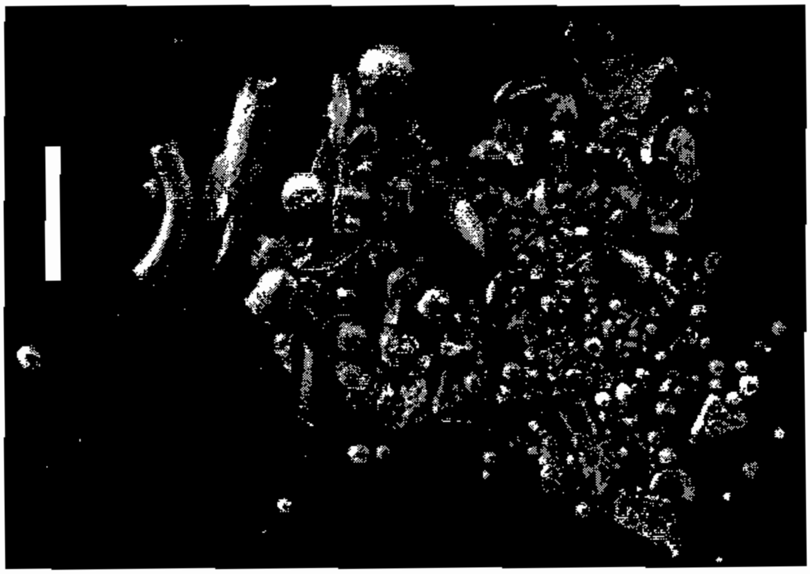

Figure 127 Gold elements collected by Paladej Srisuk in 1986 from Taling Tong locality, Srisatchanalai Sub-district, Srisatchanalai District, Sukohai Province. Scale bar equals 5 mm.

Systematic paleontology

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Superfamily Testudinoidea Batsch, 1788

Family Geoemydidae Theobald, 1868

Heosemys grandis (Gray, 1860)

(Figure 128)

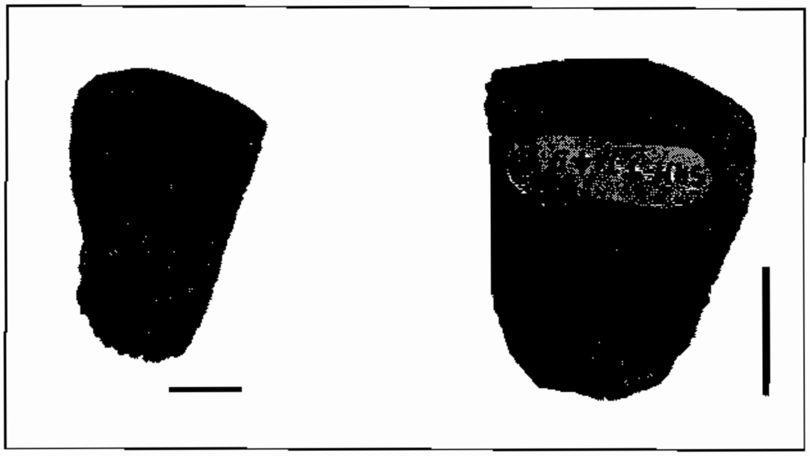

Figure 128 Right first peripheral plate of *Heosemys grandis* (Gray, 1860) (SHM-TT45) from Taling Tong locality, Srisatchanalai Sub-district, Srisatchanalai District, Sukhothai Province in dorsal (left) and visceral (right) view. Scale bars equal 2 cm.

Material: Right first peripheral plate (SHM-TT 45)

This specimen is kept in Palaeontological Research and Education Centre Collection. Mahasarakham University, Thailand.

Description:

The plate (SHM-TT 45) corresponds to a first right peripheral plate. It is rather large and have smooth surface, (Figure 128). Its anterior margin is rather smooth and displays a slightly curved outline. Its anterolateral part is expanded mesiolaterally. Its posterior part is rounded. The pleuro-marginal sulcus can be seen on the peripheral plate. The marginal sulcus is crossed in the middle of the plate and convex laterally. In visceral view, the marginal sulcus is present.

Comparison and discussion:

By comparison to living turtles of South East Asia, the described specimen can be placed into the Geoemydidae Theobald, 1868 because of the pleuro-marginal sulcus can be seen on the peripheral plate. and because the plate is relatively long. The size of the plate indicates it should belong to a large species. The sharp angle of the distal extremity of the plate is distinct from the *Batagur* group, and from *Heosemys annandalei* but similar to *Heosemys grandis*. In cross-section the visceral side of the plate is nearly straight which is also the case in *H. grandis* but different in *H. annandalei* where there is a strong demarcation at the limit of the dermo-sulcus. I therefore refer this specimen to *Heosemys grandis* (Gray, 1860). This species is a large aquatic turtle is Southeast Asia which can be found in Thailand, Myanmar, Cambodia, southern Vietnam and Malaysia (Stuart *et al*., 2001).

5.3.4 Turtles from Raksai cave, Phetchaburi Province

Locality:

Raksai cave or Tham Raksai is a part of Koa E-go located in Nong Chumpon Sub-Disctrict, Khao Yoi District, Phetchaburi Province. Khaoa E-go is a Permian limestone mountain. There are several caves around the mountain. Raksai cave is one of these. It is a small cave about 6 meters in width and 8 meters in length. Its elevation is about 360 m. above the sea level. Paladej Srisuk found this locality in March, 2000 and collected an important fossil material (P. Srisuk, pers. comm.). Most of the material belongs to mammals (1,580 pieces; Kamolrat *et al.*, 2011). Turtles bones were also found in this locality. In addition, there are also stone tools and some bone beads (Figure 129). These tools are characteristic of the Hoabinian culture and a early Holocene age can be given for that locality. At present, the background of the cave is constructed for monastic activity.

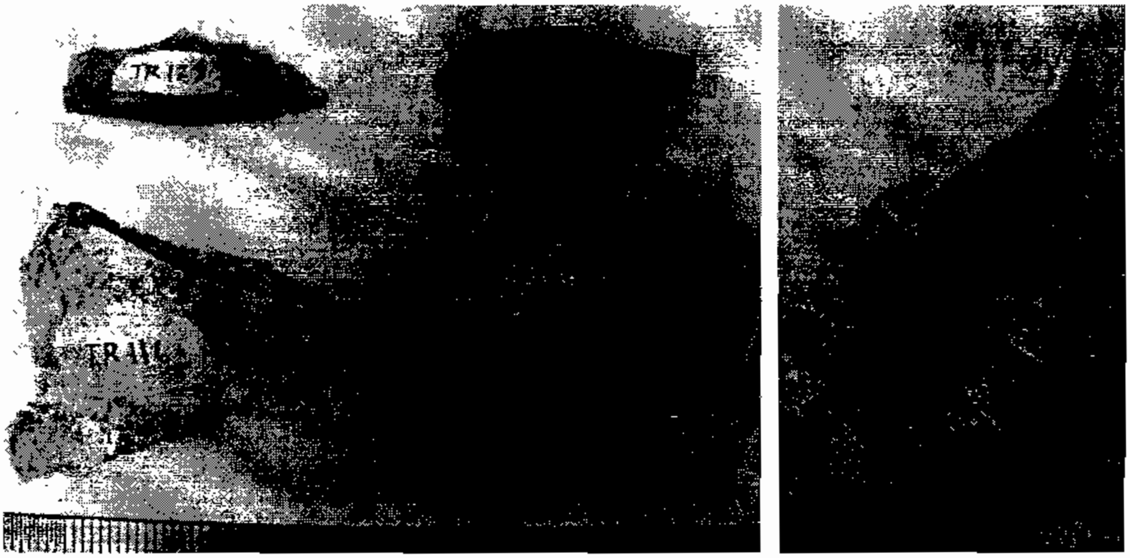

Figure 129 Stone tools (left) and bone beads (right) from Raksai cave, Nong Chumpon Sub-Disctrict, Khao Yoi District, Phetchaburi Province.

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Genus *Indotestudo* Lindholm, 1929
Indotestudo sp.
(Figure 130)

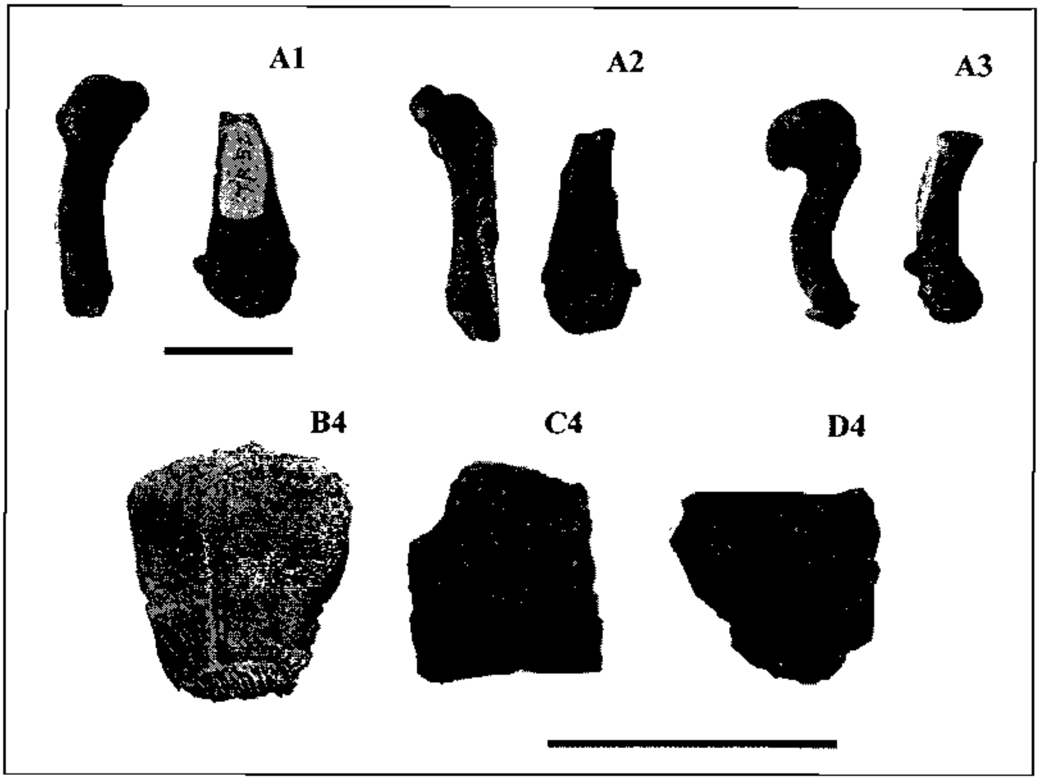

Figure 130 Humeri; TR 196, left and TR 52, right (**A**), 1st peripheral (**B**), distal part of costal (**C**), and unidentified plate (**D**) in anterior (**1**), posterior (**2**), lateral (**3**), and dorsal (**4**) views from Raksai cave, Nong Chumpon Sub-District, Khao Yoi District, Phetchaburi Province.

Material: humeri (TR 196 and TR 52), first peripheral plate (TR-unnumbered 1), distal part of costal plate (TR-unnumbered 2) and unidentified plate (TR-unnumbered 3)

The specimens are kept in Palaeontological Research and Education Centre collection, Mahasarakham University, Thailand.

Description:

The humeri are covered with a thin layer of calcite. The humerus number TR196 is not complete. Its half of the shaft with distal part is missing. The shaft is strongly curved. The *caput humeri* is oval shape. The medial and lateral processes are well developed. The lateral process is lower than the medial process even if the edge of the process is broken. The intertubercular fossa is deep but narrow. Another specimen of humerus (TR52) composes of an half of the shaft with the distal end preserved. The shaft is slightly curved. The distal end is slightly expanded. The ectepicondylar foramen cannot be observed on this bones. Carapacial fragment plates include the first left peripheral plate, the distal end of a costal plate and an unidentified bone (Figure 130). The first peripheral plate is complete. It is trapezoid in shape and expanded mesio-laterally. The inter-marginal sulcus appears in the middle of the plate. The medial margin of the plate is narrower than the lateral end. The pleuro-marginal sulcus is present on the posterior margin, very close to the costo-peripheral suture or running at the same level. Only the distal part of the costal plate is preserved. The plate is rather thin. It is crossed in the middle by the inter-pleural sulcus longitudinally. It is probably the fourth costal plate, for which the sulcus is more or less in the middle. Another plate (TR-unnumbered 3) is too fragmentary to give any precise position.

Comparison and discussion:

Based on strongly curved shaft of humerus is strongly curve and the pleuro-marginal sulcus running at the same level with costo-peripheral suture on the first peripheral plate, they are assigned to the Family Testudinidae.

In Thailand, there are two genus of Testudinidae, *Manouria* and *Indotestudo*. The humerus of *Manouria* presents a wide caput humerus and deep and wide intertubercular fossa whereas *Indotestudo* is characterized by an oval caput humeri and deep and narrow intertubercular fossa. The material described here are more similar to *Indotestudo* which is represented by one species in the country: *Indotestudo elongata*.

Therefore, the described material are assigned to *Indotestudo sp.* on the basis of morphology of humeri.

At the present, in Thailand, *Indotestudo* is commonly found in hilly area. There are also several large mammals in the cave such as primate, canivora, and artiodactyla (Kamolrat *et al.*, 2011) and also trace of stone tools and decoration. The tortoise was probably transferred into the cave by predator or humans.

5.3.5 Turtles from Keet Khin, Saraburi Province

Locality:

Keet Khin locality is located in Ban Mo Sub-district, Ban Mo District, Saraburi Province. This archeological site is about 1,000 year ago based on instable carbon isotope dating (Auetrakulvit, pers. comm.).

Systematic paleontology

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Superfamily Testudinoidea Batsch, 1788

Family Geoemydidae Theobald, 1868

Genus *Batagur* Gray, 1856

Batagur sp.

(Figure 131)

Material: a nearly complete carapace (KK-2011)

The material is kept in Silapakorn Universtiy, Bangkok, Thailand.

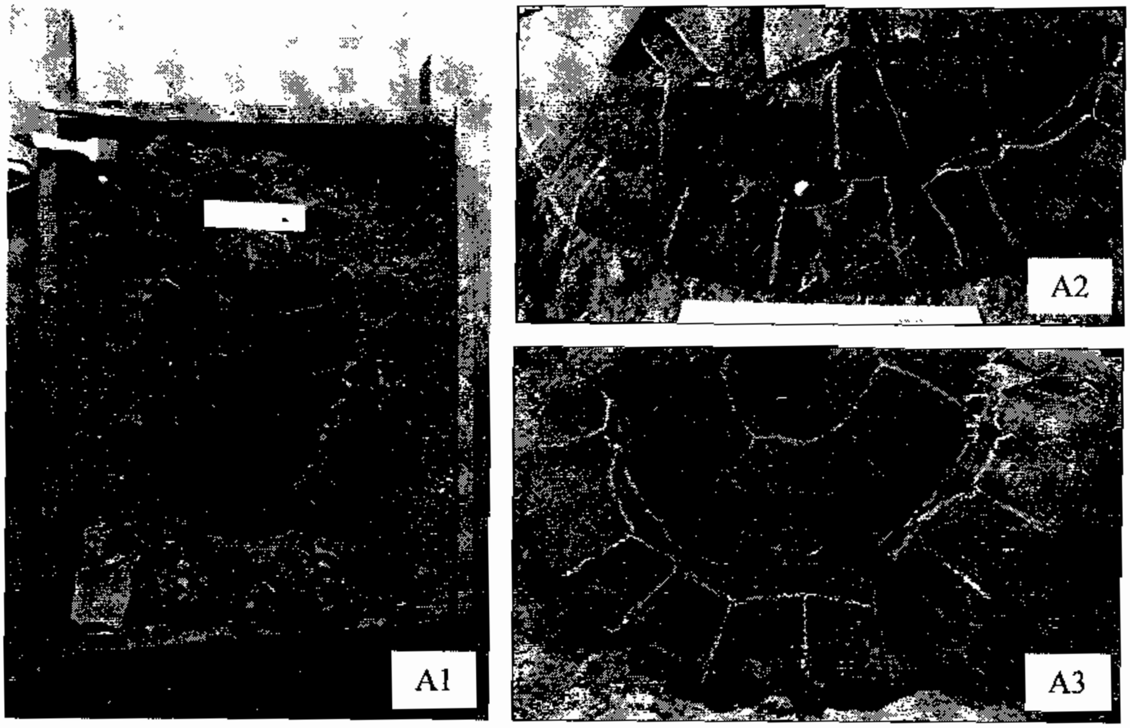

Figure 131 A nearly complete carapace of *Batagur* (KK-2011) in dorsal view from Keet Khin, Saraburi Province, Thailand; the whole carapace (**A1**), lateral side with oval fontanelles (**A2**) and posterior part with trace of cutting (**A3**).

Description:

The carapace (KK-2011) is nearly complete but some parts are broken near the area in costal plate (Figure 131). The carapace is elongated, it is slightly rounded in cross section anteriorly and more flattened on posterior part. The anterior and posterior carapace margins are smooth. The ornamentation on the carapace surface is smooth. Plates are fused together. While most of marginal scutes can be observed, except the lateral sides of the third vertebral cannot. The pleuro-marginal sulcus is clearly restricted on peripheral plate. Fontanelles are present in small and have an oval shape (Figure 131, A2). They are restricted to the lateral contact between costal plates and costal and peripherals. Three cutting traces, semicircular shape can be observed in the posterior part of the carapace (Figure 131). The fourth and fifth vertebrals can observed. The fourth vertebral is hexagonal with short anterolateral side. It is slightly wider than long. The fifth one is hexagonal with short posterolateral side. It is wider than long. Marginals are visible. They are rather long, especially the seventh to ninth peripherals. The fourth vertebral is longer than the fifth one. The plastron was not available for study.

Comparison and discussion:

This turtle specimen belongs to Geoemydidae based on the pleuro-marginal sulcus running below the costo-peripheral suture. The oval shell shape with smooth posterior margin and the presence of fontanelles is only known for *Batagur*. This specimen is separated from *Batagur bornoensis* because it shows a less distinct vertebral keel and less triangular fontanelles shape (oval here). *B. affinis* It is also different with this sub-fossil by the presence of weakly serrated central and posterior marginal scutes and a medial keel distinct and slightly pointed spines along the keel for *B. affinis edwadmolli* (Prashag *et al.*, 2009). The specimen is more similar to *Batagur baska* in shell shape, anterior and posterior margin and keel characters. Therefore, it is assigned to this mentioned species.

Batagur baska is a large geoemydid turtle which inhabits in tidal areas of the estuaries of large river (Ernst and Barbour, 1989). The discovery of this species in this locality with cutting marks in the posterior part of carapace indicated that this species was disturbed by human activity and possibly had a different distribution from today. At the present, *Batugur baska* is distributed in northeastern India from Orissa to West Bengal, Sundarbans of Bangladesh and coastline of Myanmar, perhaps northernmost west coast of peninsular Thailand (Prashag *et al.*, 2009). The map of *Batagur* species distribution is shown in Figure 132. The presence of this turtle in this archeological site may suggest it was transported by human or that its distribution became restricted recently with time.

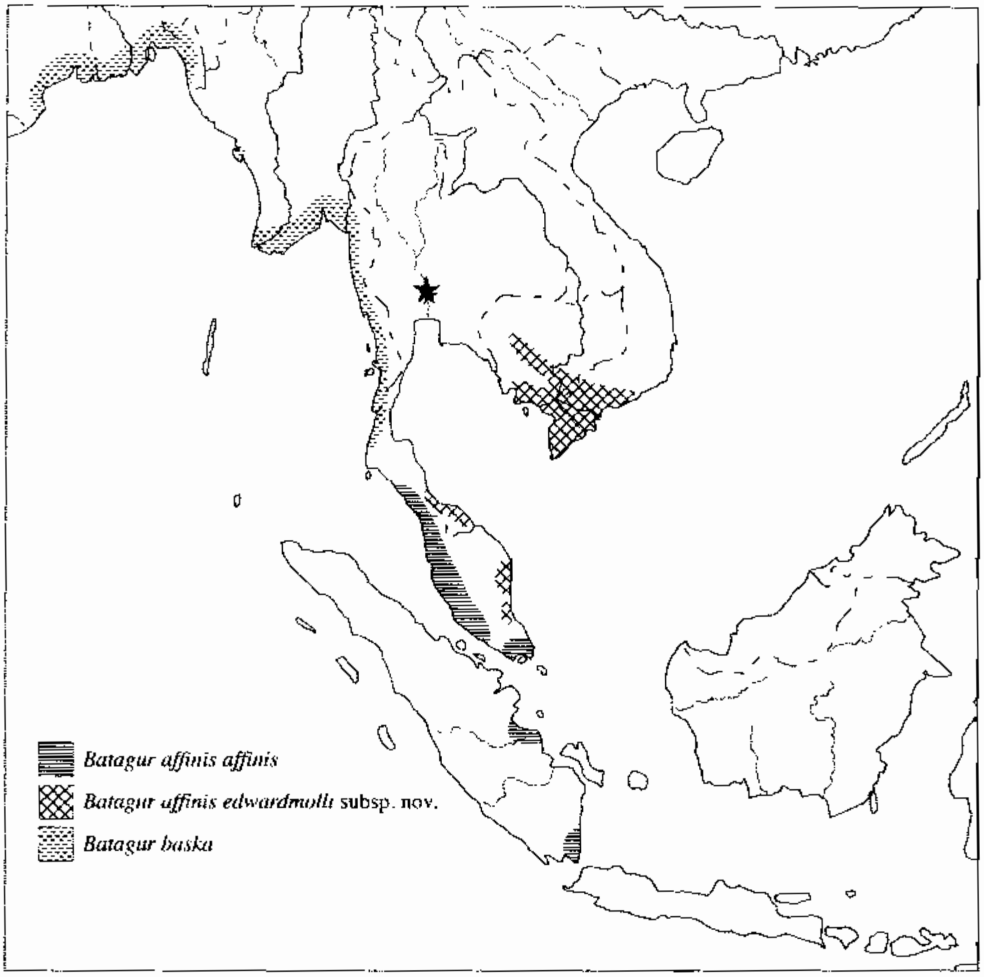

Figure 132 Distribution of *Batagur affinis affinis*, *B. affinis edwardmolli*, and *B. baska* (Prashag *et al*., 2009, p 65, Fig. 5). *Batagur baska* in Keet Khin locality indicated by black star.

Systematic paleontology

Order Testudines Linnaeus, 1758

Suborder Cryptodira Cope, 1868

Superfamily Testudinoidea Batsch, 1788

Family Geoemydidae Theobald, 1868

Heosemys annandalii Boulenger, 1930

(Figure 133)

Material: A cast of a complete carapace (KK-2006)

The material is kept in Silapakorn Universtiy, Bangkok, Thailand.

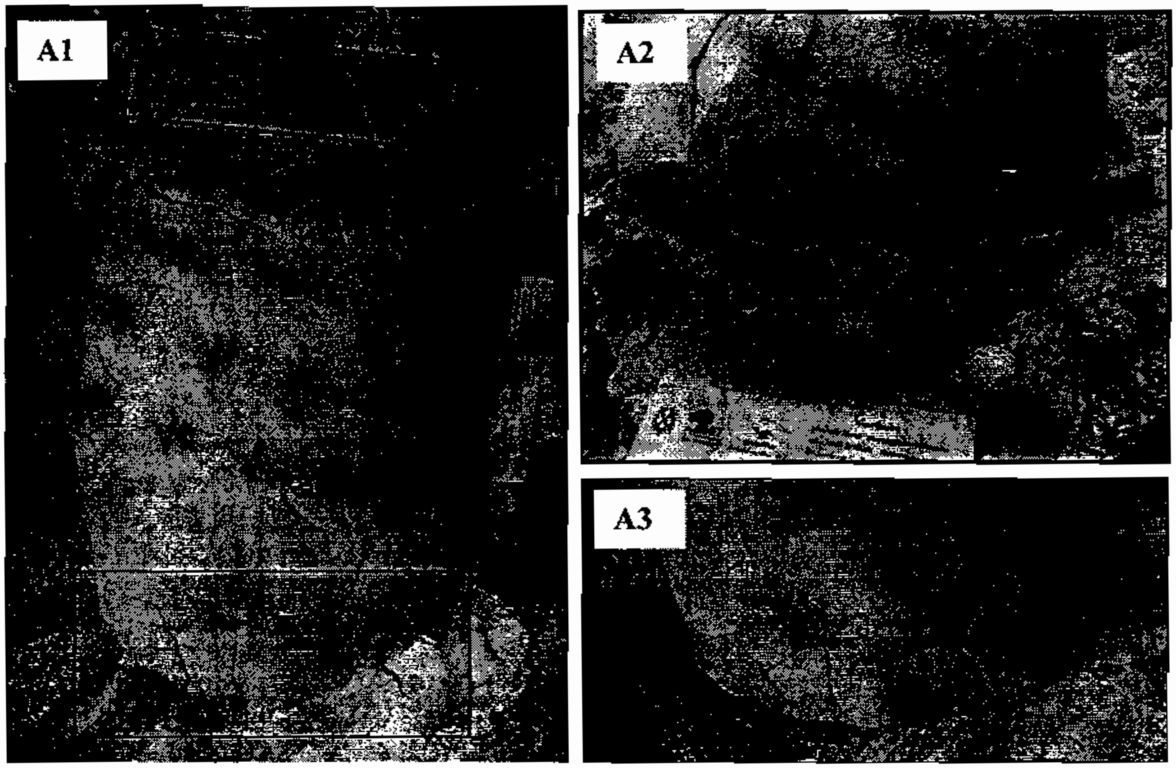

Figure 133 A complete carapace cast of *Heosemys annandalii* Boulenger, 1930 in dorsal view from Keet Khin, Saraburi Province, Thailand; the whole carapace (**A1**), anterior part with two holes (**A2**) and posterior part of carapace (**A3**).

Description:

The carapace is elongated and high. It has a vertebral keel which is distinct on the anterior and posterior part of shell (Figure 133, A1 and A3). Two holes are rounded present in the anterior part of the carapace. The anterior margin of carapace is rather smooth while the posterior margin is slightly serrated (Figure 133, A3). The scute sulci can be observed but sutures cannot be clearly seen from the cast. The cervical scute is large, triangular in shape shape and concave posteriorly (Figure 133, A2). The anterior margin of the nuchal is rather straight. There are five vertebral scutes. Most of them are longer than wide. The first vertebral scute is elongated and its anterior margin is narrower than its posterior margin. The third to fourth vertebral scutes are hexagonal and increase in length from the anterior to the posterior ones. The fifth vertebral scute is hexagonal with short posterolateral side. The first pleural scute is longer than wide. The second to fourth pleural scutes are wider than long. The first marginal scute is wide and long. The second and the third marginal scutes are mesio-laterally expanded. The lateral marginal scutes are long. The posterior marginal scutes are long. The pleuro-marginal sulcus is situated on the proximal part of peripheral plates. This sulcus is located more closely to the costo-peripheral suture. The posterior margin of pygal plate presents a tiny pygal notch.

Comparison and discussion:

The specimen can be referred to Geomydidae on the basis of the pleuro-marginal sulcus that is located below the costo-peripheral suture as in the Geomydidae. This specimen belongs to large geoemydid species as indicated by the size of the carapace. Large geoemydid correspond to the genera *Heosemys* and *Batagur* in Southeast Asia. The specimen can be excluded from *Batagur* which have an oval carapace outline with flattened posterior part and smooth anterior and posterior margins. This specimen can be assigned to *Heosemys*. Large *Heosemys* consists of *H. annandalii* and *H. grandis* while *H. spinosa* and *H. depressa* have smaller size in adult size by comparison with the specimen. *Heosemys grandis* is characterized by the anterior margin of nuchal that is emarginated, the posterior margin of carapace that is strongly serrated, by a small triangular cervical scute, and by a distinct vertebral keel while *H. annandalii* is characterized by the anterior margin of nuchal that is rather straight, the posterior margin of carapace that is slightly serrated, by a large triangular cervical scute, and by an indistinct vertebral keel. According to characters above, the specimen morphology is comparable with *Heosemys annandalii*. The presented holes are not by natural. This holes may have allowed humans to keep or to carry the species by using a rope.

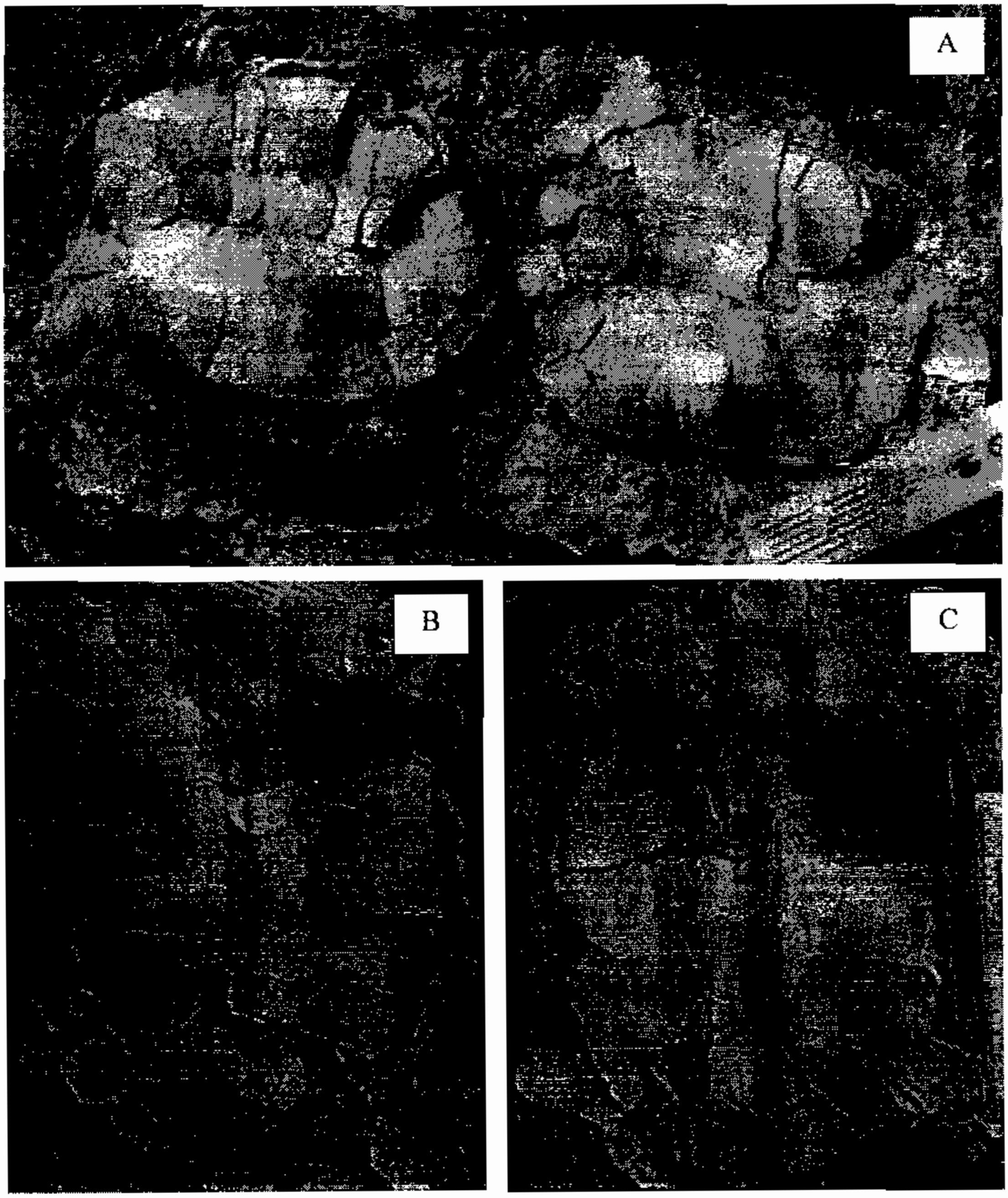

Figure 134 Nearly complete carapaces of *Malayemys* sp. in dorsal view from Keet Khin, Saraburi Province, Thailand; two carapaces (**A**), carapace (KK-2007a) (**B**) and right individual carapace (KK-2007b).

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Geoemydidae Theobald, 1868
Genus *Malayemys* Lindholm, 1931
Malayemys sp.
(Figure 134)

Material: Two nearly complete carapace (KK-2007a and KK-2007b)

The material is kept in Silapakorn Universtiy, Bangkok, Thailand.

Description:

The two turtles were preserved so that their posterior margin was in contact to each other (Figure 134). The KK-2007a is nearly complete carapace but the lateral end of costal and from the third right peripheral to pygal are broken while KK-2007b is broken on the left of the lateral end costal, left peripherals to posterior carapace (Figure 134). These shells are similar in size (about 20 cm). The anterior and posterior margins of carapace are rather smooth (Figure 134, B and C). These carapaces present distinct tricarinated keels. The scute sulci are slightly impressed. The nuchal plate is hexagonal in shape. The anterior and posterior margins are straight (Figure 134, B). The eight neurals are preserved. The first neural plate is oval shape. The second to eight neural plates are hexagonal with short anterolateral side. They are wider than long. The suprapygals are damaged, and their shape can not be determined clearly on any of the two casts of the specimen I could examine. The pygal is missing. Costal plates are small and slender except the first which is the longest. Peripheral plates are preserved from the first to ninth peripheral plates on the left side for KK-2007a and from the right first the eighth peripherals for KK-2007b. The first to the third peripheral plates are trapezoid in shape and mesio-laterally expanded. The fourth to the sixth peripheral plates are narrow. The seventh to the ninth peripheral plates are wide and mesio-laterally expanded. The scute sulci are slightly impressed. The cervical scute is triangular shape, it is narrower in KK-2007a (Figure 134, B) by comparison to KK-2007b (Figure 134, C). Its anterior and posterior margins are straight. The second to fourth vertebral scutes are hexagonal with short anterolateral side. The first vertebral scute is small and narrower than others. It is pentagonal in shape. The fifth vertebral scute cannot be observed clearly on both specimens. The first pleural scute is longer than wide. It contacts the first to the fifth marginal scutes. The second pleural scute contacts with the fourth pleural scutes. It is wider than long. The marginal scutes have expanded mesiolaterally margins. The marginal scutes covering the bridge are rectangular. The posterior marginal scutes are short and wide. The pleuro-marginal sulcus is situated below costo-peripheral suture nearly middle of peripherals. There is a circular hole at the anterior part of both carapace. The plastron cannot be observed on the cast I have examinated.

Comparison and discussion:

Tricarinated smooth carapaces are only found in Geoemydidae in Asia. Three keeled geoemydids are divided into two major groups (see Claude *et al.*, 2007), one group consisting of *Malayemys*, *Orlitia* and *Batagur* complex and the other one is *Melanochelys* complex. These specimens differ from the *Melanochelys* group which have hexagonal with short posterolateral side neurals and elongated lateral vertebrals. The neural shape of the specimens is more similar to the first group. *Orlitia* and *Batagur* differs from the fossil because they have elongated neurals while *Malayemys* have wider than long neural which is similar to these material and in other respect.

Recently, *Malayemys* genus was classified into two species members including *Malayemys subtrijuga* and *M. macrocephala* (Brophy, 2004). The difference between these two species is based on mainly external morphology, number of nasal strips, infraorbital strips, and supraorbital strips. In the geomorphometrics part of this dissertation, I showed that the carapace shape of *Malayemys* does not follow the strip pattern, therefore, this difficult to identify this at the species level in this subfossil. It is, however, similar to the Central plain morphology (and then probably may mostly correspond to *M. macrocephala*).

The shape of cervical scute of both specimens are different, (KK-2007a) is narrow triangular and another one (KK-2007b) is wide triangular cervical scute. This character probably is concerned with variation.

The presence of a circular hole on carapace nearly at the same position in both carapaces and as in *Heosemys annandalii* suggest that this turtle was similarly used by humans. However, the largest species had two holes, certainly for insuring that it could not break.

CHAPTER 6

GENERAL CONCLUSION AND DISCUSSION

This study provides for the first time an exhaustive inventory of living trionychid shell morphology in Southeast Asia. This inventory can still be improved by the inclusion of some genera such as *Palea*. However, the comparisons show that one can identify species based on carapace and plastral character. A taxonomical key hinging on skeletal characters is provided for living species.

For completing the work of my master degree, problematic genera presenting several taxonomic entities in Thailand are reanalyzed by the way of the available litterature, or by field survey. In particular the morphological variation of *Malayemys* is reassessed by the way of geometric morphometrics. Two groups of morphologies are recognized for the plastron and the carapace: one localized in the Central plain (Chao Phraya river basin) and one localized in Northeastern Thailand (Mun, Chi and Mekhong basins). The distribution of carapace morphologies does not match completely with head stripe pattern that has been used for recognizing both species. The conflict between morphological characters should be now resolved by the way of molecular data. However the congruence of information between plastron and carapace, suggests that the morphological species could probably be better discriminated on the basis of the carapace morphologies, opening the opportunity to identify *Malayemys* species also in the fossil and archaeological record.

Twenty one taxa are at least represented and discribed from the Miocene to Holocene of Thailand in this study, extending our knowledge on Thai fossil turtles in the Neogene until recent time. Summary of turtle fossil and sub-fossil taxa is shown in Table 6.1.

The three Miocene turtle localities (Ban Na Sai, Lumphun Province; Chiang Muan, Phayao Province and Mae Moh, Lampang Province) differ in the assemblage that they display. In Ban Na Sai locality three taxa including cf. *Amyda*, Trionychidae indet. and Geoemydidae indet were found. At least two, maybe three geoemydid turtles are known from the late Middle-early Late Miocene Chiang Muan. A new species of *Cuora*, *Cuora chiangmuanensis* sp. nov. (Naksri *et al.*, 2013) was discovered. The new

Cuora taxa helps to better understanding the history of the genus and the diversity of living *Cuora*. The last Miocene locality in this study, Mae Moh have yielded two taxa including Trionychidae nov. gen et sp. and Geoemydidae indet. While Chiang Muan is dominated by geoemydids, Mae Moh locality is dominated by trionychids; and Na Sai is intermediary between the two ones. It may indicates different environments between localities (or at least between the layers that yielded the fossils). Indeed, while trionychids are typically freshwater, geoemydids are more semi- terrestrial. This may also indicate that taxonomic assemblages changed during the Middle and Late Miocene. But a more systematic collecting of fossil material in these localities is needed for better understanding the stratigraphical and environmental differences between the Miocene localities.

The Miocene turtles consist of nine taxa belonging to two modern families, Geoemydidae and Trionychidae. The trionychid turtles is the first record in the Tertiary (they are not known from the Eocene or the Oligocene), and their diversity seems already high in the Miocene of Thailand. They were probably arriving in Thailand by the way of migration. The fossil record of adjacent territories being scanty, it should be also investigated for confirming this view. The Geoemydidae, by contrast are known since the late Eocene and are found in all localities. They were found first in Thailand since the late Eocene-early Oligocene (Tong et *al.*, 2006; Claude *et al.*, 2007). However, most of the specimens are fragmentary and are difficult to identify at the species level. Some are interesting for understanding the evolution of modern genera. For instance, *Cuora chiangmuanensis* provides the earliest record of the genus in 11-12 Ma (Middle Miocene or early Late Miocene) which suggests that Asian box turtles started to be present in Southeast Asia as soon as the Miocene. This is the earliest record of that genus in Asia and it documents an important part of the evolutionary history of Asian box turtles.

The Plio-Pleistocene turtles were studied from Tha Chang sandpit locality and Khok Sung locality, Nakhon Ratchasima Province. Turtles from Khok Sung, Nakhon Ratchasima Province are composed of six taxa including of *Batagur* cf. *trivittata*, *Chitra* sp. cf. *Amyda* sp., *Heosemys annandalii* and *Heosemys* cf. *grandis* (Claude *et al.*, 2011). They belong to living taxa. The discovery of *Batagur* cf. *trivittata* indicated an environment dominated by a large river system which is different from what today is.

giant tortoises from Tha Chang sandpits are assigned to *?Megalochelys*. Other fossil giant tortoises have been also reported from India, Indonesia (Java, Sulawesi, and Flores islands), Timor, Myanmar and now from Thailand. These indicate a very large distribution of giant turtles in mainland South and Southeast Asia during the Plio-Pleistocene.

The Holocene turtle record here principally comes from caves and archeological sites including Khok Farang, Buriram Province; Thammamongkol cave, Phetchaburi Province; Taling Tong, Sukhothai Province; Raksai cave, Phetchaburi Province and Kheet Khin, Saraburi Province. At Khok Farang, *Indotestudo elongata* is present. Thammamongkol cave has yielded *Indotestudo elongata* and *Heosemys grandis*. For Taling Tong, *Amyda cartilagenea* and *Heosemys grandis* can be identified. Raksai cave has yielded *Indotestudo elongata* and while Kheet Khin locality has yielded *Batagur baska, Heosemys annandalii* and *Malayemys* sp.

Indotestudo elongata is a land tortoise often found in archeological sites because it is a common species in Thailand especially for hilly area. The presence of this species in the localities is often associated with hunting or rituals. This species has also been reported to be hunted for local consumption in Thailand (Jenkins, 1995 in Sriparateep *et al*., 2013). The presence of cutting marks on *Batagur baska*, *Heosemys annandalii* and *Malayemys* sp. probably suggested that these species were consumed or used by human. The presence of *Batagur* in Saraburi Province during historical time shows that the distribution of living turtles evolved rapidly (or that this species could have been transported on long distance by humans for subsistence), maybe because of human activities (hunting) or other activities associated with landscape change. However, there are still several archeological sites in which several turtles have been found but rarely identified at the species level (Auetrakulvit, 2004) and an exhaustive inventory is now needed.

Table 6.1 Summary of Thai fossil and sub-fossil turtles from the Miocene to Holocene

Age	**Locality**	**Fossil and sub fossil taxa**
Miocene	1. Ban Na Sai	cf. *Amyda*
		Geoemydidae indet.
		Trionychidae indet.
	2. Mae Moh	Trionychidae n.g.et sp.
		Geoemydidae indet.
	3. Chiang Muan	*Cuora chiangmuanensis* sp.nov*
		cf. *Cuora chiangmuanensis*
		Testudinoidea indet.
Pleistocene	1. Khok Sung **	*Batagur* cf. *trivittata*
		Heosemys annandalii
		Heosemys cf. *grandis*
		Malayemys sp.
		Chitra sp.
		cf. *Amyda* sp.
	2. Tha Chang	? *Megalochelys*
Holocene	1. Khok Farang	*Indotestudo elongata*
	2. Thamma Mongkol cave	*Indotestudo elongata*
		Heosemys grandis
	3. Taling Tong	*Amyda cartilagenea*
		Heosemys grandis
	4. Raksai cave	*Indotestudo elongata*
	5. Keet Khin	*Batagur baska*
		Heosemys annandalii
		Malayemys sp.

Remarks *Naksri *et al.*, 2013 and **Claude *et al.*, 2011

Prospective research

1. Turtles in archeological sites are very interesting for understanding past distribution of living species and human impact on diversity. An exhaustive inventory is needed.

2. The Thai fossil record of turtles is important, this study shows that going on the field significantly help for increasing our knowledge.

3. Morphometric methods could be applied to *Cyclemys* species for better understanding their distribution and anatomical differences. *Cyclemys* could be a good candidate since its taxonomy was only recently reworked and because two (or three) species are probably present in Thailand. It would also be interesting to include more localities for analysing *Malayemys* morphological variation. Finally, it would be also interesting to make these morphometric studies in associating them with molecular data.

4. Cooperating with molecular biologists could be very useful for defining taxonomic units (*Malayemys*), in this respect, sampling around Saraburi and Eastern Thailand may help to precisely localize the hybridation line (if it exists between the two morphological groups).

REFERENCES

REFERENCES

Auetrakulvit, P. (2004). *Faunes du Pléistocène final à l'Holocène de Thaïlande: approche archéozoologigue*. PhD thesis. Marseille: Université Aix-Marseille I. (in French).

Aowphol, A. & Thirakhupt, K. (2010). Geographic distribution of the Mekong snail-eating turtle, *Malayemys subtrijuga* and the Malayan snail-eating turtle, *Malayemys macrocephala*. 14th BRT annual Meeting, Ubon Ratchathani, 10-12 October. (Abstract).

Benammi, M. Urrutia-Fucugauchi, J., Alva-Valdivia, L. M., Chaimanee, Y., Triamvichanon, S. & Jaeger, J. J. (2002). Magnetostratigraphy of the Middle Miocene continental sedimentary sequences of Mae Moh basin in northern Thailand: evidence of counterclockwise block rotation. *Earth and Planet. Sci. Lets.*, 204, 373-383.

Bookstein, F. L. (1991). *Morphometrics tool for landmark data: geometry and biology*. Cambridge: Cambridge University Press.

Bonin, F., Devaux, B. & Dupré, A. (2006) Turtles of the world. *In: English translation: The Johns Hopkins University Press, London.*

Bourret, R. (1941). Les tortues de I'Indochine. *Notes de I'institut Océanographique de I'Indochine*. 38, 1-235.

Broin de, F. (1984). *Proganochelys ruchae* n. sp., Chélonien du Trias supérieur de Thaïland. *Studia Geologica Salamanticensia*. vol. spcial 1 (Studia Palaeocheloniologica I), 87-97.

Broin de, F., Ingavat, R., Sattayarak, N. & Janvier, P. (1982). Triassic turtle remains from northeastern Thailand. *Journal of Vertebrate Paleontology*, 2, 41-46.

Brophy, T. R. (2004). Geographic variation and systematics in the South-East Asian turtles of the genus *Malayemys* (Testudines : Bataguridae). *Hamadryad*, 29, 63-79.

Cervelli, M., Oliverio, M., Bellini, A., Bologna, M., Cecconi, F., Mariottini, P. (2003). Structural and sequence evolution of U17 small nucleolar RNA (snoRNA) and its phylogenetic congruence in chelonians. *Journal of Molecular Evolution*, 57, 73-84.

Chaimanee, Y., Yamee, C., Tian, P., Khaowiset, K. (2005). *Fossils and their managements at Ban Khok Sung, Muang District, Nakhon Ratchasima Province, NE Thailand.* Acedemic report no. DMR 25/2005. Department of Mineral Resource, Bangkok: Thailand. 60 p. (In Thai).

Chiari, Y. & Claude, J. (2011). Study of the carapace shape and growth in two Galapagos tortoise lineages. *Journal of Morphology*, 272, 379-386.

Chiari, Y. & Claude, J. (2012). Morphometric identification of individuals when there are more shape variables than reference specimens: a case study in Galapagos tortoises. *Comptes rendus Biologies,* 335, 62-68.

Claude, J. (2008). *Morphometrics with R*. New York, Springer. 316 p.

Claude, J., Naksri, W., Boonchai, N., Buffetaut, E., Duangkrayom, J., Laojumpon, C., Jintasakul, P., Lauprasert, L., Martin, J., Suteethorn, V. &Tong, H. (2011). Neogene reptiles of northeastern Thailand and their paleogeographical significance. *Annales de Paléontologie*, 97(3-4), 113-131.

Claude, J., Pritchard, P.C.H., Tong, H., Paradis, E. & Auffray, J. C. (2004). Ecological correlates and the Evolutionary Divergence of the Skull of Turtles: a Geometric Morphometric Assessment. *Systematic Biology*, 56, 937-952.

Claude, J., Suteethorn, V. & Tong, H. (2007). Turtles from the terminal Eocene-basal Oligocene of the Krabi Basin (Thailand). *Bulletin de la Société Géologique de France*, 178, 305-316.

Claude, J. & Tong, H. (2004). Early Eocene turtles from Saint Papoul, France, with the comments on the early evolution of modern Testudinoidea. *Oryctos*, 5, 71-113.

Claude, J., Tong, H., Paradis, E. & Auffray, J. C. (2003). A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. *Biological Journal of the Linnean Society*, 79, 485-501.

Cuny, G., Laojumpon, C., Cheychiw, O. & Lauprasert, K. (2010). Fossil vertebrate remains from Kut Island (Gulf of Thailand, Early Cretaceous). *Cretaceous Research*, 31, 415-423.

Department of Mineral Resources. (2001). *Geology of Thailand.* Department of Mineral Resources. 556 p.

Dryden, I. E. & Mardia, K. V. (1998). *Statistical Shape Analysis*. Wiley, Chichester.

Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J.J. (1994). Ages and paleoenvironment of Miocene mammalian faunas from Thailand. *Palaeogeography,Palaeoclimatology, Palaeoecology*, 108(1-2), 108, 149-63.

Ernst, C. H. & Barbour, R. W. (1989) *Turtles of the world*. Washington, D. C., Smithsonian Institution Press.

Farkas, B., Le, D.M., Nguyen, Q.T. (2010). *Rafetus vietnamensis* Le, Le, Tran, Phan, Phan, Tran, Pham, Nguyen, Nong, Phan, Dinh, Truong and Ha, 2010-another invalid name for an invalid species of softshell turtle (Reptilia: Testudines: Trionychidae). *Russian Journal of Herpetology*, 18 (1), 65-72.

Farkas, B. & Webb, R. G. (2003). *Refetus leloii* Ha Dinh Duc, 2000--an invalid species of softshell turtle from Hoan Kiem Lake, Hanoi, Vietnam (Reptilia, Testudines, Trionychidae), *Zoologische Abhandlungen*, 53, 107-112.

Fritz, U., Guicking, D., Auer, M., Sommer, R.S., Wingk, M., Hundsdorfer, A.K. (2008). Diversity of the Southeast Asian leaf turtle genus *Cyclemys*: how many leaves on its tree of life? *Zoologica Scripta*, 37, 367-390.

Gaffney, E. S. (1979). Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History*, 164, 65-376.

Guillot, G., Renaud, S., Ledevin, R., Michaux, J. & Claude, J. (2012). A unifying model for the analysis of phenotypic, genetic and geographic data. *Systematic Biologists*, 61(5), 897-911.

Goodall, C. R. (1991). Procrustes methods in the statistical analysis of shape (with discussion). *Journal of the Royal Statistical Society*, Series B, 53, 285-339.

Kamolrat, K., Madkhamme, T. & Wongworapol, M. (2011). *Diversity of mammals in Raksai cave, Petchaburi Province*. Senior project. Mahasarakham University.

Kitimasak, W., and Thirakhupt, K. (2002). New record of *Chitra chitra* Nutphand, 1986 in Mae Ping River, Thailand. *The Natural History Journal of Chulalongkorn University* 2(1), 62-63.

Kitimasak, W. (2002). *Natural history and captive breeding of the Siamese Narrow-headed softshell turtle* Chitra chitra *Nutphand, 1986*. Doctor's Thesis. Biological Science Program, Faculty of Science, Chulalongkorn University. 128 pp.

Klingenberg, C. P. & McIntyre, G. S. (1998). Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution*, 54, 1363-1375.

Krenz, J.G, Naylor, G.J.P, Shaver, H. B., Janzen, F.J. (2005). Molecular phylogenetics and evolution of turtles. *Molecular Phylogenetics and Evolution,* 37, 178–191.

Kunimatsu, Y., Ratanasthien, B., Nakaya, H., Saegusa, H. & Nagaoka, S. (2004). Earliest Miocene hominoid from Southeast Asia. *American Journal of Physical Anthropology*, 124, 99-108.

Le, T. B., Le, Q. H., Tran, M. L., Phan, T. H., Phan, M. T., Tran, T. T. H., Pham, T. T., Nguyen, D. T., Nong, V. H., Phan, V. C., Dinh, D. K., Truong, N. H. & Ha, D. D. (2010). Comparative morphological and DNA analysis of specimens of giant freshwater soft-shelled turtle in Vietnam related to Hoan Kiem Turtle. *Tạp chí Công nghệ Sinh học*, 8(3A), 949-954.

Lourenco, J. M., Claude, J., Galtier, N., Chiari, Y. (2012). Dating cryptodiran nodes: Origin and diversification of the turtle Superfamily Testudinoidea. *Molecular Phylogenetics and Evolution*, 62, 496-507.

Martin, J., Buffetaut, E., Naksri, W., Lauprasert, K. & Claude, J. (2012). *Gavialis* from the Pleistocene of Thailand and its relevance for drainage connections from India to Java. PLoS ONE. 7(9): e44541. doi:10.1371/journal.pone.0044541 (In press)

McCord, W. P. & Pritchard, P. C. H. (2002). A review of the softshell turtles of the genus *Chitra*, with the description of new taxa from Myanmar and Indonesia (Java). *Hamadryad*, 27, 11-56.

Meylan, P. A. (1987). The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bulletin of the American museum of Natural History*, 186, 1-101.

Mustoe, G. E. & Girouard, S. P. (2001). A fossil trionychid turtle from the early Tertiary Chuckanut Formation of Northwestern Washington. *Northwest Science*, 75(3), 211-218.

Nakaya, H, Saegusa, H., Kunimatsu, Y. & Ratanasthien, B. (2002). Miocene mammalian faunas of Northern Thailand and their geological age. *Primate Research*, 18, 131-141.

Naksri, W. (2007). *Appraisal of the evolution of testudinoid turtles diversity from the Late Palaeogene and Neogene of Thailand.* Master thesis. Mahasarakham University.

Naksri, W., Tong, H., Lauprasert, K., Suteethorn, V. & Claude, J. (2013). A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance. *Geological Magazine*, 150, 908-922. doi:10.1017/S0016756812001082.

Naksri, W., Tong, H., Lauprasert, K., Suteethorn, V., Srisuk, P. & Claude, J. (2012). *The Late Oligocene Turtle Assemblage from Nong Ya Plong, Petchaburi Province, Thailand.* Symposium on turtle evolution, University of Tübingen, Germany, 2-4 June 2012. p. 31. (Abstract).

Nutaphand, V. (1979). *The turtles of Thailand.* Bangkok: Siamfarm Zoological Garden, 222 pp.

Obst, F.J. (1986). *Turtles, Tortoises and Terrapins.* New York, St. Martin's press. 231 pp.

Parham, F. J., Feldman, R. C., Boore, L. J. (2006). The complete mitochondrial genome of the enigmatic bigheaded turtle (*Platysternon*): description of unusual genomic features and the reconciliation of phylogenetic hypotheses based on mitochondrial and nuclear DNA. *BMC Evolutionary Biology*, 6, 11.

Pickford, M., Nakaya, H., Kunimatsu, Y., Saegusa, H., Fukuchi, A. & Ratanasthien, B. (2004). Age and taxonomic status of the Chiang Muan (Thailand) hominoids. *Comptes Rendus Palevol*, 3, 65-75.

Pramjai, K. (2010). *Preliminary report on an archeological site of Khok Farang*(in Thai). n.p.: n.p.

Praschag, P., Hundörfer, A. K., Reza, A. H. M. A. & Fritz, U. (2007). Genetic evidence for wild-living *Aspideretes nigricans* and a molecular phylogeny of South Asian softshell turtles (Reptilia: Trionychidae: *Aspideretes*, *Nilssonia*). *Zoologica Scripta*, 36, 301-310.

Prashag, P., Holloway, R., Georges, A., Päckert, M., Hundsdörfer & Fritz, U. (2009). A new subspecies of *Batagur affinis* (Cantor, 1847), one of the world's most critically endangered chelonians (Testudines: Geoemydidae). *Zootaxa*, 2233, 57-68.

Pritchard, P. C. H. (1979). *Encyclopedia of Turtles*, Neptune City, T.F.H. Publications. n.p.: n.p.

Pritchard, P. C. H. (2000). *Indotestudo travancorica*- a valid species of tortoise? Reptile & Amphibian Hobbyist, Feb. 2000, 18-28.

Pritchard, P. C. H., Rabett, R. J. & Piper, P. J. (2009). Distinguishing species of Geoemydid and Trionychid turtles from shell fragments: evidence from the Pleistocene at Niah Caves, Sarawak. *International Journal of Osteoarcheology*, 19, 531-550.

Pyopyo (2012). *Thai custom and human burials in Thailand from archeological evidence*. Blog: WordPress.com. (in Thai)

Racey, A. (2009). Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. Special Publications. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London, *Geological Society*, Special Publication, 315, 41-67.

Raup, M.D. (1981). Extinction: bad genes or bad luck?. *Acta Geologica Hispanica*. Concept and method in Paleontology. 16(1981) n^{os} 1-2, 25-33.

R Development Core Team (2010). *R: A language and environment for statistical computing*. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org.

Rivera, G. & Claude, J. (2008). Environmental media and shape asymmetry: a case study on turtle shells. *Biological Journal of the Linnean Society*, 94, 483-489.

Rohlf, F.J. (2004) .tpsDig. [online]. From http://life.bio.sunysb.edu/morph/. [accessed 23 junly 2012].

Rohlf, F. J. (1990). Rotational fit (Procrustes) method. In: Rohlf, F. J., Bookstein, F. L. (eds.) *Proceedings of the Michigan morphometrics workshop*. Ann Arbor: University of Michigan Museum of Zoology, 227-236.

Silaratana, T., Ratanasthien, B., Takayasu, K., Fyfe, W. S., Asnachinda, P., Kandharosa, W. & Kusakabe, M. (2004). Sulfur Isotopic Implication of Middle Miocene Marine Incursion in Northern Thailand. *Science* Asia, 30, 43-58.

Songtham, W, Ratanasthien, B., Mildenhall, D.C., Singharajwarapan, S. & Kandharosa, W. (2003). Oligocene-Miocene climatic changes in Northern Thailand resulting from extrusion tectonics of Southeast Asian landmass. *Science Asia*, 29, 221-233.

Smith, M. A. (1931). The fauna of British India, including Ceylon and Burma. *London* 1, 49-179.

Snansieng, S. & Maneekut, N. (1985). Li basin, an analysis of the oldest Cenozoic basin of Thailand. *Journal of the* Geological Society *of Thailand*, 8(1-2), 29-35.

Sriprateep, K., Aranyavalai, V., Aowphol, A. & Thirakhupt, K. (2013). Population structure and reproduction of the elongated tortoise *Indotestudo elongata* (Blyth, 1853) at Ban Kok Village, northeastern Thailand. *Tropical Natural History*, 13(1), 21-37.

Srisuk, P. (2005). Trionychid turtles from the Middle Miocene of northern Thailand. *Bulletin of the Srisuk's House Museum, Series A (Palaeontology)*, 6(1), 8-26.

Srisuk, P. (2007). Turtle remains from a Holocene cave deposit of western Thailand. *Bulletin of the Srisuk's House Museum, Series A (Palaeontology)*, 8(2), 47-55.

Stuart, B. L., van Dijk, P. P. & Hendrie, D. B. (2001). *Photographic guide to the turtles of Thailand, Laos, Vietnam and Cambodia*. Phnom Penh, Design Group.

Suganuma, Y., Hamada, T., Tanaka, S., Okada, M., Nakaya, H., Kunimatsu, Y., Saegusa, H., Nagaoka, S. & Ratanasthien, B. (2006). Magnetostratigraphy of the Miocene Chiang Muan Formation, Northern Thailand: implication for revised chronology of the earliest Miocene hominoid in Southeast Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 75-86.

Suteethorn, V., Chaimanee, Y., Buffetaut, E. & Jaeger, J.J. (1990). Vertebrate fossils in Thailand. *Development Geology for Thailand into the year 2000*. Chulalongkorn University, Bangkok, Thailand, 13-14 December 1990.

Taskavak, E. (1999). Cranial morphology of *Rafetus euphraticus* (Daudin, 1801) from Southeastern Anatolia. *Amphibia-Reptilia*, 20 (1), 35-53.

Taylor, E. H. (1970). The turtles and crocodiles of Thailand and adjacent waters. *Univ. Kansas Sci. Bull*, 49, 87-179.

Thasod, Y., Jintasakul, P., Ratanasthien, B. (2012). Proboscidean fossil from the Tha Chang sand pits, Nakhon Ratchasima Province, Thailand. *Journal of Scinece and Technology Mahasarakham University*, 31(1), 33-44.

Thasod, Y. (2007). Miocene mastodont in Thailand and paleoenvironment. Ph. D. thesis, The Graduate School, Chiang Mai University, 368 pp.

Thotsarat, R. & Kitngam, A. (2004). Report on excursion archeological site of Ban Suay, Phimai District, Nakhon Ratchasima Province. Bangkok: Office of Archeology, the Fine Arts Department. (in Thai)

Tong, H., Buffetaut, E. & Suteethorn, V. (2002). Middle Jurassic turtles from southern Thailand. *Geological Magazine*, 139, 687-697.

Tong, H., Claude, J., Buffetaut, E., Suteethorn, V., Naksri, W. & Chitsing, S. (2006). Fossil turtles of Thailand: an updated review. In: Lu, J.C., Kobayashi, Y., Huang, D & Lee, Y.-N (eds.) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Beijing, Geological Publishing House. pp. 183-184.

Tong, H., Claude, J., Naksri, W., Suteethorn, V., Buffetaut, E., Khansubha, S., Wongo, K. & Yuangdetkla, P. (2009a). *Basilochelys macrobios* n. gen. and n. and sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic-earliest Cretaceous) of the Khorat Plateau, NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., & Suteethorn, V. (eds.) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London, Geological Society, Special Publication, 315, 153-173.

Tong, H., Claude, J., Suteethorn, V., Naksri, W. & Buffetaut, E. (2009b). Turtle assemblages of the Khorat Group (Late Jurassic-Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In: Buffetaut, E., Cuny, G., Le Loeuff, J., & Suteethorn, V. (eds.) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London, Geological Society, Special Publication, 315, 141-152.

Tong, H. Buffetaut E., Claude, J., Jintasakul, P. & Suteethorn, V. (2005). The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. *International conference on geology, Geotechnology and Mineral resources of Indochina (GEOINDO 2005)*, 28-30 November 2005, Khon Kaen, Thailand.

Tong H, Buffetaut, E. & Suteethorn, V. (2006). *Isanemys*, a new adocid turtle from the Sao Khua formation (Early Cretaceous) of the Khorat Plateau, Northeastern Thailand. *Fossil Turtle Research*, 1, 128-137.

Turtle Taxonomy Working Group (van Dijk, P. P., Iverson, J. B., Shaffer, H. B., Bour, R., Rhodin, A. G. J.) (2011). Turtle of the world, 2011 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. *In*: Rhodin, A. G. J., Pritchard, P. C. H., van Dijk, P. P., Saumure, R. A., Buhlmann, K. A., Iverson, J. B., Mittermeier, R. A. (Eds.) Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5, pp. 000.165-000.242, doi:10.3854/crm.5.000.checklist. v4.2011, http://www.iucn-tftsg.org/cbftt/.

Wanchai, P., Standford, B.C., Pradatsundarasar, A., Tharapoom, K., & Thirakhupt, K. (2013). Activity budget of the impressed tortoise, *Manouria impressa* (Gunther, 1882), in Phu Luang Wildlife Sanctuary, Thailand. *Tropical Natural History*, 13(1), 39-48.

APPENDIXES

Appendix I

Sampling of individuals for the morphometric study on *Malayemys* carapace, Sampling of individuals for the morphometric study on the *Malayemys* plastron

Carapace sampling

The sample individuals of *Malayemys* in this study are all labeled. Six letters were used to generate the label. The first two characters correspond to the abbreviation of provinces as in Table 3.1. The third and fourth ones correspond to the specimen number in the locality. The fifth character corresponds to the sex, F=female, M=male, J=juvenile. The last letter correspond to the species identification according to Brophy (2004) characters, S=*Malayemys substrijuga and M= M. macrocephala*. This abbreviation is applied on both carapace and plastron samples.

BR01FM BR02FM BR03FS BR04FS BR05FS BR06FS
BR07FS BR10FS BR11FS BR12FM BR14FM BR15FS
BR16FS BR17FM BR19MS BR22MM BR24MM BR25MM
BR26MM BR28MM BR29FM
BR Total=21
BRM Total=11; BRMM=5 ; BRFM=6
BRS Total=10; BRMS=1 ; BRFS=9

SR01MS SR03FM SR04FS SR05FS SR06FS SR07MS
SR08FS SR09FS SR10FS SR12FS SR13FS SR14F
SR15MS SR16FM SR17MS SR18MS SR19MS SR20MS
SR21MS
SR Total=19
SRM Total=2; SRMM=0 ; SRFM=2
SRS Total=17; SRMS=8 ; SRFS=9

UB01FM UB02MM UB03FS UB04FM UB05FM UB06JM
UB07MS UB08JM UB10FM UB11MM UB12FM UB13JM
UB14MM UB15MS UB16JS UB17JS UB18JM UB19JM
UB20JM UB21FS UB22FS UB23FM UB24FM UB25MM
UB26MM UB27FM UB28MM UB30JM UB31FM
UB total= 29

UBM Total=22; UBMM=6; UBFM=9; UBJM=7
UBS Total=7; UBMS=2; UBFS=3; UBJS=2

CY01FM CY02FM CY03MM CY05FM CY06MM CY07FM
CY08MM CY09FM CY11MM CY12MM CY13MM CY14FM
CY15MM CY16MM CY17FM CY18FM CY19FM CY20MM
CY22JM CY23MM
CYM Total=20; CYMM=10; CYFM=9; CYJM=1

MH01FM MH02FM MH03FM MH04MM MH05MM MH06MM
MH07MM MH08MM MH09MM MH10MM MH11MM MH12MM
MH13MM MH14MM MH15MM MH16MM MH17MM MH18MM
MH19MM MH20MM MH21FM MH22FM MH23MM MH24MM
MH25MM MH26MM MH27FM MH28MM MH30MM MH31FM
MH32MM MH33MM MH34JM
MHM Total=33
MHMM=25 MHFM=7; MHJM=1

RE01MM RE02MM RE03FM RE04MM RE05MM RE06MM
RE08MM RE09FM RE10FM
REM Total=9; REMM=6; REFM=3

YT01FM YT02FM YT03MM YT04JM YT05JM YT06JM
YT07JM YT08JM YT09MM YT10MM YT11FM YT12FM
YT13MM YT14MM YT15FM YT16FM YT17FM YT18FM
YT19FM YT20FM YT21MM YT22FM YT23FM YT25MM
YT28FM YT29MM YT30MM YT31FM YT32FM YT33MM
YT34MM YT35FM YT36MM YT38FM YT39FM YT40FM
YT41MM YT42MM YT43MM YT44MM YT45MM YT46MM
YT47JM YT48JM YT49JM YT50JM YT52JM YT54MM
YT55JM YT56MM YT57FM YT58MM YT59MM YT60MM
YT61MM YT62FM YT63FM YT64MM YT65JM

YT Total=59; YTMM=25; YTFM=22; YTJM=12

MD02MM MD03JM MD05MM MD06MM MD07JM MD08JM
MD09FM MD10FM MD11FM
MDM Total=9
MDMM=3; MDFM= 3; MDJM=3

LO01MM LO02MM LO03MM LO04FM LO05MM LO06MM
LO07MM
LOM Total=7; LOMM=6; LOFM=1

NP01FM NP02FM NP04FM NP05FM NP06MM NP08FM
NP09FM NP10MM NP11JM NP12MM NP13JM NP14JM
NP15FM NP18MM NP19MM NP20FM NP22MM NP23FM
NP25JM NP26JM NP27JM NP28JM NP30MM NP31MM
NP32MM NP33MM NP34MM NP35MM NP36JM NP37MM
NP38FM NP39MM NP40MM NP41MM NP42MM NP43JM
NP44JM NP45MM NP46MM NP47JM NP48MM NP49MM
NPM Total=42; NPMM=21; NPFM=10; NPJM=11

UT01FM UT02MM UT03FM UT04MM UT05MM UT06MM
UT08FM UT09MM UT10FM UT13MM UT14MM UT16FM
UT17FM UT18FM UT20FM UT21FM UT22MM UT23FM
UTM Total=18; UTMM=8; UTFM=10

NS01FM NS02MM NS03MM NS04MM NS05FM NS06FM
NS07FM NS08FM NS09FM NS10MM NS12FM NS13FM
NS14FM NS15FM NS16MM NS18FM NS19MM NS20MM
NS21FM NS22MM NS23FM NS24FM NS25MM NS26FM
NS27MM NS28FM NS29MM NS30FM NS31MM NS32FM
NS33MM NS34FM NS35FM NS36FM NS37FM NS38FM
NS39MM NS40FM NS41JM

NSM Total=39; NSMM=14; NSFM=24; NSJM=1

SB01FM SB02FM SB03MM SB04FM SB05FM SB06FM
SB07FM SB08FM SB09FM SB10FM SB11FM SB12FM
SB13FM SB14FM SB15MM SB16JM
SBM Total=16; SBMM=2; SBFM=13; SBJM=1

Plastron sampling

BR01FM BR02FM BR03FS BR04FS BR05FS BR06F
BR07FS BR08FS BR09MS BR10FS BR11FS BR12F
BR13FS BR14FM BR15FS BR16FS BR17FM BR18MS
BR19MS BR20MM BR21MS BR22MM BR23MM BR24MM
BR25MM BR26MM BR27FM BR28MM BR29FM

BR Total=29
BRM Total=14; BRMM=7 ; BRFM=7
BRS Total=15; BRMS=4 ; BRFS=11

SR01MS SR02MS SR03FM SR04FS SR05FS SR06FS
SR07MS SR08FS SR09FS SR10FS SR11MS SR12F
SR13FS SR14FS SR15MS SR16FM SR17MS SR18
SR19MS SR20MS SR21MS
SR Total=21
SRM Total=2; SRMM=0 ; SRFM=2
SRS Total=19; SRMS=10 ; SRFS=9

UB01FM UB02MM UB03FS UB04FM UB05FM UB06JM
UB07MS UB08JM UB09FM UB10FM UB11MM UB12
UB13JM UB14MM UB15MS UB16JS UB17JS UB18JM
UB19JM UB20JM UB21FS UB22FS UB23FM UB24FM
UB25MM UB26MM UB27FM UB28MM UB29JM UB30JM
UB31FM
UB total= 31
UBM Total=24; UBMM=6; UBFM=10; UBJM=8
UBS Total=7; UBMS=2; UBFS=3; UBJS=2

CY01FM CY02FM CY03MM CY04MM CY05FM CY06MM
CY07FM CY08MM CY09FM CY10JM CY11MM CY12MM
CY13MM CY14FM CY15MM CY16MM CY17FM CY18FM
CY19FM CY20MM CY21FM CY22JM CY23MM
CYM Total=23; CYMM=11; CYFM=10; CYJM=2

MH01FM MH02FM MH03FM MH04MM MH05MM MH06MM
MH07MM MH08MM MH09MM MH11MM MH12MM MH13MM
MH14MM MH15MM MH16MM MH17MM MH18MM MH19MM
MH21FM MH22FM MH23MM MH24MM MH25MM MH26MM
MH27FM MH28MM MH29FM MH30MM MH31FM MH32MM
MH33MM MH34JM
MHM Total=32
MHMM=23 MHFM=8; MHJM=1

RE01MM RE02MM RE03FM RE04MM RE05MM RE06MM
RE08MM RE09FM RE10FM
REM Total=9; REMM=6; REFM=3

YT01FM YT02FM YT03MM YT04JM YT05JM YT06JM
YT07JM YT08JM YT09MM YT10MM YT11FM YT13MM
YT14MM YT15FM YT16FM YT17FM YT18FM YT20FM
YT21MM YT22FM YT23FM YT24FM YT25MM YT26FM
YT27MM YT28FM YT29MM YT30MM YT31FM YT32FM
YT33MM YT34MM YT35FM YT36MM YT37MM YT38FM
YT39FM YT42MM YT43MM YT44MM YT45MM YT46MM
YT47JM YT48JM YT49JM YT50JM YT51MM YT52JM
YT53JM YT54MM YT55JM YT56MM YT57FM YT58MM
YT59MM YT60MM YT61MM YT62FM YT63FM YT64MM

YT65JM

YT Total=61; YTMM=27; YTFM=21; YTJM=13

MD01FM MD02MM MD03JM MD04JM MD05MM MD06MM
MD07JM MD08JM MD09FM MD10FM MD11FM

MDM Total=11

MDMM=3; MDFM= 4; MDJM=4

LO01MM LO02MM LO03MM LO04FM LO05MM LO06MM
LO07MM

LOM Total=7; LOMM=6; LOFM=1

NP01FM NP02FM NP03FM NP04FM NP05FM NP06MM
NP07FM NP08FM NP09FM NP10MM NP11JM NP12MM
NP13JM NP14JM NP15FM NP16MM NP17MM NP18MM
NP19MM NP20FM NP21MM NP22MM NP23FM NP24JM
NP26JM NP27JM NP28JM NP29FM NP30MM NP32MM
NP33MM NP34MM NP35MM NP36JM NP37MM NP38FM
NP39MM NP40MM NP41MM NP42MM NP43JM NP44JM
NP45MM NP46MM NP47JM NP48MM NP49MM NP50MM

NPM Total=48; NPMM=24; NPFM=13; NPJM=11

UT01FM UT02MM UT03FM UT04MM UT05MM UT06MM
UT07FM UT08FM UT09MM UT10FM UT11MM UT12MM
UT13MM UT14MM UT15FM UT16FM UT17FM UT18FM
UT19FM UT20FM UT21FM UT22MM UT23FM

UTM Total=23; UTMM=10; UTFM=13

NS01FM NS03MM NS04MM NS05FM NS06FM NS07FM
NS08FM NS09FM NS10MM NS11FM NS12FM NS13FM
NS14FM NS15FM NS16MM NS17MM NS18FM NS19MM
NS20MM NS21FM NS22MM NS23FM NS24FM NS25MM

NS26FM NS27MM NS28FM NS29MM NS30FM NS31MM
NS32FM NS33MM NS34FM NS35FM NS36FM NS37FM
NS38FM NS39MM NS40FM NS41JM
NSM Total=40; NSMM=14; NSFM=25; NSJM=1

SB01FM SB02FM SB03MM SB04FM SB05FM SB06FM
SB07FM SB08FM SB09FM SB10FM SB11FM SB12FM
SB13FM SB14FM SB15MM SB16JM
SBM Total=16; SBMM=2; SBFM=13; SBJM=1

Appendix II

Carapace data analysis performed with R.2.15.2,

Plastron data analysis performed with R.2.15.2

Carapace data performed with R.2.15.2

command by J. Claude

```
setwd("D:/data")
link<-
c(1:11,34,12:14,32,30,3,NA,1,29,31,32,NA,29,30,NA,5,14,NA,7,13,NA,9,12,NA,35,36
,11,34,33,35,NA,15:25,42,26:28,40,38,17,NA,15,37,39,40,NA,37,38,NA,19,28,NA,21,
27,NA,23,26,NA,42,41,43,44,25,42,NA,43,45,35,NA,44,46,36,NA,45,46,NA,10,24,NA
,22,8,NA,20,6,NA,4,18,NA,2,16,NA,1,15)

#####Maha Sarakham
a<-scan("maha1c.tps", what="character")
namem<-a[(1:68)*99-1]
namem<-sub("IMAGE=", "", namem)
namem<-sub(".JPG", "", namem)
Am<-array(NA, dim=c(48,2,68))
for (i in 1:68){Am[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Am)<-"numeric"
AM<-array(NA, dim=c(46,2,68))
for (i in 1:68){AM[,,i]<-(Am[3:48,,i]/dist(Am[1:2,,i])) * 5}
#29;63 removed because these specimens are abnormal
AM2<-AM[,,-c(29,63)]
namem2<-namem[-c(29,63)]
locma<-as.factor(substr(namem2,2,3))
indma<-as.factor(substr(namem2,2,5))
sexma<-as.factor(substr(namem2,6,6))

#####Ubon Ratchathani
a<-scan("ubon1c.tps", what="character")
nameu<-a[(1:62)*99-1]
nameu<-sub("IMAGE=", "", nameu)
nameu<-sub(".JPG", "", nameu)
```

```
Au<-array(NA, dim=c(48,2,62))
for (i in 1:62){Au[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Au)<-"numeric"
AU<-array(NA, dim=c(46,2,62))
for (i in 1:62){AU[,,i]<-(Au[3:48,,i]/dist(Au[1:2,,i])) * 5}
#9;29;40;60 removed because the specimens are abnormal
AU2<-AU[,,-c(9,29,40,60)]
nameu2<-nameu[-c(9,29,40,60)]
locub<-as.factor(substr(nameu2,2,3))
indub<-as.factor(substr(nameu2,2,5))
sexub<-as.factor(substr(nameu2,6,6))
```

#####Buriram

```
a<-scan("buri1.tps", what="character")
nameb<-a[(1:58)*99-1]
nameb<-sub("IMAGE=", "", nameb)
nameb<-sub(".JPG", "", nameb)
Ab<-array(NA, dim=c(48,2,58))
for (i in 1:58){Ab[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ab)<-"numeric"
AB<-array(NA, dim=c(46,2,58))
for (i in 1:58){AB[,,i]<-(Ab[3:48,,i]/dist(Ab[1:2,,i])) * 5}

#8;9;13;18;20;21;23;27;37;38;42;47;49;50;52;56 removed because the specimens are abnormal
AB2<-AB[,,-c(8,9,13,18,20,21,23,27,37,38,42,47,49,50,52,56)]
nameb2<-nameb[-c(8,9,13,18,20,21,23,27,37,38,42,47,49,50,52,56)]
locbr<-as.factor(substr(nameb2,2,3))
indbr<-as.factor(substr(nameb2,2,5))
sexbr<-as.factor(substr(nameb2,6,6))
```

```
#####Surin
a<-scan("suri1c.tps", what="character")
names<-a[(1:42)*99-1]
names<-sub("IMAGE=", "", names)
names<-sub(".JPG", "", names)
As<-array(NA, dim=c(48,2,42))
for (i in 1:42){As[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(As)<-"numeric"
AS<-array(NA, dim=c(46,2,42))
for (i in 1:42){AS[,,i]<-(As[3:48,,i]/dist(As[1:2,,i])) * 5}
#2;11,23,32 removed because these specimens are abnormal
AS2<-AS[,,-c(2,11,23,32)]
names2<-names[-c(2,11,23,32)]
locsr<-as.factor(substr(names2,2,3))
indsr<-as.factor(substr(names2,2,5))
sexsr<-as.factor(substr(names2,6,6))
#####Nakhon Phanom
a<-scan("nako1c.tps", what="character")
namen<-a[(1:100)*99-1]
namen<-sub("IMAGE=", "", namen)
namen<-sub(".JPG", "", namen)
An<-array(NA, dim=c(48,2,100))
for (i in 1:100){An[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(An)<-"numeric"
AN<-array(NA, dim=c(46,2,100))
for (i in 1:100){AN[,,i]<-(An[3:48,,i]/dist(An[1:2,,i])) * 5}
AN2<-AN[,,-c(3,7,16,17,21,24,29,50,53,57,66,67,71,74,79,100)]
namen2<-namen[-c(3,7,16,17,21,24,29,50,53,57,66,67,71,74,79,100)]
locnk<-as.factor(substr(namen2,2,3))
indnk<-as.factor(substr(namen2,2,5))
sexnk<-as.factor(substr(namen2,6,6))
```

```
#####Nakhon Sawan
a<-scan("nksw1.tps", what="character")
namek<-a[(1:82)*99-1]
namek<-sub("IMAGE=", "", namek)
namek<-sub(".JPG", "", namek)
Ak<-array(NA, dim=c(48,2,82))
for (i in 1:82){Ak[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ak)<-"numeric"
AK<-array(NA, dim=c(46,2,82))
for (i in 1:82){AK[,,i]<-(Ak[3:48,,i]/dist(Ak[1:2,,i])) * 5}
# 11,17,52,58 removed because these specimens are abnormal
AK2<-AK[,,-c(11,17,52,58)]
namek2<-namek[-c(11,17,52,58)]
locns<-as.factor(substr(namek2,2,3))
indns<-as.factor(substr(namek2,2,5))
sexns<-as.factor(substr(namek2,6,6))

#####Uthai Thani
a<-scan("uttn1c.tps", what="character")
namet<-a[(1:46)*99-1]
namet<-sub("IMAGE=", "", namet)
namet<-sub(".JPG", "", namet)
At<-array(NA, dim=c(48,2,46))
for (i in 1:46){At[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(At)<-"numeric"
AT<-array(NA, dim=c(46,2,46))
for (i in 1:46){AT[,,i]<-(At[3:48,,i]/dist(At[1:2,,i])) * 5}
AT2<-AT[,,-c(7,11,12,15,19,30,34,35,38,42)]
namet2<-namet[-c(7,11,12,15,19,30,34,35,38,42)]
locut<-as.factor(substr(namet2,2,3))
indut<-as.factor(substr(namet2,2,5))
sexut<-as.factor(substr(namet2,6,6))
```

```
#####Singburi
a<-scan("sing1c.tps", what="character")
namei<-a[(1:32)*99-1]
namei<-sub("IMAGE=", "", namei)
namei<-sub(".JPG", "", namei)
Ai<-array(NA, dim=c(48,2,32))
for (i in 1:32){Ai[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ai)<-"numeric"
AI<-array(NA, dim=c(46,2,32))
for (i in 1:32){AI[,,i]<-(Ai[3:48,,i]/dist(Ai[1:2,,i])) * 10}
locsb<-as.factor(substr(namei,2,3))
indsb<-as.factor(substr(namei,2,5))
sexsb<-as.factor(substr(namei,6,6))

#####Loei
a<-scan("loe11.tps", what="character")
namel<-a[(1:14)*99-1]
namel<-sub("IMAGE=", "", namel)
namel<-sub(".JPG", "", namel)
Al<-array(NA, dim=c(48,2,14))
for (i in 1:14){Al[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Al)<-"numeric"
AL<-array(NA, dim=c(46,2,14))
for (i in 1:14){AL[,,i]<-(Al[3:48,,i]/dist(Al[1:2,,i])) * 5}
loclo<-as.factor(substr(namel,2,3))
indlo<-as.factor(substr(namel,2,5))
sexlo<-as.factor(substr(namel,6,6))
```

```
#####Chaiyaphum
a<-scan("chac1.tps", what="character")
namec<-a[(1:46)*99-1]
namec<-sub("IMAGE=", "", namec)
namec<-sub(".JPG", "", namec)
Ac<-array(NA, dim=c(48,2,46))
for (i in 1:46){Ac[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ac)<-"numeric"
AC<-array(NA, dim=c(46,2,46))
for (i in 1:46){AC[,,i]<-(Ac[3:48,,i]/dist(Ac[1:2,,i])) * 5}
#4;10;21;27;33;44 removed because these specimens are abnormal
AC2<-AC[,,-c(4,10,21,27,33,44)]
namec2<-namec[-c(4,10,21,27,33,44)]
loccy<-as.factor(substr(namec2,2,3))
indcy<-as.factor(substr(namec2,2,5))
sexcy<-as.factor(substr(namec2,6,6))

#####Roi-Et
a<-scan("roie1c.tps", what="character")
namer<-a[(1:20)*99-1]
namer<-sub("IMAGE=", "", namer)
namer<-sub(".JPG", "", namer)
Ar<-array(NA, dim=c(48,2,20))
for (i in 1:20){Ar[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ar)<-"numeric"
AR<-array(NA, dim=c(46,2,20))
for (i in 1:20){AR[,,i]<-(Ar[3:48,,i]/dist(Ar[1:2,,i])) * 5}
#7;17 removed because these specimens are abnormal
AR2<-AR[,,-c(7,17)]
namer2<-namer[-c(7,17)]
locre<-as.factor(substr(namer2,2,3))
indre<-as.factor(substr(namer2,2,5))
```

```
sexre<-as.factor(substr(namer2,6,6))

#####Yasothorn
a<-scan("yaso1c.tps", what="character")
namey<-a[(1:130)*99-1]
namey<-sub("IMAGE=", "", namey)
namey<-sub(".JPG", "", namey)
Ay<-array(NA, dim=c(48,2,130))
for (i in 1:130){Ay[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ay)<-"numeric"
AY<-array(NA, dim=c(46,2,130))
for (i in 1:130){AY[,,i]<-(Ay[3:48,,i]/dist(Ay[1:2,,i])) * 5}
#24;26;27;37;51;53;89;91;92;102;116;118 removed because the specimens are abnormal
AY2<-AY[,,-c(24,26,27,37,51,53,89,91,92,102,116,118)]
namey2<-namey[-c(24,26,27,37,51,53,89,91,92,102,116,118)]
locys<-as.factor(substr(namey2,2,3))
indys<-as.factor(substr(namey2,2,5))
sexys<-as.factor(substr(namey2,6,6))

#####Mukdahan
a<-scan("mukd1c.tps", what="character")
named<-a[(1:22)*99-1]
named<-sub("IMAGE=", "", named)
named<-sub(".JPG", "", named)
Ad<-array(NA, dim=c(48,2,22))
for (i in 1:22){Ad[,,i]<-matrix(a[2:97 + (i-1)*99],48,2,byrow=T)}
mode(Ad)<-"numeric"
AD<-array(NA, dim=c(46,2,22))
for (i in 1:22){AD[,,i]<-(Ad[3:48,,i]/dist(Ad[1:2,,i])) * 5}
#1;4;12;15 removed because these specimens are abnormal
AD2<-AD[,,-c(1,4,12,15)]
```

```
named2<-named[-c(1,4,12,15)]
locmd<-as.factor(substr(named2,2,3))
indmd<-as.factor(substr(named2,2,5))
sexmd<-as.factor(substr(named2,6,6))

#####combine data sets in one#####
name2<-as.factor(c(as.character(nameu2),as.character(namem2),
as.character(nameb2),as.character(names2),as.character(namen2),as.character(namek2),
as.character(namet2),as.character(namei),as.character(namel),as.character(namec2),as.c
haracter(namer2), as.character(namey2),as.character(named2)))
loc<-as.factor(c(as.character(locub), as.character(locma), as.character(locbr),
as.character(locsr), as.character(locnk), as.character(locns), as.character(locut),
as.character(locsb), as.character(loclo), as.character(loccy), as.character(locre),
as.character(locys), as.character(locmd)))
sex<-as.factor(c(as.character(sexub), as.character(sexma), as.character(sexbr),
as.character(sexsr), as.character(sexnk), as.character(sexns), as.character(sexut),
as.character(sexsb), as.character(sexlo), as.character(sexcy), as.character(sexre),
as.character(sexys), as.character(sexmd)))
ind<-as.factor(c(as.character(indub), as.character(indma), as.character(indbr),
as.character(indsr), as.character(indnk), as.character(indns), as.character(indut),
as.character(indsb), as.character(indlo), as.character(indcy), as.character(indre),
as.character(indys), as.character(indmd)))
colo<-c("red", "grey", "blue", "grey")[sex]

A<-array(NA, dim=c(46,2,length(name2)))
A[,,1:58]<-AU2
A[,,59:124]<-AM2
A[,,125:166]<-AB2
A[,,167:204]<-AS2
A[,,205:288]<-AN2
A[,,289:366]<-AK2
A[,,367:402]<-AT2
```

```
A[,,403:434]<-AI
A[,,435:448]<-AL
A[,,449:488]<-AC2
A[,,489:506]<-AR2
A[,,507:624]<-AY2
A[,,625:642]<-AD2

source("Rfunctions.txt")
#####plotting everything before the superimposition
plot(A[,1,], A[,2,],asp=1)
for (i in 1:642){points(A[link,,i], type="b")}
#####producing the superimposition
A1<-pgpa(A)
A1$cent.size
A2<-orp(A1$rotated)
plot(A2[,1,], A2[,2,] ,asp=1)
for (i in 1:642){points(A2[link,,i], type="b", col=colo[i])}

#####estimating measurement error
M<-matrix(NA, 642,92)
for (i in 1: 642){M[i,]<-A2[,,i]}
sM<-svd(var(M))
sM$d/sum(sM$d)
#88 because only 88 non NULL PCs
scor<-M%*%sM$u[,1:88]
mod<-lm(scor~ind)
RES<-crossprod(residuals(mod))
err<-sum(diag(RES))/321
EXP<-crossprod(scale(mod$fitted.values,scale=F))
expMS<-sum(diag(EXP))/320
expv<-(expMS-err)/2
err/(expv+err)
```

```
#####size measurement error
mod<-lm(A1$cent.size~ind)
anova(mod)
err<-sum(residuals(mod)^2)/ 321
expMS<-sum((scale(mod$fitted.values, scale=F))^2)/ 320
expv<-(expMS-err)/2
err/(expv+err)

#####computing the mean shape for every specimen####
inds<-paste(ind,sex, sep="")
indu<-unique(inds)
MI<-matrix(NA, length(indu), 92)
for (i in 1:length(indu)){MI[i,]<-apply(M[which(inds==indu[i]),],2,mean)}
Sex<-as.factor(substr(indu,5,5))
Loc<-as.factor(substr(indu, 1,2))

sMI<-svd(var(MI))
sMI$d/sum(sMI$d) #getingt the percent of shape variation for all the pcs
scor<-MI%*%sMI$u[,1:88]
cols<-c("red", "grey", "blue")[Sex]
symb<-c(3,5)[Loc]

layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(scor[,1:2], cex=0, asp=1, xlab="PC1(24.7%)", ylab="PC2(11.4%)", main="PCA on carapace")
text(scor[,1:2], labels=as.character(Loc),col=cols, cex=0.6, main="PCA on carapace")
msh<-apply(MI, 2, mean)
M1<-matrix(msh+max(scor[,1])*sMI$u[,1], 46,2)
m1<-matrix(msh+min(scor[,1])*sMI$u[,1], 46,2)
M2<-matrix(msh+max(scor[,2])*sMI$u[,2],46,2)
m2<-matrix(msh+min(scor[,2])*sMI$u[,2],46,2)
plot(M1[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
```

```
points(m1[link,], type="b", col="green")
title("variation on PC1")
plot(M2[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m2[link,], type="b", col="green")
title("variation on PC2")
plot(scor[,3:4], col=colo, pch=symb,asp=1, xlab="PC3(92.3%)", ylab="PC4(84.5%)", main="PCA on carapace")
M3<-matrix(msh+max(scor[,3])*sMI$u[,3], 46,2)
m3<-matrix(msh+min(scor[,3])*sMI$u[,3], 46,2)
M4<-matrix(msh+max(scor[,4])*sMI$u[,4],46,2)
m4<-matrix(msh+min(scor[,4])*sMI$u[,4],46,2)
plot(M3[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m3[link,], type="b", col="green")
plot(M4[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m4[link,], type="b", col="green")
plot(scor[,1:2], col=colo, asp=1, xlab="PC1(24.7%)", ylab="PC2(11.4%)", main="PCA on carapace")

##### there are some differences between localities and sexes (manova) for this analysis only adult males and females are included
##### the car library allows to perform type II sums of squares anova
library(car)
anova(lm(scor[Sex=="F" | Sex=="M", ]~Loc[Sex=="F" | Sex=="M"]*Sex[Sex=="F" | Sex=="M"]))

#####test to see whether size is related to sex or to locality
size<-numeric(length(indu))
for (i in 1:length(indu)){size[i]<-mean(A1$cent.size[which(inds==indu[i])])}
Anova(lm(size[Sex=="F" | Sex=="M"]~Loc[Sex=="F" | Sex=="M"]*Sex[Sex=="F" | Sex=="M"]))
```

```
LS<-as.factor(as.character(Loc[Sex=="F" | Sex=="M"]:Sex[Sex=="F" | Sex=="M"]))
layout(1,1,1)
plot(size[Sex=="F" | Sex=="M"]~LS)
Anova(lm(scor[Sex=="F" | Sex=="M",1:2]~(Sex[Sex=="F" |
Sex=="M"]+Loc[Sex=="F" | Sex=="M"]+size[Sex=="F" | Sex=="M"])^2))
```

##in order to visualize differences between populations, performing a linear discriminant analysis on the whole set of individuals, considering population as grouping factor. On the canonical analysis, one uses first different colors for sexes, and different colors according to the stripe pattern to see whether this factor structures the differences between populations

```
stripesp<-read.table("ind_carapace.csv")[,2]
mod<-lda(MI, Loc)
plot(predict(mod)$x, cex=0, asp=1)
text(predict(mod)$x[,1:2], labels=as.character(Loc),col=cols, cex=0.6, main="LDA on
carapace")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(mod)$x, cex=0, asp=1)
text(predict(mod)$x[,1:2], labels=as.character(Loc),col=c("black", "red")[stripesp],
cex=0.6, main="LDA on carapace")
```

drawing morphological variation along canonical axes to describe in which respect populations differ

```
mod1<-lm(MI~Loc)
dfw<-321-13
SSw<-crossprod(mod1$residuals)
VCVw<-SSw/dfw
```

```
#####premultiplying linear discriminant coefficients by intraspecific variance
covariance
LDs<-VCVw%*%mod$scaling

#####computing extreme theoretical shape on the first discriminant axis
M1<-matrix(msh+max(predict(mod)$x[,1])*LDs[,1], 46,2)
m1<-matrix(msh+min(predict(mod)$x[,1])*LDs[,1], 46,2)

#plotting the two extreme configurations
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on
LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(msh+max(predict(mod)$x[,2])*LDs[,2], 46,2)
m2<-matrix(msh+min(predict(mod)$x[,2])*LDs[,2], 46,2)

#plotting the two extreme configurations on LD2
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on
LD2", ylab="")
points(M2[link, ], type="b", col="purple")

#####in order to avoid confounding effect of sex and age,  the same analysis is
performed for just one sex
#####females#####
modf<-lda(MI[Sex=="F",], Loc[Sex=="F"])
#note that there are 149 females identified in the data set)
plot(predict(modf)$x, cex=0, asp=1)
text(predict(modf)$x[,1:2], labels=as.character(Loc[Sex=="F"]),col=c("black",
"red")[stripesp[Sex=="F"]], cex=0.6, main="LDA on carapace")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(modf)$x, cex=0, asp=1)
text(predict(modf)$x[,1:2], labels=as.character(Loc[Sex=="F"]),col=c("black",
"red")[stripesp[Sex=="F"]], cex=0.6, main="LDA on carapace")
```

```
##### drawing morphological variation along canonical axes to describe in which respect populations differ
mod1f<-lm(MI[Sex=="F",]~Loc[Sex=="F"])
dfw<-149-13
SSw<-crossprod(mod1f$residuals)
VCVw<-SSw/dfw

#####premultiplying linear discriminant coefficients by intraspecific variance covariance
LDs<-VCVw%*%mod$scaling

#####computing extreme theoretical shapes on the first discriminant axis
mshf<-apply(MI[Sex=="F",], 2, mean)
M1<-matrix(mshf+max(predict(modf)$x[,1])*LDs[,1], 46,2)
m1<-matrix(mshf+min(predict(modf)$x[,1])*LDs[,1], 46,2)

#####plotting the two extreme configurations
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(mshf+max(predict(modf)$x[,2])*LDs[,2], 46,2)
m2<-matrix(mshf+min(predict(modf)$x[,2])*LDs[,2], 46,2)

#####plotting the two extreme configurations
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD2", ylab="")
points(M2[link, ], type="b", col="purple")

#####males#####
modm<-lda(MI[Sex=="M",], Loc[Sex=="M"])
plot(predict(modm)$x, cex=0, asp=1)
```

```
text(predict(modm)$x[,1:2], labels=as.character(Loc[Sex=="M"]),col=c("black",
"red")[stripesp[Sex=="M"]], cex=0.6, main="LDA on carapace")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(modm)$x, cex=0, asp=1)
text(predict(modm)$x[,1:2], labels=as.character(Loc[Sex=="M"]),col=c("black",
"red")[stripesp[Sex=="M"]], cex=0.6, main="LDA on carapace")

#####draw morphological variation along canonical axes to describe in which
respect populations differ
mod1m<-lm(MI[Sex=="M",]~Loc[Sex=="M"])
dfw<-132-13
SSw<-crossprod(mod1m$residuals)
VCVw<-SSw/dfw
#####premultiplying linear discriminant coefficients by intraspecific variance
covariance
LDs<-VCVw%*%modm$scaling

#####computing extreme theoretical shape on the first discriminant axis
mshm<-apply(MI[Sex=="M",], 2, mean)
M1<-matrix(mshm+max(predict(modm)$x[,1])*LDs[,1], 46,2)
m1<-matrix(mshm+min(predict(modm)$x[,1])*LDs[,1], 46,2)

#####plotting the two extreme configurations on LD2
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on
LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(mshm+max(predict(modm)$x[,2])*LDs[,2], 46,2)
m2<-matrix(mshm+min(predict(modm)$x[,2])*LDs[,2], 46,2)
```

```
#####plotting the two extreme configurations on LD2
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD2", ylab="")
points(M2[link, ], type="b", col="purple")
```

Plastron morphometric analysis performed in R.2.15.2

command by J. Claude

```
setwd("D:/data_p")
link<-
c(1:7,17,NA,8:17,NA,1,23:32,NA,8,2,18,23,NA,9,3,19,24,NA,12,4,20,27,NA,15,5,21,3
0,NA,16,6,22,31,NA, 32,7,NA,8,1,NA)

#####Maha Sarakham
a<-scan("mahp1.tps", what="character")
namem<-a[(1:68)*71-1]
namem<-sub("IMAGE=", "", namem)
namem<-sub(".JPG", "", namem)
Am<-array(NA, dim=c(34,2,68))
for (i in 1:68){Am[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Am)<-"numeric"
AM<-array(NA, dim=c(32,2,68))
for (i in 1:68){AM[,,i]<-(Am[3:34,,i]/dist(Am[1:2,,i])) * 5}
#10;20;44;54 removed because these specimens are abnormal
AM2<-AM[,,-c(10,20,44,54)]
namem2<-namem[-c(10,20,44,54)]
locma<-as.factor(substr(namem2,2,3))
indma<-as.factor(substr(namem2,2,5))
sexma<-as.factor(substr(namem2,6,6))

#####Ubon Ratchathani
a<-scan("ubop1.tps", what="character")
nameu<-a[(1:62)*71-1]
nameu<-sub("IMAGE=", "", nameu)
nameu<-sub(".JPG", "", nameu)
Au<-array(NA, dim=c(34,2,62))
for (i in 1:62){Au[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
```

```
mode(Au)<-"numeric"
AU<-array(NA, dim=c(32,2,62))
for (i in 1:62){AU[,,i]<-(Au[3:34,,i]/dist(Au[1:2,,i])) * 5}
locub<-as.factor(substr(nameu,2,3))
indub<-as.factor(substr(nameu,2,5))
sexub<-as.factor(substr(nameu,6,6))

#####Buriram
a<-scan("burp1.tps", what="character")
nameb<-a[(1:58)*71-1]
nameb<-sub("IMAGE=", "", nameb)
nameb<-sub(".JPG", "", nameb)
Ab<-array(NA, dim=c(34,2,58))
for (i in 1:58){Ab[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ab)<-"numeric"
AB<-array(NA, dim=c(32,2,58))
for (i in 1:58){AB[,,i]<-(Ab[3:34,,i]/dist(Ab[1:2,,i])) * 5}
locbr<-as.factor(substr(nameb,2,3))
indbr<-as.factor(substr(nameb,2,5))
sexbr<-as.factor(substr(nameb,6,6))

#####Surin
a<-scan("surp1.tps", what="character")
names<-a[(1:42)*71-1]
names<-sub("IMAGE=", "", names)
names<-sub(".JPG", "", names)
As<-array(NA, dim=c(34,2,42))
for (i in 1:42){As[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(As)<-"numeric"
AS<-array(NA, dim=c(32,2,42))
for (i in 1:42){AS[,,i]<-(As[3:34,,i]/dist(As[1:2,,i])) * 5}
locsr<-as.factor(substr(names,2,3))
```

```
indsr<-as.factor(substr(names,2,5))
sexsr<-as.factor(substr(names,6,6))

#####Nakhon Phanom
a<-scan("nakp1.tps", what="character")
namen<-a[(1:100)*71-1]
namen<-sub("IMAGE=", "", namen)
namen<-sub(".JPG", "", namen)
An<-array(NA, dim=c(34,2,100))
for (i in 1:100){An[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(An)<-"numeric"
AN<-array(NA, dim=c(32,2,100))
for (i in 1:100){AN[,,i]<-(An[3:34,,i]/dist(An[1:2,,i])) * 5}
AN2<-AN[,,-c(25,31,75,81)]
namen2<-namen[-c(25,31,75,81)]
locnk<-as.factor(substr(namen2,2,3))
indnk<-as.factor(substr(namen2,2,5))
sexnk<-as.factor(substr(namen2,6,6))

#####Nakhon Sawan
a<-scan("nksp1.tps", what="character")
namek<-a[(1:82)*71-1]
namek<-sub("IMAGE=", "", namek)
namek<-sub(".JPG", "", namek)
Ak<-array(NA, dim=c(34,2,82))
for (i in 1:82){Ak[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ak)<-"numeric"
AK<-array(NA, dim=c(32,2,82))
for (i in 1:82){AK[,,i]<-(Ak[3:34,,i]/dist(Ak[1:2,,i])) * 5}
# 2,43 removed because the specimens are abnormal
AK2<-AK[,,-c(2,43)]
namek2<-namek[-c(2,43)]
```

```
locns<-as.factor(substr(namek2,2,3))
indns<-as.factor(substr(namek2,2,5))
sexns<-as.factor(substr(namek2,6,6))

#####Uthai Thani
a<-scan("uttp1.tps", what="character")
namet<-a[(1:46)*71-1]
namet<-sub("IMAGE=", "", namet)
namet<-sub(".JPG", "", namet)
At<-array(NA, dim=c(34,2,46))
for (i in 1:46){At[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(At)<-"numeric"
AT<-array(NA, dim=c(32,2,46))
for (i in 1:46){AT[,,i]<-(At[3:34,,i]/dist(At[1:2,,i])) * 5}
locut<-as.factor(substr(namet,2,3))
indut<-as.factor(substr(namet,2,5))
sexut<-as.factor(substr(namet,6,6))

#####Singburi
a<-scan("sinp1.tps", what="character")
namei<-a[(1:32)*71-1]
namei<-sub("IMAGE=", "", namei)
namei<-sub(".JPG", "", namei)
Ai<-array(NA, dim=c(34,2,32))
for (i in 1:32){Ai[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ai)<-"numeric"
AI<-array(NA, dim=c(32,2,32))
for (i in 1:32){AI[,,i]<-(Ai[3:34,,i]/dist(Ai[1:2,,i])) * 10}
locsb<-as.factor(substr(namei,2,3))
indsb<-as.factor(substr(namei,2,5))
sexsb<-as.factor(substr(namei,6,6))
```

```
#####Loei
a<-scan("loe1p1.tps", what="character")
namel<-a[(1:14)*71-1]
namel<-sub("IMAGE=", "", namel)
namel<-sub(".JPG", "", namel)
Al<-array(NA, dim=c(34,2,14))
for (i in 1:14){Al[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Al)<-"numeric"
AL<-array(NA, dim=c(32,2,14))
for (i in 1:14){AL[,,i]<-(Al[3:34,,i]/dist(Al[1:2,,i])) * 5}
loclo<-as.factor(substr(namel,2,3))
indlo<-as.factor(substr(namel,2,5))
sexlo<-as.factor(substr(namel,6,6))

#####Chaiyaphum
a<-scan("chap1.tps", what="character")
namec<-a[(1:46)*71-1]
namec<-sub("IMAGE=", "", namec)
namec<-sub(".JPG", "", namec)
Ac<-array(NA, dim=c(34,2,46))
for (i in 1:46){Ac[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ac)<-"numeric"
AC<-array(NA, dim=c(32,2,46))
for (i in 1:46){AC[,,i]<-(Ac[3:34,,i]/dist(Ac[1:2,,i])) * 5}
loccy<-as.factor(substr(namec,2,3))
indcy<-as.factor(substr(namec,2,5))
sexcy<-as.factor(substr(namec,6,6))

#####Roi-Et
a<-scan("roip1.tps", what="character")
namer<-a[(1:20)*71-1]
namer<-sub("IMAGE=", "", namer)
```

```
namer<-sub(".JPG", "", namer)
Ar<-array(NA, dim=c(34,2,20))
for (i in 1:20){Ar[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ar)<-"numeric"
AR<-array(NA, dim=c(32,2,20))
for (i in 1:20){AR[,,i]<-(Ar[3:34,,i]/dist(Ar[1:2,,i])) * 5}
#7;17 removed because the specimens are abnormal
AR2<-AR[,,-c(7,17)]
namer2<-namer[-c(7,17)]
locre<-as.factor(substr(namer2,2,3))
indre<-as.factor(substr(namer2,2,5))
sexre<-as.factor(substr(namer2,6,6))

#####Yasothon
a<-scan("yasp1.tps", what="character")
namey<-a[(1:130)*71-1]
namey<-sub("IMAGE=", "", namey)
namey<-sub(".JPG", "", namey)
Ay<-array(NA, dim=c(34,2,130))
for (i in 1:130){Ay[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ay)<-"numeric"
AY<-array(NA, dim=c(32,2,130))
for (i in 1:130){AY[,,i]<-(Ay[3:34,,i]/dist(Ay[1:2,,i])) * 5}
#12,19,40,41,77,84,105,106 removed because these specimens are abnormal
AY2<-AY[,,-c(12,19,40,41,77,84,105,106)]
namey2<-namey[-c(12,19,40,41,77,84,105,106)]
locys<-as.factor(substr(namey2,2,3))
indys<-as.factor(substr(namey2,2,5))
sexys<-as.factor(substr(namey2,6,6))
```

```
#####Mukdahan
a<-scan("mukp1.tps", what="character")
named<-a[(1:22)*71-1]
named<-sub("IMAGE=", "", named)
named<-sub(".JPG", "", named)
Ad<-array(NA, dim=c(34,2,22))
for (i in 1:22){Ad[,,i]<-matrix(a[2:69 + (i-1)*71],34,2,byrow=T)}
mode(Ad)<-"numeric"
AD<-array(NA, dim=c(32,2,22))
for (i in 1:22){AD[,,i]<-(Ad[3:34,,i]/dist(Ad[1:2,,i])) * 5}
locmd<-as.factor(substr(named,2,3))
indmd<-as.factor(substr(named,2,5))
sexmd<-as.factor(substr(named,6,6))

#####combine all data sets in one#####
name2<-as.factor(c(as.character(nameu),as.character(namem2),
as.character(nameb),as.character(names),as.character(namen2),as.character(namek2),as.
character(namet),as.character(namei),as.character(namel),as.character(namec),as.charac
ter(namer2), as.character(namey2),as.character(named)))
loc<-as.factor(c(as.character(locub), as.character(locma), as.character(locbr),
as.character(locsr), as.character(locnk), as.character(locns), as.character(locut),
as.character(locsb), as.character(loclo), as.character(loccy), as.character(locre),
as.character(locys), as.character(locmd)))
sex<-as.factor(c(as.character(sexub), as.character(sexma), as.character(sexbr),
as.character(sexsr), as.character(sexnk), as.character(sexns), as.character(sexut),
as.character(sexsb), as.character(sexlo), as.character(sexcy), as.character(sexre),
as.character(sexys), as.character(sexmd)))
ind<-as.factor(c(as.character(indub), as.character(indma), as.character(indbr),
as.character(indsr), as.character(indnk), as.character(indns), as.character(indut),
as.character(indsb), as.character(indlo), as.character(indcy), as.character(indre),
as.character(indys), as.character(indmd)))
colo<-c("red", "grey", "blue", "grey")[sex]
```

```
A<-array(NA, dim=c(32,2,length(name2)))
A[,,1:62]<-AU
A[,,63:126]<-AM2
A[,,127:184]<-AB
A[,,185:226]<-AS
A[,,227:322]<-AN2
A[,,323:402]<-AK2
A[,,403:448]<-AT
A[,,449:480]<-AI
A[,,481:494]<-AL
A[,,495:540]<-AC
A[,,541:558]<-AR2
A[,,559:680]<-AY2
A[,,681:702]<-AD

source("Rfunctions.txt")
#####plotting everything before the superimposition
plot(A[,1,], A[,2,],asp=1)
for (i in 1:702){points(A[link,,i], type="b")}

#####producing the superimposition
A1<-pgpa(A)
A1$cent.size
A2<-orp(A1$rotated)
plot(A2[,1,], A2[,2,] ,asp=1)
for (i in 1:702){points(A2[link,,i], type="b", col=colo[i])}

#####estimating measurement error
M<-matrix(NA, 702,64)
for (i in 1:702){M[i,]<-A2[,,i]}
sM<-svd(var(M))
sM$d/sum(sM$d)
```

```
#60 because only 60 non NULL PCs are present
scor<-M%*%sM$u[,1:60]
mod<-lm(scor~ind)
RES<-crossprod(residuals(mod))
err<-sum(diag(RES))/351
EXP<-crossprod(scale(mod$fitted.values,scale=F))
expMS<-sum(diag(EXP))/350
expv<-(expMS-err)/2
err/(expv+err)

#####size measurement error
mod<-lm(A1$cent.size~ind)
anova(mod)
err<-sum(residuals(mod)^2)/ 351
expMS<-sum((scale(mod$fitted.values, scale=F))^2)/ 350
expv<-(expMS-err)/2
err/(expv+err)

##### computing the mean shape for every specimen#####
inds<-paste(ind,sex, sep="")
indu<-unique(inds)
MI<-matrix(NA, length(indu), 64)
for (i in 1:length(indu)){MI[i,]<-apply(M[which(inds==indu[i]),],2,mean)}
Sex<-as.factor(substr(indu,5,5))
Loc<-as.factor(substr(indu, 1,2))

sMI<-svd(var(MI))
sMI$d/sum(sMI$d) #getting the percent of shape variation for all the pcs
scor<-MI%*%sMI$u[,1:60]
cols<-c("red", "grey", "blue")[Sex]
layout(matrix(c(1,1,1,1,2,3), 2,3))
```

```
plot(scor[,1:2], cex=0, asp=1, xlab="PC1(29.1%)", ylab="PC2(16.1%)", main="PCA on plastron")
text(scor[,1:2], labels=as.character(Loc),col=cols, cex=0.6)
msh<-apply(MI, 2, mean)
M1<-matrix(msh+max(scor[,1])*sMI$u[,1], 32,2)
m1<-matrix(msh+min(scor[,1])*sMI$u[,1], 32,2)
M2<-matrix(msh+max(scor[,2])*sMI$u[,2],32,2)
m2<-matrix(msh+min(scor[,2])*sMI$u[,2],32,2)
plot(M1[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m1[link,], type="b", col="green")
title("variation on PC1")
plot(M2[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m2[link,], type="b", col="green")
title("variation on PC2")

#layout(1)
plot(scor[,1:2], cex=0, asp=1, xlab="PC1(29.1%)", ylab="PC2(16.1%)", main="PCA on plastron")

plot(scor[,3:4], col=colo, pch=symb,asp=1, xlab="PC3(10.0%)", ylab="PC4(9.6%)", main="PCA on carapace")
M3<-matrix(msh+max(scor[,3])*sMI$u[,3], 32,2)
m3<-matrix(msh+min(scor[,3])*sMI$u[,3], 32,2)
M4<-matrix(msh+max(scor[,4])*sMI$u[,4],32,2)
m4<-matrix(msh+min(scor[,4])*sMI$u[,4],32,2)
plot(M3[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m3[link,], type="b", col="green")
plot(M4[link,], type="b", col="purple", asp=1, frame=F, axes=F, xlab="", ylab="")
points(m4[link,], type="b", col="green")
```

```
##### testing whether there are some differences between localities (manova)
#####load the car library to perform type II sums of squares anova and manova
library(car)
anova(lm(scor[Sex=="F" | Sex=="M", ]~Loc[Sex=="F" | Sex=="M"]*Sex[Sex=="F" | Sex=="M"]))
size<-numeric(length(indu))
for (i in 1:length(indu)){size[i]<-mean(A1$cent.size[which(inds==indu[i])])}
Anova(lm(size[Sex=="F" | Sex=="M"]~Loc[Sex=="F" | Sex=="M"]*Sex[Sex=="F" | Sex=="M"]))
layout(1)
LS<-as.factor(as.character(Loc[Sex=="F" | Sex=="M"]:Sex[Sex=="F" | Sex=="M"]))
layout(1,1,1)
plot(size[Sex=="F" | Sex=="M"]~LS)
Anova(lm(scor[Sex=="F" | Sex=="M",1:2]~(Sex[Sex=="F" | Sex=="M"]+Loc[Sex=="F" | Sex=="M"]+size[Sex=="F" | Sex=="M"])^2))

#####in order to visualize differences between populations,a linear discriminant analysis is performed on the whole set of individuals, considering population as grouping factor. On this canonical analysis,  different colors are used for sexes, and different colors  according to the stripe pattern to see whether this factor structures the differences between populations
stripesp<-read.table("ind_plastron.csv")[,2]
mod<-lda(MI, Loc)
plot(predict(mod)$x, cex=0, asp=1)
text(predict(mod)$x[,1:2], labels=as.character(Loc),col=cols, cex=0.6, main="LDA on plastron")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(mod)$x, cex=0, asp=1)
text(predict(mod)$x[,1:2], labels=as.character(Loc),col=c("black", "red")[stripesp], cex=0.6, main="LDA on plastron")
```

```
#####drawing morphological variation along canonical axes to describe in which respect populations differ
mod1<-lm(MI~Loc)
dfw<-351-13
SSw<-crossprod(mod1$residuals)
VCVw<-SSw/dfw

#####premultiplying linear discriminant coefficients by intraspecific variance covariance
LDs<-VCVw%*%mod$scaling

#####computing extreme theoretical shape on the first discriminant axis
M1<-matrix(msh+max(predict(mod)$x[,1])*LDs[,1], 32,2)
m1<-matrix(msh+min(predict(mod)$x[,1])*LDs[,1], 32,2)

#####plotting the two extreme configurations on LD2
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(msh+max(predict(mod)$x[,2])*LDs[,2], 32,2)
m2<-matrix(msh+min(predict(mod)$x[,2])*LDs[,2], 32,2)

#####plotting the two extreme configurations
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD2", ylab="")
points(M2[link, ], type="b", col="purple")

#####in order to avoid confounding effect of sex and age, perform the same analysis for just one sex
#####females#####
modf<-lda(MI[Sex=="F",], Loc[Sex=="F"])
plot(predict(modf)$x, cex=0, asp=1)
```

```
text(predict(modf)$x[,1:2], labels=as.character(Loc[Sex=="F"]),col=c("black",
"red")[stripesp[Sex=="F"]], cex=0.6, main="LDA on carapace")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(modf)$x, cex=0, asp=1)
text(predict(modf)$x[,1:2], labels=as.character(Loc[Sex=="F"]),col=c("black",
"red")[stripesp[Sex=="F"]], cex=0.6, main="LDA on plastron")
```

#####drawing morphological variation along canonical axes to describe in which respect populations differ

```
mod1f<-lm(MI[Sex=="F",]~Loc[Sex=="F"])
dfw<-161-13
SSw<-crossprod(mod1f$residuals)
VCVw<-SSw/dfw
```

#####premultiplying linear discriminant coefficients by intraspecific variance covariance

```
LDs<-VCVw%*%mod$scaling
```

#####computing extreme theoretical shape on the first discriminant axis

```
mshf<-apply(MI[Sex=="F",], 2, mean)
M1<-matrix(mshf+max(predict(modf)$x[,1])*LDs[,1], 32,2)
m1<-matrix(mshf+min(predict(modf)$x[,1])*LDs[,1], 32,2)
```

#####plotting the two extreme configurations on LD1

```
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on
LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(mshf+max(predict(modf)$x[,2])*LDs[,2], 32,2)
m2<-matrix(mshf+min(predict(modf)$x[,2])*LDs[,2], 32,2)
```

```
#####plotting the two extreme configurations on LD2
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD2", ylab="")
points(M2[link, ], type="b", col="purple")
#####males#####
modm<-lda(MI[Sex=="M",], Loc[Sex=="M"])
plot(predict(modm)$x, cex=0, asp=1)
text(predict(modm)$x[,1:2], labels=as.character(Loc[Sex=="M"]),col=c("black", "red")[stripesp[Sex=="M"]], cex=0.6, main="LDA on carapace")
layout(matrix(c(1,1,1,1,2,3), 2,3))
plot(predict(modm)$x, cex=0, asp=1)
text(predict(modm)$x[,1:2], labels=as.character(Loc[Sex=="M"]),col=c("black", "red")[stripesp[Sex=="M"]], cex=0.6, main="LDA on carapace")

##### drawing morphological variation along canonical axes to discribe in which respect populations differ
mod1m<-lm(MI[Sex=="M",]~Loc[Sex=="M"])
dfw<-146-13
SSw<-crossprod(mod1m$residuals)
VCVw<-SSw/dfw

#####premultiplying linear discriminant coefficients by intraspecific variance covariance
LDs<-VCVw%*%modm$scaling

#####computing extreme theoretical shape on the discriminant axis
mshm<-apply(MI[Sex=="M",], 2, mean)
M1<-matrix(mshm+max(predict(modm)$x[,1])*LDs[,1], 32,2)
m1<-matrix(mshm+min(predict(modm)$x[,1])*LDs[,1], 32,2)
```

```
#####plotting the two extreme configurations
plot(m1[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD1", ylab="")
points(M1[link, ], type="b", col="purple")
M2<-matrix(mshm+max(predict(modm)$x[,2])*LDs[,2], 32,2)
m2<-matrix(mshm+min(predict(modm)$x[,2])*LDs[,2], 32,2)

#####plotting the two extreme configurations
plot(m2[link, ], type="b", col="green", axes=F, asp=1, frame=F, xlab="Variation on LD2", ylab="")
points(M2[link, ], type="b", col="purple")
```

Appendix III

Basilochelys macrobios n. gen. and n. sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic-earliest Cretaceous) of the Khorat Plateau, NE Thailand

Basilochelys macrobios n. gen. and n. sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic–earliest Cretaceous) of the Khorat Plateau, NE Thailand

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Abstract: A large cryptodiran turtle, *Basilochelys macrobios* n. gen. n. sp. is described from the latest Jurassic–earliest Cretaceous Phu Kradung Formation of NE Thailand, on the basis of skull, shell and other postcranial elements. *Basilochelys* presents a combination of primitive and derived characters. The derived characters include sculptured skull roof and shell surface; deeply embedded canalis caroticus internus; foramen posterius canalis carotici interni completely surrounded by pterygoid; neural formula of $6 > 4 < 6 < 6 < 6 < 6$; anteroposteriorly expanded eleventh and twelfth marginal scutes extending onto the suprapygal and costal plates; narrow vertebral scutes; plastron sutured to the carapace, with large and wide anterior and posterior lobes, long and narrow bridge, very narrow axillary and inguinal notch; wide entoplastron; humeropectoral sulcus located on the posterior part of the entoplastron; anal notch absent. This taxon is placed in Trionychoidae and considered as the most basal member of that group.

The latest Jurassic to mid-Cretaceous non-marine beds of the Khorat Group, in NE Thailand, are rich in vertebrate remains, including turtles. Adocid and carettochelyid turtles have been described from the Early Cretaceous Sao Khua Formation (Tong *et al.* 2003, 2004*a*, 2006*a*) and the mid-Cretaceous Khok Kruat Formation (Tong *et al.* 2005); however, the turtles from the underlying Phu Kradung Formation are still poorly known (Tong *et al.* 2006*b*). Although turtle remains have been collected from several localities of that formation for several years, they were too fragmentary for an accurate systematic study. Recently, complete shells and a partial skull of a large cryptodiran turtle have been discovered in the Phu Kradung Formation at the Kham Phok locality, Mukdahan Province. The purpose of the present paper is to describe these new turtle specimens and to discuss their systematic position. The specimens are housed in the Sirindhorn Museum, Sahat Sakhan, Kalasin Province, Thailand.

Geological setting and taphonomy

Two nearly complete large turtle shells were discovered in summer 2004 near the village of Kham Phok, Mukdahan Province (Fig. 1). When discovered, both shells were lying upside down in a siltstone level with sandy to micro-conglomerate lenses. A braincase, shell fragments and other postcranial elements were collected within a few square metres around one shell (MD8-2) and probably belong to a single individual. The pelvic girdle was found inside both shells during preparation, and an incomplete femur and a cervical vertebra were found inside MD8-2. This suggests that the soft parts were at least partially decomposed before burial and that these turtles were not much transported after decomposition. Abundant shark teeth and one shark spine have been found inside the shell of MD8-1. A theropod tibia was found beneath MD8-1 (Buffetaut & Suteethorn 2007). As both turtles were found upside down and are of rather large size, we

From: BUFFETAUT, E., CUNY, G., LE LOEUFF, J. & SUTEETHORN, V. (eds) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. The Geological Society, London, Special Publications, **315**, 153–173.
DOI: 10.1144/SP315.12 0305-8719/09/$15.00

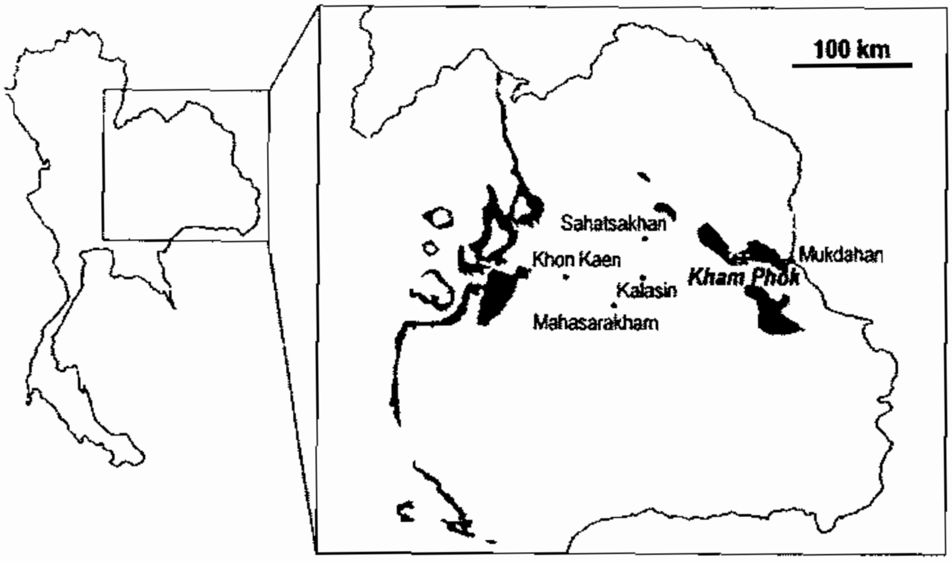

Fig. 1. Map showing location of Kham Phok locality, and outcrops of the Phu Kradung Formation (after Buffetaut & Suteethorn 2007).

suppose that getting into that position may have caused their death. Although the shells were found articulated, cracks (from 1 to 5 mm) are present in both. These cracks are not filled by calcite but probably result from the pressure of overlying sediment.

Other material studied here includes abundant shell fragments from Dan Luang and Huai Pai, and a partial carapace from the bed of Huai Sai river, in Mukdahan Province. All these specimens come from the upper levels of the Phu Kradung Formation in the eastern part of NE Thailand.

The Phu Kradung Formation consists of fluvial sandstones, siltstones and mudstones and is dated as either Late Jurassic or more probably Early Cretaceous on the basis of palynology (Racey *et al.* 1996) and detrital zircon thermochronology (Carter & Bristow 2003), whereas evidence from fossil vertebrates supports a Late Jurassic age (Buffetaut & Suteethorn 2007). Beside turtles, the vertebrates from the Phu Kradung Formation include freshwater sharks, actinopterygian fishes, lungfishes, temnospondyl amphibians, crocodilians and dinosaurs (Buffetaut *et al.* 2006).

Systematic palaeontology

Megaorder Cryptodira Cope
Parvorder Eucryptodira Gaffney
Epifamily Trionychoidae Fitzinger (*fide* Meylan & Gaffney 1989)
Genus Basilochelys new genus

Etymology. Basileus: Greek, king; *chelys*: Greek, turtle. In honour of His Majesty the King of Thailand.

Diagnosis. Cryptodiran turtle of large size, with shell length reaching 900 mm. Characterized by the combination of the following features: sculptured skull roof and shell surface; skull with large vomer separating completely the palatines, long pterygoid midline suture between the vomer and the basisphenoid, foramen posterius canalis carotici laterale exposed on ventral surface, large foramen caroticum basisphenoidale, deeply embedded canalis caroticus internus, and foramen posterius canalis carotici interni completely surrounded by pterygoid. Shell low, with smooth carapace margin and without keel; neural formula $6 > 4 < 6 < 6 < 6 < 6\ldots$; narrow vertebral scutes, second marginal scute boot-shaped, contacting the first vertebral scute; eleventh and twelfth marginals anteroposteriorly expanded, extending onto the costal and suprapygal plates. Plastron sutured to the carapace, with large and wide anterior and posterior lobes, long and narrow bridge, very narrow axillary and inguinal notch; wider than long entoplastron; humeropectoral sulcus located on the posterior part of the entoplastron; anal notch absent.

Type species. Basilochelys macrobios sp. nov.

Etymology. Macrobios: Greek, long life. In honour of His Majesty King Rama IX's eightieth birthday.

Holotype. A nearly complete carapace articulated with a partial plastron, pelvic girdle and a cervical vertebra (MD8-2, collection of the Sirindhorn Museum, Phu Kum Khao, Sahatsakhan, Kalasin Province, Thailand).

Table 1. *Shell measurements of* Basilochelys macrobios *n. gen. n. sp. from the Late Jurassic–Early Cretaceous of Phu Kradung Formation, NE Thailand (in mm)*

	MD8-1	MD8-2	MD4-1
Carapace			
Length	900	900[1]	820[1]
Width	790	720[1]	–
Plastron			
Length	720[1]	–	–
Width	600[1]	–	–
Width of anterior lobe	450[1]	–	–
Length of bridge	295	260	–
Length of posterior lobe	230	265	–
Width of posterior lobe	350	330	–

[1] Estimated.

Hypodigm. Kham Phok locality: an incomplete skull (MD8-3); a complete carapace articulated with partial plastron, and pelvic girdle (MD8-1); an isolated cervical (MD8-4); a humerus (MD8-5), an incomplete femur (MD8-6); a distal phalanx (MD8-7), and other limb bone fragments and shell fragments. Huai Sai locality: an incomplete carapace (MD4-1). Dan Luang locality: a partial shell with anterior lobe of plastron, nuchal, first costal and two peripherals (MD3-1), and numerous fragments of plates. Huai Pai locality: an incomplete anterior lobe of plastron (MD5-1), an isolated entoplastron (unnumbered, collection of Buddhabutr Temple, Mukdahan Province, Thailand) and other shell fragments (collection of the Sirindhorn Museum, Phu Kum Khao, Sahatsakhan, Kalasin Province, Thailand).

Type locality. Kham Phok, Mukdahan Province, Khorat Plateau, NE Thailand.

Horizon. Phu Kradung Formation, terminal Jurassic–basal Cretaceous.

Species diagnosis. As for genus, only species.

Measurements. See Table 1.

Description and comparisons

Skull (MD8-3; Fig. 2)

Preservation. Only the braincase is preserved, including both pterygoids, epipterygoids, prootics, opisthotics, basisphenoid and basioccipital; and incomplete quadrates, palatines, vomer, parietals, supraoccipital and exoccipitals.

General appearance. Most of the skull roof is missing; the shape and size of the temporal emargination cannot be determined. However, some free margin of the skull roof is preserved on the right side, indicating that the temporal emargination was probably fairly large, with the foramen stapedio-temporale exposed in dorsal view, unlike the fully covered skull roof of *Nanhsiungchelys* (Yeh 1966). However, judging by the width of the preserved posterior part of the parietal, the temporal emargination of the Kham Phok skull is less developed than that of *Adocus* sp. (Meylan & Gaffney 1989) and *Zangerlia neimongolensis* (Brinkman & Peng 1996). The morphology of the ventral surface of the skull is somewhat similar to that of *Adocus* sp. The pterygoid, basisphenoid and basioccipital form a flat surface; and laterally the pterygoid and the quadrate together form a large and deep anteroposteriorly directed, triangular depression (see pterygoid).

Parietal. The parietal is the only preserved skull roof element and only the posteromedial part of both parietals is preserved, with a damaged and worn surface. However, a small portion of the dorsal surface of the parietal is better preserved, showing that the skull roof was sculptured.

In lateral view, the posterior portion of the processus inferior parietalis is preserved. It contributes to the medial margin of the foramen nervi trigemini, and contacts the pterygoid anteroventrally and the epipterygoid ventrally anterior to the foramen nervi trigemini. The parietal contacts the prootic ventrally, and the supraoccipital posteriorly, posterior to the foramen nevi trigemini. In anterior view, the parietal sends a lateral process that underlies the processus trochlearis oticum, but it does not contribute to the processus on the dorsal surface. This is different from *Adocus* sp. in which the parietal forms one-third of the processus trochlearis oticum.

Vomer. Only the posterior end of the vomer is preserved. The vomer is a single bone that lies

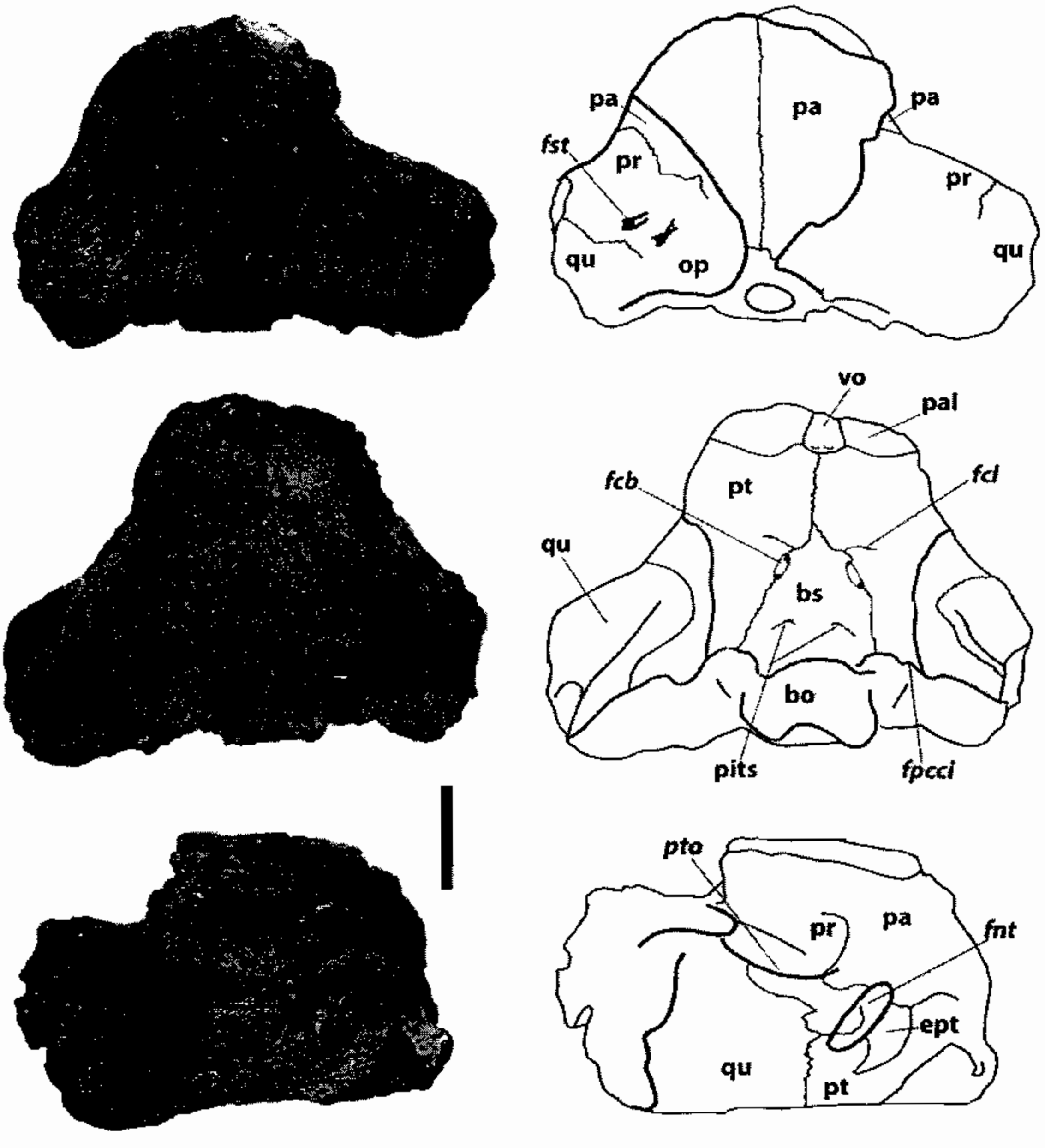

Fig. 2. Skull of ***Basilochelys macrobios*** n. gen. n. sp. (MD8-3) from the Late Jurassic–Early Cretaceous Phu Kradung Formation, Kham Phok locality, NE Thailand. Above, dorsal view; middle, ventral view; below, right lateral view. Scale bar: 50 mm. bo, basioccipital; bs, basisphenoid; ept, epipterygoid; *fcb*, foramen caroticum basisphenoidale; *fcl*, foramen posterius canalis caroticus laterale; *fnt*, foramen nervi trigemini; *fpcci*, foramen posterius calalis carotici interni; *fst*, foramen stapedio-temporale; op, opisthotic; pa, parietal; pal, palatine; pr, prootic; pt, pterygoid; *pto*, processus trochlearis oticum; qu, quadrate; vo, vomer.

between the palatines. The posterior part of the vomer is similar to that of *Adocus* sp. in that it is relatively wide with the lateral margins converging anteriorly. In addition to the palatine contact, the vomer contacts the pterygoid posteriorly. There is a pair of tubercles on the ventral surface of the vomer, close to the vomer–pterygoid suture.

Palatine. Most of both palatines are missing; only their posterior ends are preserved. The posteromedial corner of the triturating surface, preserved on the right side, is formed by the palatine. The medial limit of the triturating surface is close to the midline, which would indicate a rather wide triturating surface, at least as wide as in *Adocus* sp., rather than a narrow one as in *Dracochelys* (Gaffney & Ye 1992). Although the foramen posterius palatinus is not preserved on either side, it is unlikely that it was a large foramen as seen in *Sinemys* (Brinkman & Peng 1993*b*) and *Dracochelys*. The palatine contacts the pterygoid posteriorly and the vomer medially.

Pterygoid. Both pterygoids are nearly complete and well preserved, lacking only their anterolateral part.

In ventral view, the pterygoid, together with the basisphenoid and the basioccipital, forms a flat palatal surface. The anterolateral margin of the pterygoid is damaged; the processus pterygoideus externus is not preserved. However, the lateral margin of the right pterygoid presents a slight notch, which indicates that the base of the process is there, anterior to this notch, but its shape and size cannot be determined.

Posterolateral to the flat surface, a deep concavity is formed by the pterygoid medially and the quadrate laterally. The concavity is narrow anteriorly and becomes wider and deeper posteriorly. It is limited laterally by the quadrate process of the pterygoid and the quadrate and medially by a distinct anteroposteriorly directed ridge on the pterygoid, which extends posteriorly by a thin and nearly vertical flange on the pterygoid. The concavity is open posteriorly. This structure is very similar to that of *Adocus* sp. described by Meylan & Gaffney (1989).

The foramen caroticum basisphenoidale is a long oval opening lying on the anterior portion of the basisphenoid–pterygoid suture. It measures 5 mm in length and 1.5 mm in width on the right side and 5.5 by 1.5 mm on the left. The canalis carotici interni is deeply embedded; the depth of the canal at the foramen caroticum basisphenoidale is about 2 mm. The macrobaenids–sinemydids, such as *Dracochelys*, *Ordosemys* (Brinkman & Wu 1999; Tong *et al.* 2004*b*) and *Sinemys*, differ from this new material in that the canal is covered by a thin bone. Anterolateral to the foramen caroticum basisphenoidale, there is a pair of posteriorly facing foramina, which are interpreted here as the foramen posterius canalis caroticus laterale (Sukhanov 2000), for the palatine artery (Gaffney 1979). The posterior part of the canalis caroticus lateralis is in an open, wide and shallow depression. The position and morphology of the foramen caroticum basisphenoidale in MD8-3 is similar to that of *Adocus*, whereas the canalis caroticus lateralis is not exposed on the ventral surface in *Adocus*.

The ventrally exposed foramen posterius canalis caroticus laterale, the canalis caroticus lateralis and foramen caroticum basisphenoidale are present in *Kallokibotion* (Gaffney & Meylan 1992), xinjiangchelyids, sinemydids–macrobaenids, *Mongolochelys* (Khosatzky 1997) and *Chubutemys* (Gaffney *et al.* 2007). However, the condition in xinjiangchelyids, *Kallokibotion* and *Mongolochelys* is more primitive than in the Kham Phok skull in that the canalis caroticus internus is not covered by bone ventrally. *Meiolania platyceps* is considered also to have a canalis caroticus lateralis that is not completely enclosed in bone, but the canal is confluent with the intrapterygoid slit, an autapomorphic structure of Meiolaniidae (Gaffney 1983). The open morphology of the arterial area of the Kham Phok skull seems to be more similar to that of *Hangaiemys* (Sukhanov 2000) and *Ordosemys* (Brinkman & Wu 1999) than to that of *Sinemys*, *Kirgizemys* and *Judithemys* (Brinkman & Peng 1993*b*; Brinkman & Wu 1999; Parham & Hutchison 2003; Tong *et al.* 2004*b*; Danilov *et al.* 2006). In these forms, the arterial areas are more restricted by bony margins. In *Dracochelys* (Gaffney & Ye 1992) and *Chubutemys*, the foramen posterius canalis caroticus laterale and foramen caroticum basisphenoidale are more distant, which approaches the condition of *Kallokibotion* (Gaffney & Meylan 1992; Gaffney 1996). *Zangerlia neimongolensis* has a large depression that contains the canalis caroticus lateralis and canalis caroticus internus (Brinkman & Peng 1996), which seems comparable with the condition in the Kham Phok skull, but the poor preservation of this area prevents any detailed comparison.

The canalis caroticus internus extends posteriorly within the pterygoid. The foramen posterius canalis carotici interni is formed entirely by the pterygoid and lies near the posterior margin of the pterygoid, under a pterygoid flange, as in *Adocus*. On the ventral surface, the pterygoid contacts the vomer anteriorly and the palatine anterolaterally. Between the vomer and the basisphenoid, the left and right pterygoids meet on the midline by a long suture. Posteromedially, the pterygoid contacts the basisphenoid and posterolaterally the quadrate. The pterygoid–basisphenoid suture is clearly visible in its anterior portion, whereas its posterior part is in an area of broken bone.

In lateral view, the pterygoid is visible on both sides. The anterior contact with the palatine is not visible. Together with the parietal, the prootic, the quadrate and the epipterygoid, the pterygoid forms the foramen nervi trigemini, which is a large and oval foramen. The pterygoid contacts the parietal anterodorsally, the epipterygoid dorsally and the quadrate posteriorly.

Epipterygoid. Both epipterygoids are complete. The epipterygoid is an elongate bone, forming most of the anterior margin of the foramen nervi trigemini. Anteriorly, ventrally and posterolaterally, it is surrounded by the pterygoid; dorsally, it contacts the parietal.

Quadrate. Incomplete quadrates are preserved on both sides, whereas the cavum tympani and the processus articularis are missing on both sides.

Ventrally, the quadrate sends an anteromedial process to meet the pterygoid lateral to the pterygoid concavity (see pterygoid). It contacts the pterygoid anteromedially and medially.

Anterodorsally, the quadrate contributes to the lateral part of the processus trochlearis oticum (see prootic). It contacts the pterygoid anteroventrally, the prootic anteromedially, and the opisthotic posteromedially.

Basisphenoid. The basisphenoid is complete; only its ventral surface is exposed. The basisphenoid has a triangular and flat ventral exposure. The large foramen caroticum basisphenoidale lies on the basisphenoid–pterygoid suture (see pterygoid). A pair of small and shallow concavities can be seen on the posterior part of the basisphenoid; a similar structure is present in some sinemydids–macrobaenids, such as *Sinemys, Ordosemys, Kirgizemys* and *Judithemys* (Parham & Hutchison 2003). The basisphenoid contacts the pterygoid anteriorly and laterally, and the basioccipital posteriorly.

Basioccipital. The basioccipital is nearly complete; however, the occipital condyle is missing. The basioccipital has a rectangular and slightly concave ventral surface. The tuberculum basioccipitale is a huge and dorsoventrally flattened process. The occipital condyle is not preserved. The basioccipital contacts the basisphenoid anteriorly by a slightly anteriorly convex suture, the pterygoid laterally and the exoccipital dorsally.

Exoccipital. Both exoccipitals are damaged at their posterior end, lacking the occipital condyle. One foramen nervi hypoglossi is visible on the posterolateral surface of the exoccipital. The exoccipital contacts the basioccipital ventrally, the opisthotic laterally, the pterygoid ventrolaterally and the supraoccipital dorsally.

Prootic. The right prootic is complete; the left one is damaged, missing the lateral end. The prootic has a wide dorsal exposure, differing from the narrow prootic of *Ferganemys* (Nessov 1977), *Adocus* and a primitive adocid skull from the Late Cretaceous of Kizylkum, Uzbekistan (Danilov & Parham 2005). The prootic forms most of the processus trochlearis oticum; the quadrate contributes to its lateral portion. There is no parietal contribution to the dorsal surface of the process (see parietal). The processus trochlearis oticum is a thick, blunt and forward directed ridge. Its medial end is not well defined, but continues smoothly to the lateral surface of the braincase, whereas its lateral portion is more developed, forming a large swelling at the lateral end. The whole process, however, is not as developed as in *Adocus* sp., but more similar to that of *Zangerlia neimongolensis* (Brinkman & Peng 1996). Anteriorly, the prootic contributes to the dorsal margin of the foramen nervi trigemini (see pterygoid). The contacts with the parietal medially, the quadrate laterally and the pterygoid ventrally are clearly visible, whereas the posterior contact with the opisthotic is not clearly discernible. There are three depressions on the dorsal surface of the prootic and opisthotic; the foramen stapedio-temporale is located in the most anterior one, on or near the prootic–opisthotic suture. Although the depression is fairly large, the foramen itself is much smaller.

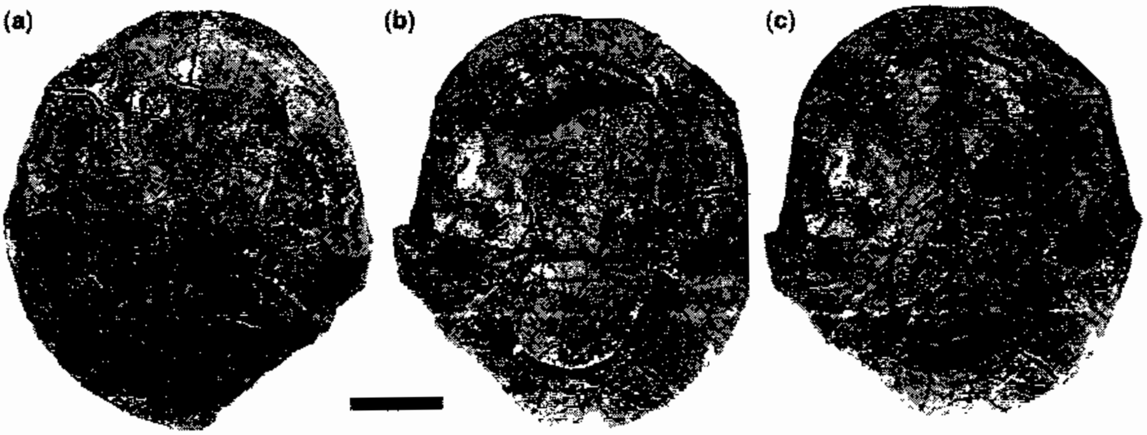

Fig. 3. Shell of *Basilochelys macrobios* n. gen. n. sp. (MD8-1) from the Late Jurassic–Early Cretaceous Phu Kradung Formation, Kham Phok locality, NE Thailand. **(a)** Dorsal view; **(b)** ventral view; **(c)** carapace in ventral view, plastron removed. Scale bar: 200 mm.

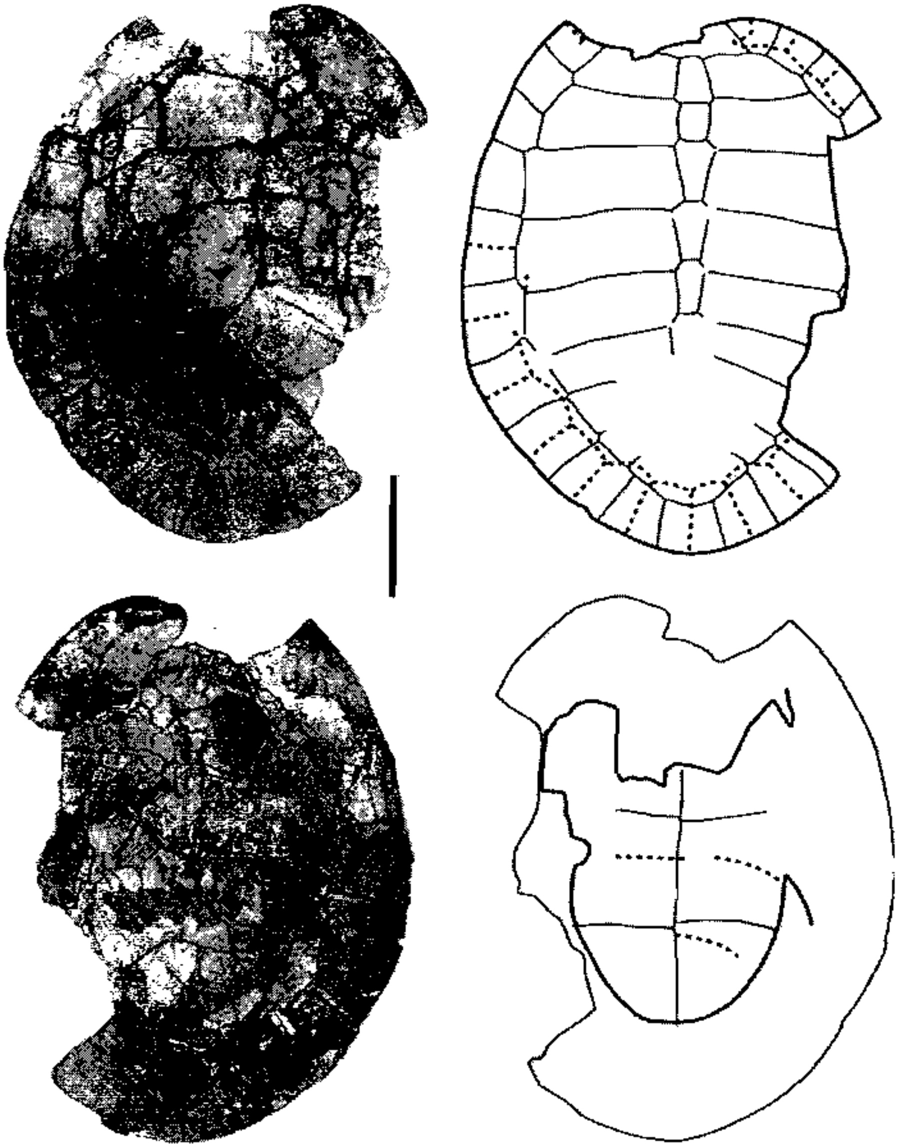

Fig. 4. Shell of *Basilochelys macrobios* n. gen. n. sp. (Type, MD8-2) from the Late Jurassic–Early Cretaceous Phu Kradung Formation, Kham Phok locality, NE Thailand. Above, dorsal view; below, ventral view. Scale bar: 200 mm.

Opisthotic. Both opisthotics are preserved but damaged. The sutures of the opisthotic are not clearly visible, and the foramen jugulare posterius and fenestra postotica are covered by matrix.

Shell (*Figs 3–6, 8*)

Shell surface ornamentation. A well-preserved shell surface is visible on the carapace from Huai Sai (MD4-1) and some isolated plates from Huai Pai and Dan Luang. In these specimens, the shell surface is covered with a distinct sculpture consisting of raised irregular ridges and tubercles, which tend to arrange themselves into a parallel pattern. The ridges are anteroposteriorly directed on the middle of the carapace, on the neurals and at least the medial part of the costals, whereas on the anterior part of the carapace they are anterolaterally directed (Fig. 5). This pattern of ornamentation is reminiscent of that of *Anomalochelys*, a nanhsiungchelyid from the Late Cretaceous of Japan (Hirayama *et al.* 2001). It differs from the pitted pattern of adocids and 'pock-mark' sculpturing of *Basilemys* and *Nanhsiungchelys* (Meylan & Gaffney 1989). On the isolated entoplastron from Huai Pai (Fig. 6c), there are light posterolaterally directed ridges radiating from the midline. In the specimens from Kham Phok, the shell surface of MD8-1 and MD8-2 is worn and covered by a layer of ferruginous matrix that is difficult to remove.

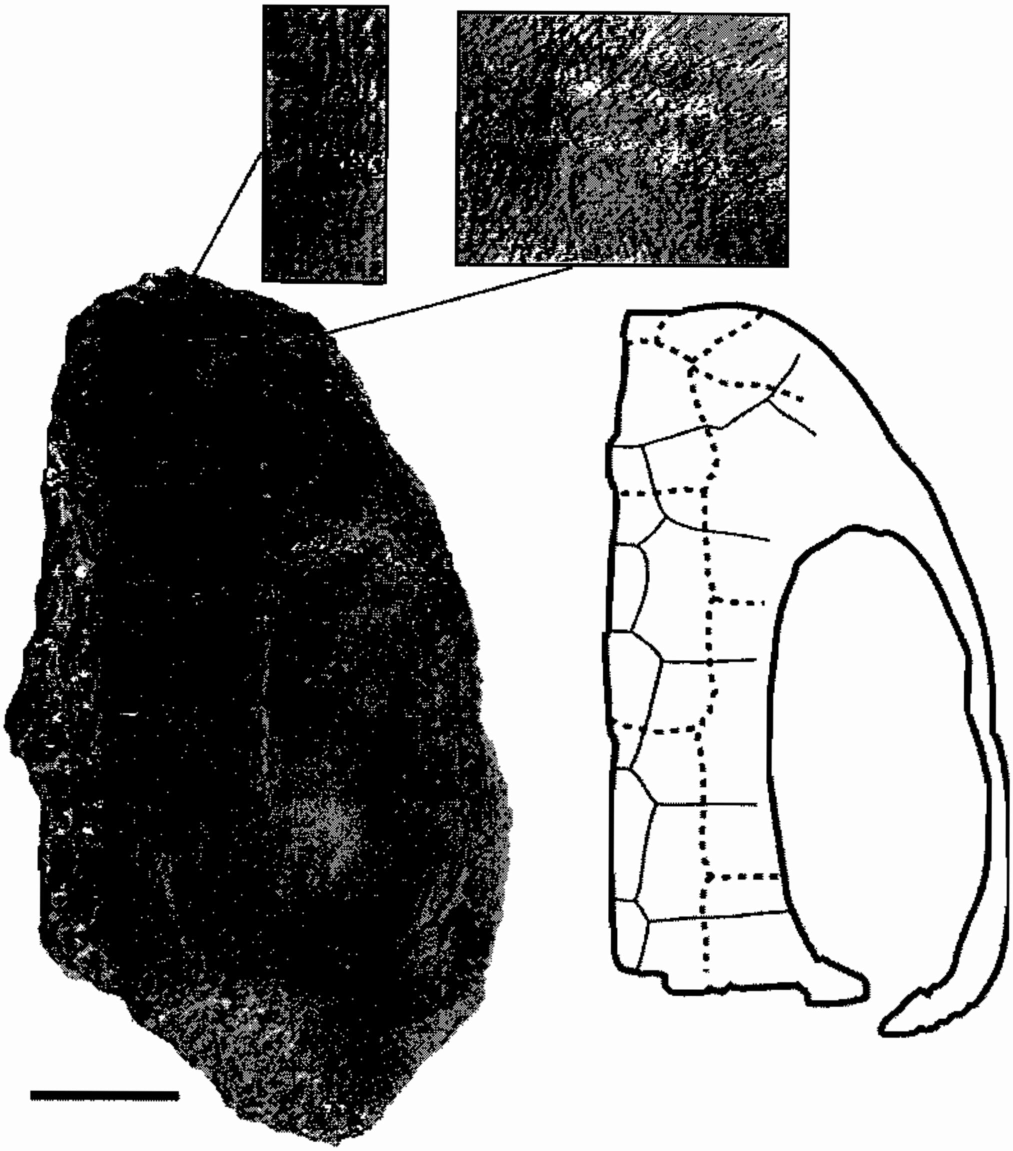

Fig. 5. Partial carapace of *Basilochelys macrobios* n. gen. n. sp. (MD4-1) from the Late Jurassic–Early Cretaceous Phu Kradung Formation, Huai Sai locality, NE Thailand. Scale bar: 200 mm.

However, the whole shell surface is rough. The vermiculated ornamentation, although not well preserved, is discernible on the anterior part of the carapace; the posterior peripherals have a rather smooth surface.

Carapace (*Figs 3–5*). The shell of MD8-1 is slightly dorsoventrally crushed. The carapace has a rounded outline with the length only slightly greater than the width. There is a wide and shallow 'notch' on the right posterolateral margin of this specimen that we interpret as an anomaly. MD8-2 is more elongated than MD8-1 (see Table 1) and slightly deformed by dorsolateral crushing. The shells are low with a smooth margin throughout and without keels or knobs on the carapace. There is no shallow central depression along the midline of the carapace. Such a depression is observed in macrobaenids–sinemydids (*Sinemys* (Brinkman & Peng 1993*b*), *Ordosemys* (Brinkman & Peng 1993*a*; Tong *et al.* 2004*b*; Danilov & Parham 2007), *Wuguia* (Matzke *et al.* 2004*b*; Danilov & Sukhanov 2006)), xinjiangchelyids (Peng & Brinkman 1993; Matzke *et al.* 2004*a*), and *Siamochelys* from the Middle Jurassic of southern Thailand (Tong *et al.* 2002).

MD8-1 and MD4-1 have a shallow nuchal emargination, whereas the anterior rim of the carapace of MD8-2 is damaged. The anterior part of the lateral margin of the shell is thickened, rounded and

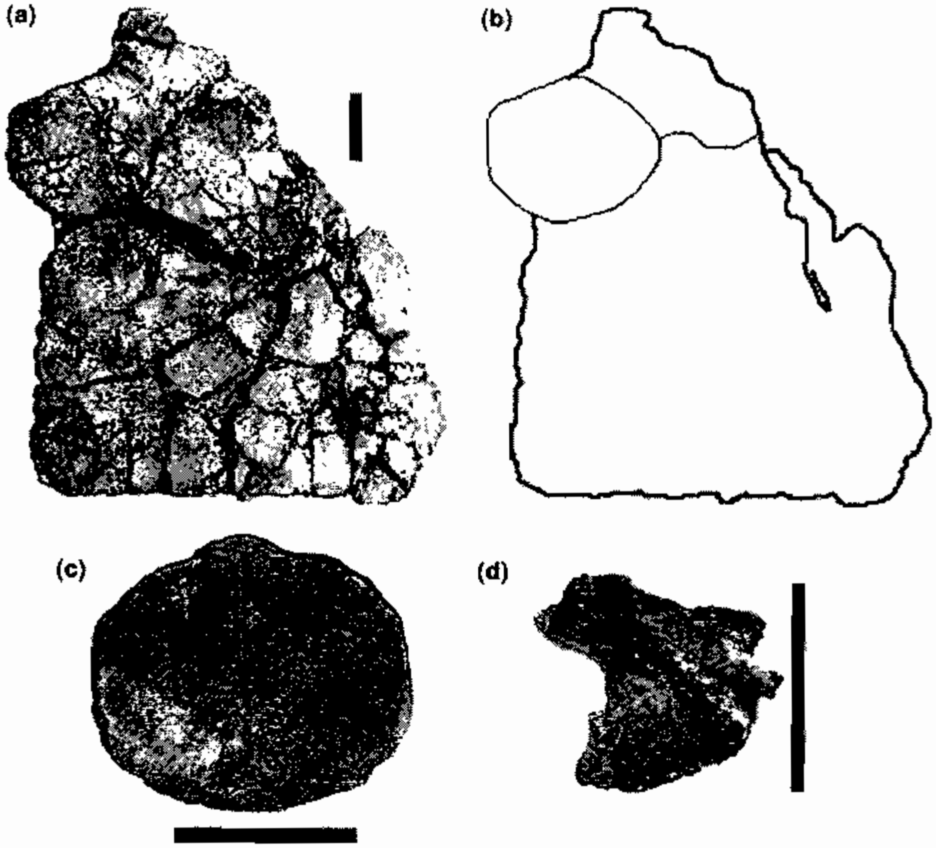

Fig. 6. *Basilochelys macrobios* n. gen. n. sp. from the Late Jurassic–Early Cretaceous Phu Kradung Formation. (**a**, **b**) partial plastron (MD5-1) from Dan Luang (scale bar: 50 mm); (**c**) entoplastron from Huai Pai (scale bar: 50 mm); (**d**) cervical vertebra (MD8-4) from Kham Phok (scale bar: 20 mm).

Fig. 7. Pelvis of *Basilochelys macrobios* n. gen. n. sp. (MD8-1) from the Late Jurassic–Early Cretaceous Phu Kradung Formation, Kham Phok locality, NE Thailand. Dorsal view. Scale bar: 50 mm.

upturned, forming a wide and shallow gutter along the margin, which is clearly visible in MD8-1, MD8-2 and MD4-1. The posterior peripherals, from the seventh to the eleventh, as well as the pygal, are flared and have a thin and rather sharp free margin, except the posterior peripherals on the right side of MD8-1, which have a rather rounded margin because of the anomaly.

The nuchal is certainly complete in MD8-1, but sutures are not visible. It is incomplete in MD8-2 and MD4-1. The nuchal of MD8-2 is wide and very short, being much wider than long and shorter than the first neural. The nuchal of MD4-1 is wide too, but longer than the first neural.

The neural series is complete in MD8-2, but only the outlines of the first to sixth neurals are distinguishable; the sutures of the posterior neurals, from the posterior part of the sixth neural to the suprapygal, are not visible. In MD8-1, neither inter-neural sutures, nor neural–costal sutures are visible, so the neurals and costals may have been completely fused together. An incomplete neural series, from the first to fifth neural, is preserved in

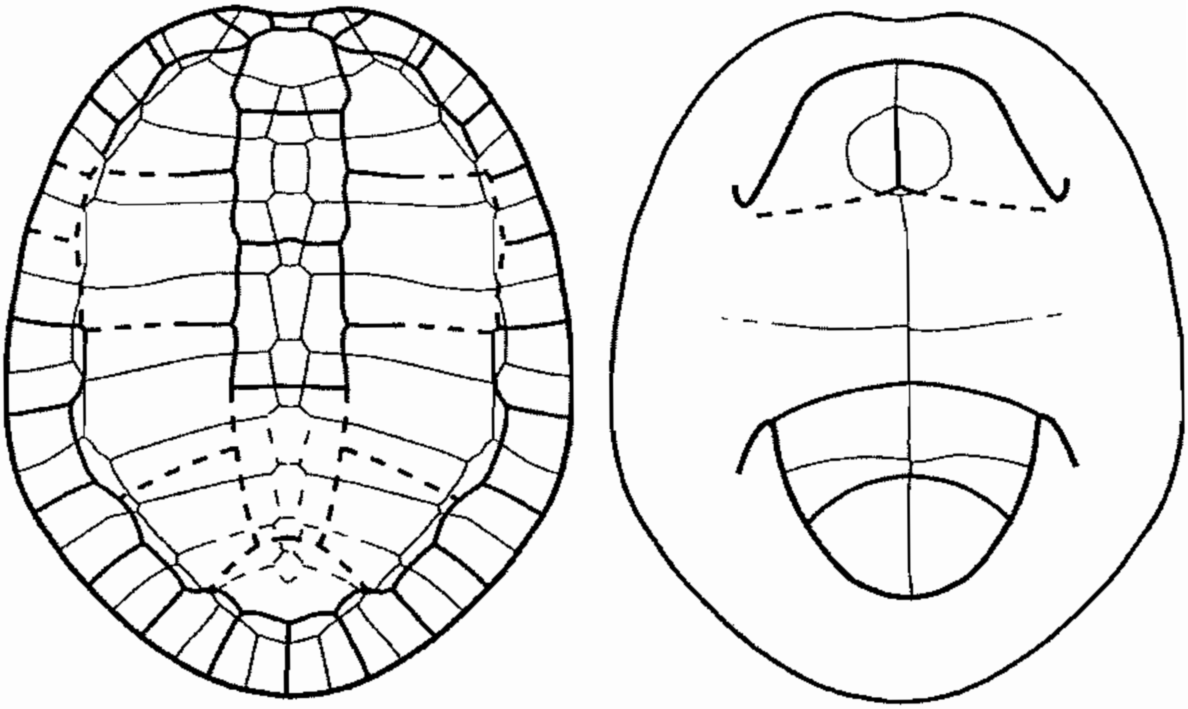

Fig. 8. Reconstruction of carapace and plastron of *Basilochelys macrobios* n. gen. n. sp. from the Late Jurassic–Early Cretaceous Phu Kradung Formation, NE Thailand, based on MD4-1, MD8-2, MD8-1 and MD5-1.

MD4-1, the fifth neural being incomplete. The neural morphology is similar in MD8-2 and MD4-1: the first neural is six-sided with short posterolateral sides. The second neural is four-sided and clearly shorter than the first. The third to sixth neurals are six-sided with short anterolateral sides. All these neurals are longer than wide, the third and the fourth neurals are the longest, and clearly longer than the first neural in both MD4-1 and MD8-2. The length of the neurals decreases from the third to the sixth. This neural pattern of $6 > 4 < 6 < 6 < 6 < 6$ is shared by adocids and nanhsiungchelyids (Meylan & Gaffney 1989; Hirayama *et al.* 2001).

Suprapygal(s) are preserved in MD8-1 and MD8-2, but sutures are not visible in MD8-1. In MD8-2, at least one large posterior suprapygal is distinguishable. The pygal plate, clearly visible in MD8-2, is slightly wider than long, with the anterior and posterior rim convex backward and the lateral borders slightly convergent forward.

Eight costal plates are present in MD8-2. The first costal is short, and as long as the second costal plate. The morphology of the first costal plate of MD4-1 and MD3-1 is similar to that of MD8-2. Other costal plates have parallel anterior and posterior sides. The first costal plate reaches the anterior margin of the third peripheral, and the eighth costal plate contacts the ninth and tenth peripheral plates.

Eleven pairs of peripherals are present in MD8-2. The first peripheral, preserved on the right side, is small and as long as wide, with the anterior free margin longer than the posterior rim. The size of the peripherals and their mediolateral width increases from the front to the back. The eighth to eleventh peripherals are mediolaterally expanded.

On the inner side of the carapace, the first costal plate bears a long and sharp transverse and anteriorly concave ridge, extending from the first dorsal rib head to the lateral margin of the plate. A strong, long stick-shaped first thoracic rib extends along this ridge laterally to the third peripheral plate. The contact is, however, not clearly preserved. A similar structure is present in *Ordosemys leios* (Brinkman & Peng 1993*a*). In *Xinjiangchelys latimarginalis* the first thoracic rib is much shorter, extending only halfway across the first costal (Peng & Brinkman 1993). All dorsal rib heads are large and flattened.

The scute sulci are clearly visible in MD4-1 (Fig. 5), whereas in MD8-1 they are discernible only on the posterior end of the shell. In MD8-2, they are preserved near the margin, on the anterior-right side and along the left and posterior margin (Fig. 4). The right half of the cervical scute is preserved on MD4-1. When it is reconstructed, the cervical scute is large and wider than long, with the posterior sulcus strongly convex anteriorly.

The right half of the first to third vertebral scutes is preserved in MD4-1. The first vertebral is roughly bell-shaped, with the anterior sulcus strongly convex anteriorly and posterolaterally convergent lateral sulci. When reconstructed, it is about as long as wide. The sulcus between the first and the second vertebral scutes crosses the first neural plate. The second and the third vertebral scutes are much longer than wide, as in some nanhsiungchelyids, such as *Hanbogdemys* (Sukhanov 2000) and *Basilemys* (Mlynarsky 1976).

The first marginal scute, visible in MD4-1 and MD8-2, is four-sided, trapezoidal in shape, with the anterior margin much longer than the posterior. The second marginal is complete in MD8-2 and nearly so in MD4-1. It is 'boot-shaped' and is anteroposteriorly longer than mediolaterally wide. The sulcus between the first and second marginals and that between the second marginal and the first pleural scute form an acute angle, extending onto the nuchal plate and barely contacting the first vertebral scute. This arrangement is clearly visible in MD8-2 and MD4-1. The third marginal scute, complete on the right side of MD8-2, is much longer than wide. The left seventh to twelfth marginals, as well as the right tenth to twelfth ones are preserved in MD8-2. The anterior marginals, from the first to the third, and the lateral ones, from the eighth to the tenth, are restricted to the peripheral plates. The seventh marginal extends onto the costal plates; and the eleventh and twelfth marginals are strongly expanded anteroposteriorly, extending onto the suprapygal and costal plates, as in most adocids and nanhsiungchelyids. The posterior marginal scutes are clearly larger than the anterior ones. The eleventh and twelfth marginals are visible in MD8-1; they are similar to those of MD8-2.

Plastron (*Figs 3, 4 and 6*). The plastron is preserved in MD8-1 and MD8-2, both lacking most of the anterior lobe. An incomplete anterior lobe, lacking the left part, is preserved in MD3-1.

The plastron is strongly sutured to the carapace. The entire plastron is strongly built, with large anterior and posterior lobes and a long bridge. The anterior lobe (MD3-1) is wide and long. The right epiplastron is nearly complete, with a long midline suture to its mate that represents about 40% of the length of the entoplastron. The entoplastron (Fig. 6c) is complete, being a five-sided plate, wider than long, with a pointed anterior end and a nearly straight and transversal posterior margin. On the inner side, a pair of rounded tubercles is present on the anterior part of this plate. The axillary buttress, preserved in MD8-1, MD8-2 and MD3-1, is long. It reaches at least the third peripheral plate, but does not extend to the costal plate. The bridge is long and narrow. It is slightly longer than the posterior lobe. The axillary and inguinal notches are very narrow. The posterior lobe, complete in both MD8-1 and MD8-2, is wide, with a rounded posterior end. The anal notch is absent. The xiphiplastron is slightly shorter than the hypoplastron. The hypoplastron–xiphiplastron suture is slightly convex anteriorly.

The general morphology of the plastron of the Phu Kradung turtles is reminiscent of adocids (*Adocus*, *Adocoides*) and nanhsiungchelyids (*Zangerlia*, *Basilemys*, *Hanbogdemys*, *Nanhsiungchelys*). The plastron of xinjiangchelyids and macrobaenids–sinemydids differs significantly from that of the Phu Kradung turtles in the loose carapace–plastron attachment, the reduced anterior and posterior lobes, the short, wide and fan-shaped bridge, and the small and much narrower entoplastron.

The sulci on the plastron are only partly visible in MD8-2 (Fig. 4). They are not preserved in MD3-1. The anal scute appears to be restricted to the xiphiplastron, not reaching the hypoplastron–xiphiplastron suture. On the isolated entoplastron from Huai Pai, the humeropectoral sulcus is preserved, on the posterior part of the entoplastron.

Vertebrae. An isolated sixth cervical vertebra is preserved inside MD8-2, exposed in left lateral view. The cervical is long and low as in *Zangerlia neimongolensis* (Brinkman & Peng 1996), unlike the short and high sixth cervical of *Dracochelys* (Brinkman 2001). The amphicoelous centrum bears a large ventral keel extending along the full length of the centrum, with a straight ventral margin. The anterior articular surface is single whereas the posterior one is double. The postzygaphophysis rises gently from the middle of the centrum posterolaterally. The transverse process is damaged; it is located under the prezygapophysis.

An isolated anterior cervical vertebra (MD8-4) has been collected near MD8-2 (Fig. 6d). This cervical is deformed, being compressed laterally. As preserved, it measures 39 mm in total length. It is narrow, high and long, being twice as long as wide. The centrum bears a thin and deep ventral keel. It is weakly amphicoelous. The anterior articular surface is slightly damaged. It is single, roughly rectangular in shape and wider than high. The posterior articular surface is single, narrow, higher than wide and appears more concave than the anterior one. The large transverse process is well separated from the prezygapophysis and located at the anterior end of the vertebra, below the prezygapophysis. There is a distinct ridge under the transverse process extending from the lateral side of the centrum to the under-surface of the transverse process. The neural arch has widely separated prezygapophyses and postzygaphophyses and a low neural spine.

The first thoracic vertebra is preserved in MD8-1 and MD8-2, articulated to the shell. The anterior articular surface of the first thoracic vertebra is concave and single, facing anteroventrally.

The amphicoelous cervical centrum is a primitive feature of cryptodires (Gaffney 1990, 1996). It is present in plesiochelyids (*Thalassemys* (Rieppel 1980)) and *Xinjiangchelys* (Peng & Brinkman 1993; Matzke *et al.* 2004*a*) among Eucryptodira. In general shape, the long and slender cervicals from Kham Phok resemble those of *Xinjiangchelys qiguensis*, *Zangerlia neimongolensis* (Brinkman & Peng 1996), *Basilemys* sp. (Brinkman 1998) and *Adocus* (Meylan & Gaffney 1989), but differ from the short cervicals of *Dracochelys* (Brinkman 2001), *Macrobaena* (Tatarinov 1959) and *Ordosemys* (Brinkman & Peng 1993*a*). The cervicals of *X. qiguensis* differ from our specimens in that the transverse process is located more posteriorly (Matzke *et al.* 2004*a*). A double articular surface between the sixth and seventh cervicals occurs in *Adocus* (Meylan & Gaffney 1989) and the nanhsiungchelyids *Zangerlia neimongolensis* and *Basilemys* sp. (Brinkman 1998). They differ from the cervicals from Kham Phok in the opisthocoelous second to seventh cervicals. In addition, *Z. neimongolensis* has a double central articulation between the eighth cervical and the first thoracic vertebrae, whereas the first thoracic vertebra from Kham Phok has a single anterior central articulation. *Adocus* has a single but concave posterior central articulating surface of the eighth cervical.

A complete series of 10 dorsal vertebrae is preserved in MD8-1 and MD8-2, articulated to the shell. They are long, slender and high, with a rounded ventral surface.

Pectoral and pelvic girdle

The complete ilium, pubis and ischium are preserved in MD8-1 (Fig. 7); the pubis and ischium remain articulated to each other, but turned 90° to the left, and both ilia are crushed. A disarticulated pelvis is preserved in MD8-2.

The ilium is short and stout, with an enlarged distal end to form the iliac blade. There is no evidence of a thelial process.

The pubis and ischium, exposed in dorsal view in MD8-1, form a longer than wide ventral plate. The pubis is narrow and long. The epipubis is not ossified. The pectineal process is absent or very weak, not visible in dorsal view. This is different from *Adocus*, in which a short pectineal process is present at the mid-length of the pubis. The ischium has a very strong and long metischial process, which is directed backwards and slightly outwards. Both the pubic and ischiac symphyses are long. The thyroid fenestra is not completely divided; a short space separates the pubis from the ischium on the midline, as in *Adocus* (Meylan & Gaffney 1989).

The general morphology of the pelvis is most similar to that of *Adocus* sp. (Meylan & Gaffney 1989), but very different from that of *Lissemys* and other trionychids (Meylan 1987). The absence of the pectineal process is unusual among turtles. The long metischial process is found also in *Xinjiangchelyis* (Peng & Brinkman 1993; Matzke *et al.* 2004*a*), macrobaenids (Tatarinov 1959; Brinkman & Peng 1993*a*; Parham & Hutchison 2003), *Adocus* (Meylan & Gaffney 1989), *Basilemys* (Meylan & Gaffney 1989), and an undescribed new genus and species of trionychoid from the Early Cretaceous of Japan (Hirayama 2000, 2002). The pubis of xinjianchelyids is different from that of the Kham Phok specimens because it is wider than long and bears a well-developed and long pectineal process (Peng & Brinkman 1993; Matzke *et al.* 2004*a*).

Limb bones

A right humerus (MD8-5) was found near MD8-2 and an incomplete femur (MD8-6) was found inside MD8-2. The humerus is nearly complete, but the medial process and the head are a little damaged. The humerus is 160 mm long, which represents only 18% of the shell length of MD8-2. The shoulder is not developed. The shaft is slightly curved ventrally. The posterior half of the humerus is strongly expanded. The condyles are well developed and face ventrally. The ectepicondyle foramen is crushed.

The femur (MD8-6) has both its proximal and distal ends damaged. Its length is similar to or slightly larger than that of the humerus. It has a slightly curved shaft.

One isolated nearly complete distal phalanx (MD8-7), 51 mm long, is preserved. It is laterally compressed, with a higher than wide articular surface.

Discussion

The large turtles from the Phu Kradung Formation described above clearly belong to the Cryptodira, as the pelvis is not sutured to the shell and the processus trochlearis oticum is present. They belong to Eucryptodira because the carotid artery is enclosed by the pterygoid posteriorly and the mesoplastra are absent (Gaffney & Meylan 1988; Gaffney 1996).

Among Eucryptodira, the amphicoelous cervical vertebrae of the Phu Kradung turtles is a primitive feature that is reminiscent of the early Eucryptodira, such as the xinjiangchelyid *Xinjiangchelys* (Peng & Brinkman 1993) and the plesiochelyid *Thalassemys* (Rieppel 1980). The Phu Kradung turtles are excluded from xinjiangchelyids and plesiochelyids because the posterior portion of the canalis caroticus internus is covered by bone, a derived character found in Centrocryptodira.

Several characters are shared by the Phu Kradung turtles and the Early Cretaceous turtles that have been placed in the families Sinemydidae and Macrobaenidae. These characters include the ventrally exposed foramen posterius canalis caroticus laterale, the unossified posterior portion of the canalis caroticus lateralis, a large foramen caroticum basisphenoidale, and the presence of a pair of pits on the ventral surface of the basisphenoid. In addition, the Phu Kradung turtles have a long first thoracic rib that extends along the full width of the first costal plate, a character observed also in the macrobaenid *Ordosemys leios* from the Early Cretaceous of Inner Mongolia, China (Brinkman & Peng 1993*a*). The Phu Kradung turtles are separated from sinemydids–macrobaenids by several derived characters. The deeply embedded canalis caroticus internus is characteristic of Polycryptodira. The plastron sutured to the carapace, the broad epiplastra, the large and broad entoplastron, the large plastron with wide anterior and posterior lobes, and the long and narrow bridge are shared with Trionychoidea and Testudinoidea. In addition, the first thoracic vertebra of the Phu Kradung turtles has an anteroventrally facing anterior central articulation. This character is part of the neck retraction mechanism characteristic of advanced cryptodires. Although measuring this character is delicate, it suggests that these large turtles were probably capable of retracting the head inside the shell. The plastral buttresses not reaching the costal plates exclude the Phu Kradung turtles from Testudinoidea.

Among Trionychoidea, the very ventral position of the foramen posterior canalis carotici interni, which is completely enclosed by the pterygoids in the Kham Phok skull, is characteristic of Trionychoidae (Meylan & Gaffney 1989). Furthermore, the skull and shells of the Phu Kradung turtles share several derived characters with both Adocidae and Nanhsiungchelyidae. Several previous studies considered Adocidae and Nanhsiungchelyidae as a monophyletic group (Brinkman & Peng 1996; Brinkman 1998; Joyce 2007). According to Brinkman & Peng (1996), the clade Adocidae–Nanhsiungchelyidae is supported by four unambiguous characters. With the exception of the first character (scute sulci on skull roof), which is not preserved in the Kham Phok skull, the other three characters are all present in the Phu Kradung turtles.

The neural formula $6 > 4 < 6 < 6 < 6 < 6$ occurs in nearly all Adocidae and Nanhsiungchelyidae, with a single exception in adocids: *Isanemys* from the Early Cretaceous of Thailand (Tong *et al.* 2006*a*). This character is used as a synaphomorphy to unite these two families (Gaffney & Meylan 1988; Brinkman & Peng 1996; Hirayama *et al.* 2001; Joyce 2007), or considered as an independent occurrence (Meylan & Gaffney 1989; Tong *et al.* 2006*a*). In Nanhsiungchelyidae, the neural series is complete, reaching the suprapygal; whereas in Adocidae, there is a diminution of the number of neurals, the posterior costals meeting on the midline. Only the shape of the first six neurals could be determined in the large turtles from the Phu Kradung Formation (see reconstruction, Fig. 8).

The pectoral scute reaching the entoplastron is present in all nanhsiungchelyids and advanced adocids, but absent in primitive adocids, including *Isanemys*, *Ferganemys*, the undescribed trionychoid from the Neocomian of Japan (Hirayama *et al.* 2000), and *Yehguia tatsuensis*, a primitive trionychoid closely related to adocids and nanhsiungchelyids (Danilov & Parham 2006). Thus this character could be also considered as occurring independently in Adocidae and Nanhsiungchelyidae.

The advanced adocids, such as *Adocus* and *Adocoides*, have the lateral and posterior marginals mediolaterally expanded, overlapping the costal plates, whereas in most adocids, including primitive adocids, and most nanhsiungchelyids, only the eleventh and twelfth marginals are anteroposteriorly expanded, being clearly longer than wide, extending beyond the peripheral plates. In adocids, this occurs in *Ferganemys*, *Adocus*, *Adocoides*, the undescribed trionychoid from Japan, *Shachemys baibolatica* and *S. ancestralis* (Nessov 1986; Danilov *et al.* 2007). In *Shachemys laosiana*, the twelfth marginals are elongated and narrow as in the Phu Kradung turtles, overlapping the suprapygal, whereas the eleventh marginals are included in the peripheral plates (de Lapparent de Broin 2004). In nanhsiungchelyids, this character is observed in *Hanbogdemys*, *Bulganemys* (Sukhanov 2000; Sukhanov & Narmandakh 2006), *Basilemys variolosa* (Langston 1956), but not in *Zangerlia testudimorpha* (Mlynarski 1972). The eleventh and twelfth marginals are short, and wider than long in sinemydids–macrobaenids. They are square in some xinjiangchelyids. In these forms, either the eleventh and twelfth marginals are included in the pygal and peripherals or only the twelfth marginals extend onto the posterior suprapygal. Testudinoids also have short eleventh and twelfth marginals. The twelfth pair of marginals extending onto the pygal in this group is due to the short pygal plate, but not due to the elongation of the marginals.

Table 2. *Distribution of characters from the Appendix*

	10	20	30	40	50	60	70	80
Proganochelys	0000000000	00?0000000	?000000000	0000000000	000001?00?	00??000000	01000000?0	0000
Pleurodira	0000010000	0000001000	100000aaa0	001fe0100a	00a0000ca0	0abaa00100	001110e00a	0010
Kayentachelys	0011001000	00?0000000	0000000??0	00?0000?00	000???0010	1010000000	0100000000	0000
Kallokibotion	0011011100	0000?00000	0000000??0	00?0000?00	000???0010	0030000100	0011?000?0	0010
Pleurosternidae	0011011110	1001101000	000010a??0	00?0000?00	00???0011c	10b0000100	001c100000	00a0
Baenidae	0011011110	1011101000	0000001100	001e00a000	0000000c10	00b0000110	0a1a100000	00a0
Plesiochelyidae	0111011111	a000001000	0000001??0	0010001?00	?????00010	0a001001?0	001a10000a	0100
Xingjiangchelys	???????111	0000?11??0	??000?1??0	10?0000001	??0?0?0110	0000101000	0010100000	0101
Meiolaniidae	0011011111	01?0000000	1000000001	0001100000	000001?11?	00??101001	001?0000?1	0?0?
Sinemys	0011111111	0000011110	10000?1??1	1??220??00	????00110	001010101?	001?1??00a	1?00
Dracochelys	?111111111	00?0?111?0	00000?1101	0??2200001	??????0110	00111110?1	00101??001	1??0
Ordosemys	0011011111	0000?11100	00000?1?01	1?11200000	111??00110	00001110??	00101?0001	0100
Judithemys	0111011111	11?0?11100	00000?11?1	1111101001	111??00110	00001110?1	0010110000	0100
Chelydridae	1111011111	1110001100	100000a001	1111101111	11000002a0	0000111011	0010110001	1100
Chelonioidea	0111011111	1100001100	000000a001	1111111111	0110000210	00b01a1011	0010110001	1000
Adocus	1111011111	?110001110	0010011111	1112211111	?1?0101212	1121100010	0012101000	0001
Carettochelyidae	1111011111	1110001111	1011110111	1012211111	011010021?	112?111010	00111????0	a?0?
Trionychidae	1111011111	1110001110	1011111111	1012211111	011?100???	112?1a101?	00121????1	a???
Basilochelys	?????11111	0100?11??1	?00?0????0	11????1?10	???01?1211	1??1100010	00121?10?0	000?
Basilemys	11?1??1???	??????1110	1?00??1011	1112?111??	????111210	1a11100010	111210?010	0001
Zangerlia	1111011111	???0?01110	10100?11?1	1112211111	????111211	10a1100010	11121020a0	0001
Nanhsiungchelys	0111011???	11????0001	1?0?1?00?1	?????????	???0?11111	1011100??0	1112102010	0001
Dermatemys	1111011111	1110001110	0100010001	1113111111	0111100210	01c1100010	001211?100	0011
Staurotypus	1111011111	1110001110	0100010001	1113111111	0111100210	0a2?110010	001111?100	1000
Testudinoidea	1111011111	11100011a0	a000001a01	111dc11111	a1a00aae1a	0aa010a110	aa1111e000	00a0

Taxon/character matrix: a = (01); b = (02); c = (12); d = (13); e = (012); f = (023).

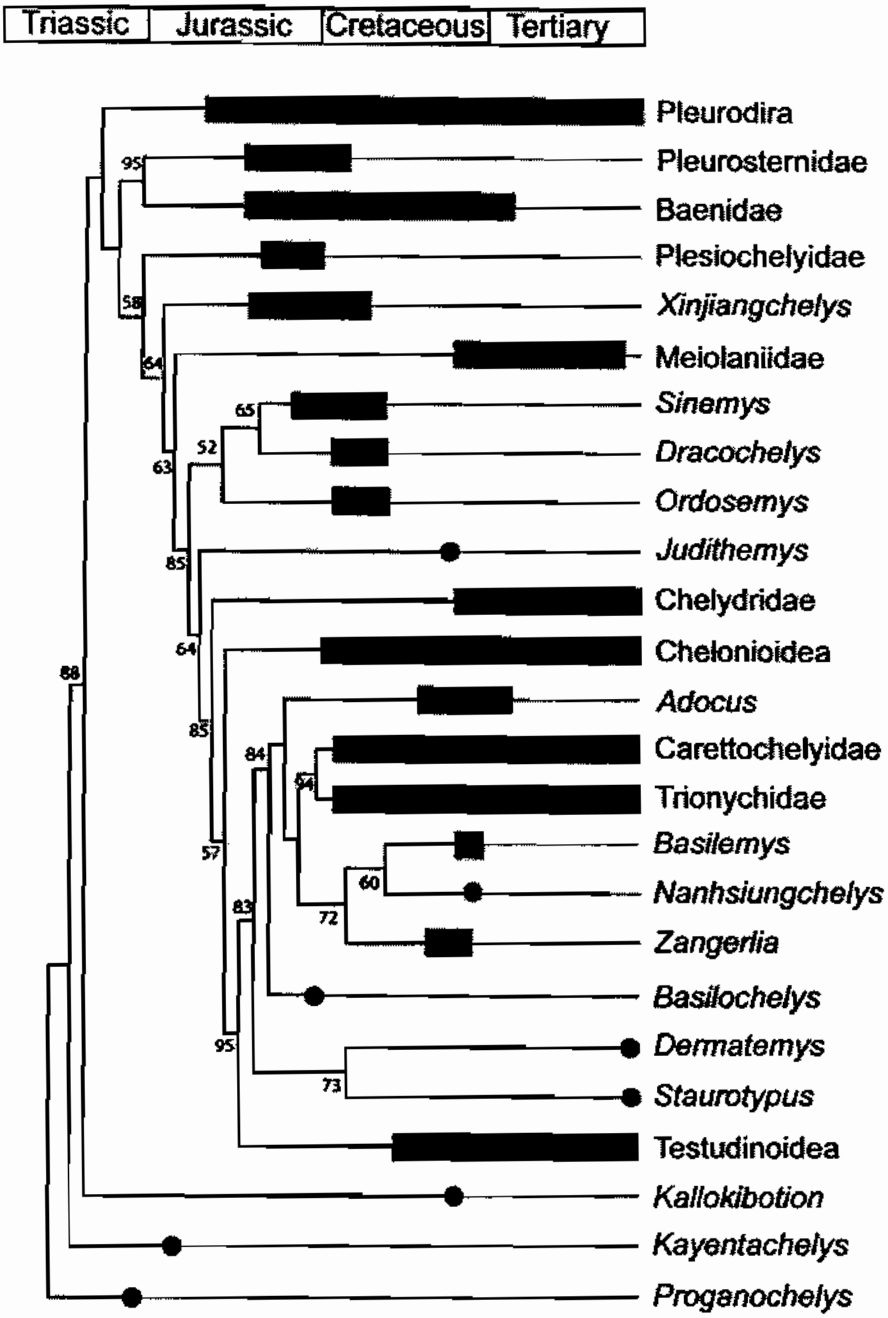

Fig. 9. Strict consensus cladogram produced from the data matrix in Table 2.

Two additional characters can be added to the above-mentioned characters of the Adocidae and Nanhsiungchelyidae: both the shell and the skull roof surface are sculptured and the vertebral scutes are narrow. A sculptured shell surface is found in most Trionychoidea, including Trionychidae, Carettochelyidae, Adocidae, Nanhsiungchelyidae and Dermatemydidae. The pattern of the ornamentation seen on the Huai Sai carapace is most similar to that of *Anomalochelys*, a nanhsiungchelyid from the Late Cretaceous of Japan (Hirayama *et al.* 2001). The sculpturing of both shell and skull roof surface occurs in *Nanhsiungchelys* (Yeh 1966) and *Carettochelys*, whereas in *Zangerlia neimongolensis* only the shell is sculptured (Brinkman & Peng 1996). The skull roof of *Basilemys* sp. is also sculptured, but it does not match the sculpturing of the carapace (Brinkman 1998). Both adocids and nanhsiungchelyids have narrow vertebrals. The very narrow vertebrals, with the second to the fourth vertebrals much longer than wide as seen in the Phu Kradung turtles, are present in some nanhsiungchelyids, such as *Hanbogdemys orientalis* and *Basilemys variolosa*, and some testudinoids. This is also the case in carettochelyid, when the scutes are present on the shell.

As shown in the description and comparisons, the general morphology of the Kham Phok skull presents strong similarities to that of *Adocus* from the Late Cretaceous of North America (Meylan & Gaffney 1989). The skull of *Adocus* is more derived than that from Kham Phok in that the palatine artery is fully embedded in bone; thus the foramen posterius canalis caroticus laterale is no longer visible on the ventral surface, although a foramen caroticum basisphenoidale is still present. Another derived feature that separates *Adocus* from the Phu Kradung turtles is the significant contribution of the parietal to the processus trochlearis oticum. For these two characters, the condition of the Phu Kradung turtles is closer to that of nanhsiungchelyids. *Zangerlia neimongolensis* also has the canalis caroticus lateralis and canalis caroticus internus exposed in a large depression, but the poor preservation of that region in *Zangerlia* prevents a detailed comparison (Brinkman & Peng 1996). The significant contribution of the parietal to the processus trochlearis oticum, considered as a synapomorphy of Trionychoidae by Meylan & Gaffney (1989) is observed in the adocid *Adocus*, *Ferganemys* and a primitive adocid skull from the Late Cretaceous of Uzbekistan (Danilov & Parham 2005), but absent in the nanhsiungchelyid *Basilemys* sp. and also in *Nanhsiungchelys* according to Brinkman (1998).

We performed a cladistic analysis based on previously defined data matrices (Meylan 1987; Meylan & Gaffney 1989; Rougier *et al.* 1995; Brinkman & Peng 1996; Gaffney 1996; Shaffer *et al.* 1997; Brinkman & Wu 1999; Hirayama *et al.* 2000, 2001; Joyce 2007) using the parsimony algorithm of PAUP 4.0 (Swofford 1996). We considered *Hanbogdemys* and *Nanhsiungchelys* as belonging to a monophyletic entity, following Brinkman & Nicholls (1993).

The different states of 74 characters were scored for 25 taxa (Table 2 and Appendix). The analysis resulted in a single tree of 177 steps (Fig. 9) with a consistency index of 0.47 and retention index of 0.74, suggesting that homoplasy is rampant in the dataset. On the 74 characters, 42 were observed in *Basilochelys*. Our analysis agrees with the cladogram obtained by Gaffney (1996) for interfamilial relationships except for the position of *Kayentachelys* and *Kallokibotion*, and with that of Meylan & Gaffney (1989) for the relationships within Trionychoidea, in placing *Adocus* as the sister group of Nanhsiunchelyidae + Trionychia. *Basilochelys* is in a early position within the monophyletic Trionychoidae and closely related to *Adocus* and nanhsiungchelyids.

The high homoplasy rate in the tree implies that the relationships must be considered with caution. There is no exclusive apomorphy for uniting Trionychoidea, Trionychoidae or Nanhsiungchelyidae. These groups are defined more by character combinations than by a series of unambiguous autapomorphies. In contrast, several characters (e.g. 34, 35) occur only in Trionychoidae (Trionychia, *Adocus* and Nanhsiungchelyidae) and in some macrobaenid–sinemydid turtles, which suggests that the Trionychoidae may have an earlier position within eucryptodiran turtles. This may explain both the early occurrence of Trionychoidae in the fossil record, in contrast to Kinosternoidae, Chelydroidea or Testudinoidea; and the non-monophyletic nature of Kinosternoidea + Trionychoidae based on recent molecular phylogenies (Shaffer *et al.* 1997; Fujita *et al.* 2004), although the tree that we have obtained does not support this scenario. The association of primitive and derived characters in *Basilochelys* would also support a more primitive position for Trionychoidae. Further discoveries could therefore challenge the current scenario.

Conclusion

The large turtles from the terminal Jurassic–earliest Cretaceous Phu Kradung Formation of the Khorat Group, NE Thailand, described herein represent a new genus and new species of Eucryptodira, *Basilochelys macrobios* n. gen. n. sp. This taxon is placed in Trionychoidae and considered as the most basal member of that group. The combination of primitive and derived characters of *Basilochelys* suggests that the group Trionychoidae may have originated from xinjiangchelyids and their close relatives. *Siamochelys* from the Middle Jurassic of the southern peninsula of Thailand may represent the sister taxon of Trionychoidae, because of its ligamentous carapace–plastron attachment, sculptured shell surface and wide entoplastron. These new discoveries add significantly to the still poorly known turtle fauna from the Late Jurassic–Early Cretaceous of SE Asia and provide important information about the origin and early evolution of modern cryptodiran turtles.

This work was supported by the Department of Mineral Resources, Thailand, the ECLIPSE Programme of CNRS, France, the TRF-CNRS Special Programme for Biodiversity Research and Training (BRT/BIOTEC/NSTDA), Grant BRT R-24507; and the PHC 'Evolution et biodiversité des vertébrés aquatiques Mésozoiques et Cénozoiques en Thaïlande' (16610UG). We thank all the people who took part in the field work and prepared the specimens; and P. Meylan (Saint Petersburg, Florida) and D. Brinkman (Drumheller, Alberta) for reviewing the paper. This is publication ISEM 2007-166 of J.C.

Appendix: Definition of characters and their states used in the analysis of relationships of *Basilochelys*

Character state definition:
Skull:

1. Nasals: present = 0; absent = 1 (Gaffney 1996: 1).
2. Prefrontals: do not meet in midline = 0; meet in midline = 1 (Gaffney 1996: 2).
3. Prefrontal–vomer contact: absent = 0; present = 1 (Gaffney 1996: 3).
4. Vertical flange on processus pterygoideus externus: absent = 0; present = 1 (Gaffney 1996: 4).
5. Foramen palatinum posterius: relatively small = 0; relatively large = 1 (Gaffney 1996: 5).
6. Interpterygoid vacuity: open = 0; closed = 1 (Gaffney 1996: 6).
7. Processus trochlearis oticum: absent = 0; present = 1 (Gaffney 1996: 7).
8. Middle ear with ossified floor formed by posteromedial process of pterygoid: pterygoid process absent = 0; pterygoid process present = 1 (Gaffney 1996: 8).
9. Canalis caroticus internus at least partially formed by pterygoid: not formed by pterygoid to any extent = 0; partially or entirely formed by pterygoid = 1 (Gaffney 1996: 9).
10. Canalis caroticus internus formed entirely by pterygoid posteriorly (distally): formed partially or not by pterygoid = 0; formed entirely by pterygoid = 1 (Gaffney 1996: 10).
11. Canalis caroticus internus and canalis caroticus lateralis completely embedded in bone: both canals open ventrally = 0; both canals embedded in bone = 1 (Gaffney 1996: 11).
12. Thickness of pterygoid floor of canalis caroticus internus: thin or absent = 0; thick = 1 (Gaffney 1996: 12).
13. Canalis caroticus lateralis versus canalis caroticus internus: canalis caroticus lateralis equal to or larger than canalis caroticus internus = 0; canalis caroticus lateralis smaller than canalis caroticus internus = 1 (Gaffney 1996:13; some scores according to Shaffer *et al.* 1997)
14. Foramen posterius canalis carotici interni: not formed by basisphenoid and pterygoid = 0; formed by basisphenoid and pterygoid, midway along basisphenoid–pterygoid suture = 1 (Gaffney 1996: 14).
15. Fenestra perilymphatica: relatively large = 0; relatively small = 1 (Gaffney 1996: 15).
16. Paired pits on ventral surface of basisphenoid: pits absent = 0; pits present = 1 (Gaffney 1996: 16).
17. Posterior temporal emargination: not developed = 0; at least partially developed = 1 (Gaffney 1996: 17).
18. Parietal–squamosal contact: present = 0; absent = 1 (Gaffney 1996: 18).
19. Postorbital–squamosal contact: present = 0; absent = 1 (Gaffney 1996: 19).
20. Skull roof surface sculptured: no = 0; yes = 1 (Brinkman & Peng 1996: 15).
21. Incisura columellae auris: open = 0; closed = 1 (Meylan & Gaffney 1989: 13).
22. Foramen stapedio-temporale: large = 0; absent or small = 1 (Shaffer *et al.* 1997: 92).
23. Contribution of parietal to processus trochlearis oticum: little or none = 0; large = 1 (Meylan & Gaffney 1989: 44)
24. Fused premaxillae: no = 0; yes = 1 (Meylan 1987: 44).
25. Ventral contact between left and right pterygoid: present = 0; absent = 1 (Meylan & Gaffney 1989: 12).
26. Palatine contribution to the side wall of braincase: small or absent = 0; large = 1 (Shaffer *et al.* 1997: 68).
27. Lower cheek emargination: absent or shallow, with processus pterygoidei externus concealed from lateral = 0; deep, with processus pterygoidei externus exposed from lateral = 1 (Meylan & Gaffney 1989: 42).

Lower jaw:

28. Coronoid tall and located in the middle of the mandible: no = 0; yes = 1 (Meylan & Gaffney 1989: 43).
29. Retroarticular process: absent = 0; present = 1 (Meylan & Gaffney 1989: 18).

Axial skeleton:

30. Central articulations of cervical vertebrae: unformed (platycoelous or amphicoelous) = 0; formed (concavo-convex) = 1 (Gaffney 1996: 20).
31. Transverse processes of cervical vertebrae: on middle of centrum = 0; on anterior of centrum = 1 (Gaffney 1996: 21).
32. Posterior cervicals with strong ventral process: absent = 0; present = 1 (Gaffney 1996: 22; and see Joyce 2007, for codings in Trionychia).
33. Cervical ribs: present = 0; absent = 1 (modified from Gaffney 1996: 23, according Joyce 2007).
34. Fourth cervical central articulation (unordered): amphicoelous = 0; biconvex = 1; opisthocoelous = 2; procoelous = 3 (Gaffney 1996: 24).
35. Eighth cervical central articulation (unordered): amphicoelous = 0; procoelous 1; biconvex or opisthocoelous = 2 (modified from Gaffney 1996: 25).
36. Double (i.e. transversely paired) central articulations between the seventh and eighth cervicals: absent = 0; present = 1 (Gaffney 1996: 26).

37. Cervical vertebra having a distinct double transverse process (i.e. diapophysis and parapophysis): present in at least some cervicals = 0; absent = 1 (Gaffney 1996: 27).
38. Neural spine on eighth cervical: high = 0; low = 1 (Gaffney 1996: 28).
39. Anterior articulation of first thoracic centrum: faces anteriorly or slightly anteroventrally = 0; faces strongly anteroventrally = 1 (Gaffney 1996: 33).
40. First thoracic rib: extends to peripherals or nearly so and lies behind the tip of the axillary buttress = 0; extends less than halfway across first costal = 1 (Gaffney 1996: 32).
41. A biconcave caudal near base of tail: absent = 0; present = 1 (Gaffney 1996: 29; *Sinemys* unknown as suggested by Joyce for this character).
42. Caudal central articulations: all centra amphicoelous or opisthocolous = 0; at least first two caudals procoelous = 1 (Gaffney 1996: 30).
43. Chevrons: well developed and present on nearly all caudals = 0; small to absent (if present, only on a few anterior caudals) = 1 (Gaffney 1996: 31; score according to Joyce 2007).

Girdles:

44. Thelial process: absent = 0; present = 1 (Meylan & Gaffney 1989: 37).
45. Thyroid fenestra: subdivided by midline contact of pubis and ischium = 0; confluent = 1 (Shaffer *et al.* 1997: 114; testudinoids coded as non-confluent).

Appendicular skeleton:

46. Phalangeal formula: most digits with three phalanges = 0; most digits with two phalanges = 1 (Meylan & Gaffney 1989: 40).

Carapace:

47. Neural formula $6 > 4 < 6 < 6 < 6 < 6$: no = 0; yes = 1 (Meylan & Gaffney 1989: 20).
48. 2nd to 4th vertebral scutes: much broader than pleural scute = 0; as broad as pleural and wider than long = 1; narrower than pleurals and longer than wide = 2 (modified from Hirayama *et al.* 2000: 59; ordered).
49. Supramarginal scutes: present = 0; absent = 1 (Gaffney 1996: 36).
50. Marginal scutes reaching costal plates: no = 0; posteriorly only = 1; posteriorly and laterally = 2 (Meylan & Gaffney 1989: 47; ordered).
51. Shell ornamentation with pits, ridges or vermiculation: absent = 0; present = 1.
52. Posterior costals meeting on the midline: no = 0; yes = 1 (Meylan & Gaffney 1989: 21).
53. Suprapygal: nearly equally divided into two = 0; first suprapygal much smaller than second = 1; first suprapygal absent = 2; second suprapygal much smaller than first or absent = 3 (Hirayama *et al.* 2000: 61).
54. Second suprapygal: contacts peripheral 11 = 0; contacts peripheral 10 and 11 = 1 (Hirayama *et al.* 2001: 23).

Plastron:

55. Mesoplastra: present = 0; absent = 1 (Gaffney 1996: 34).
56. Length of bridge: long = 0; short = 1 (Brinkman & Wu 1999: 52).
57. Attachment of carapace and plastron: sutured = 0, ligamentous = 1 (Gaffney 1996: 35).
58. Axillary buttress reach costal bone: absent = 0; present = 1 (Meylan & Gaffney 1989: 24).
59. Dorsal process on epiplastron: present = 0; absent = 1 (Gaffney 1996: 37).
60. Epiplastron: broad = 0; narrow = 1 (Gaffney 1996: 39).
61. Thick epiplastron with broad dorsal extension of gular scute: absent = 0; present = 1 (Hirayama *et al.* 2001: 35).
62. Epiplastron projected beyond the anterior margin of carapace: no = 0; yes = 1 (Hirayama *et al.* 2001: 36).
63. Entoplastron separating epiplastra: yes = 0; no = 1 (Gaffney 1996: 38).
64. Entoplastron: narrow ($W \ll L$, like *Ordosemys*) = 0; broad ($W = L$ or $W < L$, like testudinoids) = 1; very broad ($W \gg L$, like nanhsiungchelyids and *Adocus*) = 2 (modified from Hirayama *et al.* 2000: 72, with one more character state) (ordered).
65. Entoplastron: size of posterior entoplastral process: present = 0; absent = 1 (Rougier *et al.* 1995: 46).
66. Loss of plastral scute set 2 (gulars or extragulars): full set of scales 1 and 2 (gular, extragular see Hutchison & Bramble 1981; equal to intergular, gular of older terminology) = 0; one set of scales absent (scale set 2 of Hutchison & Bramble 1981) = 1 (Gaffney 1996: 40).
67. Entoplastron: plastral scute set 4 (pectorals) well behind entoplastron = 0; plastral set 4 reaching the posterior end of entoplastron = 1; plastral set 4 reaching half length of the entoplastron = 2 (modified from Meylan & Gaffney 1989: 33).
68. Plastral scute set 4: present = 0; absent = 1 (Meylan & Gaffney 1989: 32).
69. 6th pair of marginal scutes greatly expanded ventromedially: no = 0; yes = 1 (Hirayama *et al.* 2001: 30).
70. Plastral fontanelle between hyoplastra and hypoplastra: absent = 0; retained in adult = 1 (Hirayama *et al.* 2000: 63).
71. Xiphiplastron: broad = 0; narrow = 1 (Hirayama *et al.* 2000: 75).
72. Femoro-anal sulcus reaching hypoplastral–xiphiplastral suture: no = 0; yes = 1 (Hirayama *et al.* 2000: 68).

73. Anal notch: absent = 0; present = 1 (Hirayama *et al.* 2000: 76).
74. Midline plastral sulcus sinuous: no = 0; yes = 1 (Meylan & Gaffney 1989: 30).

References

Brinkman, D. 1998. The skull and neck of the Cretaceous turtle *Basilemys* (Trionychoidea, Nanhsiungchelyidae), and the interrelationships of the genus. *Paludicola*, **1**, 150–157.

Brinkman, D. 2001. New material of *Dracochelys* (Eucryptodira:Sinemydidae) from the Junggar Basin, Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **38**, 1645–1651.

Brinkman, D. & Nicholls, E. L. 1993. New specimen of *Basilemys praeclara* Hay and its bearing on the relationships of the Nanhsiungchelyidae (Reptilia: Testudines). *Journal of Paleontology*, **67**, 1027–1031.

Brinkman, D. & Peng, J.-H. 1993*a*. *Ordosemys leios* n. gen., n. sp., a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. *Canadian Journal of Earth Sciences*, **30**, 2128–2138.

Brinkman, D. & Peng, J.-H. 1993*b*. New material of *Sinemys* (Testudines, Sinemydidae) from the Early Cretaceous of China. *Canadian Journal of Earth Sciences*, **30**, 2139–2152.

Brinkman, D. & Peng, J.-H. 1996. A new species of *Zangerlia* (Testudines: Nanhsiungchelyidae) from the Upper Cretaceous redbeds at Bayan Mandahu, Inner Mongolia, and the relationships of the genus. *Canadian Journal of Earth Sciences*, **33**, 526–540.

Brinkman, D. & Wu, X.-C. 1999. The skull of *Ordosemys*, an Early Cretaceous turtle from the Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). *Paludicola*, **2**, 134–147.

Buffetaut, E. & Suteethorn, V. 2007. A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. *Bulletin de la Société Géologique de France*, **178**, 497–502.

Buffetaut, E., Suteethorn, V. & Tong, H. 2006. Dinosaur assemblages from Thailand: A comparison with Chinese faunas. *In*: Lü, J., Kobayashi, Y., Huang, D. & Lee, Y. (eds) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing, 19–37.

Carter, A. & Bristow, C. S. 2003. Linking hinterland evolution and continental basin sedimentation by using detrital zircon thermochronology: A study of the Khorat Plateau Basin, eastern Thailand. *Basin Research*, **15**, 271–285.

Danilov, I. & Parham, J. F. 2005. A reassessment of the referral of an isolated skull from the Late Cretaceous of Uzbekistan to the stem-testudinoid turtle genus *Lindholmemys*. *Journal of Vertebrate Paleontology*, **25**, 784–791.

Danilov, I. & Parham, J. F. 2006. A redescription of *Plesiochelys tatsuensis* from the Late Jurassic of China, with comments on the antiquity of the crown clade Cryptodira. *Journal of Vertebrate Paleontology*, **26**, 573–580.

Danilov, I. G. & Parham, J. F. 2007. The type series of '*Sinemys*' *wuerhoensis*, a problematic turtle from the Lower Cretaceous of China, includes at least three taxa. *Palaeontology*, **50**, 431–444.

Danilov, I. G. & Sukhanov, V. B. 2006. A basal eucryptodiran turtle '*Sinemys*' *efremovi* (=*Wuguia efremovi*) from the Early Cretaceous of China. *Acta Palaeontologica Polonica*, **51**, 105–110.

Danilov, I. G., Averianov, A. O., Skutchas, P. P. & Rezvyi, A. S. 2006. *Kirgizemys* (Testudines, 'Macrobaenidae'): New material from the Lower Cretaceous of Buryatia (Russia) and taxonomic revision. *Russian Journal of Herpetology*, **13**(Supplement), 46–62.

Danilov, I., Syromyatnikova, E. V. & Sukhanov, V. B. 2007. Turtles of the genus *Shachemys* from the Upper Cretaceous of Asia. *In*: Rozanov, A. Y., Lopatin, A. V. & Parkhaev, P. Y. (eds) *Modern Paleontology: Classical and New Methods—2007. Third all-Russian School 2006*. Palaeontological Institute, Moscow, 59–72.

de Lapparent de Broin, F. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: Preliminary data. *Comptes Rendus Palévol*, **3**, 387–396.

Fujita, M. K., Engstrom, T. N., Starkey, D. E. & Shaffer, H. B. 2004. Turtle phylogeny: Insights from a novel nuclear intron. *Molecular Phylogenetics and Evolution*, **31**, 1031–1040.

Gaffney, E. S. 1979. Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History*, **164**, 67–376.

Gaffney, E. S. 1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *Bulletin of the American Museum of Natural History*, **175**, 361–479.

Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, **194**, 1–263.

Gaffney, E. S. 1996. The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History*, **229**, 1–166.

Gaffney, E. S. & Meylan, P. A. 1988. A phylogeny of turtles. *In*: Benton, M. J. (ed.) *The Phylogeny and Classification of the Tetrapods*. Clarendon Press, Oxford, 157–219.

Gaffney, E. S. & Meylan, P. A. 1992. The Transylvanian turtle, *Kallokibotion*, a primitive Cryptodire of Cretaceous age. *American Museum Novitates*, **3040**, 1–37.

Gaffney, E. S. & Ye, X.-K. 1992. *Dracochelys*, a new Cryptodiran turtle from the Early Cretaceous of China. *American Museum Novitates*, **3048**, 1–13.

Gaffney, E. S., Rich, T. H., Vickers-Rich, P., Constantine, A., Vacca, P. & Kool, L. 2007. *Chubutemys*, a new Eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *American Museum Novitates*, **3599**, 1–35.

Hirayama, R. 2000. Fossil turtles from the Kiwajima Formation (Tetori Group; Early Cretaceous) of Kaseki-Kabe, Shiramine-mura, Ishikawa Prefecture, Central

Japan. *In*: MATSUOKA, H. (ed.) *Fossils of the Kuwajima 'Kaseki-Kabe' (Fossil bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan*. Shiramine-mura Education Board, Ishikawa, 75–92.

HIRAYAMA, R. 2002. Preliminary report of the fossil turtles from the Kitadani Formation (Early Cretaceous) of the Tetori Group of Katsuyama, Fukui Prefecture, Central Japan. *Memoir of the Fukui Prefectural Dinosaur Museum*, **1**, 29–40.

HIRAYAMA, R., BRINKMAN, D. & DANILOV, I. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology*, **7**, 181–198.

HIRAYAMA, R., SAKURAI, K., CHITOKU, T., KAWAKAMI, G. & KITO, N. 2001. *Anomalochelys angulata*, an unusual land turtle of Family Nanhsiungchelyidae (Superfamily Tronychoidea; Order Testudines) from the Upper Cretaceous of Hokkaido, North Japan. *Russian Journal of Herpetology*, **8**, 127–138.

HUTCHISON, J. H. & BRAMBLE, D. M. 1981. Homology of the plastral scales of the Kinosternidae and related turtles. *Herpetelogica*, **37**, 73–85.

JOYCE, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, **48**, 3–102.

KHOSATZKY, L. I. 1997. Big turtle of the Late Cretaceous of Mongolia. *Russian Journal of Herpetology*, **4**, 148–154.

LANGSTON, W. JR. 1956. The shell of *Basilemys variolosa* (Cope). *Bulletin and Annual Report of the National Museum of Canada*, **142**, 155–163.

MATZKE, A. T., MAISCH, M. W., GE, S. & PFRETZSCHNER, H.-U. 2004*a*. A new xinjiangchelyid turtle (Testudines, Eucryptodira) from the Jurassic Qigu Formation of the southern Junggar Basin, Xinjiang, north-west China. *Palaeontology*, **47**, 1211–1266.

MATZKE, A. T., MAISCH, M. W., PFRETZSCHNER, H.-U., SUN, G. & STÖHR, H. 2004*b*. A new basal sinemydid turtle (Reptilia: Testudines) from the lower Cretaceous Tugulu Group of the Junggar Basin (NW China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2004**, 151–167.

MEYLAN, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bulletin of the American Museum of Natural History*, **186**, 1–101.

MEYLAN, P. A. & GAFFNEY, E. S. 1989. The skeletal morphology of the Cretaceous Cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. *American Museum Novitates*, **2941**, 1–60.

MLYNARSKI, M. 1972. *Zangerlia testudinimorpha* n. gen. n. sp., a primitive land tortoise from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, **27**, 85–92.

MLYNARSKY, M. 1976. *Testudines*. Fischer, Stuttgart.

NESSOV, L. A. 1977. Skull morphology of Early Cretaceous turtle belonging to the family Adocidae. *Trudy Zoologicheskogo Instituta AN SSSR*, **74**, 74–79.

NESSOV, L. A. 1986. Some Late Mesozoic and Paleocene turtles of Soviet Middle Asia. *Studia Geologica Salamanticensia, Volumen Especial 2, Studia Palaeochelonilogica*, **2**, 7–22.

PARHAM, J. F. & HUTCHISON, J. H. 2003. A new eucryptodiran turtle from the Late Cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). *Journal of Vertebrate Paleontology*, **23**, 783–798.

PENG, J.-H. & BRINKMAN, D. 1993. New material of *Xinjiangchelys* (Reptilia:Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. *Canadian Journal of Earth Sciences*, **30**, 2013–2026.

RACEY, A., LOVE, M. A., CANHAM, A. C., GOODALL, J. G. S., POLACHAN, S. & JONES, P. D. 1996. Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. 1. Stratigraphy and sedimentary evolution. *Journal of Petroleum Geology*, **19**, 5–40.

RIEPPEL, O. 1980. The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase. *Palaeontographica*, **171**, 105–140.

ROUGIER, G. W., FUENTE, D. L. M. S. & ARCUCCI, A. B. 1995. Late Triassic turtles from South America. *Science*, **268**, 855–858.

SHAFFER, H. B., MEYLAN, P. A. & MCKNIGHT, M. L. 1997. Tests of turtle phylogeny: Molecular, morphological, and paleontological approches. *Systematic Biology*, **46**, 235–268.

SUKHANOV, V. B. 2000. Mesozoic turtles of Middle and Central Aisa. *In*: BENTON, M. J., SHISHKIN, M. A., UNWIN, D. M. & KUROCHKIN, E. N. (eds) *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, 309–367.

SUKHANOV, V. B. & NARMANDAKH, P. 2006. New taxa of Mesozoic turtles from Mongolia. *Russian Journal of Herpetology*, **13**(Supplement), 119–127.

SWOFFORD, D. L. 1996. *PAUP*: Phylogenetic Analysis using Parsimony (*and other Methods), Version 4.0*. Sinauer, Sunderland, MA.

TATARINOV, L. P. 1959. New turtle of the family Baenidae from the Lower Eocene of Mongolia. *Paleontologicheskii Zhurnal*, **1**, 100–113.

TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2002. Middle Jurassic turtles from southern Thailand. *Geological Magazine*, **139**, 687–697.

TONG, H., BUFFETAUT, E., SUTEETHORN, V. & SRISUK, P. 2003. Turtle remains from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. (abstract). *In*: DANILOV, I. G., CHEREPANOV, G. O., HIRAYAMA, R. & PARHAM, J. F. (eds) *Symposium on Turtle Origin, Evolution and Systematics*. Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, **30**.

TONG, H., BUFFETAUT, E., SUTEETHORN, V. & SRISUK, P. 2004*a*. First carettochelyid turtle from the Lower Cretaceous of Thailand (abstract). *In*: DOSTAL, O., GREGORAVA, R. & IVANOV, M. (eds) *2nd EAVP Meeting*. Moravian Museum, Brno, 44.

TONG, H., JI, S.-A. & JI, Q. 2004*b*. *Ordosemys* (Testudines: Cryptodira) from the Yixian Formation of Liaoning Province, Northeastern China: New specimens and systematic revision. *American Museum Novitaes*, **3438**, 1–20.

TONG, H., SUTEETHORN, V., CLAUDE, J., BUFFETAUT, E. & JINTASAKUL, P. 2005. The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. *In*: WANNAKAO, L., YOUNGME, W., SRISUK, K. & LERTSIRIVORAKUL, R. (eds) *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005)*. Khon Kaen University, Khon Kaen, 610–614.

TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2006*a*. *Isanemys*, a new adocid turtle from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. *Russian Journal of Herpetology*, **13**(Supplement), 128–137.

TONG, H., CLAUDE, J., BUFFETAUT, E., SUTEETHORN, V., NAKSRI, W. & SUWANNA, C. 2006*b*. Fossil turtles of Thailand: An updated review. *In*: LÜ, J. C., KOBAYASHI, Y., HUANG, D. & LEE, Y.-N. (eds) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing, 183–194.

YEH, X.-K. 1966. A new Cretaceous turtle of Nanhsiung, northern Kwangtung. *Vertebrata Palasiatica*, **10**, 191–200.

Appendix IV

Turtle assemblages of the Khorat Group (Late Jurassic-Early Cretaceous) of NE Thailand and their palaeobiogeographical significance

Turtle assemblages of the Khorat Group (Late Jurassic–Early Cretaceous) of NE Thailand and their palaeobiogeographical significance

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Abstract: The turtle assemblages from the Khorat Group consist mainly of trionychoids. They include the primitive Trionychoidae *Basilochelys* and basal eucryptodiran turtles from the Phu Kradung Formation (?Late Jurassic); the adocid *Isanemys srisuki*, the carettochelyid *Kizylkumemys* sp. and undetermined Trionychoidea from the Sao Khua Formation (Early Cretaceous); and the carettochelyid *Kizylkumemys khoratensis* and the adocid *Shachemys* sp. from the Khok Kruat Formation (Aptian). Our study shows some faunal links between the turtle faunas from the Khorat Group and those from the peripheral regions of Asia during the time span of the Khorat Group. Thus the coastal regions of Asia, and more particularly SE Asia, may have been important places for the origin and early diversification of the trionychoids.

The Mesozoic turtle record of Thailand ranges in age from the Late Triassic to the Early Cretaceous. It includes *Proganochelys ruchae* from the Late Triassic Huai Hin Lat Formation of NE Thailand (de Broin *et al.* 1982; de Broin 1984) and *Siamochelys peninsularis* from the Middle Jurassic of the southern peninsula (Tong *et al.* 2002). However, most turtle remains come from the Late Jurassic to Early Cretaceous Khorat Group, in the northeastern part of the country (Tong *et al.* 2003*a*, *b*, 2004*a*, 2005, 2006*a*, *b*). In this paper, we present an updated review that focuses on the turtles from the Khorat Group, as they constitute a succession of turtle assemblages during a crucial period for the evolution of Testudines, when many modern groups appeared. The Thai turtle assemblages are compared with coeval assemblages from other regions of Asia, especially those from China and Japan, to assess the palaeogeographical distribution of turtles in Asia during the Late Jurassic and Early Cretaceous and to gain a better understanding of turtle evolution during that period.

The Khorat Group is a succession of non-marine deposits occurring on the Khorat Plateau, a vast tabular area in the northeastern part of Thailand. It overlies uncomformably the Late Triassic Nam Phong Formation. According to the current interpretations (Racey *et al.* 1996), the Khorat Group consists of five formations. They are, from bottom to top, the Phu Kradung, Phra Wihan, Sao Khua, Phu Pan and Khok Kruat Formations. Three of them (Phu Kradung, Sao Khua and Khok Kruat) have yielded turtle remains.

The Late Jurassic(?) Phu Kradung Formation

The Phu Kradung Formation consists of sandstones, siltstones and mudstones of mainly fluvial origin (Racey *et al.* 1996). It is dated as either Late Jurassic or more probably basal Cretaceous on the basis of palynology (Racey *et al.* 1996) and detrital zircon thermochronology (Carter & Bristow 2003), whereas the evidence from fossil vertebrates supports a Late Jurassic age for this formation (Buffetaut *et al.* 2006; Buffetaut & Suteethorn 2007). The vertebrate fauna of the Phu Kradung Formation includes freshwater sharks, actinopterygian fishes, temnospondyl amphibians, turtles, crocodiles, and sauropod, theropod and ornithopod dinosaurs (Buffetaut *et al.* 2006). Turtle remains are abundant in some localities, but they are often very fragmentary and poorly preserved.

From: BUFFETAUT, E., CUNY, G., LE LOEUFF, J. & SUTEETHORN, V. (eds) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. The Geological Society, London, Special Publications, **315**, 141–152.
DOI: 10.1144/SP315.11 0305-8719/09/$15.00

The recently discovered material of a large turtle, *Basilochelys macrobios*, found in Mukdahan Province, includes a braincase, two shells and elements of the appendicular skeleton (Tong *et al.* 2009). *Basilochelys* has a low shell without a keel on the carapace, with a shell length reaching 900 mm. Although it is primitive in some aspects, several derived features support its trionychoid affinity. These characters include sculpture on both skull roof and shell surface, a neural formula of $6 > 4 < 6 < 6 < 6 < 6$, very narrow vertebral scutes, anteroposteriorly elongated eleventh and twelfth marginal scutes overlapping the suprapygal and costal plates, a plastron sutured to the carapace, with large anterior and posterior lobes, a long bridge, a wide entoplastron and narrow axillary and inguinal notches. However, the presence of a large foramen basisphenoidale, the foramen posterius canalis caroticus laterale exposed on the ventral surface of the skull, amphicoelous cervical vertebrae and long first thoracic ribs extending to the lateral end of the first costal are primitive characters reminiscent of basal eucryptodiran turtles such as xinjiangchelyids or macrobaenids. The phylogenetic analysis placed *Basilochelys* in a basal position among Trionychoidae and near the origin of Nanhsiungchelyidae and Adocidae. The remains of *Basilochelys* are common in the Phu Kradung Formation; they have been collected at most localities of that age on the Khorat Plateau. Other shell fragments collected in the Phu Kradung Formation suggest the occurrence of more than one morphotype of large trionychoids.

Isolated and fragmentary shell plates, collected near Ban Khok Sanam, in Kalasin Province, indicate the presence of other taxa. Fragments of plastron with a peg-like process on the lateral plastral margin indicate a ligamentous attachment between the carapace and plastron, as in xinjiangchelyids and macrobaenids. The surface of the neurals and costals shows fine plications arranged in a radiating manner, which is reminiscent of some *Xinjiangchelys* species, such as *X. latimarginalis* from the Late Jurassic Shangshaximiao Formation of Sichuan, China (Young & Chow 1953; Ye 1994). Such ornamentation is, however, not limited to xinjiangchelyids, but also occurs in some macrobaenids–sinemydids, such as *Wuguia efremovi* (Danilov & Sukhanov 2006). These turtle remains are thus referable to xinjiangchelyids or macrobaenids–sinemydids.

If the above-mentioned specimens belong to xinjiangchelyids, the turtle assemblage from the Phu Kradung Formation could be correlated with the Late Jurassic turtle fauna of China and Mongolia. Xinjiangchelyids are known from the Middle Jurassic to Early Cretaceous and were the dominant group of turtles during the Late Jurassic in Asia. In western China, the Qigu Formation of the Shishugou Group in Xinjiang has yielded two species of *Xinjiangchelys*: *X. latimarginalis* (including *X. junggarensis* (Ye 1986)) and *X. qiguensis* (Peng & Brinkman 1993; Matzke *et al.* 2004*a*). Most turtles from the Shangshaximiao Formation and equivalent beds in Sichuan, and the Upper Lufeng Formation in Yunnan, which were previously referred to *Plesiochelys* (Young & Chow 1953; Ye 1963, 1973*a*, 1994; Ye & Fang 1982; Peng *et al.* 2005) can also be assigned to *Xinjiangchelys* or Xinjiangchelyidae. In Mongolia, several taxa of xinjiangchelyids (*Annemys latiens*, *A. levensis*, *Shartegemys laticentralis* and *Undjulemys platensis*) have been reported from the Late Jurassic Shar Teeg in the Transaltai Gobi and Önjüül in Central Mongolia (Sukhanov 2000; Sukhanov & Narmandakh 2006).

The large trionychoid *Basilochelys* from the Phu Kradung Formation has no counterpart in the Late Jurassic of anywhere else in Asia. On the whole, the Jurassic trionychoid record is poor. An incomplete shell originally described as '*Plesiochelys*' *tatsuensis* (Ye 1963) from the Late Jurassic of Dazu, Chongqing was later renamed as *Yehguia* and considered as an adocid (Nessov 1977*b*; Meylan & Gaffney 1989) or closely related to Adocidae and Nanhsiungchelyidae (Danilov & Parham 2006). Originally attributed to the Trionychidae (Young & Chow 1953), *Sinaspideretes wimani*, an incomplete shell from ?Late Jurassic or Early Cretaceous deposits along the Chengyu railway, Sichuan, was later tentatively placed in the Carettochelyidae (Meylan & Gaffney 1992). Considered as one of the basal-most members of Trionychoidae, *Basilochelys* represents an important evolutionary link between the basal Eucryptodira from the Jurassic and more advanced trionychoids from the Cretaceous.

At the moment, the turtle assemblage from the Phu Kradung Formation does not provide much information about its age. The primitiveness of the large trionychoid *Basilochelys* with regard to the Cretaceous nanhsiungchelyids would support the idea that the Phu Kradung Formation is older than mid-Cretaceous, and can be either Late Jurassic or Early Cretaceous in age. What can be noticed is that the composition of the Phu Kradung turtle assemblage is unusual when compared with those from the Late Jurassic or Early Cretaceous of mainland Asia, in that it is mainly composed of trionychoids. The occurrence of basal eucryptodiran xinjiangchelyids or macrobaenids–sinemydids in the Phu Kradung Formation may provide a possible correlation with the turtle faunas located farther north in Asia, but better material from Thailand is needed for further comparative studies. Furthermore, the Phu Kradung turtle assemblage seems to be more closely related to that of southern

China than to those farther north, because of the occurrence in the Late Jurassic of Chongqing of *Yehguia*, a primitive trionychoid that is considered as a primitive relative of Adocidae + Nanhsiungchelyidae (Danilov & Parham 2006). It should be noted also that some Chinese Late Jurassic turtle assemblages may be older than the Phu Kradung Formation, as the Shangshaximiao Formation and Qigu Formation were both placed in the lower part of the Late Jurassic (Dong 1992; Peng & Brinkman 1993; Peng *et al.* 2005).

The Early Cretaceous Sao Khua Formation

The Early Cretaceous Sao Khua Formation consists of red sandstones, mudstones and conglomerates, deposited in low-energy, meandering rivers and on extensive floodplains (Mouret *et al.* 1993; Racey *et al.* 1996). The age of the Sao Khua Formation is considered as ante-Aptian and probably not basal Cretaceous (Mouret *et al.* 1993; Buffetaut & Suteethorn 1999). The Sao Khua Formation has yielded the most abundant and most diversified vertebrate fauna of the Khorat Group, comprising sharks, bony fishes, turtles, crocodiles, dinosaurs and birds (Cavin *et al.* 2007).

Turtle remains are frequently found in the Sao Khua Formation. The adocid turtle *Isanemys srisuki* Tong, Buffetaut and Suteethorn, 2006 (Figs 1 and 2) was originally based on more than 20 shells collected from two localities: Phu Kum Khao, in Kalasin Province and Phu Wat 1, in Khon Kaen Province (Tong *et al.* 2006*a*). Additional isolated shell plates of *I. srisuki* have

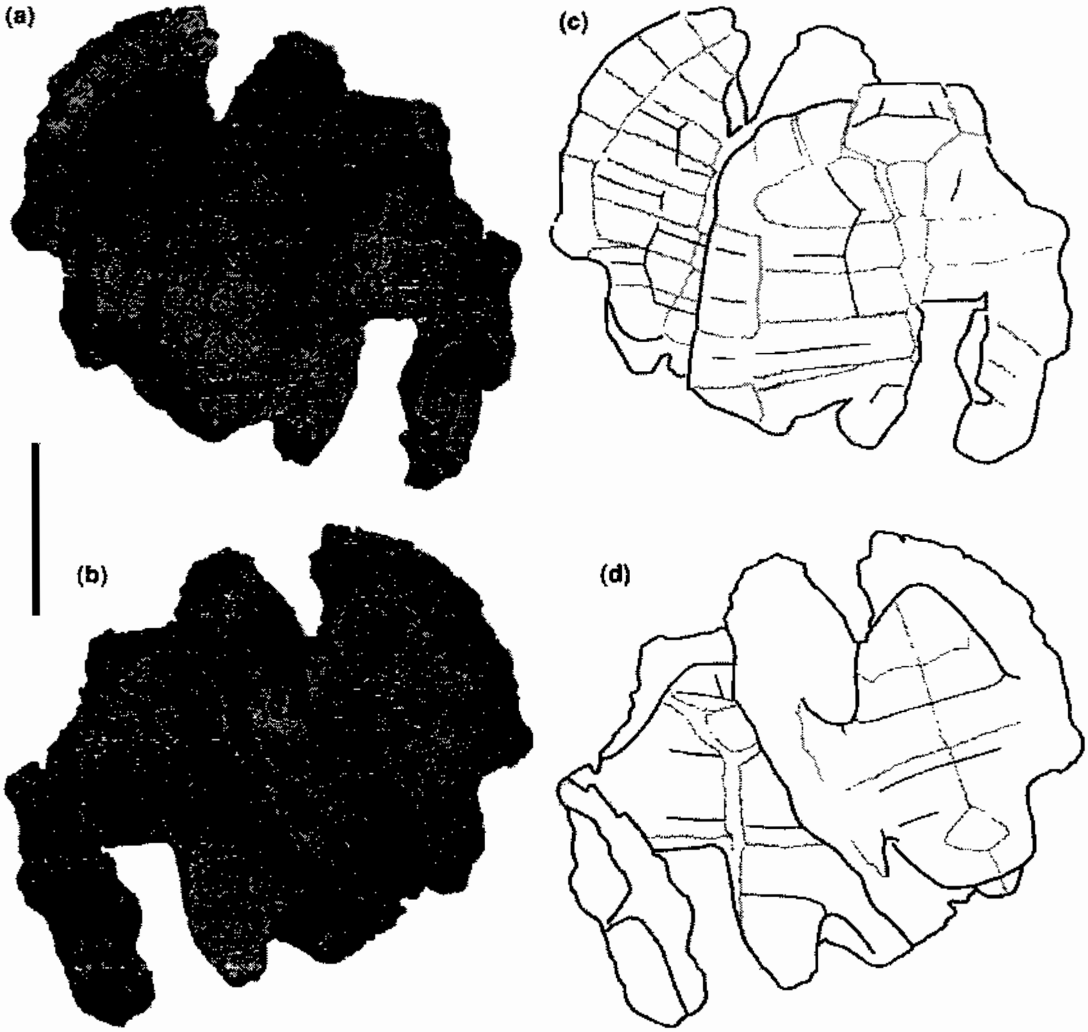

Fig. 1. The adocid *Isanemys srisuki* (K4-658 (holotype, right (**a**, **c**) left (**b**, **d**)) and K4-659) from the Early Cretaceous Sao Khua Formation; Phu Kum Khao locality, Kalasin Province, NE Thailand. (**a**, **c**) dorsal view; (**b**, **d**) ventral view. Scale bar: 50 mm. (After Tong *et al.* 2006*a*.)

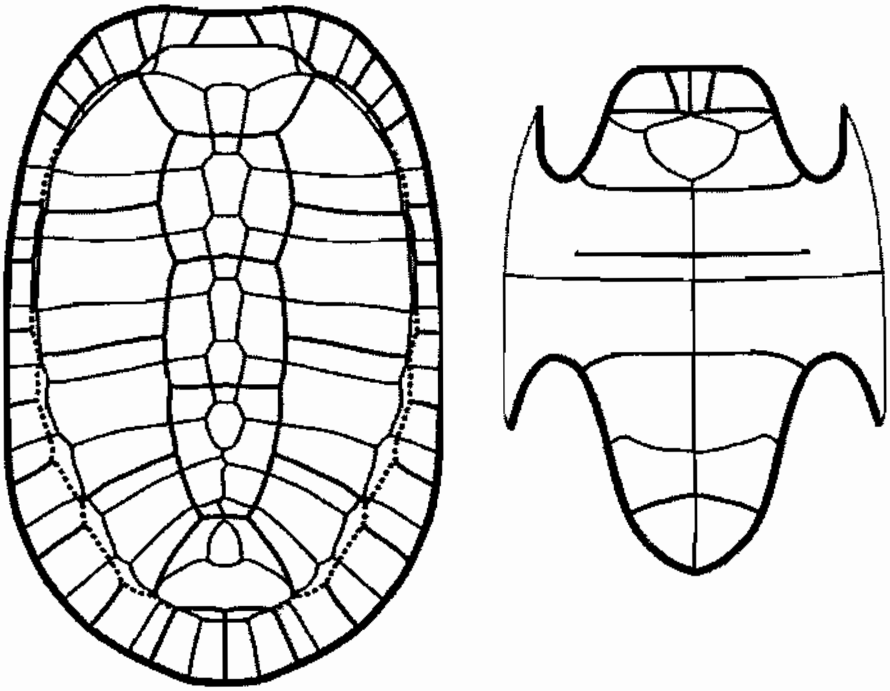

Fig. 2. Reconstruction of *Isanemys srisuki* from the Early Cretaceous Sao Khua Formation, NE Thailand (modified from Tong *et al.* 2006*a*).

been recovered from Ban Na Krai, in Kalasin Province, and Phu Phok, in Sakon Nakhon Province. *Isanemys* presents various adocid characters, including the punctuate ornamentation of the shell surface, an incomplete neural series with the posterior costals meeting on the midline, two suprapygals, the first one very small and the second much larger, and the plastron shorter than the carapace, with a truncated anterior lobe and a straight anterior margin. The shell of *Isanemys* is primitive relative to that of other adocids, including *Adocus* from the Late Cretaceous of North America (Meylan & Gaffney 1989), *Adocoides* from the Late Cretaceous of Mongolia (Narmandakh 1985; Sukhanov 2000; Sukhanov & Narmandakh 2006), *Ferganemys* from the mid-Cretaceous of Kirghizstan and Uzbekistan (Nessov & Khozatskii 1977; Sukhanov 2000) and an unnamed trionychoid from the Neocomian of Japan (Hirayama 2000; Hirayama *et al.* 2000). The primitive characters of *Isanemys* include the neural formula of 4 > 6 > 6 > 6 > 6 > 5(7), a longer and not medially expanded pectoral scute and a larger cervical scute. *Isanemys* is thus considered as the sister taxon of all other known adocids.

The carettochelyid turtle, *Kizylkumemys* sp. (Fig. 3c–f) is represented by abundant, but very fragmentary shell plates from Phu Wat 2, in Khon Kaen Province (Tong *et al.* 2004*a*). Additional material of *K.* sp. has been collected at Phu Mai Paw and Khok Kong, Kalasin Province, and Phu Phan Thong, Nong Bua Lamphu Province. The strongly keeled neural plates closely resemble *K. schultzi* from the Late Cretaceous of Uzbekistan and Mongolia (Nessov 1977*a*, 1981; Sukhanov 2000), but the fragmentary nature of the specimens prevents detailed comparisons. An isolated nuchal plate collected from the Phu Paeng locality, Kalasin Province, represents a third taxon of trionychoids. It is much wider than long and presents strong vermiculated ridges on the surface (Tong *et al.* 2003*b*).

It is not easy to compare the Sao Khua turtle assemblage with those from China and Central Asia as the Early Cretaceous beds of these regions have yielded mainly macrobaenid–sinemydid turtles. In China, the formations roughly equivalent to the Sao Khua Formation on the basis of their geological age that have yielded turtle remains include the Yixian and Jiufotang Formations in Liaoning, the Tugulu Group in the Junggar Basin, Xinjiang, the Mengyin Formation in Shandong, and the Luohandong Formation in Inner Mongolia. Based on radiometric dating, the Yixian and Jiufotang Formations of Liaoning, in NE China, are considered as ranging from Barremian to Aptian in age (Ji *et al.* 2004). The Yixian Formation

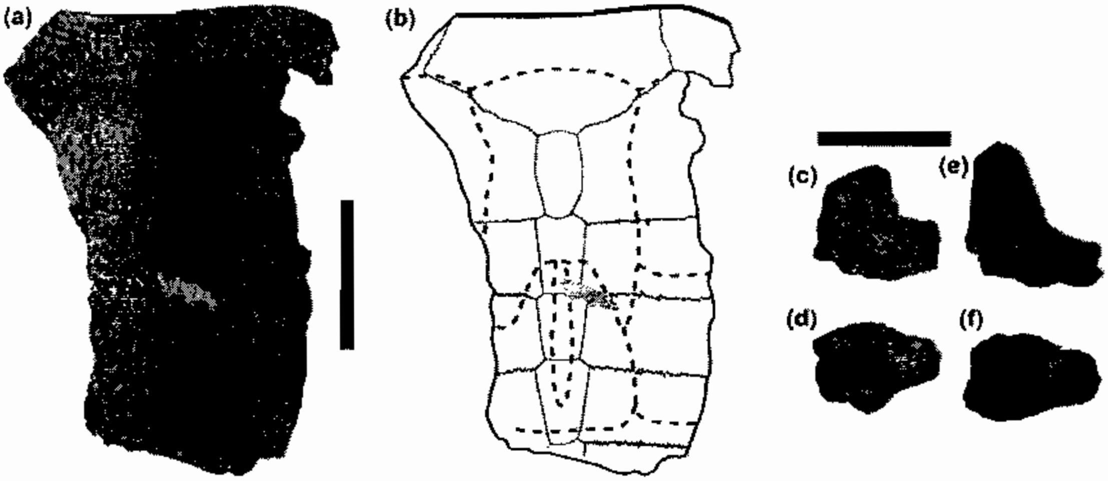

Fig. 3. The carettochelyid *Kizylkumemys* from the Khorat Plateau, NE Thailand. (**a**, **b**) Partial carapace of *K. khoratensis* (NRRU A1861, holotype) from the late Early Cretaceous Khok Kruat Formation (Ban Saphan Hin, Nakhon Ratchasima Province). Scale bar: 20 mm (after Tong *et al.* 2005). (**c**, **f**) Neurals of *Kizylkumemys* sp. from the Early Cretaceous Sao Khua Formation (Phu Wat 2, Khon Kaen Province), in lateral (c, **e**) and dorsal (**d**, f) views. Scale bar: 10 mm. (After Tong *et al.* 2006*b*.)

has yielded abundant specimens of the macrobaenid *Ordosemys liaoxiensis* (Ji 1995; Li & Liu 1999; Tong *et al.* 2004*b*). A sinemydid, *Manchurochelys manchoukuoensis*, has been reported from equivalent beds in the same area (Endo & Shikama 1942). Turtle remains have also been reported from the overlying Jiufotang Formation (Liu 2003), but they have not been described.

In eastern China, the Mengyin Formation, in Shandong, has yielded *Sinemys lens*, *Scutemys tecta* and *Sinochelys applanata*. This turtle fauna is dominated by far by the sinemydid *S. lens* (Wiman 1930; Brinkman & Peng 1993*b*). *Sinochelys* and *Scutemys* were placed later in the Sinochelyidae (Chkhikvadze 1987). The Mengyin Formation is regarded as either Early Cretaceous (Wiman 1930), or Late Jurassic (Dong 1992) in age.

In Inner Mongolia, the Luohandong Formation contains the macrobaenid *Ordosemys leios* and the sinemydid *Sinemys gamera* (Brinkman & Peng 1993*a*, *b*; Brinkman & Wu 1999).

Further to the west, in Xinjiang, two formations of the Tugulu Group have yielded turtles along the southern margin of the Junggar Basin: *Wuguia hutubeiensis* from the Hutubei Formation (Matzke & Maisch 2004; Matzke *et al.* 2004*b*) and *Dracochelys wimani* (a synonym of *Wuguia efremovi* according to Danilov & Sukhanov (2006)) from the overlying Lianmouxin Formation (Maisch *et al.* 2003). From the northwestern part of the Junggar basin, Ye (1973*b*) reported a dozen turtles from the Early Cretaceous Tugulu Group in the Wuerho area. Most of these turtles were assigned to *Sinemys wuerhoensis* (Ye 1973*b*) and one skull was described as *Dracochelys bicuspis* (Gaffney & Ye 1992). Additional material of *D. bicuspis* has recently been described from the same horizon in Xinjiang (Brinkman 2001). The revision of the type series of *S. wuerhoensis* revealed that the specimens actually belong to three taxa: most of them belong to the macrobaenid *Ordosemys* (*O. brinkmania*); the type specimen is referred to *Xinjiangchelys* sp. and one isolated skull is attributed to Trionychia (Danilov & Parham 2007). The Tugulu Group is considered as Early Cretaceous in age, with the Hutubei Formation of Hauterivian–Barremian age and the Lianmuxin Formation of Aptian–Albian age (Eberth *et al.* 2001).

In Russia, the Neocomian Gusinoje Ozero Group in the Baikal Lake region contains mainly specimens of the macrobaenid *Kirgizemys dmitrievi* (Nessov 1984; Danilov *et al.* 2006).

To sum up, the Early Cretaceous turtle assemblages from China and Central Asia predominantly contain macrobaenids–sinemydids. In contrast to the turtle assemblage from the Sao Khua Formation, the trionychoids are fairly rare. Beside the Trionychia skull from Wuerho mentioned above, other trionychoid records include *Aspideretes maortuensis*, a nearly complete trionychid shell from Dashukou, Maortu, Inner Mongolia, and *Sinamyda fuchienensis*, a carapace from Hekou, Fujian, but the Early Cretaceous age of both specimens is uncertain (Ye 1965, 1974, 1994; Chkhikvadze 2000). Some fragmentary trionychid specimens have also been reported from the Early Cretaceous On Gong Formation of Inner Mongolia (Young & Chow 1953).

The difference in composition between the turtle assemblage from the Sao Khua Formation and those from China and Central Asia suggests that SE Asia was more isolated from mainland Asia during the Early Cretaceous than before: a conclusion also supported to some extent by the composition of the dinosaur fauna from the Sao Khua Formation (Buffetaut *et al.* 2006) and by the analysis of whole vertebrate assemblage (Fernandez *et al.* 2009). On the other hand, the Sao Khua turtle fauna is more comparable with that from the Neocomian Kuwajima Formation of the Tetori Group in Central Japan. The lacustrine deposits of the Kuwajima Formation have yielded trionychoids, possible testudinoids and sinemydids (Hirayama 2000; Hirayama *et al.* 2000). The same trionychoid turtles, as well as a xinjiangchelyid (Hirayama 2006) are also reported from the equivalent Okurodani Formation. Based on shell morphology, these trionychoids are members of Adocidae, as is *Isanemys* from the Sao Khua Formation. The Neocomian age of this horizon is well supported by fission-track dating of the overlying tuff from the Okurodani Formation and palaeontological evidence (Hirayama *et al.* 2000).

The late Early Cretaceous Khok Kruat Formation

The Khok Kruat Formation is the geologically youngest formation of the Khorat Group. It consists mainly of red siltstones, sandstones and conglomerates, indicative of a predominantly fluvial depositional environment (Racey *et al.* 1996). The age of the Khok Kruat Formation is well constrained as Aptian–Albian by the occurrence of the freshwater hybodont shark *Thaiodus ruchae* (Cappetta *et al.* 1990). It is considered as Aptian based on palynology (Racey *et al.* 1996; Racey & Goodall 2009). The vertebrate fauna of the Khok Kruat Formation includes hybodont sharks, actinopterygian fishes, turtles, crocodiles, and sauropod, theropod and ornithopod dinosaurs (Buffetaut *et al.* 2005).

Only trionychoids have been hitherto recorded from the Khok Kruat Formation. The carettochelyid *Kizylkumemys khoratensis* Tong, Suteethorn, Claude, Buffetaut & Jintasakul 2005 is represented by shell material from the Ban Saphan Hin and Ban Khok Kruat localities, in Nakhon Ratchasima Province, and the Khok Pa Suam locality in Ubon Ratchathani Province (Tong *et al.* 2005). *K. khoratensis* presents the typical morphology of the vertebral scutes of Anosteirinae, with the very large first vertebral scute extending from the nuchal to the third costal plate and the second vertebral bounded laterally by the first vertebral scute. The presence of a small central scute on the second to fourth neurals and included in the second vertebral scutes, and the sulcus between the first and the second vertebral scutes crossing the second neural are characteristic of *Kizylkumemys*. The carapace of *K. khoratensis* reaches 350 mm in length. It differs from the type species of *Kizylkumemys*, *K. schultzi* Nessov, 1977 from the Cenomanian–Turonian of Karakalpakia, Uzbekistan (Nessov 1977*a*), mainly by the absence of the dorsal keel (Fig. 3a and b). Although the high keel on the carapace of *K. schultzi* presents some sexual dimorphism, both males and females had a strong keel on the carapace. The male probably had a higher dorsal keel than the female (Nessov 1986).

Adocids are represented by shell material recovered from Ban Sapan Hin, in Nakhon Rachasima Province (Tong *et al.* 2005) and Khok Pa Suam, in Ubon Ratchatani Province (Fig. 4). The tiny pores on the shell surface, the large plastron with wide posterior lobe and narrow inguinal notch, and the presence of large inframarginal scutes are reminiscent of *Shachemys*. *Shachemys* is a freshwater turtle characterized by a hinge between the epiplastra and ento-hyoplastra, and by the absence of all or nearly all neural plates. The Thai *Shachemys* is too incomplete for specific assignment. Three species of *Shachemys* have been so far described: *S. laosiana* from the late Early Cretaceous of Laos (Lapparent de Broin 2004), and *S. baibolatica* and *S. ancestralis* from the Late Cretaceous of Central Asia (Kuznetzov 1976; Nessov & Krasovskaya 1984; Nessov 1986; Danilov *et al.* 2007). Although the Thai *Shachemys* and *S. laosiana* are similar in age, the size of *Shachemys* from Thailand (shell length 400 mm) is clearly larger than that of *S. laosiana* (165–200 mm), but similar to that of *S. baibolatica*. In addition, a few fragmentary shell plates collected near Khorat are referable to Trionychidae.

Comparison with approximately coeval turtle faunas from other countries in Asia may begin with the 'Grès supérieur' Formation in Laos, dated as Aptian–Albian by the occurrence of the fresh water bivalve *Trigonioidea*. That formation is considered as an equivalent of the Khok Khruat Formation on the eastern fringe of the Khorat Plateau (Buffetaut 1991). The turtle assemblage from the red floodplain deposits of that formation in Savannakhet province contains mainly trionychoids, which include the adocid *Shachemys laosiana*, Carettochelyidae, Trionychidae, and an uncertain basal eucryptodira referred to Aff. *Xinjiangchelys* sp. (de Lapparent de Broin 2004). This turtle fauna closely resembles that from the Khok Kruat Formation in the trionychoid-dominated composition, and in the presence of *Shachemys* and carettochelyids, although the assignment to *Xinjiangchelys* is doubtful.

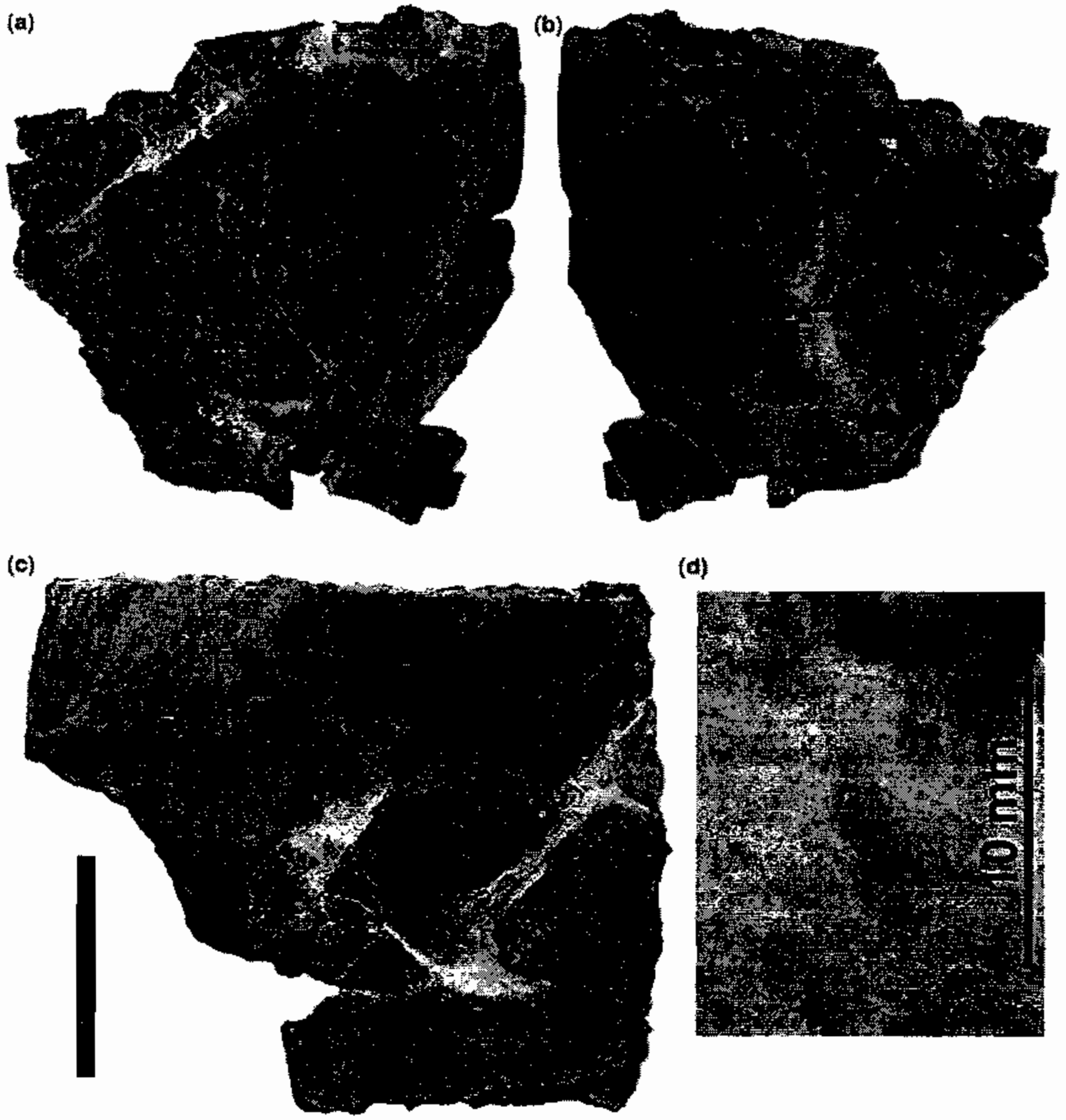

Fig. 4. The adocid *Shachemys* sp. from the late Early Cretaceous Khok Kruat Formation (Ban Saphan Hin, Nakhon Ratchasima Province). (**a, b**) Fragment of carapace with right seventh and eighth peripherals and lateral part of the fifth and sixth costal plates (NRRU A1254) in dorsal (a) and ventral (b) views; (**c**) right hypoplastron (NRRU A1864) in ventral view. Scale bar: 40 mm. (**d**) Detail of ornamentation on plastron (NRRU A1864). (After Tong *et al.* 2006*b*.)

The Khok Kruat turtle fauna is comparable with that from the Kitadani Formation of the Tetori Group, in central Japan. The Kitadani Formation is considered as Barremian or Aptian in age and contains mainly trionychoids (the adocid *Adocus* sp., the nanhsiungchelyid *Basilemys* sp. and Trionychidae), and a few Sinemydidae and Testudinoidea (Hirayama 2002).

Some resemblances can also be noted between the turtle assemblage from the Khok Kruat Formation and those from Central Asia. The turtles from the Alamyshyk Formation (Albian) of Kylodzhun, in the Fergana Depression (Kirghizstan) consist of the adocid *Ferganemys*, the trionychid *Trionyx* and the macrobaenid *Kirgizemys*. The lower and middle parts of the Khodzhakul Formation (Upper Albian (Nessov 1984) or Lower Cenomanian (Averianov & Archibald 2005)), western Sultanuvais Ridge, in Uzbekistan, have yielded macrobaenids, adocids, nanhsiungchelyids, carettochelyids and testudinoids (Nessov 1984). As mentioned above, the adocid *Ferganemys* is more advanced than *Isanemys* from the Sao Khua Formation (Tong *et al.* 2006*a*).

On the other hand, the turtle assemblages from the late Early Cretaceous of China and Mongolia are different from that from the Khok Kruat Formation. There are few late Early Cretaceous deposits in China that have yielded turtle remains. In Gansu, several turtle taxa (*Osteopygis, Peishanemys, Heishanemys, Tsaotanemys* and *Yumenemys*) were collected by the Sino-Swedish expedition from the Early Cretaceous beds in the Jiayuguan area in 1929–1930 (Bohlin 1953). According to Dong (1992), these specimens come from the Chijinbao Formation, which belongs to the Jehol Biota. The Chijinbao Formation is the lowermost of three formations of the Xinminbao Group (Ma *et al.* 1982). Based on the invertebrates and vertebrates collected in the neighbouring Mazhongshan area, the age of the Xinminbao Group is considered as ranging from the Late Barremian to the Albian (Tang *et al.* 2001). Among the turtle remains from Jiayuguan described by Bohlin (1953), the so-called *Osteopygis* was recently referred to the macrobaenid *Kirgizemys* (Danilov *et al.* 2006), *Tsaotanemys* is considered as a primitive testudinoid (Lindholmemydidae) (Hirayama *et al.* 2000), and *Peishanemys* (probably including *Heishanemys*) is placed in the Sinochelyidae (Chkhikvadze 1987). *Peishanemys* is also reported from Aptian–Albian deposits in Mongolia (Nessov & Verzilin 1981; Nessov 1987) and from the Qingshan Formation of Shandong, eastern China (Chow 1954). Based on isotopic dating, the age of the Qingshan Formation is Aptian (Dong 1992). In Mongolia, the Aptian–Albian turtle assemblage from Höövör is dominated by the macrobaenid *Kirgizemys* (*Hangaiemys*) *hoburensis* (Sukhanov 2000).

To sum up, the turtle assemblage from the Khok Kruat Formation in the Khorat Plateau (including the 'Grès supérieurs' Formation in Laos) resembles those from Japan and Central Asia in being dominated by trionychoids and in the occurrence of the carettochelyid *Kizylkumemys*. The Chinese and Mongolian turtle assemblages are different, being dominated by macrobaenids. Two macrobaenid genera had a wide geographical distribution during that period: *Kirgizemys* (including *Hangaiemys* according to Danilov *et al.* (2006)), represented by five species and some *Kirgizemys* sp. records, is known from Barremian to Albian deposits in Mongolia, Kirghizstan, northern China, South Korea and Russia (Sukhanov 2000; Averianov *et al.* 2006; Danilov *et al.* 2006); and *Ordosemys*, roughly coeval with *Kirgizemys*, represented by four species, is recorded from northern and NE China and Mongolia (Brinkman & Peng 1993*a*; Tong *et al.* 2004*b*; Danilov & Parham 2007).

Conclusion

The turtle assemblages from the Khorat Group consist mainly of trionychoids, which include the primitive Trionychoidae *Basilochelys* from the Late Jurassic(?) Phu Kradung Formation; the adocid *Isanemys srisuki*, the carettochelyid *Kizylkumemys* sp., and undetermined Trionychoidea from the Sao Khua Formation; and the carettochelyid *Kizylkumemys khoratensis* and the adocid *Shachemys* sp. from the Khok Kruat Formation. Basal eucryptodiran xinjiangchelyids or macrobaenids–sinemydids are represented in the Phu Kradung Formation by a few fragmentary remains. The turtle fauna from the Sao Khua Formation appears to be more similar to that from the Khok Kruat Formation than to that of the Phu Kradung Formation. Adocids and carettochelyids are recorded from both Sao Khua and Khok Kruat Formations; however, they are represented by different taxa.

On the basis of the above comparison with the Late Jurassic to Early Cretaceous turtle faunas from other areas of Asia, the turtle assemblage from the Phu Kradung Formation can be correlated with either the Late Jurassic or the Early Cretaceous turtle assemblages of China, because of the presence of basal eucryptodiran xinjiangchelyids or macrobaenids–sinemydids, and it shows apparently more similarities to the turtle fauna from southern China than to those from more northerly areas. The turtles from the Sao Khua Formation show similarities to those from the Neocomian Kuwajima Formation in Japan, with the occurrence of adocids, but are different from those of China, which are dominated by macrobaenids–sinemydids. This may suggest that SE Asia became more isolated than before from mainland Asia during the Early Cretaceous. The differences between the Sao Khua dinosaur assemblage and the roughly coeval assemblages in China, notably those from the Jehol Group of NE China, have already been noted, and several hypotheses have been put forward, including differences in taphonomic conditions, and the existence of geographical or environmental barriers (Buffetaut *et al.* 2006; Fernandez *et al.* 2009). One possible bias may be that there are very few Early Cretaceous vertebrate localities in southern China and turtles of that age are particularly poorly known from that region. The close resemblance between the turtle fauna of the Khok Kruat Formation and the 'Grès supérieur' Formation in Laos supports that they belonged to the same palaeobiogeographical province during the late Early Cretaceous. They closely resemble the faunas from the Kitadani Formation of Japan and from Central Asia, but are very different from those from China and Mongolia. On the whole, within a palaeogeographical context, there are some faunal links between SE Asia and other peripheral regions during the time span of the Khorat Group.

In conclusion, our study supports the hypothesis of Hirayama *et al.* (2000), according to which during the Late Jurassic and Early Cretaceous there were two main palaeobiogeographical areas in Asia that controlled turtle distribution: the palaeogeographically coastal area (including SE Asia (Thailand and Laos), Japan and Central Asia (Uzbekistan, Kirghizstan and Kazakhstan)), which was dominated by trionychoid turtles, and the palaeogeographically inland area (China, Mongolia and the Lake Baikal region of Russia), which was dominated by basal eucryptodiran turtles such as xinjiangchelyids and macrobaenids–sinemydids. The coastal regions of Asia, and more particularly SE Asia, may have been an important area for the origin and early diversification of the trionychoids.

This work was supported by the Department of Mineral Resources, Thailand, the ECLIPSE Programme of CNRS, France, the TRF-CNRS Special Programme for Biodiversity Research and Training (BRT/BIOTEC/NSTDA), Grant BRT R-24507, and the PHC 'Evolution et biodiversité des vertébrés aquatiques Mésozoiques et Cénozoiques en Thaïlande' (16610UG). We thank I. Danilov (St Petersburg) and R. Hirayama (Tokyo) for reviewing the manuscript. This is publication ISEM 2008-011 of J.C.

References

AVERIANOV, A. O. & ARCHIBALD, J. D. 2005. Mammals from the mid-Cretaceous Khodzhakul Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research*, **26**, 593–608.

AVERIANOV, A. O., VORONKEVICH, A. V., LESHCHINSKIY, S. V. & FAYNGERTZ, A. V. 2006. A ceratopsian dinosaur *Psittacosaurus sibiricus* from the Early Cretaceous of West Siberia, Russia and its phylogenetic relationships. *Journal of Systematic Palaeontology*, **4**, 359–395.

BOHLIN, B. 1953. *Fossil reptiles from Mongolia and Kansu*. Statens Etnografiska Museum, Stockholm.

BRINKMAN, D. 2001. New material of *Dracochelys* (Eucryptodira: Sinemydidae) from the Junggar Basin, Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **38**, 1645–1651.

BRINKMAN, D. & PENG, J.-H. 1993*a*. *Ordosemys leios* n. gen., n. sp., a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. *Canadian Journal of Earth Sciences*, **30**, 2128–2138.

BRINKMAN, D. & PENG, J.-H. 1993*b*. New material of *Sinemys* (Testudines, Sinemydidae) from the Early Cretaceous of China. *Canadian Journal of Earth Sciences*, **30**, 2139–2152.

BRINKMAN, D. & WU, X.-C. 1999. The skull of *Ordosemys*, an Early Cretaceous turtle from the Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). *Paludicola*, **2**, 134–147.

BUFFETAUT, E. 1991. On the age of the Cretaceous dinosaur-bearing beds of southern Laos. *Newsletter on Stratigraphy*, **24**, 59–73.

BUFFETAUT, E. & SUTEETHORN, V. 1999. The dinosaur fauna of the Sao Khua Formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **150**, 13–23.

BUFFETAUT, E. & SUTEETHORN, V. 2007. A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. *Bulletin de la Société Géologique de France*, **178**, 497–502.

BUFFETAUT, E., SUTEETHORN, V., LE LOEUFF, J., KHANSUBHA, S., TONG, H. & WONGKO, K. 2005. The dinosaur fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. *In*: WANNAKAO, L., YOUNGME, W., SRISUK, K. & LERTSIRIVORAKUL, R. (eds) *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005)*. Khon Kaen University, Khon Kaen, 575–581.

BUFFETAUT, E., SUTEETHORN, V. & TONG, H. 2006. Dinosaur assemblages from Thailand: A comparison with Chinese faunas. *In*: LÜ, J., KOBAYASHI, Y., HUANG, D. & LEE, Y. (eds) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing, 19–37.

CAPPETTA, H., BUFFETAUT, E. & SUTEETHORN, V. 1990. A new hybodont shark from the Lower Cretaceous of Thailand. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **11**, 659–666.

CARTER, A. & BRISTOW, C. S. 2003. Linking hinterland evolution and continental basin sedimentation by using detrital zircon thermochronology: A study of the Khorat Plateau Basin, eastern Thailand. *Basin Research*, **15**, 271–285.

CAVIN, L., SUTEETHORN, V., BUFFETAUT, E., CLAUDE, J., CUNY, G., LE LOEUFF, J. & TONG, H. 2007. The first sinamiid fish (Holostei, Halecomorpha) from southeast Asia (Early Cretaceous of Thailand). *Journal of Vertebrate Paleontology*, **27**, 827–837.

CHKHIKVADZE, V. M. 1987. Sur la classification et les caractères de certaines tortues fossiles d'Asie rares et peu étudiées. *Studia Palaeocheloniologica*, **2**, 55–86.

CHKHIKVADZE, V. M. 2000. On the systematic position of some extinct trionychids of North America and Asia. *Trudy Tbilisskogo gosudarstvennogo pedagogicheskogo universiteta*, **7**, 199–213.

CHOW, M.-C. 1954. Cretaceous turtles from Laiyang, Shantung. *Acta Palaeontologica Sinica*, **2**, 395–410.

DANILOV, I. G. & PARHAM, J. F. 2006. A redescription of *Plesiochelys tatsuensis* from the Late Jurassic of China, with comments on the antiquity of the crown clade Cryptodira. *Journal of Vertebrate Paleontology*, **26**, 573–580.

DANILOV, I. G. & PARHAM, J. F. 2007. The type series of '*Sinemys*' *wuerhoensis*, a problematic turtle from the Lower Cretaceous of China, includes at least three taxa. *Palaeontology*, **50**, 431–444.

DANILOV, I. G. & SUKHANOV, V. B. 2006. A basal eucryptodiran turtle '*Sinemys*' *efremovi* (= *Wuguia efremovi*) from the Early Cretaceous of China. *Acta Palaeontologica Polonica*, **51**, 105–110.

Danilov, I. G., Averianov, A. O., Skutchas, P. P. & Rezvyi, A. S. 2006. *Kirgizemys* (Testudines, 'Macrobaenidae'): New material from the Lower Cretaceous of Buryatia (Russia) and taxonomic revision. *Fossil Turtles Research, Vol. 1, Russian Journal of Herpetology*, **13**(Supplement), 46–62.

Danilov, I. G., Syromyatnikova, E. V. & Sukhanov, V. B. 2007. Turtles of the genus *Shachemys* from the Upper Cretaceous of Asia. *In*: Rozanov, A. Y., Lopatin, A. V. & Parkhaev, P. Y. (eds) *Modern Paleontology: Classical and New Methods—Third all-Russian School 2006*. Palaeontological Institute, Moscow, 59–72.

de Broin, F. 1984. *Proganochelys ruchae* n. sp., Chélonien du Trias supérieur de Thaïlande. *Studia Geologica Salamanticensia, Studia Palaeocheloniologica I, Special Volume*, **1**, 87–97.

de Broin, F., Ingavat, R., Sattayarak, N. & Janvier, P. 1982. Triassic turtle remains from northeastern Thailand. *Journal of Vertebrate Paleontology*, **2**, 41–46.

de Lapparent de Broin, F. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: Preliminary data. *Comptes Rendus Palévol*, **3**, 387–396.

Dong, Z.-M. 1992. *Dinosaurian Faunas of China*. China Ocean Press, Springer, Berlin.

Eberth, D. A., Brinkman, D. B., Chen, P.-J., Yuan, F.-T., Wu, X.-C., Li, G. & Xian-Shen, C. 2001. Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Juggar Basin, Xijiang Autonomous Region, People's Republic of China. *Canadian Journal of Earth Sciences*, **38**, 1627–1644.

Endo, R. & Shikama, T. 1942. Mesozoic fauna in the Jehol mountainland, Manchoukuo. *Bulletin of Central National Museum of Natural History, Manchoukuo*, **3**, 1–23.

Fernandez, V., Claude, J., Escarguel, G., Buffetaut, E. & Suteethorn, V. 2009. Biogeographical affinities of Jurassic and Cretaceous continental vertebrate assemblages from SE Asia. *In*: Buffetaut, E., Cuny, G., Le Loeuff, J. & Suteethorn, V. (eds) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. Geological Society, London, Special Publications, **315**, 281–296.

Gaffney, E. S. & Ye, X. 1992. *Dracochelys*, a new Cryptodiran turtle from the Early Cretaceous of China. *American Museum Novitates*, **3048**, 1–13.

Hirayama, R. 2000. Fossil turtles from the Kiwajima Formation (Tetori Group; Early Cretaceous) of Kaseki-Kabe, Shiramine-mura, Ishikawa Prefecture, Central Japan. *In*: Matsuoka, H. (ed.) *Fossils of the Kuwajima 'Kaseki-Kabe' (Fossil bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan*. Shiramine-mura Education Board, Ishikawa, 75–92.

Hirayama, R. 2002. Preliminary report of the fossil turtles from the Kitadani Formation (Early Cretaceous) of the Tetori Group of Katsuyama, Fukui Prefecture, Central Japan. *Memoir of the Fukui Prefectural Dinosaur Museum*, **1**, 29–40.

Hirayama, R. 2006. Review of fossil turtles of Japan. *Fossils*, **80**, 47–59.

Hirayama, R., Brinkman, D. & Danilov, I. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology*, **7**, 181–198.

Ji, Q., Chen, W., Wang, W.-L. *et al.* 2004. *Mesozoic Jehol Biota of Western Liaoning, China*. Geological Publishing House, Beijing.

Ji, S.-A. 1995. Reptilia. *In*: Ren, D., Lu, L.-W., Guo, Z.-L. & Ji, S.-A. (eds) *Faunae and Stratigraphy of Jurassic–Cretaceous in Beijing and Adjacent Areas*. Seismic Press, Beijing, 140–158.

Kuznetzov, V. V. 1976. A freshwater turtle from the Senonian of northeastern Cisaralia. *Paleontological Journal*, **1976**, 498–500.

Li, J.-L. & Liu, J. 1999. The skull of *Manchurochelys laoxiensis* (Testudines: Sinemydidae) from the Yixian Formation of Beipiao, Liaoning and phylogenetic position of this taxon. *In*: Chen, P.-J. & Jin, F. (eds) *Palaeoworld II, Jehol Biota*. Press of University of Sciences and Technology of China, Hebei, 281–295.

Liu, J. 2003. Turtles. *In*: Zahng, M.-M., Chen, P.-J., Wang, Y.-Q., Wang, Y. & Miao, D.-S. (eds) *The Jehol Biota*. Shanghai Scintific and Technical Publishers, Shanghai, 86–87.

Ma, Q.-H., Lin, Q.-B., Ye, C.-H. & Sheng, Y.-B. 1982. Division and correlation of the Xinminbao Group and the Chijinbao Formation in western Jiuquan Basin. *Journal of Stratigraphy*, **6**, 112–120.

Maisch, M. W., Matzke, A. T. & Sun, G. 2003. A new sinemydid turtle (Reptilia: Testudines) from the Lower Cretaceous of the Juggar Basin (NW China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2003**, 705–722.

Matzke, A. T. & Maisch, M. W. 2004. New information and specimens of *Wuguia hutubeiensis* (Reptilia: Testudines) from the Lower Cretaceous Tugulu Group of the southern Juggar Basin (NW China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2004**, 473–495.

Matzke, A. T., Maisch, M. W., Ge, S. & Pfretzschner, H.-U. 2004*a*. A new xinjiangchelyid turtle (Testudines, Eucryptodira) from the Jurassic Qigu Formation of the southern Junggar Basin, Xinjiang, north-west China. *Palaeontology*, **47**, 1211–1266.

Matzke, A. T., Maisch, M. W., Pfretzschner, H.-U., Sun, G. & Stöhr, H. 2004*b*. A new basal sinemydid turtle (Reptilia: Testudines) from the lower Cretaceous Tugulu Group of the Junggar Basin (NW China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2004**, 151–167.

Meylan, P. A. & Gaffney, E. S. 1989. The skeletal morphology of the Cretaceous Cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. *American Museum Novitates*, **2941**, 1–60.

Meylan, P. A. & Gaffney, E. S. 1992. *Sinaspideretes* is not the oldest trionychid turtle. *Journal of Vertebrate Paleontology*, **12**, 257–259.

Mouret, C., Heggemann, H., Gouadain, J. & Krisadasima, S. 1993. Geological history of the siliciclastic Mesozoic strata of the Khorat Group in the Phu Phan Range area, northeastern Thailand.

In: THANASUTHIPITAK, T. (ed.) *Proceedings of the International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies and Paleontology*. Chiang Mai University, Chiang Mai, 23–49.

NARMANDAKH, P. 1985. A new species of *Adocus* from the Late Cretaceous of Mongolia. *Paleontologicheskii Zhurnal*, **1985**, 85–93.

NESSOV, L. A. 1977*a*. A new genus of pitted-shelled turtle from the Upper Cretaceous of Karakalpakia. *Paleontological Journal*, **1**, 96–107

NESSOV, L. A. 1977*b*. Skull morphology of Early Cretaceous turtle belonging to the family Adocidae. *Trudy Zoologicheskogo Instituta AN SSSR*, **74**, 74–79.

NESSOV, L. A. 1981. On turtles of the family Dermademydidae from the Cretaceous of the Amur river basin, and some other rare discoveries of the remains of ancient turtles of Asia. *In*: BORKIN, L. J. (ed.) *Herpetological Investigations in Siberia and the Far East*. Zoological Institute of the Russian Academy of Sciences, Leningrad, 69–73.

NESSOV, L. A. 1984. Data on Late Mesozoic turtles from the USSR. *Studia Geologica Salamanticensia, Volumen Especial 1, Studia Palaeocheloniologica*, **1**, 215–224.

NESSOV, L. A. 1986. Some Late Mesozoic and Paleocene turtles of Soviet Middle Asia. *Studia Geologica Salamanticensia, Volumen Especial 2, Studia Palaeocheloniologica*, **2**, 7–22.

NESSOV, L. A. 1987. On some Mesozoic turtles of the Soviet Union, Mongolia and China, with comments on systematics. *Studia Geologica Salamanticensia, Volumen Especial 2, Studia Palaeocheloniologica*, **2**, 87–102.

NESSOV, L. A. & KHOZATSKII, L. I. 1977. Freshwater turtle from the Early Cretaceous of Fergana. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **20**, 248–262.

NESSOV, L. A. & KRASOVSKAYA, T. B. 1984. Transformations in the composition of turtle assemblages in the Cretaceous of Middle Asia. *Vestnik Leningradeskogo Universiteta*, **3**, 15–25.

NESSOV, L. A. & VERZILIN, N. N. 1981. Remains of turtles from Aptian–Albian deposits of the Transaltai Gobi in Mongolia and conditions of their burial. *In*: BARSBOLD, R. *ET AL*. (eds) *Fossil Vertebrates of Mongolia*. Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleotologicheskoi Ekspeditsii, Moscow, **15**, 12–26.

PENG, J.-H. & BRINKMAN, D. 1993. New material of *Xinjiangchelys* (Reptilia : Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. *Canadian Journal of Earth Sciences*, **30**, 2013–2026.

PENG, G.-Z., YE, Y., GAO, Y.-H., SHU, C.-K. & JIANG, S. (eds) 2005. *Jurassic Dinosaur Fauna in Zhigong*. Shichuan People's Press, Chengdu.

RACEY, A. & GOODALL, J. G. S. 2009. Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. *In*: BUFFETAUT, E., CUNY, G., LE LOEUFF, J. & SUTEETHORN, V. (eds) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. Geological Society, London, Special Publications, **315**, 67–81.

RACEY, A., LOVE, M. A., CANHAM, A. C., GOODALL, J. G. S., POLACHAN, S. & JONES, P. D. 1996. Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. 1. Stratigraphy and sedimentary evolution. *Journal of Petroleum Geology*, **19**, 5–40.

SUKHANOV, V. B. 2000. Mesozoic turtles of Middle and Central Asia. *In*: BENTON, M. J., SHISHKIN, M. A., UNWIN, D. M. & KUROCHKIN, E. N. (eds) *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, 309–367.

SUKHANOV, V. B. & NARMANDAKH, P. 2006. New taxa of Mesozoic turtles from Mongolia. *Russian Journal of Herpetology*, **13**(Supplement), 119–127.

TANG, F., LUO, Z.-X., ZHOU, Z.-H., YOU, H.-L., GEORGI, J.-A., TANG, Z.-L. & WANG, X.-Z. 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Research*, **22**, 115–129.

TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2002. Middle Jurassic turtles from southern Thailand. *Geological Magazine*, **139**, 687–697.

TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2003*a*. Mesozoic turtles of Thailand. *Mahasarakham University Journal*, **22**(Special Issue 2003), 41–48.

TONG, H., BUFFETAUT, E., SUTEETHORN, V. & SRISUK, P. 2003*b*. Turtle remains from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. Abstract. *In*: DANILOV, I. G., CHEREPANOV, G. O., HIRAYAMA, R. & PARHAM, J. F. (eds) *Symposium on Turtle Origin, Evolution and Systematics*. Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, **30**.

TONG, H., BUFFETAUT, E., SUTEETHORN, V. & SRISUK, P. 2004*a*. First carettochelyid turtle from the Lower Cretaceous of Thailand (abstract). *In*: DOSTAL, O., GREGORAVA, R. & IVANOV, M. (eds) *2nd EAVP Meeting*. Moravian Museum, Brno, 44.

TONG, H., JI, S.-A. & JI, Q. 2004*b*. *Ordosemys* (Testudines: Cryptodira) from the Yixian Formation of Liaoning Province, Northeastern China: New specimens and systematic revision. *American Museum Novitates*, **3438**, 1–20.

TONG, H., SUTEETHORN, V., CLAUDE, J., BUFFETAUT, E. & JINTASAKUL, P. 2005. The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. *In*: WANNAKAO, L., YOUNGME, W., SRISUK, K. & LERTSIRIVORAKUL, R. (eds) *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005)*. Khon Kaen University, Khon Kaen, 610–614.

TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2006*a*. *Isanemys*, a new adocid turtle from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. *Russian Journal of Herpetology*, **13**(Supplement), 128–137.

TONG, H., CLAUDE, J., BUFFETAUT, E., SUTEETHORN, V., NAKSRI, W. & SUWANNA, C. 2006*b*. Fossil turtles of Thailand: an updated review. *In*: LÜ, J. C., KOBAYASHI, Y., HUANG, D. & LEE, Y.-N. (eds) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing, 183–194.

TONG, H., CLAUDE, J. *ET AL*. 2009. *Basilochelys macrobios* n. gen. and n. sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic–earliest Cretaceous) of the Khorat Plateau, NE Thailand.

In: BUFFETAUT, E., CUNY, G., LE LOEUFF, J. & SUTEETHORN, V. (eds) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. Geological Society, London, Special Publications, **315**, 151–170.

WIMAN, C. 1930. Fossile Schildkröken aus China. *Palaeontologia Sinica, Series C*. **6**, 5–53.

YE, X.-K. 1963. Fossil turtles of China. *Palaeontologia Sinica*, **150**, 1–112.

YE, X.-K. 1965. New materials of fossil turtles of Inner Mongolia. *Vertebrata Palasiatica*, **9**. 47–48.

YE, X.-K. 1973*a*. Discovery of *Plesiochelys* from Upper Lufeng Series, Oshan, Yunnan and its stratigraphical significance. *Vertebrata Palasiatica*, **11**, 160–164.

YE, X.-K. 1973*b*. Fossil turtles from Wuerho. Reports of the palaeontological expedition to the Xinjiang 2. The Pterosaurian fauna from Wuerho. *Academia Sinica, Institute of Vertebrate Palaeontology and Palaeoanthropology, Memoirs*, **11**, 8–11.

YE, X.-K. 1974. A new fossil *Trionyx* from Fuchien. *Vertebrata Palasiatica*, **12**, 190–192.

YE, X.-K. 1986. A Jurassic turtle from Junggar, Xinhjiang. *Vertebrata Palasiatica*, **24**, 171–181.

YE, X.-K. 1994. *Fossil and Recent Turtles of China*. Science Press, Beijing.

YE, X.-K. & FANG, Q.-R. 1982. A new species of fossil *Plesiochelys* from Jingyuan, Sichuan. *Acta Herpetologica Sinica*, **1**, 63–68.

YOUNG, C. C. & CHOW, M.-C. 1953. New fossil reptiles from Szechuan, China. *Acta Scientica Sinica*, **2**, 216–243.

Appendix V

Fossil turtles of Thailand: An updated review

FOSSIL TURTLES OF THAILAND: AN UPDATED REVIEW

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ABSTRACT Turtle remains are known from both Mesozoic and Cenozoic formations in Thailand. Most Mesozoic turtles are from the non-marine beds of the Khorat Plateau, in northeastern Thailand, but the southern peninsula of Thailand has also yielded Mesozoic turtles. The turtle remains from the Middle Jurassic of the southern peninsula of Thailand include a primitive cryptodiran, *Siamochelys peninsularis*. The turtle assemblages from the Khorat Plateau include one of the most ancient turtles in the world, *Proganochelys ruchae* from the Upper Triassic Huai Hin Lat Formation, trionychoids from the Upper Jurassic Phu Kradung Formation, the adocid *Isanemys srisuki* and the carettochelyid *Kizylkumemys* sp. from the Lower Cretaceous Sao Khua Formation, and the carettochelyid *Kizylkumemys khoratensis* and the adocid *Shachemys* sp. from the upper Lower Cretaceous Khok Kruat Formation. The Cenozoic beds of Thailand have yielded testudinids, geoemydids and trionychids.

INTRODUCTION

Since the first discovery of Mesozoic turtle remains in Thailand in the 1980s, our knowledge of fossil turtles of Thailand has increased considerably, especially during the last few years. The purpose of the present paper is to provide an up to date overview of the fossil turtles of Thailand, which complements an earlier review of the Mesozoic turtles (Tong *et al.*, 2003a) with new finds. A brief summary on the Cenozoic turtles of Thailand is also included.

From: Lü, J. C., Kobayashi, Y., Huang, D. & Lee, Y.-N. (eds). 2006. *Papers from the* 2005 *Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing. 183 ~ 194.

From a palaeogeographical point of view, Thailand consists of two blocks or microcontinents: the northeastern part (Khorat Plateau) is part of the Indochina Block and the western part of the country belongs to the Shan-Thai Block. The Indochina Block has been part of mainland of Asia possibly since the Late Permian, while the Shan-Thai Block has collided with the Asian mainland later, during the Mesozoic, probably before the Jurassic (Metcalfe, 1998). Most of the Mesozoic turtle remains from Thailand have been found in the non-marine beds of the Khorat Plateau, as summarised below:

Khok Kruat Formation (late Early Cretaceous: Aptian-Albian): carettochelyids, adocids.

Sao Khua Formation (Early Cretaceous): carettochelyids, adocids.

Phu Kradung Formation (? Late Jurassic): trionychoids.

Huai Hin Lat Formation (Late Triassic: Norian): proganochelyids.

The southern peninsula of Thailand, which was part of the Shan-Thai Block, has also yielded Mesozoic turtles. Cenozoic turtles are interesting for understanding the biogeographical history of modern groups in this area.

MESOZOIC TURTLES

TURTLES FROM THE SHAN-THAI BLOCK

Middle Jurassic Turtles from the Southern Peninsula of Thailand

Complete and partial shells of a cryptodiran turtle, *Siamochelys peninsularis* Tong, Buffetaut and Suteethorn (Tong *et al.*, 2002) were discovered at the Mab Ching locality, Nakhon Si Tammarat Province, in the southern peninsula of Thailand. In addition to the turtle remains, the vertebrate assemblage from Mab Ching includes large hybodont sharks, *Lepidotes*-like actinopterygian fishes, lungfishes, temnospondyl amphibians and crocodiles, indicative of a lacustrine environment. The charophytes from that locality suggest a Middle Jurassic age (Buffetaut *et al.*, 1994a, 1994b).

Siamochelys is a medium-sized turtle, with a carapace length of about 315 mm. It is characterized by the shell surface covered with a distinctive ornamentation consisting of raised vermiculated ridges and tubercles, the presence of a pair of mesoplastra meeting on the midline and lying on both pectoral and abdominal scutes, a loose plastron-carapace attachment, absence of the dorsal process of epiplastron, a significant dorsal thickening of the lateral edge of the second to seventh peripheral plates, an upturned anterolateral margin of the carapace forming a gutter, extension of the anal scute to the hypop-xiphiplastral suture or onto the hypoplastron, and a sinusoidal midline sulcus of the plastron (Fig. 1). This combination of primitive and derived characters shows that *Siamochelys* differs from *Pleisiochelys* from the Jurassic of Europe, but closely resembles *Chengyuchelys*, and more particularly *Xinjiangchelys* from the Middle to Late Jurassic of China and Central Asia (Peng and Brinkman, 1993; Ye, 1994; Sukhanov, 2000). However, *Siamochelys*

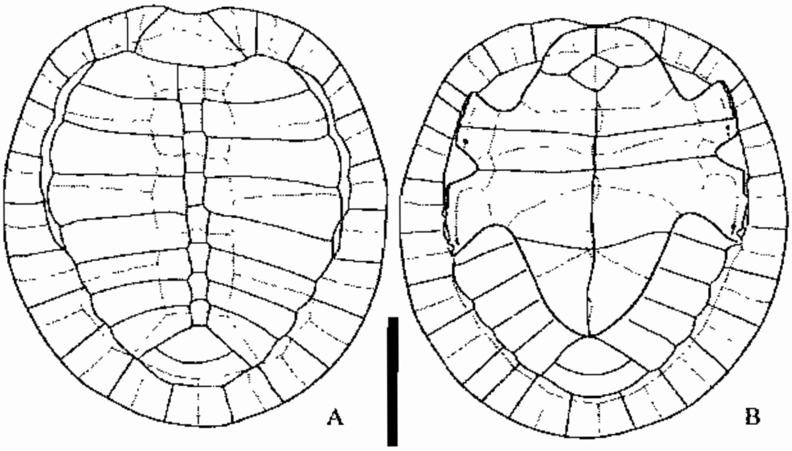

Fig. 1 Reconstruction of *Siamochelys peninsularis* Tong, Buffetaut and Suteethorn, 2002 from the Middle Jurassic of Mab Ching, southern peninsula of Thailand (after Tong *et al.*, 2002). A. Carapace; B. Plastron. Scale bar = 100 mm.

differs from *Xinjiangchelys* by the presence of a pair of mesoplastra, the absence of a dorsal process of the epiplastron, a broad entoplastron and ornamentation on the shell surface. The discovery of *Siamochelys* supports a Middle Jurassic age for the vertebrate-bearing beds of Mab Ching and indicates that the Shan-Thai (Sibumasu) Block was in contact with the Asian mainland by that time (Tong *et al.*, 2002).

TURTLES FROM THE KHORAT PLATEAU, NE THAILAND

Late Triassic Turtles from the Huai Hin Lat Formation

The Upper Triassic Huai Hin Lat Formation (probably Norian) (Buffetaut and Suteethorn, 1998) has yielded one of the most ancient turtles in the world: *Proganochelys ruchae* Broin de (Broin de, 1984). The remains of this species have been collected in lacustrine bituminous shales and limestones at three localities NW of the city of Chum Phae, in northeastern Thailand. They only consist of incomplete shell elements. The plastron presents an anterior and a lateral projection and a strong dorsal process on the epiplastron, as in *Proganochelys quenstedti* from the Late Triassic of Germany (Gaffney, 1990). However, it differs from *P. quenstedti* in having a more simple ornamentation on the shell surface and a more transversally directed and more dorso-ventrally flattened epiplastral projection. The estimated shell length of *P. ruchae* ranges from 300 to 500 mm (Broin de *et al.*, 1982; Broin de, 1984; Tong *et al.*, 2003a).

Late Jurassic (?) Turtles from the Phu Kradung Formation

The Phu Kradung Formation is dated as either Late Jurassic or basal Cretaceous on the basis of palynomorphs (Racey *et al.*, 1994, 1996) and contains fishes, temnospondyl amphibians, crocodiles, theropod, sauropod and ornithopod dinosaurs (Buffetaut *et al.*, 1997, 2003). The turtles from the Phu Kradung Formation are still poorly known. Their remains are abundant in some localities but mostly very fragmentary and poorly preserved. Some isolated plates with parallel striations and ridges appear to be reminiscent of certain trionychoids. Recently, complete shells of large trionychoid turtles have been discovered in Mukdahan Province, they are currently under study.

The Early Cretaceous Turtle Fauna from the Sao Khua Formation

The Early Cretaceous Sao Khua Formation has yielded the most abundant and the most diverse vertebrate assemblage of the Khorat Group. The Sao Khua Formation consists of red clays, sandstones and conglomerates, indicating deposition in a floodplain with meandering rivers. The vertebrate assemblage includes turtles, fishes, crocodiles, sauropod and theropod dinosaurs, and birds. According to its stratigraphical position, the Sao Khua Formation is considered as ante-Aptian and probably not basal Cretaceous (for a detailed review see Buffetaut and Suteethorn (1999)).

Turtle remains from the Sao Khua Formation include two taxa, both are trionychoids. *Isanemys srisuki* Tong, Buffetaut and Suteethorn (Tong *et al.*, 2006) was discovered at two localities in the Sao Khua Formation: Phu Wat, in Khon Kaen Province and Phu Kum Khao, in Kalasin Province. The material consists of more than twenty specimens, all being shells. *Isanemys* is an adocid turtle with an oval and moderately domed shell. The shell length ranges from 170 to 265 mm. The shell surface is covered with a punctated ornamentation. It is characterized by an incomplete neural series of 6 neurals, with the posterior pairs of costals meeting on the midline; two suprapygals, the first one very small and triangular and the second much larger; the plastron shorter than the carapace, with a truncated anterior lobe and a straight anterior margin (Fig. 2). However, this adocid

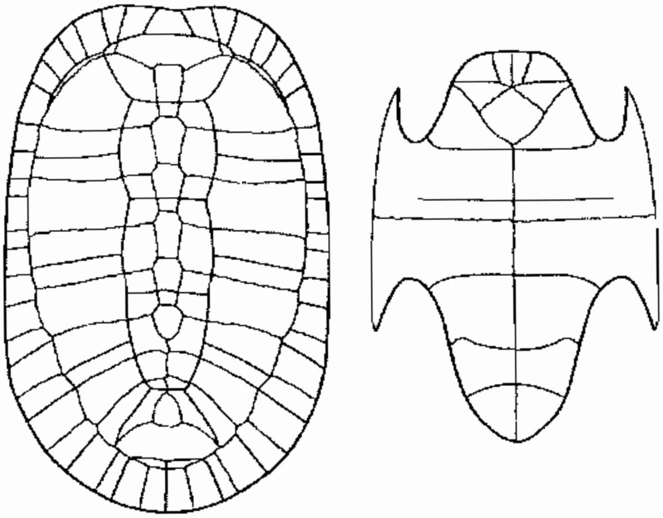

Fig. 2　Reconstruction of *Isanemys srisuki* from the Early Cretaceous Sao Khua Formation, Khorat Plateau, NE Thailand (after Tong *et al.*, 2006).

turtle presents several features which are more primitive than those of other adocids, including *Adocus* from the Late Cretaceous of North America (Meylan and Gaffney, 1989), *Adocoides* from the Late Cretaceous of Mongolia (Narmandakh, 1985; Sukhanov, 2000; Sukhanov and Narmandakh, 2006), *Ferganemys* from the mid-Cretaceous of Kirgizstan and Uzbekistan (Nessov and Khozatskii, 1977; Sukhanov, 2000) and an unnamed trionychoid turtle from the Neocomian of Japan (Hirayama *et al.*, 2000). These primitive characters include a neural formula of 4 >6 >6 >6 >6 >5(7), with a six-sided second neural with short anterolateral sides, a large cervical scute which is wider than long, and a longer and not medially expanded pectoral scute. *Isanemys* is therefore considered as the sister taxon of all other adocids (Tong *et al.*, 2003b, 2006).

Isolated shell plates of a carettochelyid turtle were collected from the Phu Wat locality, in Khon Kaen Province. This turtle has the shell surface covered with a pitted ornamentation, a wide nuchal, neurals bearing a high dorsal keel (Fig. 3) and a serrated margin of the carapace. All these features are reminiscent of *Kizylkumemys*, an anosteirine turtle (Carettochelyidae) known from the late Early Cretaceous to the Late Cretaceous of Central Asia (Nessov, 1977, 1981, 1984; Sukhanov, 2000; Tong *et al.*, 2004). Some isolated plates with similar shell ornamentation from the Late Cretaceous of Japan have been attributed to Anosteirinae gen. et sp. indet. (Hirayama, 1998).

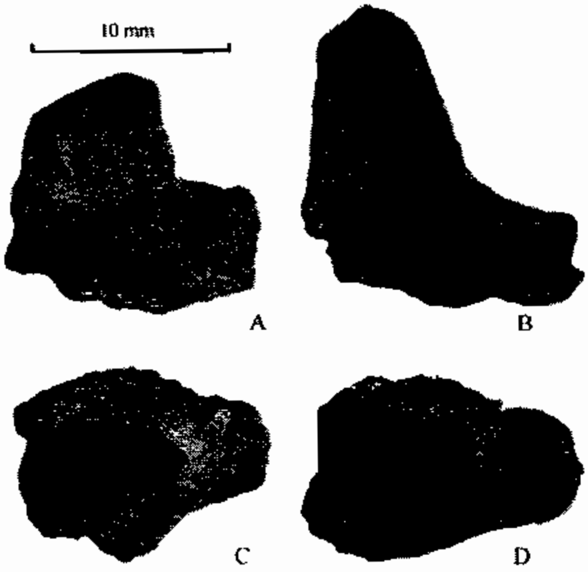

Fig. 3 Neural plates of keeled carettochelyid turtle from Phu Wat (Early Cretaceous, Sao Khua Formation), Khon Kaen Province, NE Thailand. A – B, lateral view; C – D, dorsal view.

The Late Early Cretaceous Turtle Assemblage from the Khok Kruat Formation

The Khok Kruat Formation is the geologically youngest vertebrate-bearing formation of the

Khorat Group in northeastern Thailand. It consists mainly of red siltstones, sandstones and conglomerates, indicative of a predominantly fluvial depositional environment (Racey *et al.*, 1996). The Khok Kruat Formation is well dated as late Early Cretaceous (Aptian-Albian) on the basis of palynomorphs (Racey *et al.*, 1996) and fresh-water sharks (Cappetta *et al.*, 1990). Turtle remains are quite abundant but fragmentary at some localities, including the carettochelyid *Kizylkumemys* and the adocid *Shachemys* (Tong *et al.*, 2005). Besides turtles, the Khok Kruat Formation has yielded hybodont sharks, semionotiform fishes, crocodiles, dinosaurs and pterosaurs (Buffetaut *et al.*, 2005).

Kizylkumemys khoratensis Tong, Suteethorn, Claude, Buffetaut and Jintasakul (Tong *et al.*, 2005) was described on the basis of shell material. Numerous shell fragments of this medium-sized carettochelyid (350 mm of shell length) have been collected at Ban Saphan Hin and Khok Kruat, in Nakhon Ratchasima Province and Khok Pa Suam, in Ubon Ratchathani Province. The shell surface is covered with a strong sculpture, consisting of raised vermiculated ridges and tubercles. The morphology of the scutes, particularly the anterior part of the second vertebral scute bounded by the very large first vertebral scute, is characteristic of Anosteirinae, a subfamily of Carettochelyidae. The subfamily Anosterininae includes several genera from the late Early Cretaceous-Late Cretaceous and Early Tertiary of Asia and North America, including *Kizylkumemys schultzi* from the Late Cretaceous of Central Asia (Nessov, 1977, 1984; Sukhanov, 2000). Although the dorsal keel observed in *Kizylkumemys schultzi* is absent in the Thai specimens, other characters are clearly reminiscent of *Kizylkumemys*. These characters include the presence of a small central scute on the second to fourth neurals and included in the second vertebral scute, the first vertebral scute not divided and the anterior sulcus of the second vertebral scute crossing the second neural (Fig. 4).

Shell fragments of an adocid turtle have been discovered at Ban Saphan Hin, Nakhon Rat-

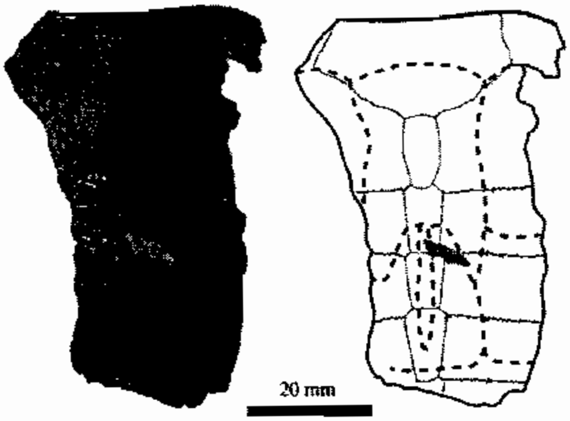

Fig. 4 Type specimen of *Kizylkumemys khoratensis* Tong, Suteethorn, Claude, Buffetaut and Jintasakul, 2005 from Ban Saphan Hin (late Early Cretaceous, Khok Kruat Formation), Nakhon Ratchasima Province, NE Thailand (NRRU A1861, collection of the Museum of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Thailand) (after Tong *et al.*, 2005).

chasima Province (Fig. 5). The tiny pores on the shell surface, the large plastron with wide posterior lobes and a narrow inguinal notch, and the presence of large inframarginal scutes observed in these specimens are reminiscent of *Shachemys*. *Shachemys* is a fresh-water turtle which is characterised by a hinge on the anterior lobe of the plastron, placed between the epi-entoplastron and hyoplastron, and by the absence of all or nearly all neurals. The genus *Shachemys* contains two species: *S. baibolatica* Kuznetsov, 1976 from the Late Cretaceous of Kazakhstan and Uzbekistan (Kuznetzov, 1976; Sukhanov, 2000), and *S. laosiana* from the late Early Cretaceous of Laos (Lapparent de Broin de, 2004). An epiplastron of *Shachemys* sp. has been reported from the Late Cretaceous of Japan (Hirayama, 1998). Although the Thai *Shachemys* is similar in age to *S. laosiana*, its size is larger (shell length: 400 mm) and more similar to that of *S. baibolatica* (300 – 400 mm) than to that of *S. laosiana* (165 – 200 mm). The Thai specimens are too incomplete for specific assignment.

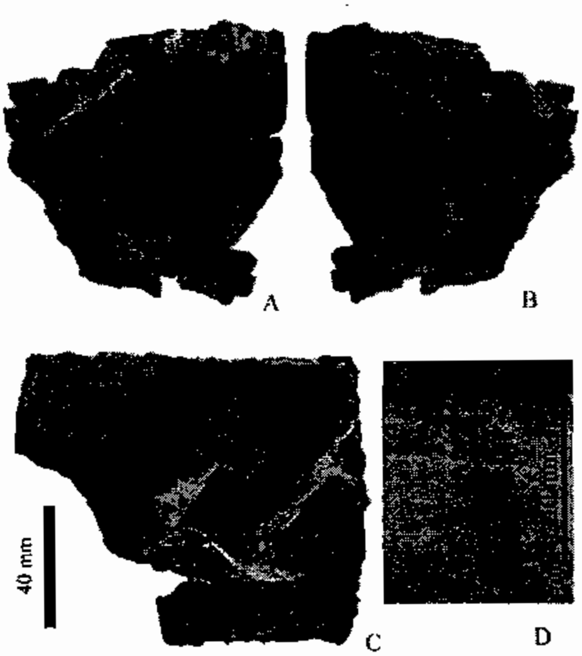

Fig. 5 *Shachemys* sp. from Ban Saphan Hin (late Early Cretaceous, Khok Kruat Formation), Nakhon Ratchasima Province, NE Thailand.

A – B, fragment of carapace (NRRU A1254) in dorsal (A) and ventral (B) views; C, right hypoplastron (NRRU A1864) in ventral view; D, detail of shell surface ornamentation on plastron (collection of the Museum of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Thailand) (after Tong *et al.*, 2005)

CENOZOIC TURTLES

Although not yet described in detail, turtles are present in various Tertiary formations of Thailand. All of them have been discovered in continental basins.

So far, only three modern families (Geoemydidae, Testudinidae and Trionychidae) are represented in the Tertiary of Thailand. The Late Eocene fossiliferous lignite pits at Krabi (Krabi Province), in the southern peninsula of Thailand, have yielded geoemydid and testudinid turtles, among which three taxa can be identified: a three-keeled Geoemydidae which can be referred to the living genus *Mauremys*, a species related to the living geoemydid *Hardella*, and a possible Testudinidae (Claude *et al.*, 2003). These geoemydids are the earliest occurrences in Southeast Asia, although they are known as early as the Early Eocene in Europe and North America.

The lignite mines of the Nong Ya Plong Basin (Petchaburi Province), in the northern part of the peninsula of Thailand, have also yielded turtle remains. Several mammals discovered in these lignite mines indicate a Late Oligocene age (Marivaux *et al.*, 2004). The turtles belong to two or three geoemydid species. Amazingly, although a rich trionychoid fauna is recorded from the Middle Eocene of Myanmar (Hutchison *et al.*, 2004), this group is absent from both Eocene and Oligocene localities in Thailand. This may be the result of environmental and facies differences between the Thai and Burmese localities.

Geoemydid, testudinid and trionychid turtles have been found in the Neogene lignite mines (Mae Moh, Chiang Muan, Na Sai and Mae Sot basins) of the northwestern part of Thailand. Near Nakhon Ratchasima, the Miocene to probably Pleistocene deposits of the Moon River contain a rich turtle fauna including testudinids, geoemydids and trionychids. Geoemydids and trionychids are represented by species close to or conspecific with their living counterparts, whereas isolated plates and nearly complete shells of Testudinidae (Fig. 6) closely resemble the giant terrestrial turtles of similar size found in the Neogene beds of the Siwalik Hills, described during the second part of the nineteenth century (Lydekker, 1885).

Fig. 6 Giant terrestrial turtle (Testudinidae) from the Neogene of Nakhon Ratchasima Province, Thailand. The carapace length is estimated as about 1.5 metres.

CONCLUSION

Although the fossil turtle record of Thailand is still incomplete and discontinuous, both Mesozoic and Cenozoic formations have yielded what is currently the most important succession of turtle faunas in Southeast Asia. The Mesozoic turtle record, from both the Indochina and Shan-Thai Blocks, ranges from the Late Triassic to the mid-Cretaceous. Although the turtles from the Phu Kradung Formation are still poorly known, large trionychoids are already present in this formation. Both the Sao Khua and Khok Kruat formations have so far yielded only trionychoid turtles. The turtle fauna from the Sao Khua Formation appears to be different from the roughly coeval Early Cretaceous turtle fauna from northeastern China, which is dominated by macrobaenids. This may suggest climatic and/or environmental differences. Early representatives of trionychoid turtles seem to play an important part in the Late Jurassic and Early Cretaceous ecosystems of Southeast Asia, before their later diversification in the Late Cretaceous of Central Asia. The turtle record from Thailand thus provides important evidence not only about faunal succession in Southeast Asia, but also about the origin and evolution of trionychoid turtles.

ACKNOWLEDGMENTS

Our research on fossil turtles, which is part of the joint Thai-French research programme on vertebrate palaeontology in Thailand, is supported by the TRF-CNRS Special Programme for Biodiversity Research and Training (BRT/BIOTEC/NSTDA), Grant BRT R-24507, the Department of Mineral Resources (DMR), Thailand, the Centre National de la Recherche Scientifique (ECLIPSE Programme), France and the Department of Biology, University of Mahasarakham, Thailand. Thanks to all French and Thai colleagues who took part in the field work.

LITERATURE CITED

Broin de, F. 1984. *Proganochelys ruchae* n. sp., Chélonien du Trias supérieur de Thaïlande. Studia Geologica Salamanticensia vol. special 1 (Studia Palaeocheloniologica I):87 – 97

Broin de, F., R. Ingavat, N. Sattayarak, and P. Janvier. 1982. Triassic turtle remains from northeastern Thailand. Journal of Vertebrate Paleontology 2:41 – 46.

Buffetaut, E., L. Raksaskulwong, V. Suteethorn, and H. Tong. 1994a. First post-Triassic temnospondyl amphibians from the Shan-Thai Block: intercentra from the Jurassic of peninsular Thailand. Geological Magazine 131:837 – 839.

Buffetaut, E., and V. Suteethorn. 1998. The biogeological significance of the Mesozoic vertebrates from Thailand; pp. 83 – 90 *in* R. Hall and J. D. Holloway (eds.), Biogeography and Geological Evolution of SE Asia. Backhuys, Leiden.

Buffetaut, E., and V. Suteethorn. 1999. The dinosaur fauna of the Sao Khua Formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia. Palaeogeography, Palaeoclimatology, Palaeoecology 150:13 – 23.

Buffetaut, E., V. Suteethorn, G. Cuny, S. Khansubha, H. Tong, J. Le Loeuff, and L. Cavin. 2003. Dinosaurs in Thailand. Proceedings of 1st International Conference on Palaeontology of Southeast Asia. Mahasarakham University Journal 22 (Special Issue 2003):69 – 82.

Buffetaut, E., V. Suteethorn, J. Le Loeuff, S. Khansubha, H. Tong, and K. Wongko. 2005. The dinosaur fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand; pp. 575 – 581 *in* L. Wannakao, W. Youngme, K. Srisuk and R. Lertsirivorakul (eds.), Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005). Khon Kaen University, Khon Kaen.

Buffetaut, E., V. Suteethorn, H. Tong, Y. Chaimanee, and S. Khansubha. 1997. New dinosaur discoveries in the Jurassic and Cretaceous of northeastern Thailand; pp. 177 – 187 *in* The International Conference on Stratigraphy and Tectonic Evolution of Southeast Asia and the South Pacific. Bangkok, Thailand.

Buffetaut, E., H. Tong, V. Suteethorn, and L. Raksaskulwong. 1994b. Jurassic vertebrates from the southern peninsula of Thailand and their implications. A preliminary report; pp. 253 – 256 *in* P. Angsuwathana, T. Wongwanich, W. Tansathien, S. Wongsomsak and J. Tulyatid (eds.) Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia. Department of Mineral Resources, Bangkok.

Cappetta, H., E. Buffetaut, and V. Suteethorn. 1990. A new hybodont shark from the Lower Cretaceous of Thailand. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 11:659 – 666.

Claude, J., H. Tong, and V. Suteethorn. 2003. Geoemydid turtles from the Eocene of Krabi (Thailand): Preliminary report. Proceedings of 1st International Conference on Palaeontology of Southeast Asia, Mahasarakham University Journal 22 (Special Issue 2003):101.

Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. Bulletin of the American Museum of Natural History 194:1 – 263.

Hirayama, R. 1998. Fossil turtles from the Mifune Group (Late Cretaceous) of Kumamoto Prefecture, western Japan; pp. 85 – 99 *in* Report of the Research on the Distribution of Important Fossils in Kumamoto Prefecture. Dinosaurs from the Mifune Group, Kumamoto Prefecture, Japan. Mifune Town Education Board.

Hirayama, R., D. Brinkman, and I. Danilov. 2000. Distribution and biogeography of non-marine Cretaceous turtles. Russian Journal of Herpetology 7:181 – 198.

Hutchison, J. H., P. A. Holroyd, and R. L. Ciochon. 2004. A preliminary report on southeast Asia's oldest Cenozoic turtle fauna from the late Middle Eocene Pondaung Formation, Myanmar. Asiatic Herpetological Research 10:38 – 52.

Kuznetzov, V. V. 1976. A freshwater turtle from the Senonian of northeastern Cisaralia. Paleontological Journal 1976:498 – 500.

Lapparent de Broin de, F. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data. Comptes Rendus Palevol 3:387 – 396.

Lydekker, R. 1885. Siwalik and Narbada Chelonia. Memoir Geological Survey of India 10:155 – 208.

Marivaux, L., Y. Chaimanee, P. Srisuk, and J.-J. Jaeger. 2004. Discovery of ***Fallomus ladakhensis*** Nanda & Sahni, 1998 (Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Petchaburi Province, Thailand): systematic, biochronology and paleoenvironmental implications. Geodiversitas 26:493 – 507.

Metcalfe, I. 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography; pp. 25 – 41 *in* R. Hall and J. D. Holloway (eds.). Biogeography and Geological Evolution of SE Asia. Backhuys, Leiden.

Meylan, P. A., and E. S. Gaffney. 1989. The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. American Museum Novitates 2941:1 – 60.

Narmandakh, P. 1985. A new species of *Adocus* from the Late Cretaceous of Mongolia. Paleontologicheskii Zhurnal 1985:85 – 93.

Nessov, L. A. 1977. A new genus of pitted-shelled turtle from the Upper Cretaceous of Karakalpakia. Paleontological Journal 1:96 – 107.

Nessov, L. A. 1981. On turtles of the family Dermatemydidae from the Cretaceous of the Amur River basin, and some other rare discoveries of the remains of ancient turtles of Asia; pp. 69 – 73 *in* L. J. Borkin (ed.), Herpetological Investigations in Siberia and the Far East. Leningrad.

Nessov, L. A. 1984. Data on Late Mesozoic turtles from the USSR. Studia Geologica Salamanticensia, vol. especial 1, Studia Palaeochelonioilogica 1:215 – 224.

Nessov, L. A., and L. I. Khozatskii. 1977. Freshwater turtle from the Early Cretaceous of Fergana. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 20:248 – 262.

Peng, J. H., and D. Brinkman. 1993. New material of *Xinjiangchelys* (Reptilia, Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. Canadian Journal of Earth Sciences 30:2013 – 2026.

Racey, A., J. G. S. Goodall, M. A. Love, S. Polachan, and P. D. Jones. 1994. New age data for the Mesozoic Khorat Plateau of Northeast Thailand; pp. 245 – 252 *in* P. Ansuwathana, T. Wongwanich, W. Tansathien, S. Wongsomak and J. Tulyatid (eds.), Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia. Department of Mineral Resources, Bangkok.

Racey, A., M. A. Love, A. C. Canham, J. G. S. Goodall, S. Polachan, and P. D. Jones. 1996. Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. 1. Stratigraphy and sedimentary evolution. Journal of Petroleum Geology 19:5 – 40.

Sukhanov, V. B. 2000. Mesozoic turtles of Middle and Central Asia; pp. 309 – 367 *in* M. J. Benton, M. A. Shishkin, D. M. Unwin and E. N. Kurochkin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge.

Sukhanov, V. B., and P. Narmandakh. 2006. New taxa of Mesozoic turtles from Mongolia; pp. 119 – 127 *in* I. Danilov and J. F. Parham (eds.), Fossil Turtle Research, Vol. 1, Russian Journal of Herpetology.

Tong, H., E. Buffetaut, and V. Suteethorn. 2002. Middle Jurassic turtles from southern Thailand. Geological Magazine 139:687 – 697.

Tong, H., E. Buffetaut, and V. Suteethorn. 2003a. Mesozoic turtles of Thailand. Proceedings of 1st International Conference on Palaeontology of Southeast Asia, Mahasarakham University Journal 22 (Special Issue 2003):41 – 48.

Tong, H., E. Buffetaut, and V. Suteethorn. 2006. *Isanemys*, a new adocid turtle from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand; pp. 128 – 137 *in* I. Danilov and J. F. Parham (eds.), Fossil Turtle Research, Vol. 1, Russian Journal of Herpetology.

Tong, H., E. Buffetaut, V. Suteethorn, and P. Srisuk. 2003b. Turtle remains from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. Abstract, pp. 30 *in* Symposium on Turtle Origin, Evolution and Systematics. Saint Petersburg.

Tong, H., E. Buffetaut, V. Suteethorn, and P. Srisuk. 2004. First carettochelyid turtle from the Lower Cretaceous of Thailand. Abstract, pp. 44 *in* 2nd EAVP Meeting. Brno.

Tong, H., V. Suteethorn, J. Claude, E. Buffetaut, and P. Jintasakul. 2005. The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand; pp. 610 – 614 *in* L. Wannakao, W. Youngme, K. Srisuk and R. Leetsirivorakul (eds.). Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005). Khon Kaen University, Khon Kaen.

Ye, X.-K. 1994. Fossil and Recent Turtles of China. Science Press, Beijing, 112 pp.

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Appendix VI

A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance

Geol. Mag.: page 1 of 15. © Cambridge University Press 2013
doi:10.1017/S0016756812001082

A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance

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(*Received* 23 September 2012; *accepted* 10 December 2012)

Abstract – A new species of *Cuora*, *Cuora chiangmuanensis* sp. nov., is described on the basis of a nearly complete shell with limb bones from the late Middle – early Late Miocene Chiang Muan Mine, Phayao Province (Northern Thailand). *C. chiangmuanensis* is distinguished from other fossil and living *Cuora* species mainly on the basis of its plastral morphology. Among fossil and extant *Cuora* taxa, the new species appears to be a missing link between the taxa from Southeast Asia and those from East Asia. It represents the earliest record of the genus and demonstrates that by 11–12 Ma, Asian box turtles were already present in Southeast Asia.

Keywords: *Cuora*, Geoemydidae, Miocene, Thailand, evolution, Southeast Asia.

1. Introduction

Cuora Gray, 1855 is a living and fossil genus of Geoemydidae, which is geographically restricted to Asia. Living species of *Cuora* are found in both continental areas and insular regions of Southeast and East Asia (Iverson, 1992; Parham *et al.* 2001) as shown in Figure 1. During the last three decades, the genus has received scientific interest in terms of systematics and taxonomy (Parham *et al.* 2004; Stuart & Parham, 2004; Blanck, McCord & Le, 2006; Spinks, Thomson & Shaffer, 2009; Spinks *et al.* 2012). Hypotheses regarding phylogenetic relationships within the genus are diverse (Yasukawa, Hirayama & Kikida, 2001; Honda *et al.* 2002; Stuart & Parham, 2004; Spinks & Shaffer, 2007; Zhang *et al.* 2008; Spinks, Thomson & Shaffer, 2009; Spinks *et al.* 2012). Among major findings, recent phylogenetic studies (Spinks, Thomson & Shaffer, 2009) suggest that the genera *Pyxidea* Gray, 1863 and *Cistoclemmys* Gray, 1863 should be included in *Cuora* for the genus to be monophyletic, a position that we adopt here. In addition to uncertainties regarding the phylogeny of the genus, species delimitation hardly reaches a consensus: the number of recognized species within the genus *Cuora* still varies from author to author from 10 living species (Fritz & Havas, 2006) to 12 or 13 living species (Iverson, 2008; Spinks, Thomson & Shaffer, 2009; Turtle Taxonomy Working Group, 2011). Taxonomy and systematics is rendered difficult for at least three reasons:

(1) Some species have a small geographical range or are unknown in the wild. For instance, *Cuora yunnanensis* was considered extinct until it was recently rediscovered (Zhou & Zhao, 2004; Blanck, 2005; He *et al.* 2007); species such as *C. mccordi* were for a long time unknown in the wild (Zhou *et al.* 2008).

(2) The presence of nuclear mitochondrial pseudogenes has led to misinterpretations in molecular-based phylogenies (Spinks, Thomson & Shaffer, 2009).

(3) Incomplete lineage sorting and introgression seems common between species of *Cuora* and between *Cuora* and other geoemydid genera (Stuart & Parham, 2007; Spinks, Thomson & Shaffer, 2009). This complexity is well illustrated by the species *C. serrata* Iverson & McCord, 1992. This species was thought to result from hybridization in a turtle farm for the pet trade since it was not known in the wild (Parham *et al.* 2001; Stuart & Parham, 2004, 2007). This taxon was later discovered in the wild and analysed showing that the hybridization was not necessarily driven by farming practices only (Shi *et al.* 2005; Spinks, Thomson & Shaffer, 2009).

Thanks to an increasing number of studies, the systematics of *Cuora* has nevertheless progressed, but problems in species delimitation still impact the way we understand it. Different genes provide different signals, possibly owing to introgression and hybridization (Spinks, Thomson & Shaffer, 2009). Recently, Spinks *et al.* (2012) provided one of the most detailed molecular studies, which resulted in much clearer and better supported nodes within the *Cuora* genus.

On the other hand, the fossil record of the genus is poorly documented, especially for pre-Neolithic times. A better knowledge of fossil *Cuora* can certainly help form a better understanding of the systematics and

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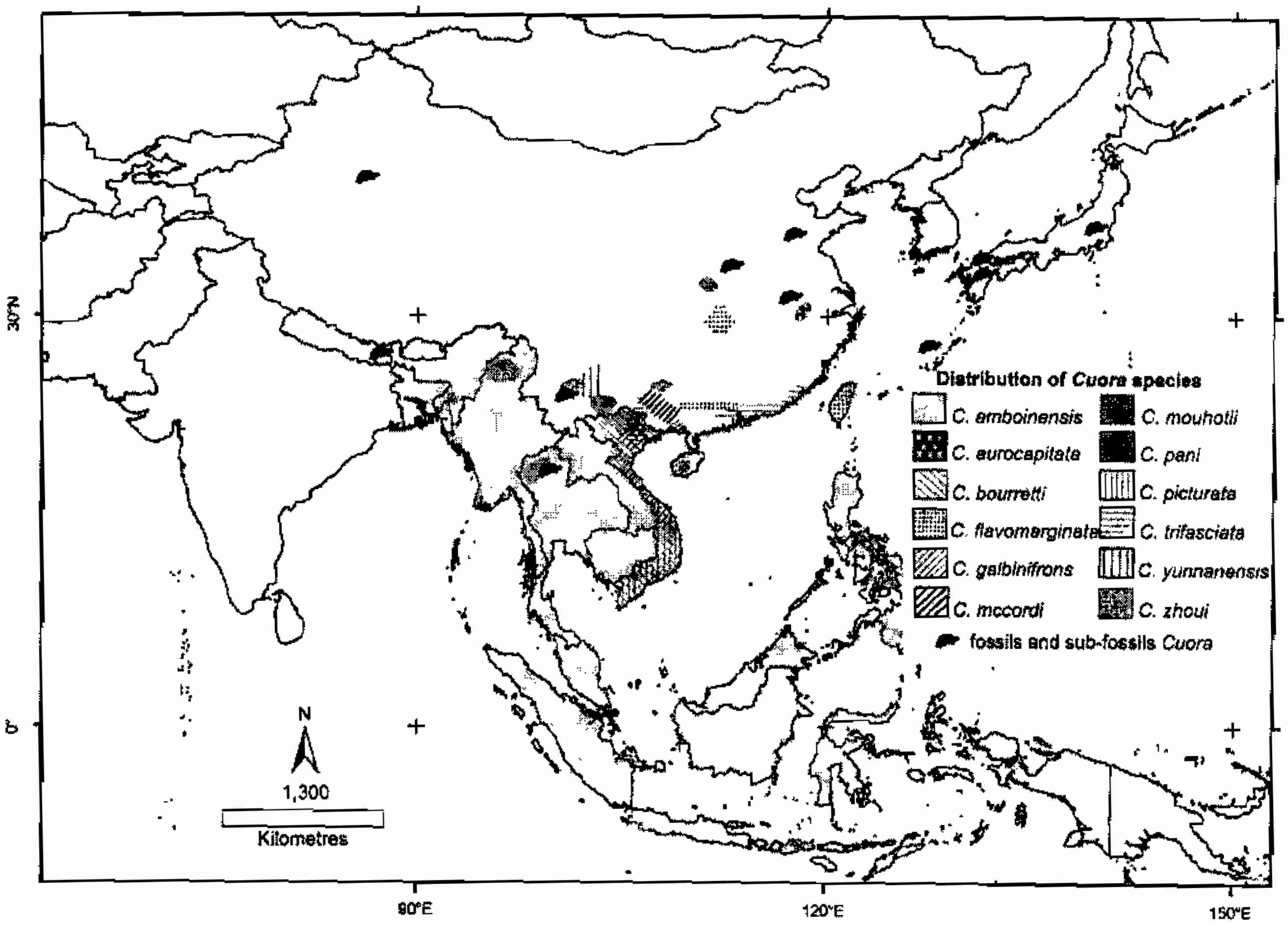

Figure 1. (Colour online) Distribution of living, sub-fossil and fossil *Cuora* species (the living distribution was compiled from Nutaphand, 1979; McCord & Iverson, 1991; Fong, Parham & Fu, 2002; Bonin, Devaux & Dupre, 2006; Turtle Taxonomy Working Group, 2011; Spinks *et al.* 2012).

evolution of the genus. Fossil *Cuora* have been recorded (see Fig. 1) from the Late Miocene to the Neolithic of China and Japan (Yeh, 1994*b*; Takahashi, Otsuka & Ota, 2008), including *Cuora pitheca* Yeh, 1981 from the Late Miocene of Lufeng, Yunnan, China; *C. miyatai* (Shikama, 1949) from the Middle Pleistocene of Oita Prefecture in Kyushu, and Tochigi and Yamaguchi prefectures in Honshu, Japan (Hirayama, 2007); *Cuora* sp. from the Pliocene of Anhui, China (Yeh, 1994*a*); and *C. flavomarginata* from the Late Pleistocene and Neolithic of China (Zhejiang, Shandong, Henan; Yeh, 1961, 1983, 1985*a,b*; Yeh & Zhang, 1994) and the Late Pleistocene of the Ryukyu Archipelago, Japan (Takahashi, Otsuka & Ota, 2008).

In this paper, we report on a recently discovered specimen of *Cuora* from the late Middle – early Late Miocene of the Chiang Muan coal mine in Northern Thailand. The detailed description and systematic study of that specimen is presented here. It is assigned to a new species, *Cuora chiangmuanensis* sp. nov. Its morphology and phylogenetic relationships with modern taxa shed new light on the origin and evolutionary history of Asian box turtles.

2. Geological setting

Chiang Muan coal mine is located in the Chiang Muan Basin, Tambon Ban Sra, Chiang Muan District, Phayao Province, Northern Thailand (Fig. 2). The Tertiary sedimentary rocks of the Chiang Muan coal mine consist of alternating beds of conglomerates, sandstones, mudstones, claystones and coal, which have yielded a rich vertebrate fauna. The palaeomagnetic study and mammalian fossils indicate a late Middle Miocene to an early Late Miocene age for this sequence (about 11–12 Ma, Kunimatsu *et al.* 2004; Pickford *et al.* 2004; Silaratana *et al.* 2004 or 9.8–13 Ma, Suganuma *et al.* 2006). The vertebrate assemblage from Chiang Muan Mine includes fishes, crocodiles, birds, mammals, snakes and turtles (Nakaya *et al.* 2002; Silaratana *et al.* 2004). Most turtle remains are shell elements which belong to geoemydid turtles. There are at least two geoemydid turtles based on the morphology of the xiphiplastron. In addition, Nakaya *et al.* (2002) reported Testudines, fam., gen. et sp. indet. Most specimens are represented by isolated plates. The specimen of *Cuora* studied in this work is one of the most complete geoemydid turtle specimens. It was collected by Mr Nikorn Wongchai, a geologist of the mine at that time, from the CMu 6 level, a ligneous claystone level under the lower massive coal seam (LM).

3. Material analysed and fossil preparation

The studied specimen (Cme-1/1) is housed at the Chiang Muan Mine museum, Phayao Province, Thailand. It comprises an articulated shell and a humerus and femur as disarticulated elements, all belonging to one individual. The material is fragile and was partly embedded within lignite. The material was first prepared using a needle to remove the matrix, then cleaned using 10 % sodium hydroxide (NaOH) to allow more details of sulci and sutures to be visible. It was then rinsed in water and the surface was cleaned using a soft brush and finally dried.

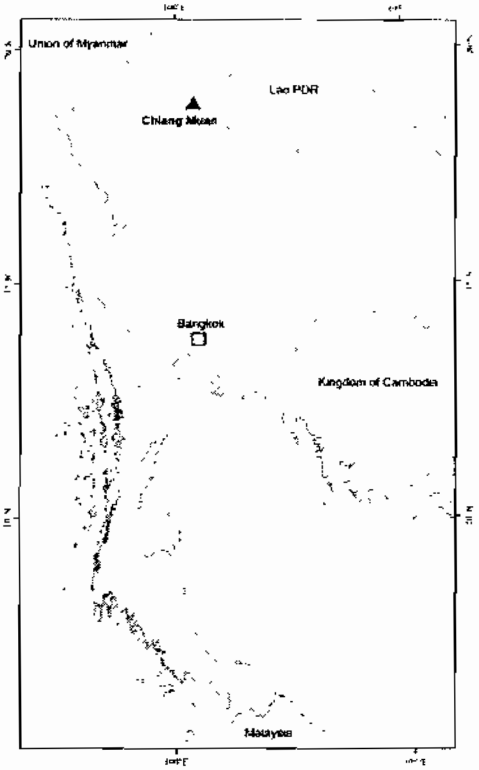

Figure 2. Map showing the location of Chiang Muan coal mine in Phayao Province, Northern Thailand (indicated by black triangle).

The specimens consulted for the comparison section of this study are listed in Table 1.

Institutional abbreviations. CIB – Chengdu Institute of Biology, Chinese Academy of Sciences, China; Cme – Chiang Muan Mine museum; CUMZ(R) – Chulalongkorn University Museum Zoology (Reptile), Bangkok, Thailand; IVPP – Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; PRC – Palaeontological Research and Education Centre, Mahasarakham, Thailand; RH – Ren Hirayama's Collection; THUb – Teikyo Heisei University, Japan; YY – Yuichiro Yasukawa's Collection, Japan.

Anatomical abbreviations. Ab – abdominal; An – anal; C – costal; Cv – cervical; Fe – femoral; H – humerus; hyp – hypoplastron; m – marginal; n – neural; N – nuchal; p – peripheral; Pl – pleural; sp – suprapygal; V – vertebral; xi – xiphiplastron.

Table 1. List of *Cuora* specimens in the comparison section of this study

Species	Specimen number and/or references
Cuora chiangmuanensis	Cme-1/1
C. pitheca Yeh, 1981	IVPP V.6178; IVPP V.6178.1; IVPP V.6178.2
C. miyatai (Shikama, 1949)	IGPS Reg. 65667; Hagesawa & Ota,1980
C. amboinensis (Riche, 1801)	CUMZ(R) 1996-01-08(1); CUMZ(R) 1997-12-25(2); CUMZ(R) 1997-12-25(3); CUMZ(R) 2008-08-06(7); RH 149; RH 838
C. aurocapitata Luo & Zong, 1988	RH 915; THUb 13; THUb 14
C. bourreti Obst & Reimann, 1994	Shi, 2008; Stuart & Parham, 2004
C. flavomarginata (Gray, 1863)	ICB 639084; ICB 64 III 088; IVPP V. 2520; RH 65; RH 104; RH 105; RH 106; RH 208; RH 429; RH 431; RH 432; RH 433; RH 435; RH 436; RH 438; RH 446; RH 629; RH 697; RH 928; RH 942
C. galbinifrons Bourret, 1939	ICB 64 III 088; RH 773; RH895; RH 900; RH 916
C. mccordi Ernst, 1988	RH 934; RH 950; RH 989; RH 1078
C. mouhotii (Gray, 1862)	CUMZ(R)-unnumbered; Stuart & Parham, 2004
C. pani Song, 1984	RH 903; RH 951; RH 989; RH 1079; Parham & Li, 1999
C. picturata Lehr, Fritz & Obst, 1998	Shi, 2008; Stuart & Parham, 2004
C. trifasciata (Bell, 1825)	RH 250; YY1; YY2
C. yunnanensis (Boulenger, 1906)	Shi, 2008
C. zhoui Zhao, 1990	RH 1157; Shi, 2008

4. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758
Suborder CRYPTODIRA Cope, 1868
Superfamily TESTUDINOIDEA Batsch, 1788
Family GEOEMYDIDAE Theobald, 1868
Genus *Cuora* Gray, 1855
Cuora chiangmuanensis sp. nov.
Figure 3

Etymology. The species name refers to the type locality.

Holotype. An articulated carapace and a complete posterior lobe of a plastron, a humerus and a femur (Cme-1/1).

Type locality and horizon. Chiang Muan coal mine, Tambon Ban Sra, Chiang Muan District, Phayao Province, Northern Thailand; CMu 6, ligneous claystone under lower massive coal seam (LM), late Middle or early Late Miocene.

Diagnosis. A species of *Cuora* of moderate size (carapace length around 20 cm); carapace oval in shape with smooth margin. It is diagnosed by the following combination of characters: absence of vertebral keel extending anteriorly; first vertebral wide anteriorly nearly reaching the second marginal; smooth posterior margin (differs from *C. mouhotii* and *C. serrata*); fully divided anal scutes (unlike *C. bourreti*, *C. flavomargianata*, *C. galbinifrons* and *C. picturata*); very small anal notch present but smaller than that of *C. pitheca*, *C. mccordi*, *C. pani*, *C. mouhotii*, *C. trifasciata* and *C. zhoui*; well-developed lips on the posterior lobe of the plastron.

Measurements. See Table 2.

Table 2. Shell measurements (in millimetres) of the holotype of *Cuora chiangmuanensis* sp. nov.

Length of carapace (estimated)	200
Length of posterior lobe	125
Midline length of abdominal	45
Midline length of femoral	12
Midline length of anal	60
Midline length of hypoplastron	60
Width of hypoplastron	125
Midline length of xiphiplastron	52
Width of xiphiplastron	118
Length of nuchal	30
Greatest width of nuchal	43
Anterior width of nuchal	30
Posterior width of nuchal	18
Length of neural I	20
Greatest width of neural I	25
Length of neural II	24
Greatest width of neural II	28

4.a. Description

Preservation. The holotype (Cme-1/1) consists of a nearly complete carapace, the posterior half of a plastron, a left humerus and a femur. The carapace is broken into two parts along the midline and the left part of the carapace is turned over to lie on the ventral surface of the plastron. The posterior lobe of the plastron is turned 90° to the right (see Fig. 3).

The shell is flattened dorso-ventrally and the anterior margin of the carapace is damaged. Sulci and sutures are well preserved except for the fifth vertebral sulcus, which cannot be observed. The preserved part of the carapace consists of the nuchal plate, the first to eleventh left and right peripheral plates, the first to fifth and distal part of the sixth to eighth left costal plates and the first to eighth right costals. The medial portions of the fifth to eighth costal plates of the right side are broken. The first and second neural plates are preserved in their original position and presented in dorsal view, while four other neural plates are disarticulated from the carapace and scattered on the visceral side of the left costal plates, presented on the internal view. Other neural plates are not preserved. The first suprapygal and pygal are missing. The second suprapygal is preserved but the anterior and left parts are missing. On the plastron, only the hypoplastra and xiphiplastra are preserved.

Carapace. (Fig. 3a, b) The shell has an oval outline. The carapace outer surface is smooth without ornamentation or growth annuli. There are no fontanelles on the carapace (Fig. 3a, b). The carapace is not sutured to the plastron. The anterior and posterior carapace margins are smooth. The vertebral keel is indistinct.

The nuchal plate is hexagonal in shape with a narrow posterior end. The anterior rim of this plate is damaged. The first and second neural plates, preserved *in situ*, are hexagonal with short postero-lateral sides. The first neural is as wide as it is long. The second neural is slightly wider than long and longer than the first neural. The outline of the medial margin of the costal plates suggests that the third to fifth neural plates are also wider than long and hexagonal with short postero-lateral sides (see Fig. 3a1, b1). The four scattered neurals, presented in internal view, are interpreted as the third to sixth neurals. The neural formula

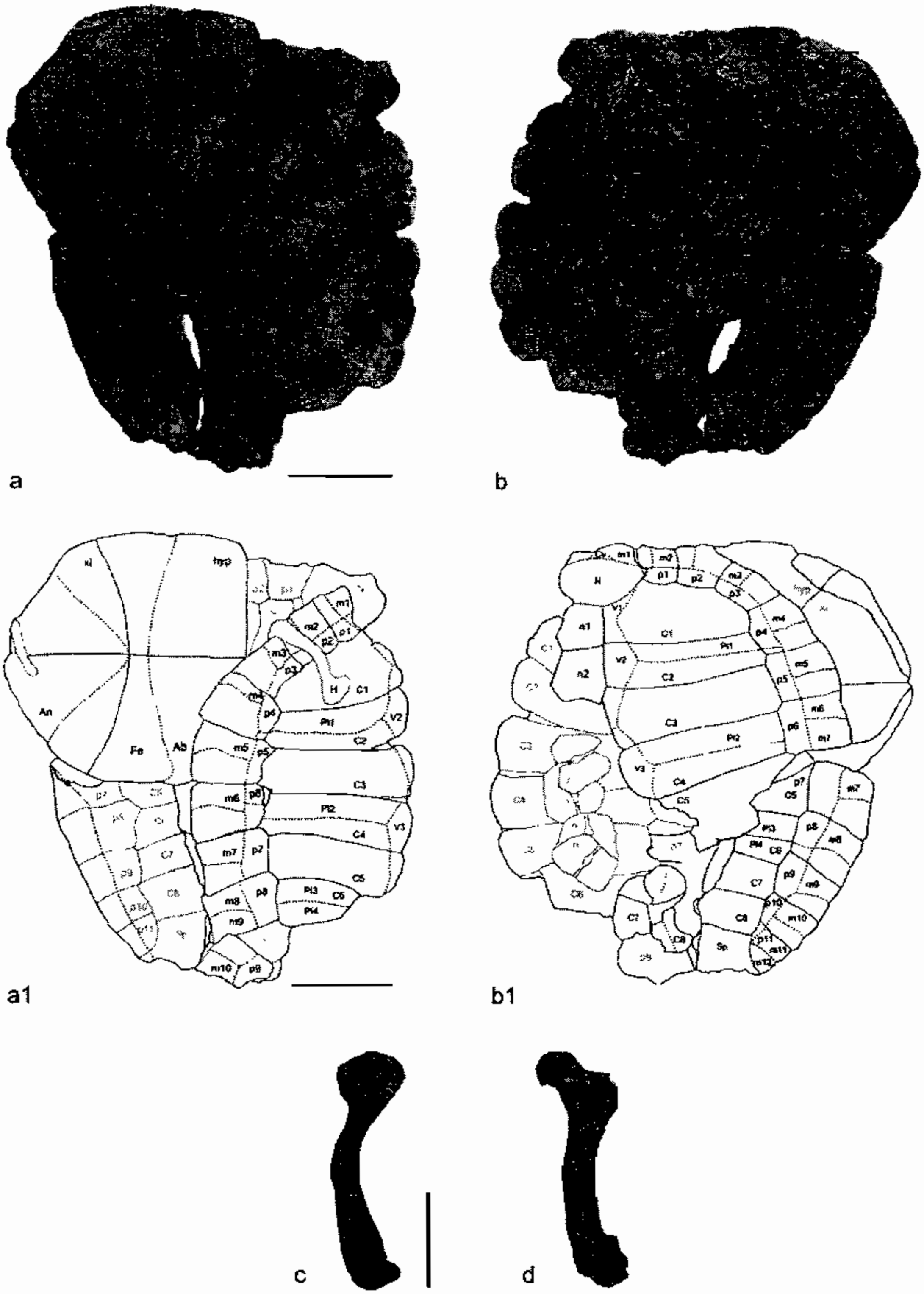

Figure 3. (Colour online) Shell and limb bones of *Cuora chiangmuanensis* sp. nov. from Chiang Muan Mine, Phayao Province. Holotype (Cme-1/1): (a, b) carapace and plastron; (c) humerus; (d) femur. Inguinal buttress is indicated by arrow. Scale bar of shell is 5 cm and that of limb bones is 2 cm.

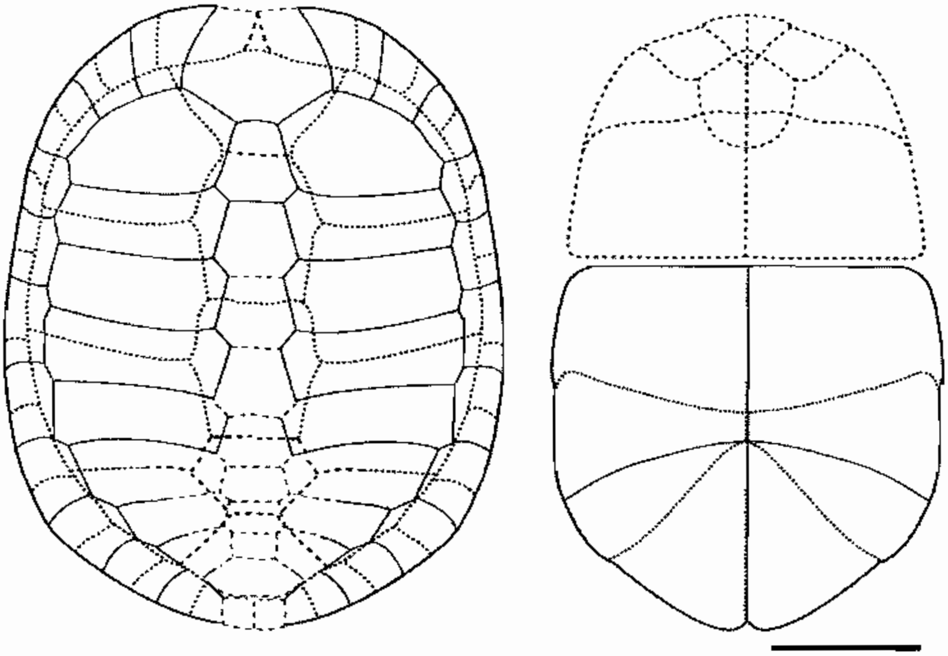

Figure 4. Reconstruction of the shell of *Cuora chiangmuanensis* sp. nov. Scale bar is 5 cm.

is, therefore, 6P,6P,6P,6P,6P,6P,?,?. The wide sixth neural with a long posterior margin indicates the presence of the seventh neural, but whether the eighth neural is present or absent is indeterminate. The presence and shape of the first suprapygal cannot be determined. As indicated by the outline of the peripherals, the eighth costals and by its preserved portions, the second suprapygal plate is probably hexagonal in shape. The pygal plate is not preserved. The first costal plate is the longest. It contacts the first peripheral plate to the anterior half of the fourth peripheral plate. The second to fourth costal plates are relatively short, slightly decreasing in length backwards. The fifth costal plate is curved posteriorly and reaches the eighth peripheral plate. There is a very short inguinal scar on the inner surface of the lateral end of the left sixth costal and seventh peripheral (see in Fig. 3a). The sixth and seventh costal plates are smaller and narrower; they are also curved posteriorly. The sixth costal plate contacts the eighth and ninth peripheral plates. The seventh costal plate contacts the ninth and tenth peripheral plates. The eighth costal plate contacts the tenth and eleventh peripheral plates. The first peripheral plate is longer than wide. The second to eleventh peripheral plates are more slender, mesio-laterally expanded and reduced in size posteriorly. The right seventh peripheral plate exhibits a distinct musk duct foramen on the ventral surface (see Fig. 3a1).

The cervical scute is incomplete. Its posterior part is rather wide. The first vertebral scute is as wide as the nuchal. It is wider anteriorly with the anterior margin more than twice its posterior margin, and nearly reaches the second marginal scute. The second and third vertebral scutes are rather narrow and hexagonal in shape with the posterior half narrower than their anterior half. The first pleural scute is long and extends posteriorly until the anterior half of the second costal plate, and contacts the anterior half of the fifth marginal scute. The second and third pleural scutes are shorter. The second pleural scute contacts the fifth and the sixth marginals, which can be observed clearly on the left side. The third pleural scute reaches the sixth to eighth marginal scutes. The fourth pleural scute is the smallest of all. It is slightly longer than wide. The pleuro-marginal sulcus is situated below the costo-peripheral suture.

Plastron. (Fig. 3a, b) Only the posterior half of the plastron is preserved. The plastral surface is smooth. The posterior border of the posterior plastral lobe is rounded. A very small anal notch is present. The hypoplastron is as long as the xiphiplatron in the midline. The anterior border of the hypoplastron corresponding to the pectoro-abdominal sulcus is straight and clearly rounded, indicating a hinge between the hyoplastra and hypoplastra. The hypo-xiphiplastral suture is slightly convex anteriorly. The abdomino-femoral sulcus is convex posteriorly. There is no constriction on the lateral borders of the xiphiplastra at the femoro-anal sulcus. The maximum length of the anal scutes is longer than the midline length of the abdominal scutes, which are both much longer than the midline length of the femoral scutes. The partial scute formula for the plastron is An > Ab > Fe. The maximum length of the anal scutes is 5.8 times greater than that of the femoral scutes. The femoro-anal sulci form a right angle between each other and oblique to the midline. This sulcus reaches the hypo-xiphiplastral suture at the midline.

On the inner surface of the plastron, a weak inguinal buttress is preserved on the left side (see Fig. 3b). The lip is well developed; it is very wide and flat on the anterior part, and becomes narrower posteriorly. The anal lip is rather wide and thick. The reconstruction of the shell is shown in Figure 4.

Humerus. (Fig. 3c) The left humerus was preserved as an isolated element on the left side of the carapace (Fig. 3a). It is 4.5 cm in length. It is nearly complete but flattened, especially the proximal and distal parts. The shaft is slender and slightly curved. The caput humerus is compressed. The lateral process is not preserved. The ectepicondyle foramen is damaged; its distal part is an open groove.

Femur. (Fig. 3d) A disarticulated femur was preserved above the left side of carapace before it was removed for preparation. It is 3.5 cm in length. It is complete but compressed laterally. The shaft is slender and slightly curved. Both the trochanter minor and trochanter major are damaged. The intertrochanter fossa is deep, narrow and open.

4.b. Comparison and discussion

4.b.1 Systematic assignment

The specimen from Chiang Muan displays geoemydid synapomorphies as indicated by the presence of inguinal musk duct foramina on the seventh peripheral (Hirayama, 1985; Gaffney & Meylan, 1988; Yasukawa, Hirayama & Kikida, 2001; Claude & Tong, 2004). The presence of a distinct hinge between the hyoplastron and hypoplastron and the absence of a distinct bony bridge are known in several independent geoemydid lineages (*Cuora*, *Cyclemys*, *Ptychogaster*). The reduced anal notch and the regular and wide hexagonal neural plates with short postero-lateral sides seen in Cme-1/1 are diagnostic of the genus *Cuora*. The large size and absence of the carapacial fontanelles between the costals and peripherals indicates that this specimen belongs to an adult individual. Following Spinks, Thomson & Shaffer (2009) and Spinks *et al.* (2012), we consider that the genus *Cuora* includes 12 evolving units that could be considered as extant species: *C. mccordi*, *C. galbinifrons*, *C. picturata*, *C. bourreti*, *C. trifasciata*, *C. amboinensis*, *C. mouhotii*, *C. yunnanensis*, *C. flavomarginata*, *C. zhoui*, *C. pani*, *C. aurocapitata*, plus the hybrid *C. serrata*.

In comparison with extant species of *Cuora* (see Table 3), the specimen from Chiang Muan clearly differs from *C. mouhotii* and *C. serrata* by its smooth carapacial margin and its smaller anal notch. It differs from *C. bourreti*, *C. picturata*, *C. flavomarginata* and *C. galbinifrons* in the presence of an anal notch and in lacking a vertebral keel. In *Cuora amboinensis*, *C. flavomarginata*, *C. bourreti* and *C. galbinifrons* the anal notch is absent, while *C. mccordi* and *C. pani* have a larger anal notch in comparison with our specimen. The specimen from Chiang Muan differs from *C. aurocapitata*, *C. pani*, *C. trifasciata*, *C. mouhotii*, *C. yunnanensis* and *C. zhoui* in the absence of the vertebral keel; this character, however, can vary during ontogeny. In addition, *C. chiangmuanensis* shares with *C. amboinensis*, *C. aurocapitata*, *C. galbinifrons* and *C. mccordi* the presence of a musk duct that is a closed foramen located in the middle of the seventh peripheral plate. In other species of *Cuora*, the musk duct is incised in the ligamentous area. *Cuora chiangmuanensis* differs from *C. bourreti*, *C. flavomarginata*, *C. galbinifrons* and *C. picturata* by having fully divided anal scutes as seen in other members of Geoemydidae. It differs from *C. amboinensis*, *C. bourreti*, *C. flavomarginata*, *C. galbinifrons* and *C. picturata* by the presence of a very small anal notch which is, however, smaller than in *C. mccordi*, *C. pani*, *C. trifasciata* and *C. zhoui*. *C. chiangmuanensis* has a flat lateral lip on the posterior lobe, which is still wide on the xiphiplastral part. This is similar to *C. mouhotii* but different from all other *Cuora* species. Furthermore, the femoral scute has a very short midline length in *C. chiangmuanensis* as in *C. amboinensis*, *C. flavomarginata* and *C. picturata*, while other *Cuora* species have a longer femoral midline length.

In addition to living taxa, a few fossil *Cuora* species have been reported: *C. pitheca* Yeh, 1981 from the Late Miocene of Lufeng, Yunnan and *C. miyatai* (Shikama, 1949) from the middle Pleistocene of Japan (Hasegawa & Ota, 1980; Yeh, 1981, 1985). *Cuora chiangmuanensis* differs from *C. pitheca* in having a trapezoid first vertebral scute which is much wider anteriorly than posteriorly, nearly reaching the second marginal scute, and in having the clearly longer than wide second vertebral. In *C. pitheca*, the first vertebral scute is roughly rectangular in shape, with the anterior border only slightly wider than the posterior one and reaching laterally to the mid-width of the first marginal scute; the second vertebral scute is slightly wider than long (Yeh, 1981, 1985). *Cuora miyatai* is similar to *C. chiangmuanensis* in the first vertebral scute reaching the second marginal scute. These two species differ from one another in the shape of the first vertebral scute: the anterior border of that scute is much longer than the posterior one in *C. chiangmuanensis*, while the anterior border is only slightly longer than the posterior one in *C. miyatai*. Furthermore, *C. miyatai* differs from *C. chiangmuanensis* in the second and third vertebral scutes, which are wider than long.

Concerning the plastron, *Cuora chiangmuanensis* and *C. miyatai* are similar in having a slightly wider than long posterior lobe, while the posterior lobe of *C. pitheca* is longer than wide. The abdominal is shorter than the anal scute in *C. chiangmuanensis*, differing from *C. pitheca* and *C. miyatai* in which the abdominal is longer than the anal scute. The ratio of anal/femoral midline length is less than three in *C. pitheca*, while this ratio is greater in *C. chiangmuanensis* and *C. miyatai*. In addition, *C. chiangmuanensis* shares with *C. pitheca* a wide lateral lip on the visceral surface of the posterior lobe; but the lip is flat in our specimen, while *C. pitheca* has a more prominent lip (IVPP V6718.2 and Yeh, 1985, fig. 1). Furthermore, *Cuora chiangmuanensis* differs from *C. pitheca* and *C. miyatai* in having a very small anal notch. The anal notch is clearly deeper in *C. pitheca*, and it is absent in *C. miyatai* (see Table 3; Figs 5, 6).

On the basis of the comparisons given above, *Cuora* from Chiang Muan differs from all other *Cuora* species by a combination of characters (see diagnosis), particularly in the posterior half of the plastron. It is, therefore, assigned to a new species, *Cuora chiangmuanensis* sp. nov. Among the extant and fossil *Cuora*, the new species from Thailand is most similar to *C. amboinensis* and *C. miyatai* with 9.66/13 and 8.66/12 shared characters, respectively. Similarities and differences between the living and fossil taxa are summarized in Table 3 (see the method of computation in the footnote [1] of the table).

Table 3. Comparison of *Cuora chiangmuanensis* sp. nov. with extinct and living species of *Cuora*

Characters/species of *Cuora*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
The first vertebral scute reaches the second marginal scute	yes	no	yes	no	yes	no	no	no	no	no	yes	no	yes	yes	yes
Medial carapace carina extending anteriorly	no	no	yes	no	yes	no	yes	no	yes	yes	yes	no	yes	no/yes	yes
Lip on the visceral side of hypoplastron	flat	elevated	flat	flat	elevated	?	flat	flat	elevated	flat	flat	?	elevated	?	elevated
Lateral anal lip on the visceral side of xiphiplastron	wide	wide	narrow	narrow	narrow	?	narrow	narrow	wide	wide	narrow	?	wide	?	wide
Fully divided anal scute	yes	yes	yes	yes	yes	no	no/partial	no	yes	yes	yes	no	yes	yes	yes
Anal notch	small	deep	absent	absent	small	absent	absent	absent	small	deep	small & deep	absent	small	small or deep	small
Width to length ratio for the posterior plastral lobe (behind the hinge)[*]	A	C	A	B	C	A	B	C	A	A	B	A	C	C	A
Abdominal/anal midline length[†]	F	F	D	E	E	D	E	E	E	D	E	D	D	D	E
Abdomino-femoral sulcus[‡]	G	G	G	G	H	I	H	G	H	H	H	I	H	I	I
Musk duct foramina enclosed in seventh peripheral plate	present	?	?	present	present	?	present	absent	present	absent	absent	?	absent	?	absent
Anal to femoral midline length ratio[§]	J	K	J	J	K	K	J	K	K	K	K	J	K	K	K
Contact between the tenth marginal scute and the fifth vertebral scute	no	no	no	no	no	no	no	no	yes	yes	no	?	no	no	no
Plastral hinge	present	present	present	present	present	present	present	present	present	present	present	present	present	present	present
Characters shared with *C. chiangmuanensis*[¶]	–	7.33/12	8.66/12	9.66/13	7/13	4.66/10	6.66/13	7.16/13	8/13	5.83/13	7.16/13	4.99/9	6.5/13	5.16/10	5.16/10

1 – *C. chiangmuanensis*; 2 – *C. pitheca*; 3 – *C. miyatai*; 4 – *C. amboinensis*; 5 – *C. aurocapitata*; 6 – *C. bourreti*; 7 *C. flavomarginata*; 8 – *C. galbinifrons*; 9 *C. mccordi*; 10 *C. mouhotii*; 11 - *C. pani*; 12 *C. picturata*; 13 – *C. trifasciata*; 14 – *C. yunnanensis*; 15 – *C. zhoui*.

[*] A – wider than long; B – wider than long or longer than wide; C – longer than wide;

[†] D – abdominal longer than anal scute; E – abdominal longer, equal to, or shorter than anal scute; F – abdominal shorter than anal scute;

[‡] G – convex posteriorly; H – convex posteriorly or straight; I – straight;

[§] J – more than 3; K – less than 3.

[¶] We computed a ratio quantifying similarity between *C. chiangmuanensis* and other *Cuora* species. The denominator indicates the number of available characters, while the numerator indicates the number of similar characters. Since intermediate character states exist for multistate and ordered characters, they were given an inferior weight than if taxa differed by extreme states. Resemblance was therefore calculated so that closer states would proportionally account for more resemblances than distant states on a unit scale.

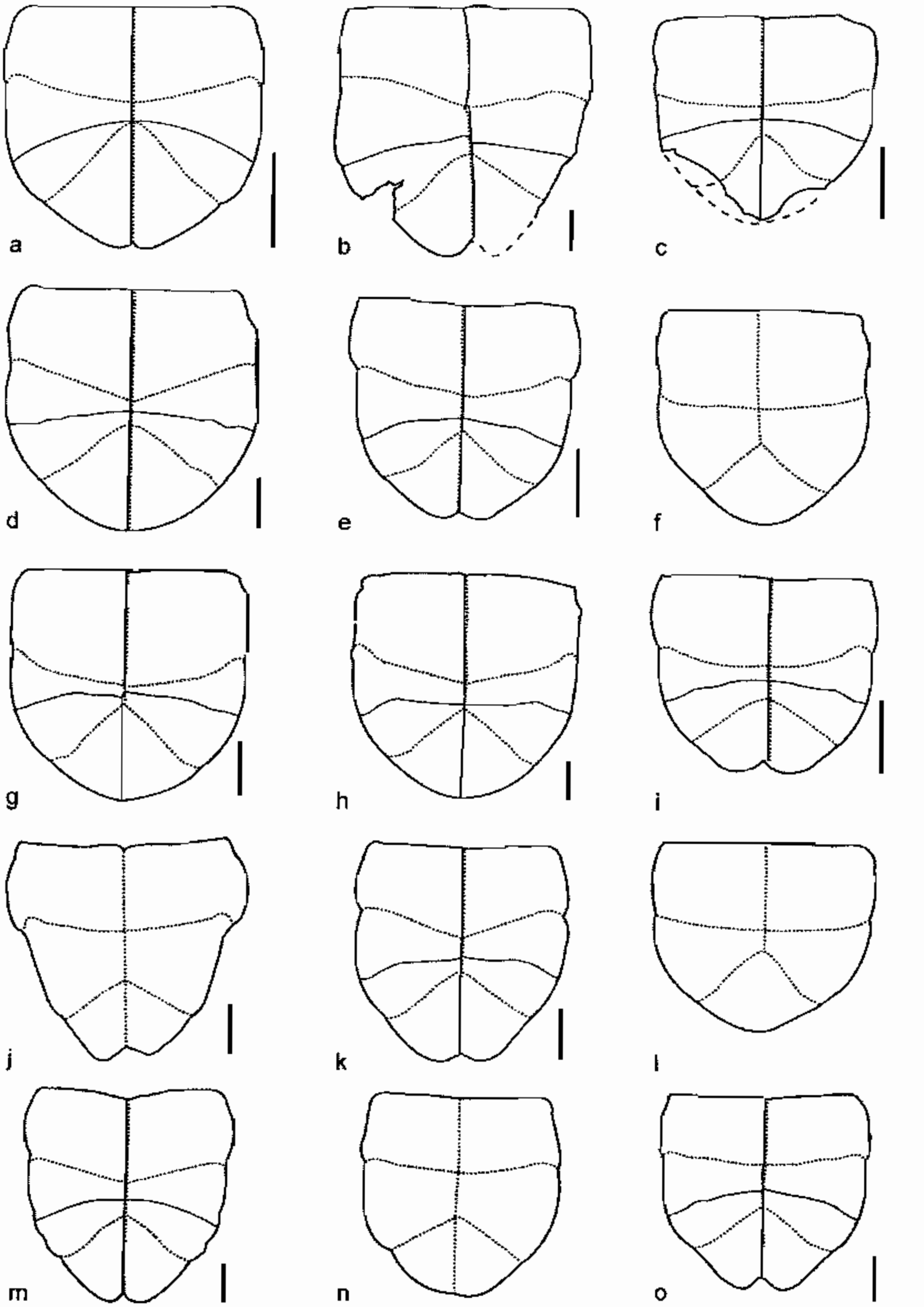

Figure 5. Posterior half of plastrons of *Cuora* in ventral view. (a) *C. chiangmuanensis* (Cme-1/1), (b) *C. pitheca* (IVPP, V.6178.2), (c) *C. miyatai* (IGPS Reg. 65667), (d) *C. amboinensis* (CUMZ(R) 1997–12–25(2)), (e) *C. aurocapitata* (RH 905), (f) *C. bourreti* (after Shi, 2008), (g) *C. flavomarginata* (RH9 82), (h) *C. galbinifrons* (RH 916), (i) *C. mccordi* (RH 950), (j) *C. mouhotii* (CUMZ(R)-unnumbered), (k) *C. pani* (RH 1079), (l) *C. picturata* (after Shi, 2008), (m) *C. trifasciata* (YY1). (n) *C. yunnanensis* (after Shi, 2008) and (o) *C. zhoui* (RH 1157). Scale bars are 2 cm.

Figure 6. (Colour online) Posterior half of plastrons of *Cuora* in visceral view. (a) *C. chiangmuanensis* (Cme-1/1), (b) *C. pitheca* (IVPP, V.6178.2), (c) *C. amboinensis* (CUMZ(R)-1997–2–25(2)), (d) *C. aurocapitata* (TUTb14), (e) *C. flavomarginata* (RH982), (f) *C. galbinifrons* (RH894), (g) *C. mccordi* (RH989), (h) *C. mouhotii* (CUMZ(R)-unnumbered), (i) *C. pani* (RH1079), (j) *C. trifasciata* (YY2) and (k) *C. zhoui* (RH 1157). Scale bars are 2 cm.

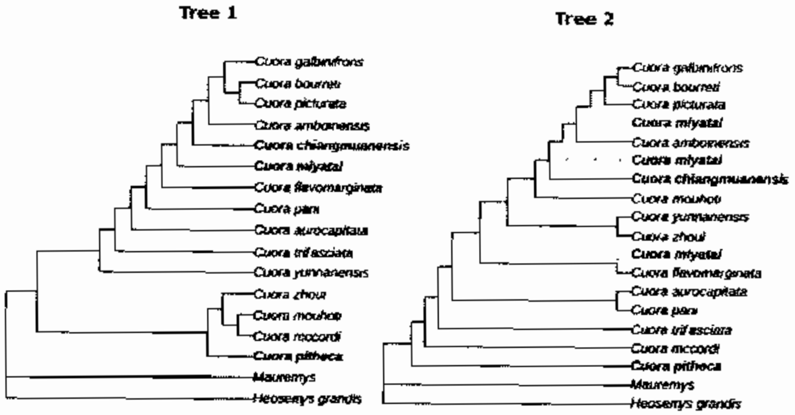

Figure 7. Most parsimonious phylogenetic hypotheses resulting from our study. Tree 1 is based only on morphological characters, while tree 2 presents the three most parsimonious hypotheses, constrained by the molecular scaffold following Spinks *et al.* (2012).

4.b.2. Phylogenetic relationships

Although the phylogenetic relationships among *Cuora* species are not completely congruent among authors, the most recent molecular phylogenies (Honda *et al.* 2002; Parham *et al.* 2004; Stuart & Parham, 2004; Blanck, McCord & Le, 2006; He *et al.* 2007; Iverson *et al.* 2007; Spinks & Shaffer, 2007; Spinks, Thomson & Shaffer, 2009) show that: (i) *C. bourreti*, *C. galbinifrons* and *C. picturata* form a monophyletic clade (characterized by absence of anal notch, absence of vertebral keel and fused anal scutes); (ii) *C. pani and C. aurocapitata* form a monophyletic clade (characterized by relatively flat shell, presence of vertebral keel and presence of small anal notch); and (iii) *C. amboinensis*, *C. mouhotii*, *C. bourreti*, *C. galbinifrons* and *C. picturata* tend to branch closer to each other (but not all phylogenies demonstrate this; see Spinks & Shaffer, 2007). This group, the majority of which are found in the southern range of *Cuora*, is characterized by at least one feature that can be interpreted as a symplesiomorphy: the first vertebral scute does not reach the second marginal (also found in *C. mccordi*).

Using nuclear DNA, Spinks *et al.* (2012) better resolved the phylogenetic relationships within *Cuora*. In this study, only the phylogenetic relationship of *Cuora mouhotii* with other southeastern *Cuora* was not well supported.

In order to determine the phylogenetic relationships of *C. chiangmuanensis*, a data matrix of 13 informative characters was gathered on the 12 living species and three fossil species. The tree was rooted with the help of two outgroups: *Heosemys grandis* (Gray, 1860) and *Mauremys sensu lato*. *Mauremys mutica* (Cantor, 1842), *Mauremys reevesi* (Gray, 1831) and *Mauremys leprosa* (Schweigger, 1812) were scored for determining the states of the *Mauremys sensu lato* tip.

Two analyses were run, the first one using only morphological characters and the second one constraining the relationships among living taxa using a molecular scaffold based on the phylogeny obtained from the nuclear data of Spinks *et al.* (2012). In that scaffold, only nodes that received bootstrap support above 95 % were considered; therefore, *Cuora mouhotii* formed a polytomy with Southeast Asian *Cuora* (*C. amboinensis*, *C. bourreti*, *C. picturata* and *C. galbinifrons*) and the group formed by other East Asian *Cuora*. Character descriptions and distributions are given in Appendix 1. Polymorphic characters were interpreted as intermediate characters. Characters were ordered, and all ordered multi-state characters were scaled so that those characters did not have a disproportionate effect over the binary characters in phylogeny estimation.

Parsimony analyses were performed in PAUP 4.0 b10 (Swofford, 1998) using random addition sequence, and the tree bisection-reconnection branch swapping algorithm across 10 000 replicates.

While the unconstrained analysis resulted in a single tree (Fig. 7), three most parsimonious hypotheses were found in using the molecularly constrained tree, which differed in the position of *Cuora miyatai*, either nesting it within the Southeast Asian taxa *C. chiangmuanensis*, *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis* or forming a clade with *C. flavomariginata*. *C. chiangmuanensis* always formed a clade with the living *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis*. *Cuora pitheca* roots all other *Cuora* in the molecularly constrained tree but forms a monophyletic group with *C. zhoui*, *C. mccordi* and *C. mouhotii* in the unconstrained tree. One should keep in mind that rooting the tree differently may challenge the understanding of the evolutionary history of *Cuora*, especially regarding whether the East Asian group constitutes a plesion or a clade. Nevertheless, the major finding of our analysis is that the position of *Cuora chiangmuanensis* is close to the Southeast Asian group formed by *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis*. Interestingly, *C. mouhotii* is sister rooting the Southeast Asian group in the molecularly constrained analysis, while it forms a basal clade with other *Cuora* in the unconstrained phylogeny.

5. Concluding remarks

An adult geoemydid turtle from the Miocene of the Chiang Muan coal mine, Northern Thailand is described as a new species of *Cuora*, *C. chiangmuanensis*, sp. nov. This is the earliest record of that genus in the Middle Miocene or early Late Miocene and it documents an important part of the evolutionary history of Asian box turtles. Based on the mammalian fauna, the age of the hitherto known oldest *Cuora*, *C. pitheca* from the Late Miocene of Lufeng, China is of 8–9 Ma (Wang & Qi, 2005; Deng, 2006) or even younger (7 Ma, Deng & Qi, 2009). *C. chiangmuanensis* is thus likely older than *C. pitheca*, even if it appears more 'derived'. This shows that the group was already diversified before the end of the Miocene.

If we consider that *C. chiangmuanensis* forms a monophyletic group with the extant Southeast Asian *Cuora* species (*C. amboniensis*, *C. galbinifrons*, *C. picturata* and *C. bourreti*) and that *C. chiangmuanensis* is also from this region, it is possible that *C. chiangmuanensis* represents the fossil link between Southeast Asian and East Asian *Cuora*. The systematic position of *Cuora miyatai* is not resolved in our study, but it is clear that it diverged from a continental group earlier than the Middle Pleistocene. While Hirayama (2007) and one of our analyses suggested it may be a close relative of *C. flavomarginata*, some equally parsimonious hypotheses suggest it may share a common ancestry with Southeast Asian *Cuora*, suggesting an alternative biogeographic origin. According to our analyses, *Cuora mouhotii* may either represent a member of this Southeast Asian group demonstrating a vicariant evolution within the genus or a more primitive member of *Cuora* (demonstrating iterative migrations). The fossil record being still scanty and molecular constraints being unavailable for the root, it would be speculative to polarize these migrations, but palaeogeography undoubtedly influenced the diversification of the genus *Cuora*.

Acknowledgements. This work was supported by a Science Achievement Scholarship of Thailand, Mahasarakham University Development Fund (Creative Works and Paper Presentation Scholarship), Palaeontological Research and Education Centre, Faculty of Science, Mahasarakham University and Mahasarakham University fiscal year 2012 grant. We thank the Chiang Muan Mine authorities and Nikorn Wongchai for facilities during our work; Jeremy Martin (Bristol University) for his help to prepare the specimen and improve the manuscript; Kumthorn Thirakhupt (Chulalongkorn University), Fang Zheng, Lu Li (Institute of Vertebrate Palaeontology and Palaeoanthropology), Shengquan Li, Yueying Chen, Yuezhao Wang, Jianping Jiang (Chengdu Institute of Biology), Ren Hirayama (Waseda University), Teppei Sonoda (Ibaraki University), Akio Takahashi (Okayama University of Science), Hideo Nakaya (Kagawa University) and Yuichiro Yasukawa (University of the Ryukyus) for providing comparative materials and useful data and suggestions; Eric Buffetaut (CNRS), Suravech Suteethorn, Paladej Srisuk, Arnauld Filoux (PRC), Jean Le Loeuff (Musée des Dinosaures, Espéraza) for useful suggestions and correction; and Atthiwat Wattanapituksakul (PRC) for the map of the locality. Thanks to everyone who took part in our fieldwork. We are grateful to the two anonymous reviewers who significantly improved an earlier version of this manuscript.

References

BATSCH, A. J. G. C. 1788. *Versuch einer Anleitung zur Kenntniss und Geschichte der Thiere und Mineralien. Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere. Vögel, Amphibien und Fische*. Jena: Akademischen Buchhandlung, 528 pp.

BELL, T. 1825. A monograph of the tortoise having a moveable sternum, with remarks on their arrangement and affinities. *Zoological Journal* **2**, 299–310.

BLANCK, T. 2005. *Cuora yunnanensis* (Boulenger, 1906), the Yunnan box turtle, rediscovered after one-hundred years? *Radiata* **14**, 10–33.

BLANCK, T., MCCORD, W. P. & LE, M. 2006. *On the Variability of Cuora trifasciata (Bell, 1825)*. Frankfurt am Main: Edition Chimaira.

BONIN, F., DEVAUX, B. & DUPRE, A. 2006. *Turtles of the World*. London: Johns Hopkins University Press.

BOULENGER, G. A. 1906. Descriptions of new reptiles from Yunnan. *Annals and Magazine of Natural History, Series 7* **17**, 567–8.

BOURRET, R. 1939. Notes herpétologiques su l'Indochine française. XVIII. Reptiles et batraciens reçus au Laboratoire des Sciences Naturelles de l'Université au cours de l'année 1939. Descriptions de quatre espèces et d'une variété nouvelles. *Bulletin Générale d'Instruction Publique* 4 (annexe), 5–40.

CANTOR, T. 1842. General features of Chusan, with remarks on the flora and fauna of that island. *Annals and Magazine of Natural History, Series 1* **9**, 265–78, 361–70, 481–93.

CLAUDE, J. & TONG, H. 2004. Early Eocene turtles from Saint Papoul, France, with the comments on the early evolution of modern Testudinoidea. *Oryctos* **5**, 71–113.

COPE, E. D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20**, 242–300.

DENG, T. 2006. Chinese Neogene mammal biochronology. *Vertebrata Palasiatica* **44**, 143–63.

DENG, T. & QI, G.-Q. 2009. Rhinocerotids (Mammalia, Perissodactyla) from *Lufengpithecus* site, Lufeng, Yunnan. *Vertebrata PalAsiatica* **47**, 135–52.

ERNST, C. H. 1988. *Cuora mccordi*, a new Chinese box turtle from Guangxi Province. *Proceedings of the Biological Society of Washington* **101**, 466–70.

FRITZ, U. & HAVAS, P. 2007. Checklist of chelonians of the world. *Vertebrate Zoology* **57**, 149–368.

FONG, J., PARHAM, J. & FU, J. 2002. A reassessment of the distribution of *Cuora flavomarginata* Gray, 1868 on mainland China. *Russian Journal of Herpetology* **9** (1), 9–14.

GAFFNEY, E. S. & MEYLAN, P. A. 1988. A phylogeny of turtles. In *The Phylogeny and Classification of the Tetrapods, Vol. 1: Amphibians, Reptiles, Birds* (ed. M. J. Benton), pp. 157–219. Oxford: Clarendon Press.

GRAY, J. E. 1831. *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I. – Cataphracta Tortoises, Crocodiles, and Enaliosaurians*. London: Treuttel, Wurz and Co., 85 pp.

Gray, J. E. 1855. On some new species of freshwater tortoises from North America, Ceylon and Australia, in the collection of the British Museum. *Proceedings of the Zoological Society of London* **23**, 197–202.

Gray, J. E. 1860. On some new species of Mammalia and tortoises from Cambojia. *Annals and Magazine of Natural History, Series 3* **6**, 217–18.

Gray, J. E. 1862. Notice of a new species of *Cyclemys* from the Lao Mountains, in Siam. *Annals and Magazine of Natural History, Series 3* **10**,157.

Gray, J. E. 1863. Observations on the box tortoises, with the descriptions of three new Asiatic species. *Proceedings of the Zoological Society of London* **1863**, 173–8.

Hasegawa, Y. & Ota, M. 1980. Report on a Pleistocene terrapin, *Cyclemys* from Katayama Marble Quarry, Mine City, Japan. *Science Reports of the Yokohama National University, Section II* **27**, 47–52.

He, T., Zhou, T., Rao, T.-Q. & Zhang, Y.-P. 2007 Molecular identification and phylogenetic position of *Cuora yunnanensis*. *Chinese Science Bulletin* **52** (23), 3305–9.

Hirayama, R. 1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); a preliminary result. In *Studio Palaeocheloniologica I. Stvdia Geologica Salmanticensia Volumen Especial 1* (eds. F. de Broin & E. Jiménez-Fuentes), pp. 141–57.

Hirayama, R. 2007. Revision of the systematics of the fossil turtles from Japan. *Jubilee Publication in Commemoration of Professor Kamei Tadao's 80th Birthday*, 145–53.

Honda, M., Yasukawa, Y., Hirayama, R. & Ota, H. 2002. Phylogenetic relationships of the Asian box turtles of the genus *Cuora* sensu lato (Reptilia: Bataguridae) inferred from mitochondrial DNA sequences. *Zoological Science* **19**, 1305–12.

Iverson, J. B. 2008. A checklist of the turtles of the world. http://www.earlham.edu/biology/documents/TurtleNamesOct07.

Iverson, J. B. 1992. *A Revised Checklist with Distribution Maps of the Turtles of the World*. Richmond, Indiana: Privately Printed.

Iverson, J. B., Brown, R. M., Akre, T. S., Near, T. J., Le, M., Thomson, R. C. & Starkey, D. E. 2007. In search of the tree of life for turtles. In *Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Freshwater Turtles and Tortoises* (eds H. B. Shaffer, N. N. Fitz Simmons, A. Georges & A. G. J. Rhodin). *Chelonian Research Monographs* **4**, 85–106.

Iverson, J. B. & McCord, W. P. 1992. A new subspecies of *Cuora galbinifrons* (Testudines: Batagurinae) from Hainan Island, China. *Proceedings of the Biological Society of Washington* **105**, 433–9.

Kunimatsu, Y., Ratanasthien, B., Nakaya, H., Saegusa, H. & Nagaoka, S. 2004. Earliest Miocene hominoid from Southeast Asia. *American Journal of Physical Anthropology* **124**, 99–108.

Lehr, E., Fritz, U. & Obst, F. J. 1998. *Cuora galbinifrons picturata* subsp. nov., eine neue Unterart der Hinterindischen Scharnierschildkröte. *Herpetofauna* **20** (113), 5–11.

Linnaeus, C. 1758. *Systema Naturae, per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima, Reformata*. [10th ed.]. Holmiae [Stockholm]: Laurentii Salvii, 824 pp.

Luo, B. & Zong, Y. 1988. A new species of *Cuora* – *Cuora aurocapitata*. *Acta Herpetologica Sinica* **3**, 13–15.

McCord, W. P. & Iverson, J. B. 1991. A new box turtle of the genus *Cuora* Testudines Emydidae with taxonomic notes and a key to the species. *Herpetologica* **47**, 407–20.

Nakaya, H., Saegusa, H., Kunimatsu, Y. & Ratanasthien, B. 2002. Miocene mammalian faunas of Northern Thailand and their geological age. *Primate Research* **18**, 131–41 (in Japanese with English abstract).

Nutaphand, V. 1979. *The Turtles of Thailand*. Bangkok: Siamfarm Zoological Garden, 222 pp.

Obst, F. J. & Reimann, M. 1994. Bemerkenswerte Variabilität bei *Cuora galbinifrons* Bourret, 1939, mit Beschreibung einer neuen geographischen Unterart: *Cuora galbinifrons bourreti* subsp. nov. (Reptilia: Testudines: Criptodira: Bataguridae). *Zoologische Abhandlungen, Staatliches Museum für Tierkunde Dresden* **48**, 125–39.

Parham, J. F. & Li, D. 1999. A new locality for *Cuora pani* Song 1984 with comments on its known range. *Asiatic Herpetological Research* **8**, 111–13.

Parham, J. F., Simison, W. B., Kozak, K. H., Feldman, C. R. & Shi, H. 2001. New Chinese turtles: endangered or invalid. A reassessment of two species using mitochondrial DNA, allozyme electrophoresis and known-locality specimens. *Animal Conservation* **4**, 357–67.

Parham, J. F., Stuart, B. L., Bour, R. & Fritz, U. 2004. Evolutionary distinctiveness of the extinct Yunnan box turtle (*Cuora yunnanensis*) revealed by DNA from an old museum specimen. *Proceedings of the Royal Society Biological Sciences Series B* **271**, S391–S394.

Pickford, M., Nakaya, H., Kunimatsu, Y., Saegusa, H., Fukuchi, A. & Ratanasthien, B. 2004. Age and taxonomic status of the Chiang Muan (Thailand) hominoids. *Comptes Rendus Palevol* **3**, 65–75.

Riche, M. 1801. *Testudo amboinensis*. In *Histoire Naturelle, á Générale et Particulière, des Reptiles*. Tome Second (ed. F. M. Daudin), pp. 309–12. Paris: Dufart.

Schweigger, A. F. 1812. Prodromus monographiae Cheloniorum. *Königsberger Archive für Naturwissenschaftliche und Mathematik* **1**, 271–368, 406–58.

Shi, H. 2008. *Identification Manual for Trade Turtles in China*. Beijing: Encyclopedia of China Publishing House.

Shi, H., Parham, J. F., Simison, W. B., Wang, J., Gong, S. & Fu, B. 2005. A report on the hybridization between two species of threatened Asian box turtles (Testudines: Cuora) in the wild on Hainan Island (China) with comments on the origin of 'serrata'-like turtles. *Amphibia-Reptilia* **26** (3): 377–81.

Shikama, T. 1949. The Kuzuü Ossuaries: geological and palaeontological studies of the limestone fissure deposits, in Kuzuü, Totigi Prefecture. *Science Report of Tohoku University, 2nd Series (Geology)* **23**, 1–201.

Silaratana, T., Ratanasthien, B., Takayasu, K., Fyfe, W. S., Asnachinda, P., Kandharosa, W. & Kusakabe, M. 2004. Sulfur isotopic implication of Middle Miocene marine incursion in Northern Thailand. *Science Asia* **30**, 43–58.

Song, M. T. 1984. A new species of the turtle genus *Cuora* (Testudoformes: Testudinidae). *Acta Zootaxonomica Sinica* **9** (3), 330–32.

Spinks, P. Q. & Shaffer, H. B. 2007. Conservation phylogenetics of the Asian box turtles (Geoemydidae, *Cuora*): mitochondrial introgression, numts, and inferences from multiple nuclear loci. *Conservation Genetics* **8**, 641–57.

Spinks, P. Q., Thomson, R. C., Shaffer, H. B. 2009. A reassessment of *Cuora cyclornata* Blanck, McCord and

Le, 2006 (Testudines, Geoemydidae) and a plea for taxonomic stability. *Zootaxa* **2018**, 58–68.

Spinks, P. Q., Thomson, R. C., Zhang, Y., Che, J., Wu, Y. & Shaffer, H. B. 2012. Species boundaries and phylogenetic relationships in the critically endangered Asian box turtle genus *Cuora*. *Molecular Phylogenetics and Evolution* **63**, 656–67.

Stuart, B. & Parham, J. F. 2004. Molecular phylogeny of the critically endangered Indochinese box turtle (*Cuora galbinifrons*). *Molecular Phylogenetics and Evolution* **31**, 164–77.

Stuart, B. & Parham, J. F. 2007. Recent hybrid origin of three rare Chinese turtles. *Conservation Genetics* **8**, 169–75.

Suganuma, Y., Hamada, T., Tanaka, S., Okada, M., Nakaya, H., Kunimatsu, Y., Saegusa, H., Nagaoka, S., & Ratanasthien, B. 2006. Magnetostratigraphy of the Miocene Chiang Muan Formation, Northern Thailand: implication for revised chronology of the earliest Miocene hominoid in Southeast Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **239**, 75–86.

Swofford, D. L. 1998. PAUP*: phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Sunderland, MA.

Takahashi, A., Otsuka, H. & Ota, H. 2008. Systematic review of Late Pleistocene turtles (Reptilia: Chelonii) from the Ryukyu Archipelago, Japan, with special reference to paleogeographical implication. *Pacific Science* **62** (3), 395–402.

Theobald, W., Jr. 1868. *Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal*. Journal of the Asiatic Society, Extra Number. Calcutta: Printed at the Baptist Mission Press, 88 pp.

Turtle Taxonomy Working Group [Van Dijk, P. P., Iverson, J. B., Shaffer, H. B., Bour, R. & Rhodin, A. G. J.]. 2011. Turtles of the World, 2011 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. In *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group* (eds A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson & R. A. Mittermeier). *Chelonian Research Monographs* **5**, pp. 000.165–000.242. doi:10.3854/crm.5.000.checklist.v4.2011, http://www.iucn-tftsg.org/cbftt/.

Wang, B.-Y. & Qi, G.-Q. 2005. A procupine (Rodentia, Mammalia) from *Lufengpithecus* site, Lufeng, Yunnan. *Vertebrata PalAsiatica* **43**, 11–23.

Yasukawa, Y., Hirayama, R. & Kikida, T. 2001. Phylogenetic relationships of Geoemydine turtles (Reptilia: Bataguridae). *Current Herpetology* **20**, 105–33.

Yeh, H.-K. 1961. The first discovery of a box-turtle in China. *Vertebrata PalAsiatica* **3**, 58–64.

Yeh, H.-K. 1981. New fossil *Cuora* (Emydidae) from Early Pliocene of Yunnan. *Vertebrata PalAsiatica* **19**, 239–46.

Yeh, H.-K. 1983. New remains of *Cuora* from Zhejiang. *Vertebrata PalAsiatica* **21**: 49–53.

Yeh, H.-K. 1985*a*. Studies on fossils of *Cuora* of China and Japan. *Acta Hepetologica Sinica* **4**, 81–7.

Yeh, H.-K. 1985*b*. New materials of *Cuora pitheca* and its generic history. *Acta Anthropologiga Sinica* **6**, 113–17.

Yeh, H.-K. 1994*a*. Notes on a fossil *Cuora* (Testudines) from Tongshan, Anhui. *Vertebrata PalAsiatica* **32**, 66–8.

Yeh, H.-K. 1994*b*. *Fossil and Recent Turtles of China*. Beijing: Science Press.

Yeh, H.-K. & Zhang, J. 1994. Turtle remains from Jiahu site at Wuyang, Henan. *Acta Anthropologiga Sinica* **13**, 32–9.

Zhang, L., Nie, L. W., Cao, C. H. & Zhang, Y. 2008. The complete mitochondrial genome of the keeled box turtle *Pyxidea mouhotii* and phylogenetic analysis of major turtle groups. *Journal of Genetics and Genomics* **35**, 33–40.

Zhao, E. 1990. *Cuora zhoui*. In *A new Chinese box turtle (Testudinata: Emydidae) - Cuora zhoui* (eds E. Zhao, T. Zhou & P. Ye), pp. 213–16. In *From Water Onto Land* (ed. E. Zhao). Beijing: Chinese Society for the Study of Amphibians and Reptiles (in Chinese).

Zhou, T., Blanck, T., McCord, W. P. & Li, P.-P. 2008. Tracking *Cuora mccordi* Ernst, 1988: the first record of its natural habitat; a re-description; with data on captive populations and its vulnerability. *Hamadryad* **32**, 57–69.

Zhou, T. & Zhao, E. 2004. On the occurrence of living *Cuora yunnanensis* since fifty-eight years, and its description. *Sichuan Journal of Zoology* **23**, 325–6.

Appendix 1. Character definition

Characters

1. First vertebral scute:
   0. does not reach the second marginal scute
   1. polymorphic
   2. reaches the second marginal scute
2. Medial carapace carina extending on anterior neurals:
   0. absent
   1. absent in some individuals
   2. present
3. Lip on the visceral side of the hypoplastron:
   0. elevated
   1. flat
4. Lateral anal lip on the visceral side of the xiphiplastron:
   0. wide
   1. narrow
5. Fully divided anal scute:
   0. yes
   1. incomplete for some specimens
   2. no
6. Anal notch:
   0. deep
   1. small or deep
   2. small
   3. absent
7. Width to length ratio for the posterior plastral lobe (behind the hinge):
   0. wider than long
   1. wider than long or longer than wide
   2. longer than wide
8. Abdominal/anal midline length:
   0. abdominal longer than anal scute
   1. abdominal longer, equal, or shorter than anal scute
   2. abdominal shorter than anal scute
9. Abdomino-femoral sulcus:
   0. convex posteriorly
   1. polymorphic
   2. straight

10. Musk duct foramina enclosed in seventh peripheral plate:
    0. absent
    1. present
11. Ratio of anal/femoral midline length:
    0. less than 3
    1. more than 3
12. Contact between the tenth marginal scute and the fifth vertebral scute:
    0. absent
    1. present
13. Plastral hinge:
    0. absent
    1. present

Taxa/character matrix

Cuora chiangmuanensis	2010020201 101
Cuora pitheca	000000220? 001
Cuora miyatai	221103000? 101
Cuora amboinensis	0011031101 101
Cuora aurocapitata	2201022111 001
Cuora bourreti	00??23002? 001
Cuora flavomarginata	0211131110 101
Cuora galbinifrons	0011232101 001
Cuora mccordi	0200020111 011
Cuora mouhotii	0210000010 011
Cuora pani	2211011110 001
Cuora picturata	00??23002? 1?1
Cuora trifasciata	2200022010 001
Cuora yunnanensis	21??01202? 001
Cuora zhoui	2200000120 001
Mauremys	1210002021 000
Heosemys grandis	0200002001 000

Appendix VII

Neogene reptiles of northeastern Thailand and their palaeogeographical significance

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Original article

Neogene reptiles of northeastern Thailand and their paleogeographical significance

Les reptiles néogènes du nord-est de la Thaïlande et leur intérêt paléogéographique

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Abstract

In the last ten years, several fossil localities in Nakhon Ratchasima Province (northeastern Thailand) have yielded late Neogene turtle and crocodile taxa. Although not always well dated, the age of all these fossils is constrained between Middle Miocene and Pleistocene. Several crocodile taxa have been discovered: Crocodylidae, Alligatoridae and Gavialidae. In particular, the presence of *Gavialis* is attested in northeastern Thailand during the Pleistocene. Fossil turtles belong to several families: Geoemydidae, Testudinidae, and Trionychidae. In addition to the discovery of giant continental tortoises, some large aquatic trionychid and geoemydid turtles are present. The latter are only found in larger river systems and no longer encountered in the Mun or Chi Rivers of northeastern Thailand. Most fossil forms correspond to modern species and reveal interesting changes in biogeographical distribution patterns. These changes are likely related to changes in

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doi:10.1016/j.annpal.2011.08.002

the size of the drainage and direction of the Mun River system. We suggest that the Mun River was probably not flowing from west to east to the Mekong River system as today but that it was flowing from east to west to the Chao Phraya River system.

Keywords: Crocodiles; Turtles; Southeast Asia; Cenozoic; Paleohydrogeography

Résumé

Plusieurs localités fossilifères ont livré des restes de vertébrés néogènes dans la province de Nakhon Ratchasima ces dernières années. Ces sites, souvent mal datés, sont calés stratigraphiquement entre le Miocène moyen et le Pléistocène. Parmi les vertébrés mis au jour, on note la présence d'une faune intéressante de tortues et de crocodiles, comportant en particulier des gavialidés, des crocodilidés et des alligatoridés. La faune de tortues est représentée par les familles des géoémydidés, des testudinidés (avec en particulier des tortues géantes) et des trionychidés. La plupart des formes aquatiques retrouvées sont caractéristiques de grands cours d'eaux, et ne sont pas retrouvées aujourd'hui dans les rivières Mun et Chi qui sont les deux majeurs cours d'eau du Nord-est de la Thaïlande. Ces fossiles comparables aux formes actuelles suggèrent des modifications importantes des systèmes fluviaux de la région. La biogéographie de ces faunes soutient l'hypothèse que la rivière Mun coulait d'Est en Ouest vers la Chao Phraya.

Mots clés : Crocodiles ; Tortues ; Asie du Sud-est ; Cénozoïque ; Paléohydrogéographie

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1. Introduction

1.1. General context

Specific studies of Neogene reptiles from mainland Southeast Asia are extremely rare in the literature. The first mention is probably "*Geoclemys palaeannamitica*" from a Neolithic site of Vietnam (Bourret, 1941). This species was later referred to the genus "*Chinemys*" by Bour in 1980 (Bour, 1980). Although fossil remains of freshwater reptiles are not rare in the Cenozoic of mainland Southeast Asia, few of them were described in detail from the Paleogene (in Thailand, Claude et al., 2007; Martin and Lauprasert, 2010; in Myanmar, Hutchison et al., 2004), and even less have been described or mentioned from the Neogene (most records are from Thailand, see Tong et al., 2006 for an overview). Although little has been published about freshwater vertebrates; they can, however, contribute to test hypotheses concerning the complex hydrogeographic history of the area (Gregory, 1925; Hutchison, 1989). Indeed, most hypotheses regarding paleohydrogeography are inferred from geomorphological data and confronted to the distribution of living species and variation of molecular data (e.g. Attwood and Johnston, 2001; Meijaard and Groves, 2006), but rarely related to past organisms distribution known from fossils. In Thailand, turtles and crocodiles are known from Miocene localities in the north and in the northeastern parts of the country, but have not been studied in detail. Middle Miocene localities of northern Thailand have yielded freshwater geoemydids, trionychids, and testudinid tortoises, and alligatorids, which have been found in lacustrine environments. These faunas will be described in detail in a future study. By contrast to northern Thai localities, the geological context of northeastern Thailand is younger and clearly fluvial. This context can be very informative for understanding the late evolution of the hydrogeographic system in Southeast Asia via the use of freshwater fossil organisms. The purposes of this paper are to provide preliminary specimen descriptions and taxonomic lists for the northeastern localities in terms of reptile diversity and to discuss the hydrogeographic history of the Mun River, within the framework of hypotheses regarding its relationships with the Mekong and other river systems.

1.2. Abbreviations and collections

All fossils described in this paper are kept in the collections of the Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima, Thailand (RIN); and in the collections of the Department of Mineral Resources (DMR) in Bangkok, Khok Sung village (Nakhon Ratchasima Province), and Sirindhorn Museum, Sahat Sakhan (Kalasin Province).

1.3. Geographical context

The three localities having yielded Neogene reptiles in northeastern Thailand are located in Nakhon Ratchasima Province (Figs. 1 and 2), close to the Mun River. Today, the Mun originates in the Sankamphaeng range (or Sankambeng range) in Khao Yai National Park and flows northwards and then eastwards to join the Mekong River in Khong Chiam city in Ubon Rachatani Province (Fig. 1). The main tributary of the Mun is the Chi River (the longest Thai river), which runs north of the Mun River but carries less water.

1.4. Geological context

Fossils were usually found when digging reservoirs or during gravel and sand extraction, these activities being commonly undertaken in Neogene sediments in Nakhon Ratchasima Province (in contrast to the lower part of the Mun River). Neogene sediments in this region consist of layers of sand, conglomerate, or mud and were clearly deposited in a fluvial context. These sediments were accumulated and preserved around the present Mun River and overlie Cretaceous formations (Khok Kruat or Mahasarakham Formation in this area). Outcrops or pits are often temporary, superficial and pits become rapidly flooded. Moreover, lateral continuity of the sedimentary bodies is usually not well developed, precluding litho stratigraphic correlations between the various pits. It is also likely that a lot of material has been reworked in this sedimentological context. According to the amount of Neogene sediments, and the nature of conglomerates, it is not clear whether these sediments were deposited by the present-day Mun River (see the discussion). According to the mammal assemblages, the Neogene sediments around Nakhon Ratchasima are thought to have been deposited from the Middle or Late Miocene to the Pleistocene (Department of Mineral Resources, 2005; Hanta et al., 2008).

2. Tha Chang Area

Fossils have been found in the area of Tha Chang in Chaloem Pra Kiat district during excavation and mining in sand pits (Fig. 1) (Plate 1). In this area, the current day Mun River flows very close to the fossil beds (pits are dug on both sides of the river). Eight sand pits at least are said to have yielded fossil vertebrates in this area, especially elephant teeth (Hanta et al., 2008). The fossils are usually recovered during the extraction of sand from the walls of the pits with a high-pressure water jet. In this context, most of the fossils are collected by local villagers working in the sand pits. Few fossils are brought by villagers and kept in institutions

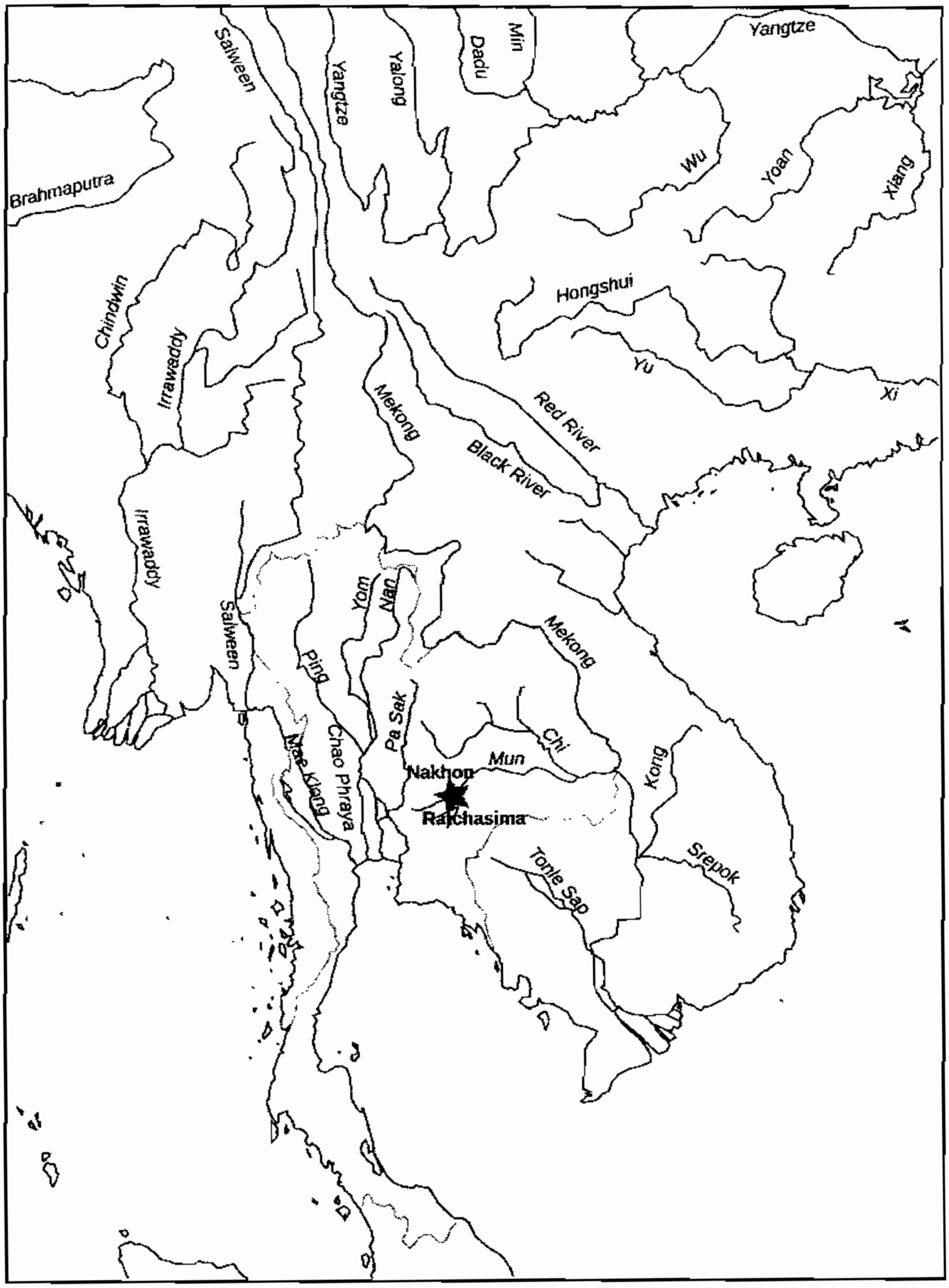

Fig. 1. **Hydrogeographical and geographic context.**
Contexte géographique et hydrogéographique.

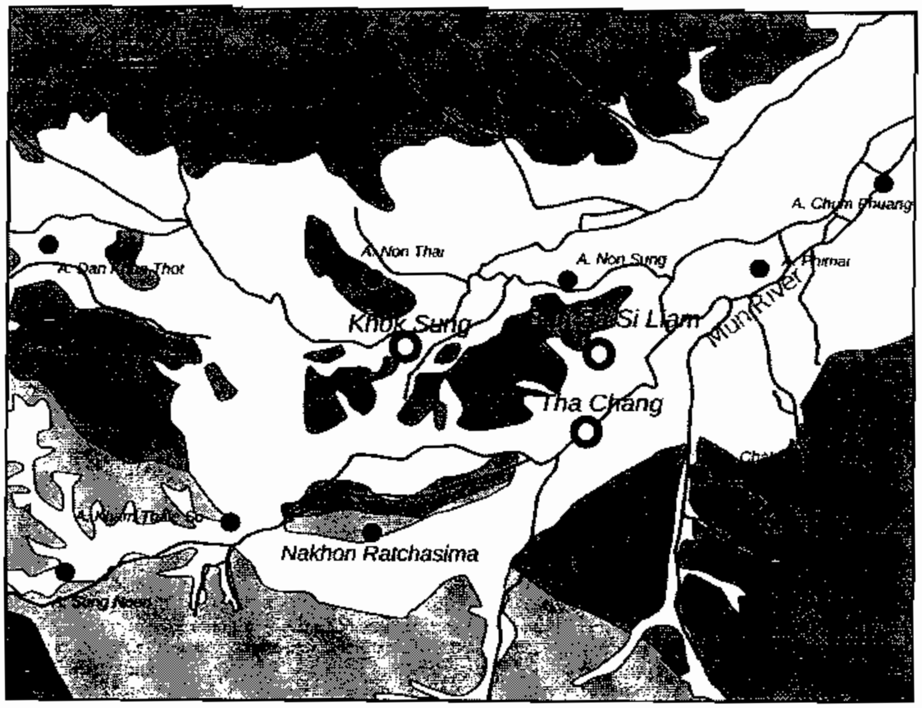

Fig. 2. Locations of Neogene fossil vertebrate sites in northeastern Thailand. Light grey: Khok Kruat Formation; dark gray: Mahasarakham formation; white: Neogene + Quaternary alluvial deposits.
Localités fossiles du Néogène de Thaïlande du Nord-est. Gris clair : Formation de Khok Kruat ; gris foncé : formation de Mahasarakham ; blanc : dépôts alluviaux néogènes et quaternaires.

since they tend to sell part of their discoveries to antique dealers and fossil collectors. Therefore, both the mode of extraction and the mode of collection do not allow to accurately position the fossils in the pits (or even to know from which pits come the fossils). Correlations between the pits are made difficult by the lack of sufficient lateral continuity in the fluvial context. One can, however, recognize one upper oxidizing unit (developed on few meters) and one lower reducing unit (up to 30 m in depth) in all pits. It is not clear whether these units can be considered as stratigraphic units or as pedological features related with the level of the water table. Few vertebrate fossils were collected *in situ* by scientists. Mammalogists think that there are at least three assemblages in the pits: a Middle Miocene, a Late Miocene and a Pleistocene assemblage (Hanta et al., 2008). The fossils belonging to the latter are found in a hard ferruginous matrix that characterizes the upper oxidizing unit of the sand pits while other fossils (the majority) are found in deeper levels that characterize a lower "reducing" unit. At least two sand pits have yielded fossil reptiles: the sand pit no. 8 or Somsak sand pit and the sand pit no. 9 or Siam sand pit.

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
?Megalochelys (Plate 1: A, B, C)

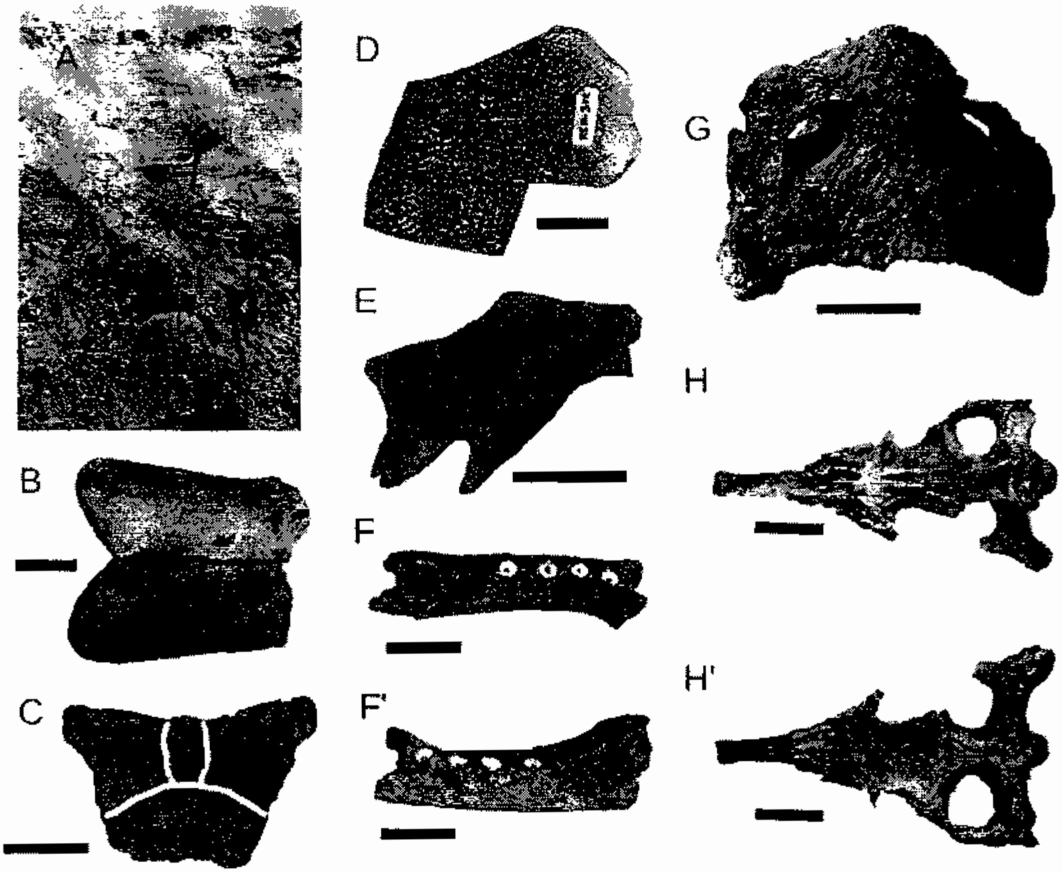

Plate 1. Locality and fossil reptiles of the area of Tha Chang. A. The Siam pit locality with the giant tortoise *in situ*. B. ?*Megalauchelys*: epiplastral process (RIN-862). C. ?*Megalauchelys*: nuchal plate (RIN-543). D. *Chitra* sp.: anterior associated costal bones (RIN-144). E. Trionychinae indet: hypoplastron (RIN-843). F. *Crocodylus* sp.: dentary bone in dorsal view (RIN-820). F'. Same specimen in labial view. G. *Crocodylus* sp.: skull table (RIN-5). H. *Gavialis* sp.: skull in dorsal view (RIN-112). H'. Same specimen in ventral view. All scale bars: 5 cm.

Localité et reptiles fossiles aux alentours de Tha Chang. A. Le puits « Siam » avec une tortue géante in situ. B. ?Megalauchelys : processus épiplastraux (RIN-862). C. ?Megalauchelys : plaque nucale (RIN-543). D. Chitra sp. : plaques costales antérieures en connexion (RIN-144). E. Trionychinae indet : hypoplastron (RIN-843). F. Crocodylus sp. : dentaire en vue dorsale (RIN-820). F'. Même spécimen en vue labiale. G. Crocodylus sp. : toit cranien (RIN-5). H. Gavialis sp. : crâne en vue dorsale (RIN-112). H'. Même spécimen en vue ventrale. Toutes les barres d'échelles représentent 5 cm.

Two giant tortoises were found *in situ* during the excavation of the Siam sand pit (Plate 1: A). This pit is now flooded. Unfortunately, the first specimen disappeared during the pit excavation, while the second collapsed during its extraction by the DMR. The latter was partially restored by the DMR at Phu Wiang Museum. The tortoises come from a sand layer some 13 m below the surface of the pit, below a more conglomeratic bed. The giant tortoises have therefore been collected below the upper oxidizing unit but above the lower levels having yielded fossil mammals in this pit (some 25 m below the surface). These tortoises were found below another horizon having yielded fossil mammals that is developed some 10 m below the surface (Chaimanee et al., 2005). If we believe that depth can be used for performing correlation, the giant tortoises are probably younger than one of the few fossil mammals found *in situ*: *Merycopotamus thachangensis* (Hanta et al., 2008) discovered in the closest sand pit (Somsak sand pit) and which could be Late Miocene in age. The two carapaces were approximatively 1.5 m in length. Isolated bony plates and bones of giant tortoises have also been found elsewhere in the area of Tha Chang, all coming from the lower reducing unit: they are therefore older than fossils of the more superficial Pleistocene, upper oxidizing unit. We tentatively associate isolated material with the shells discovered in Siam sand pit on the basis of their very large size. These specimens display characters of the testudinid family (alternative costal pattern, strong epiplastral process, presence of an anal notch) and belong to a giant tortoise lineage that was flourishing at this time in Asia. Large tortoises belonging to different species or morphotypes are known in the Pliocene and Pleistocene sediments of the Siwaliks (Lydekker, 1889). The best-known species of that group, *Megalochelys sivalensis* (Falconer and Cautley, 1837) is represented by several specimens in Pleistocene deposits of the Siwaliks in India and Pakistan, in Indonesia, and in Timor (Setiyabudi, 2009 for a review). In the Thai specimens, epiplastral processes are well developed but they are not forked, which is a different condition from that characterizes *Megalochelys sivalensis*.

Testudinoidea indet.

A few isolated, often fragmentary plates with smooth outer surface belong to turtles of smaller size (these specimens are kept in the Northeastern Research Institute of Petrified Wood and Mineral resources). This fragmentary material does not allow a precise assignment. While large fragments could be assigned to the adult giant Testudinidae, some smaller plates could belong either to smaller testudinids (possibly including juvenile forms of the giant specimens, but the different kinds of sulcus pattern suggest that more than one taxon is present) or to freshwater geoemydids.

Superfamily Trionychoidea Gray, 1825
Family Trionychidae Gray, 1825
Subfamily Trionychinae Gray, 1825
Genus *Chitra* Gray, 1844
Chitra sp. (Plate 1: D)

Several shell plates of trionychids have been collected in the pits, most of them, if not all, come from the lower reduced unit of the sand pits. Their vermiculated ornamentation is typical of Trionychidae. Large carapace plate fragments display an ornamentation different from that of *Amyda cartilaginea* (Boddaert, 1770) or *Rafetus swinhoei* (Gray, 1873) but reminiscent of *Chitra* or *Pelochelys*. The lateral undulation found on the partially associated first to third costals (RIN-144) is found in *Chitra* but not in *Pelochelys*. In addition, bony plates are rather thick as in *Chitra* by comparison with *Pelochelys*. Therefore we tentatively assign these large specimens to *Chitra*. Nowadays, *Chitra* inhabits permanent water bodies, in major rivers of India, western Pakistan, Myanmar, Sumatra, Java, peninsular Malaysia and the Chao Phraya river basin in Thailand.

Trionychinae indet. (Plate 1: E)

Some other turtles of the subfamily Trionychinae were present based on the variety of carapace ornamentations and because one of the plastral plates is different from those found in

Chitra. However, most plates (e.g., RIN-843) are too fragmentary to be diagnostic at the genus level.

Order Crocodilia Gmelin 1789
Family Crocodylidae Laurenti, 1768
Genus *Crocodylus* Laurenti, 1768
Crocodylus sp. (Plate 1: F, F', G)

Several jaw fragments pertaining to an indeterminate crocodylid taxon are housed in the collections of the Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima. Most of the material is uninformative but at least two specimens provide the following information. The anterior extremity of an articulated lower jaw preserves the first two alveoli and the anterior margin of the third alveolus. The completely preserved dentary symphysis extends at least to the level of the third alveolus and most probably to the level of the fourth. The splenial does not participate in the dentary symphysis and is not visible in this specimen. Another specimen (RIN 820) consists of a posterior portion of a left dentary, which shows the anterior extension of the splenial. This morphology is consistent with the observations made on the first specimen, indicating the exclusion of the splenial from the symphysis. Here, the splenial extends anteriorly to the level of the seventh alveolus. Four other specimens (a right surangular + articular; a right posterior portion of a dentary; a left portion of surangular + dentary and a fragmentary maxilla) are too fragmentary to be informative but the relatively large size of all the referred material and the pattern of ornamentation with large pits on the external surface of the bone indicate that they most probably belong to the same taxon. To sum up, the present combination of a fourth enlarged dentary alveolus, the exclusion of the splenial from the symphysis and the short length of the symphysis are indicative of the presence of *Crocodylus* sp.

A partial posterior part of crocodilian skull (RIN-5) is embedded in a hard conglomeratic oxidized matrix that is found in the upper section of the sand pit. It requires further preparation but allows some observations. The posterior skull table exhibits two supratemporal fenestrae of moderate size. The skull table is broader than long. The sutural organization around the orbitotemporal foramen is the same as in *Crocodylus*.

Although it is nearly extinct in Thailand, *Crocodylus siamensis* was rather common in the Chao Phraya basin, central and southern Thailand and in the lower Mekong River during the 19th and early 20th centuries (Smith, 1931; Simpson and Bezuijen, 2010), and was widespread all the way to Indonesia during the Pleistocene (Delfino and De Vos, 2010). It may have been present also in northeastern Thailand since the species is still found in Laos in Savannakhet Province, and is known from Iron age sites in Cambodia (O'Reilly et al., 2006; Voen, 2008). Further studies and discoveries are needed to check the relationships between the fossil and living species.

Family Gavialidae Adams, 1854
Genus *Gavialis* Oppel, 1811
Gavialis sp. (Plate 1: H, H')

Several gavialid remains have been discovered in the sand pits of the Tha Chang area. According to the matrix, gavialid specimens are found in the reduced lower unit. Usually these remains correspond to part of the rostrum or parts of the lower jaw or posterior skull tables. These specimens are overall similar to the living species or to the Pleistocene *Gavialis bengawanicus* Dubois, 1908 from Java in that they have a rather rounded temporal fenestra by comparison with the living species, *Gavialis gangeticus*. However, a more complete specimen (RIN-112) corresponds to a partial skull and shows rather long palatine fenestrae as in the Pliocene *Gavialis browni* Mook, 1932 from the lower middle Siwaliks of northern Pakistan (Nathot locality). It differs, however, from that species by its broader frontal and more widely spaced orbits -as do modern gavials-. The Asian genus *Gavialis* has a good fossil record in Pakistan, India and Nepal, especially in the Siwaliks area where several species have been described (Lull, 1944; Piras and Kotsakis, 2005). It is also represented by the Early Pleistocene species *G. bengawanicus* Dubois, 1908 in Java. The recent species had a much larger geographical range in historical times, some authors citing eastern occurrences in northern Myanmar at the beginning of the 20th century (Smith, 1931).

3. Khok Sung locality

During 2005, several vertebrate fossils were discovered during gravel extraction near the village of Khok Sung. The specimens were found in a sandy to conglomeratic level that was rather rich in organic matter (Plate 2, A). The material is displayed in a local museum in Khok Sung village. Mammals are represented by bovids, hyaena, *Stegodon*, and deer (Department of Mineral Resources, 2005), while fishes are represented predominantly by large silurids (JC, personal observations). Fossil plants have been studied by Grote, 2007. The site is 15 km north of Nakhon Ratchasima city, close to the 205 Highway. The locality is now flooded, covered by sediments and no longer accessible.

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Geoemydidae Theobald, 1868
Genus *Batagur* Gray, 1855
Batagur cf. *trivittata* (Duméril and Bibron, 1835) (Plate 2: G, H, I)

Several adult shells of medium size (40–50 cm) display very strong axillary and inguinal buttresses (DMR-KS0305-24-1), short epiplastral lips, rather short gulars (DMR-KS05-03-2446, DMR-KS0503-15-4), a humero-pectoral sulcus far behind the entoplastron (DMR-KS05-03-24-46) and quadrangular vertebral scutes (DMR-KS0305-24-1). This morphology is found in highly aquatic geoemydids belonging to the *Batagur-Pangshura-Morenia-Hardella* clade. Some specimens (DMR-KS05-03-16-01) exhibit carapace or plastron bone ankylosis (disappearance of sutures) as do adults of the species *Batagur borneoensis* (Schlegel and Müller, 1844), *Batagur baska* (Gray, 1831), *Batagur trivittata* (Duméril and Bibron, 1835) and *Batagur affinis* (Cantor, 1847), and more occasionally large individuals of *Batagur kachuga* (Gray, 1831). The overall shape of the shell is very similar to that of *B. borneoensis, B. trivittata, B. affinis,* and *B. baska*. All these species have rather similar shells. The rather elevated shell, the vertebral pattern with the posteriorly slightly constricted third vertebral, the elongated fourth vertebral scute, and the presence of persistent rounded lateral fontanelles (as in DMR-KS0305-24-1) allow, however, to refer the fossils from Khok Sung either to *B. borneoensis* or to *B. trivittata*. In addition, as seen in DMRKS0305-24-1, the posterior end of the fifth vertebral scute is more constricted than in *B. baska* or *B. affinis* and only contacts the eleventh and twelfth marginal scutes, as in *B. borneoensis* or in *B. trivittata*. *B. borneoensis* and *B. trivittata* are phylogenetically very close (Praschag et al., 2009) and have very similar skeletons. No characters allow to distinguish the fossil specimens from these species. Nowadays, *B. borneoensis* is found in estuaries and

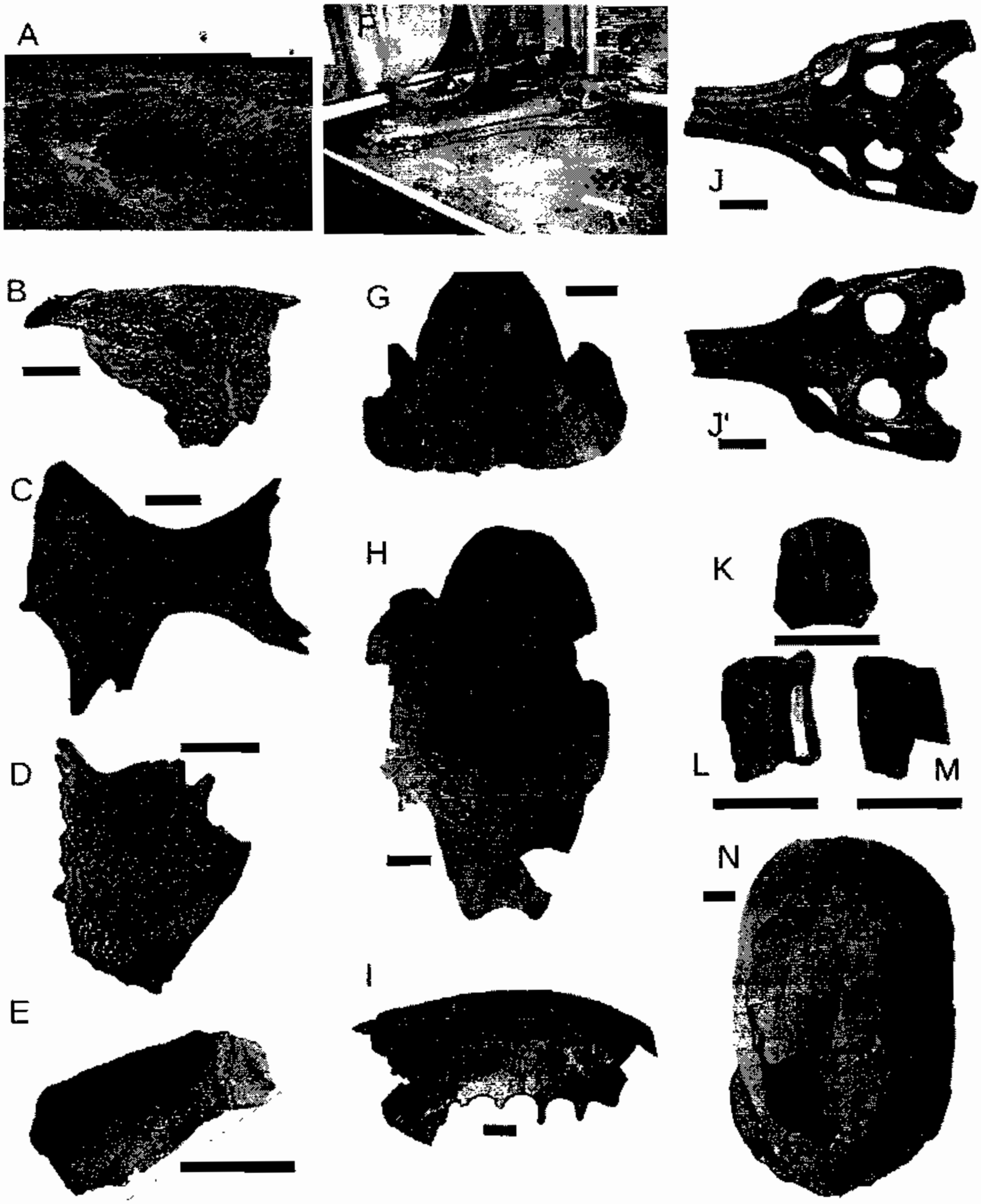

Plate 2. Locality and fossil reptiles of Khok Sung. A. The locality when it was exploited in 2005. B. *Chitra* sp.: anterior carapace (DMR-KS0506-22-2). C. cf. *Amyda* sp.: associated hyo- and hypoplastron (DMR-KS0503-3111 and DMR-KS0503-3112). D. cf. *Amyda* sp.: xiphiplastron (DMR-KS0503-2645). E. *Malayemys* sp.: fifth costal plate (DMR-KS201102-1). F. *Gavialis* sp.: skull and jaw as exhibited in the Khok Sung Museum. G. *Batagur* cf. *trivittata*: anterior plastral lobe (DMR-KS0503-2446). H. *Batagur* cf. *trivittata*: plastron showing strong ankylosis between plates (DMR-KS0503-16-1). I. *Batagur* cf. *trivittata*: carapace in lateral view showing the developpement of lateral fontanelles (DMR-KS0503-24-1). J. *Gavialis* sp.: skull in dorsal view (DMR-KS-0503-25-23). J'. Same specimen than J in ventral

mangroves in southern Thailand, Brunei, peninsular Malaysia and Indonesia (Sumatra), while its closest relative, *B. trivittata* lives in the Irrawady delta, and upstream of the delta in large water bodies of the Irrawady and Salween River systems (Praschag et al., 2009). Based on the ecology of the overall fauna (no clear marine influence), we tentatively refer the fossils from Khok Sung to *B. trivittata*.

Genus *Heosemys* Stejneger, 1902

Heosemys annandalii (Boulenger, 1903) (Plate 2: N)

Several complete shells (DMR-KS201102-05) of large size (up to 50 cm), display neurals with shorter posterior sides, a discontinuous central carina, a large anal notch and wide anterior plastral lobes. The posterior margin is undulated to smooth. These turtles can be assigned to the species *Heosemys annandalii* (formerly *Hieremys annandalii*). *Heosemys annandalii* inhabits permanent water bodies in swamps and rivers in central, southern, and eastern Thailand, in peninsular Malaysia, in the South of Cambodia, and in the South of Vietnam.

Heosemys cf. *grandis* (Gray, 1860) (Plate 2: K, L, M)

A few neural plates (DMR-KS201102-2) with a strong carina and some posterior peripheral plates (DMR-KS201102-3 and DMR-KS201102-4) exhibiting well-developed serrations indicate that another large geoemydid turtle was present. A nuchal plate does not show the special visceral indentation that is found in *Heosemys annandalii*. According to the size and shape, these plates could belong to the species *Heosemys grandis*. *Heosemys grandis* inhabits swamps and rivers in central, western, eastern and southern Thailand, southern Myanmar, southern Cambodia, and southern Vietnam.

Genus *Malayemys* Lindholm, 1931

Malayemys sp. (Plate 2: E)

A tricarinate turtle is present and is attested by the presence of a fifth costal plate (DMR-KS201102-1). Internally, it shows a rather well-developed scar for the inguinal buttress insertion (which also articulates with the sixth costal plate). The intervertebral sulcus is posterior on this plate. This fossil belongs to the genus *Malayemys* because the lateral carina is extremely pronounced and forms a strong knob. Two species are known in *Malayemys* (Brophy, 2004); however, skeletal differences between these species have not been described precluding a more

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Plate 2. view. K. *Heosemys grandis*: neural plate (DMR-KS201102-2). L. *Heosemys grandis*: posterior peripheral plate (DMR-KS201102-3). M. *Heosemys grandis*: posterior peripheral plate (DMR-KS201102-4). N. *Heosemys annandalii*: Carapace in dorsal view (DMR-KS201102-5). All scale bars: 5 cm.

Localité et reptiles fossiles de Khok Sung. A. La localité lorsqu'elle a été exploitée en 2005. B. Chitra sp.. carapace antérieure (DMR-KS0506-22-2). C. cf. Amyda sp. : hyoplastron et hypoplastron en connexion anatomique (DMR-KS0503-3111 and DMR-KS0503-3112). D. cf. Amyda sp. : xiphiplastron (DMR-KS0503-2645). E. Malayemys sp. : cinquième plaque costale (DMR-KS201102-1). F. Gavialis sp. : crâne et mandibule tels qu'ils sont présentés dans le musée local de Khok Sung. G. Batagur cf. trivittata : lobe plastral antérieur (DMR-KS0503-2446). H. Batagur cf. trivittata : plastron présentant une forte ankylose entre les plaques osseuses (DMR-KS0503-16-1). I. Batagur cf. trivittata : carapace en vue latérale montrant le développement des fontanelles latérales (DMR-KS0503-24-1). J. Gavialis sp. : crâne en vue dorsale (DMR-KS-0503-25-23). J'. Même spécimen en vue ventrale. K. Heosemys grandis : plaque neurale (DMR-KS201102-2). L. Heosemys grandis : plaque périphérique postérieure (DMR-KS201102-3). M. Heosemys grandis : plaque postérieure périphérique (DMR-KS201102-4). N. Heosemys annandalii : Carapace en vue dorsale (DMR-KS201102-5). Toutes les barres d'échelles représentent 5 cm.

precise determination. *Malayemys* is a common turtle found in rivers and swamps in mainland Southeast Asia and Indonesia.

Superfamily Trionychoidea Gray, 1825
Family Trionychidae Gray, 1825
Subfamily Trionychinae Gray, 1825
Genus *Chitra* Gray, 1844
Chitra sp. (Plate 2: B)

Articulated nuchal, first costal and first neural plates of large size (DMR KS0506-22-2) are very similar to *Chitra* in both the ornamentation and the morphology of plates (e.g. first neural with lateral sides that are convergent anteriorly). The bony carapace would have reached around 50 cm in length, which corresponds to a large individual. Several plates of Trionychinae of large size could also belong to this genus but their taxonomic assignment is more uncertain because they are not diagnostic at the generic level.

Genus *Amyda* Geoffroy Saint-Hilaire, 1809
cf. *Amyda* sp. (Plate 2: C, D)

A partial plastron consisting of the hypo- and hyoplastron (DMRKS0305-31-11, DMRKS0305-31-12, DMRKS0305-31-13) shows strong notches and well-developed callosities as seen as in *Amyda*. A triangular xiphiplastron (DMR KS05032645) is also similar to those found in large individuals of this genus. The size was large (estimated plastral width: 40 cm), and is among the largest individuals in the size range known for the only living species of that genus. *Amyda* is a monotypic genus living in permanent bodies of water (rivers, lakes) of Thailand, Myanmar, Bengladesh, Brunei, Laos, Vietnam, Singapore, Cambodia, Malaysia and Indonesia.

Order Crocodilia Gmelin, 1789
Family Gavialidae Adams, 1854
Genus *Gavialis* Oppel, 1811
Gavialis sp. (Plate 2: F, J, J')

Several osteoderms, cranial and postcranial remains belong to the genus *Gavialis*. The skulls are easily recognized by their very long and narrow rostrum, dilated at the anterior end. The nasal bones are short relative to the rostrum and do not reach the premaxillae. Twenty-five or 26 teeth are present on the upper jaw (21 or 22 maxillary teeth), while 21 or 22 teeth were present on the dentary. In large specimens (DMR-KS0503-2523), the orbital rim is raised, and the lateral rim of the maxilla exhibits clear festooning. As in the living species, the orbits are widely spaced by comparison with fossil forms such as *G. browni* Mook, 1932. The rostrum is narrow as in the living species and *G. bengawanicus* and different from the Neogene species from Pakistan (*Gavialis breviceps* Pilgrim, 1912, *Gavialis curvirostris*, Pilgrim, 1912). The specimens show several similarities with *G. bengawanicus* Dubois, 2008 from the Pleistocene of Java (number of dentary teeth, rounded shape of temporal fenestra) and similarities with the living species (maxilla with festooning, relatively high number of maxillary teeth). In later publications, we will perform further comparisons to find out whether this intermediary condition corresponds to an underestimation of possible intraspecific variation in *Gavialis gangeticus* or whether it really represents an intermediary form between the two species. However, by its geographical position, the Thai taxon might possibly be considered as the missing (geographical or evolutionary) link between the Indian and Indonesian specimens.

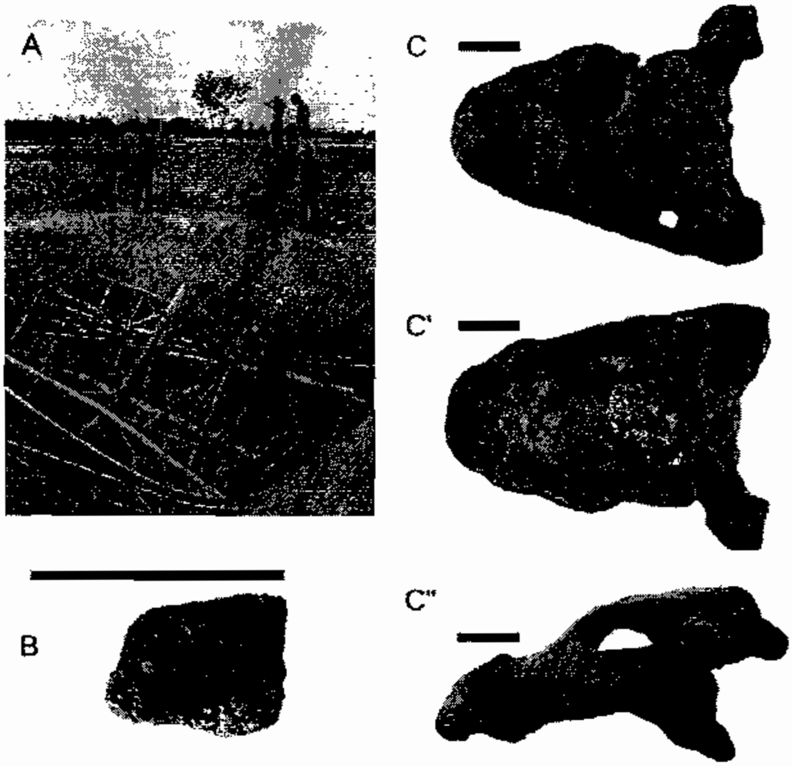

Plate 3. Locality and fossil reptiles of Ban Si Liam. A. The locality. B. Turtle carapace plate fragment (DMR-BSL2011-1). C. *Alligator* cf. *sinensis*: skull in dorsal view (DMR-BSL2011-2). C'. Same specimen: ventral view. C''. Same specimen: lateral view. All scale bars: 5 cm.

Localité et reptiles fossiles de Ban Si Liam. A. La localité. B. Fragment de plaque de tortue (DMR-BSL2011-1). C. Alligator cf. sinensis : crâne en vue dorsale (DMR-BSL2011-2). C'. Même spécimen en vue ventrale. C''. Même spécimen en vue latérale. Toutes les barres d'échelles représentent 5 cm.

4. Ban Si Liam locality

The Ban Si Liam locality, Mai Subdistrict, Non Sung district was discovered by villagers in 2005 while they were excavating a reservoir in the region of Non Sung. The fossils were found in a sandy level some 5 m below the surface (Plate 3, A). Several vertebrates were discovered in the locality. The mammalian fauna is at least represented by a suid and a giraffid. These faunal elements have not been studied in detail but do not seem to give good age constraints for the locality. On the basis of the presence of Giraffidae, the locality is believed to be Late Miocene to Pleistocene. The fact that crocodile material can be attributed to a living species suggests that the locality is relatively recent.

Order Testudines Linnaeus, 1758
Superfamily Testudinoidea Batsch, 1788
Testudinoidea indet. (Plate 3: B)

A few isolated fragments of plastral plates (DMR-BSL2011-1) with a smooth outer surface likely belong to terrestrial testudinids or aquatic geoemydids. The plates do not allow a more precise taxonomic assignment.

Order Crocodilia Gmelin 1789
Family Alligatoridae Gray, 1844
Genus *Alligator* Cuvier, 1807
Alligator cf. *sinensis* Fauvel, 1879 (Plate 3: C-C")

A complete skull of a short-snouted crocodilian (DMR-BSL2011-2) is preserved and requires further preparation as no sutures can be observed yet. The skull is about 25 cm long, robust, and very short. Additionally, the U-shaped outline of the upper jaw suggests that it can be referred to the family Alligatoridae. The posterior skull margin is straight and the distance from the posterior margin of the skull table to the upper temporal fenestra is rather long. The skull table is broad, and wider than long. There is a well-developed internarial bar. All these characters can be found in *Alligator sinensis*. A 25 cm long skull would correspond to a rather large specimen for this species (between 2 and 3 m). Nowadays *A. sinensis* is restricted to scattered places on the lower Yangtze river. However, historical records for that species show that it had a much larger distribution in the past (Thorbjarnarson et al., 2002). Few other species of alligatorids are reported from the Neogene of Eastern and Southern Asia (Taplin and Grigg, 1989).

5. Discussion

5.1. The large Neogene tortoises

The presence of large tortoises in Thailand during the late Neogene is not surprising since giant tortoises are known in the Siwalik beds of India and Pakistan, in Timor and in Indonesia. Special attention should be paid in the future to the stratigraphy and the taxonomy of these giant tortoises. During the Neogene, it is clear that giant tortoises were widespread inland (especially at the end of the the Plio-Pleistocene). They are known in several places in Europe during the Pliocene, and also in Asia from the late Neogene of Pakistan and India, the Early Pleistocene of Indonesia (Java, Sulawesi, Flores) and Timor, the late Neogene of Myanmar, and now in Thailand. In historical times or today, giant tortoises of different lineages are known from several islands (Aldabra, Mauritius, Réunion, Galapagos, and Madagascar). Gigantism in tortoises has long been presented in textbooks as resulting from insular conditions; however, the presence of giant tortoises inland demonstrates that insular conditions are not necessary for tortoises to reach a very large size. Because giant tortoises are known geologically rather late in South and Southeast Asia, the age of the beds having yielded the giant tortoise in Thailand is probably Pliocene or Pleistocene.

5.2. The middle Pleistocene large aquatic turtles and gavialids

The presence of large aquatic turtles and gavialid crocodilians in the Middle Pleistocene of northeastern Thailand contrasts very much with the present herpetological diversity of the Mun River in Nakhon Ratchasima Province. Nowadays, in this upper part of the stream, turtles consist of *Malayemys*, possibly some other small taxa such as *Cyclemys* or/and *Cuora amboinensis*, and the moderately large *Amyda cartilaginea* softshell turtle. Large turtles inhabiting estuarine or large fluvial systems are absent. This is probably because the Mun River near Nakhon Ratchasima Province is too small a river today to host large forms found in Neogene sediments (*Chitra*, *Hieremys*, *Batagur*). It is, however, unlikely that the upper part of that stream was developed as an estuary if the Mun River took its source at the same place as today. Moreover, the large aquatic fossil turtles found in Nakhon Ratchasima are also absent today in northeastern Thailand and in the Thai and Lao section of the Mekong Basin. They inhabit, however, the Chao Phraya River system, and are present in the southern large river systems of mainland Southeast Asia and Indonesia. As to *Gavialis*, this taxon is known to occur or to have occurred in India, Nepal, Myanmar in historical times and in Indonesia in the Pleistocene. Thailand was probably one necessary route for *Gavialis* to disperse into Indonesia. This "bridge" can also explain why today *B. borneoensis* is found in southern Indochina without geographical connection with its closest relative *B. trivittata*, which is found only in the Irrawady and Salween river systems. As for *Gavialis*, the *Batagur* from Khok Sung can be considered as a biogeographical missing link between northwestern Indochina and Indonesia. Surprisingly none of these species are known in the lower Mekong basin, and no exclusive species of the lower Mekong Basin are present in the Pleistocene deposits of Nakhon Ratchasima Province. We propose that at the time of the deposition of the Khok Sung sediments, rather than flowing from west to east toward the Mekong River, the Mun River was flowing from east to southwest in the direction of the Chao Phraya system (Fig. 3). This could explain the Pleistocene or earlier presence in the Mun River of "western" freshwater reptiles such as *Gavialis*, *Batagur*, or *Chitra*. This scenario could also explain the large amount of Neogene sediments in this area by contrast with the eastern section of the river (i.e., closer to the current day Mekong). Since the Nakhon Ratchasima area would not correspond at that time to the upper Mun River, the accumulation of sediments could be more considerable by comparison with what it is today in the upper part of the stream (today the Mun is principally eroding the Khorat Plateau, and not depositing sediments). Since it was larger and closer to the seashore in terms of river length to the ocean, the Mun River could have been hosting larger freshwater reptiles. At that time and place, some reptile species such as *B. trivittata* could keep gene flows with populations of the Irrawady river sysem, and southern peninsular populations that later differentiated into *B. borneoensis*. Because we find the closest sister groups of Southeast Asian *Chitra*, *Gavialis*, and *Batagur* in the Ganges/Brahmaputra river systems, India can probably be considered as the origin of Southeast Asian populations and species. Therefore one must consider that the populations from Myanmar were also once connected to Indian populations with a connection between the Irrawady/Salween river basin and the Ganges/Brahmaputra river systems (Fig. 3), either rather upstream at the level of the Ping river, or downstream between the Salween and Mae Khlong river systems (Fig. 3). Part of these hypotheses were also presented to explain the biogeography of gastropods by Atwood et al. (2001), and have also been considered to explain vertebrate biogeography (Meijaard and Groves, 2006).

5.3. The presence of Alligator sinensis

The only alligator species present in Asia today has a northern distribution by comparison with other crocodiles, which are predominantly found in more southern areas. The presence of alligatorids in the Neogene deposits of northeastern Thailand is unexpected and requires an explanation. Furthermore, even if we have no clear evidence of co-occurrence with *Gavialis*, this possibility is extremely unusual and possibly unique. It should be reminded that the geographical distribution of *A. sinensis* was much larger in the past and that human activities have considerably restricted the range of this species. The specimen from Ban Si Liam shows that northeastern Thailand was once part of the range of *Alligator*. It is also possible that the Chao Phraya river system was draining the upper parts of the Mekong River and possibly Yangtze River basins where the species may have been present (Fig. 3). However, it is unlikely that the species was found in mountainous areas (even though it can survive during cold weather in winter). It is likely

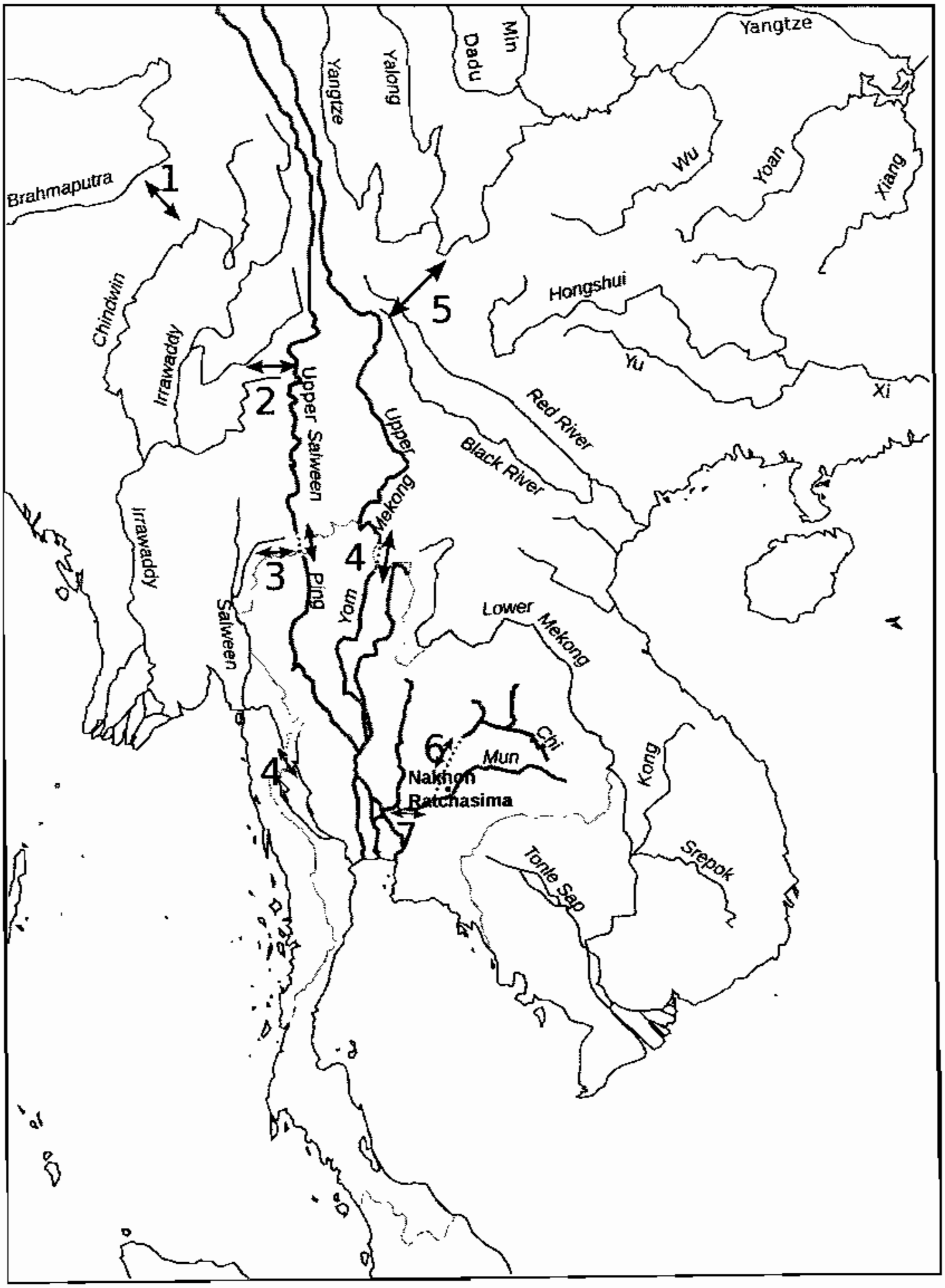
Yangtze
Min
Dadu
Yalong
Yangtze
Brahmaputra
1
Wu
Yoan
Xiang
Chindwin
Irrawaddy
Hongshui
5
2
Upper Salween
Upper Mekong
Yu
Xi
Red River
Black River
Irrawaddy
3
Ping
4
Yom
Salween
Lower Mekong
Chi
6
Mun
Nakhon Ratchasima
4
7
Kong
Tonle Sap
Srepok

Fig. 3.

that *Alligator* populations also extended to the Red and Black river systems, therefore offering a possible continuity with northeastern Thailand.

5.4. Paleohydrogeography

It has been proposed for a long time that the hydrogeographical history of the Chao Phraya and Mun Rivers was connected to the history of the Mekong and possibly of the Yangtze and Salween Rivers (Gregory, 1925; Hutchison, 1989), and this is also supported by the fossil data presented here (Fig. 3). Some interesting scenarios have been proposed to explain the distribution of gastropods in the lower Mekong basin (Attwood and Johnston, 2001), and seem to be accepted by the scientific community (e.g., Meijaard and Groves, 2006; Sterling et al., 2006). However, few palaeontological data document this hydrogeographical history. The freshwater reptilian fauna of northeastern Thailand seems to shed interesting light on the past hydrogeography of mainland Southeast Asia and China. Thailand has been a possible place of exchanges between Indian and Southeast Asian faunas (e.g., *Gavialis*, *Batagur*) but also between Southeast Asian fauna and Eastern Asia (e.g., *A. sinensis*). Further sedimentological analyses could be very interesting to test our hypotheses and provide a chronology. If the above-mentioned hypotheses are correct, one would expect to find in the Pleistocene and pre-Pleistocene deposits of the Chao Phraya basin sediments coming from both the rivers of northeastern Thailand, and from the upper Mekong (and possibly Salween and Yangtze) River.

5.5. The Age of the Deposits

In our study, most reptilian faunas do not show clear evidence of typical Miocene taxa in the area. Rather, most taxa are likely Pliocene or Pleistocene (cf. the giant tortoise, gavialids, and the absence of ancient forms for the other species). Because it could allow correlation with marine sediments, a stratigraphical and sedimentological analysis of deltaic sediments of the Chao Phraya River could be very interesting to provide further correlations and attest or not the presence of Miocene rocks in northeastern Thailand. Overall the fauna is very similar in taxonomic content to early Pleistocene fauna from Java where gavials, giant tortoises, large freshwater turtles are present (Jaekel, 1911; Janensch, 1911). Most fossils of Miocene mammals have not been found *in situ* and are often fragmentary (e.g., isolated elephant teeth, primate jaws, and other remains), and it is possible that this material is reworked and that most of the deposition was Pleistocene in age. This would indicate that the hydrogeographical system in northeastern Thailand got its present configuration recently.

Fig. 3. Putative changes in hydrogeography during the Neogene. Black dotted lines correspond to possible river capture, double arrows to faunal interchange during the Neogene; 1: between Gange/Brahmaputra and Irrawady; 2: between Irrawady and Salween river systems; 3: between the Salween and Chao Phraya river systems; 4: between the Chao Phraya and Upper Mekong river systems; 5: between the Mekong and Yangtze river systems; 6: between the Chi river systems and the Mun and Chao Phraya river systems; 7: between the Mun and the Chao Phraya river system. The possible former Mekong River is represented in grey dashed lines.

Changements possibles de l'hydrogéographie au cours du Néogène. Les lignes noires pointillées correspondent à de possibles captures de rivières, les flèches doubles aux échanges fauniques durant le Néogène ; 1 : entre le Gange/Brahmaputr et les fleuves Irrawady et Salween river systems ; 2 : entre la Salween et l'Irrawady ; 3 : entre la Chao Phraya et le Salween ; 4 : entre la Chao Phraya et le haut Mékong ; 5 : entre le Mékong et le Yangtze ; 6 : entre la Chi et le système Mun-Mékong ; 7 : entre la Mun et la Chao Phraya. Le cours ancien possible du Mékong est représentée en ligne pointillée grise.

Acknowledgements

This publication was sponsored by the PHC Evolution of aquatic vertebrate biodiversity in Thailand through the past to the present (2007–2008). We thank Yupa Thasod for providing information concerning specimens kept in RIN.

References

Attwood, S.W., Johnston, D.A., 2001. Nucleotide sequence differences reveal genetic variation in *Neotricula aperta* (Gastropoda: Pomatiopsidae), the snail host of schistosomiasis in the Lower Mekong Basin. Biological Journal of the Linnean Society 73, 23–41.

Brophy, T.R., 2004. Geographic variation and systematics in the south-east Asian turtles of the genus *Malayemys* (Testudines: Bataguridae). Hamadryad 29, 63–79.

Bour, R., 1980. Position systématique de Geoclemys palaeannamitica Bourret, 1941 (Reptilia-Testudines-Emydidae). Amphibia-Reptilia 1, 149–159.

Bourret, R., 1941. Les tortues de l'Indochine. Notes Inst. Oceanographique de l'Indochine. Stn. Marit. Cauda, Nhatrang. p. 235.

Chaimanee, Y., Yamee, C., Tian, P., Khaowiset, K., 2005. Biodiversity of ancient elephants in Nakhon Ratchasima Province (2nd. ed). Academic report no. DMR 21/2003. Thailand Deparment of Mineral Resources, p.75, (In Thai).

Claude, J., Suteethorn, V., Tong, H., 2007. Turtles from the Late Eocene-Early Oligocene of the Krabi Basin (Thailand). Bulletin de Société Geologique de France 178 (4). 305–316.

Delfino, M., De Vos, J., 2010. A revision of Dubois crocodylians, *Gavialis bengawanicus* and *Crocodylus ossifragus*, from the Pleistocene *Homo erectus* beds of Java. Journal of Vertebrate Paleontology 30 (2), 427–441.

Department of Mineral Resources, 2005. Biodiversity and palaeoenvironments of caenozoic of northeastern Thailand in Her Majesty the Queen and the conservation on natural resources and environments. Monre Special Publication, pp. 10-11.

Gregory, J.W, 1925. The evolution of the river system of southeastern Asia. Scottish Geographical Journal 41, 129–141.

Grote, P., 2007. Studies of fruits and seeds from the Pleistocene of northeastern Thailand. Courier Forschunginstitut Senckenberg 258, 171–181.

Hanta, R., Ratanasthiena, B., Kunimatsub, Y., Saegusa, C.H., Nakaya, D.H., Nagaoka, E.S., et al., 2008. A new species of Bothriodontinae, *Merycopotamus thachangensis* (Cetartiodactyla, Anthracotheriidae) from the Late Miocene of Nakhon Ratchasima, North-eastern Thailand. Journal of Vertebrate Paleontology 28 (4), 1182–1188.

Hutchison, C.S., 1989. Geological Evolution of Southeast Asia. Oxford Science Publications.

Hutchison, J.H., Holroyd, P.A., Ciochon, R.L., 2004. A preliminary report on Southeast Asia's oldest Cenozoic turtle fauna from the Late Middle Eocene Pondaung formation. Myanmar Asiatic Herpetological Research 10, 38–52.

Jaekel, O., 1911. Die fossilen Schildkröten reste von Trinil. Plate XIV, XV in Die *Pithecantropus*-Schichten auf Java. In: Selenka, L., Blackenbraum, M. (Eds.). Geologische und Paläontologishche Ergenbisse der Trinil Expedition (1907 und 1908). Verlag von Wilhelm Engelmann, Leipzig, pp. 75–81.

Janensch, W., 1911. In: Selenka, L., Blackenbraum, M. (Eds.), Die Reptilienreste (exkl. Schildkröten). Plate XII, XIII in Die *Pithecantropus*-Schichten auf Java. Geologische und Paläontologishche Ergenbisse der Trinil Expedition (1907 und 1908). Verlag von Wilhelm Engelmann, Leipzig, pp. 61–74.

Lull, R.S., 1944. Fossil gavials from India. American Journal of Science 242, 417–430.

Lydekker, R., 1889. On the land tortoises of the Siwaliks. Records of Geological Survey of India 22. 209–212.

Martin, J.A., Lauprasert, K., 2010. A new primitive alligatorine from the Eocene of Thailand: relevance of Asiatic members to the radiation of the group. Zoological Journal of the Linnean Society 158 (3), 608–628.

Meijaard, E., Groves, C., 2006. The geography of mammals and rivers in mainland Southeast Asia. In: Lehmann, S.M., Fleagle, J.G. (Eds.), Primate biogeography: progress and prospects. Springer, New York, pp. 305–329.

O'Reilly, O., Von den Driesch, A., Voeun, V., 2006. Archaeology and archaeozoology of Phum Snay: a late prehistoric cemetery in North-western Cambodia. Asian Perspectives 45 (2), 188–211.

Piras, P., Kotsakis, T., 2005. A new gavialid from the Early Miocene of southeastern Pakistan (Preliminary Report). Rendiconti Societa Paleontologica Italiana 2, 201–207.

Praschag, P., Holloway, R., Georges, A., Päkert, M., Hundsdörfer, A., Fritz, U., 2009. A new subspecies of *Batagur affinis* (Cantor 1847), one of the world's most critically endangered chelonian (Testudines, Geoemydidae). Zootaxa 2233, 57–68.

Setiyabudi, E., 2009. An early Pleistocene giant tortoise (Reptilia; Testudines; Testudinidae) from the Bumiayu area, Central Java, Indonesia. Journal of Fossil Research 42 (1), 1–11.

Simpson, B.K., Bezuijen, M.R., 2010. Siamese crocodile *Crocodylus siamensis*. In: Manolis, S.C., Stevenson, C. (Eds.). Crocodiles. Status survey and conservation action pla, Third Edition. Crocodile Specialist Group, Darwin, pp. 120–126.

Smith, M.A., 1931. The Fauna of British India including Ceylon and Burma, Reptilia and Amphibia. Taylor and Francis. London.

Sterling, E.J., Hurley, M.M., Le, M.D., 2006. Vietnam: a natural history. Yale University Press, New Haven and London.

Taplin, L.E., Grigg, G.C., 1989. Historical zoogeography of the Eusuchian crocodilians: a physiological perspective. American Zoologist 29, 885–901.

Thorbjarnarson, J., Wang, X., Ming, S., He, L., Ding, Y., Wu, Y., et al., 2002. Wild populations of the Chinese alligator approach extinction. Biological Conservation 103, 93–102.

Tong, H., Claude, J., Buffetaut, E., Suteethorn, V., Naksri, W., Chitizing, S., 2006. Fossil turtles of Thailand: an updated review. In: Lü, J.C., Kobayashi, Y., Huang, G D., Lee, Y.-N. (Eds.). Papers from the 2005 Heyuan International dinosaur symposium. Geological Publishing House, Beijing, pp. 183–194.

Voen, V., 2008. Zooarchaeological study from Phum Snay – a prehistoric cemetery in Northwest Cambodia. Mémoire de Master Erasmus Mundus, Muséum national d'Histoire naturelle.

Appendix VIII

Manuscript ; Giant Neogene tortoises from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand

Giant Neogene tortoises from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand

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Abstract

Giant tortoises have been found in the Neogene sediments from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand together with a rich vertebrate fauna not older than Late Miocene in age. These tortoises are represented by several individuals and are described based on carapace, plastron, limb bones and isolated plates. Three different morphotypes of epiplastra are recognized. Based on their large size and the presence of epiplastral projection, Thai giant tortoises probably could be close to the *Megalochelys* genus, although they strongly differ from the type species of the genus. Pending for a revision of the genus and for more complete Thai material, the descriptions of these fossils contributes to better understand the geographic distribution of giant tortoises and their morphology in South and Southeast Asia during at that time.

Keywords: giant tortoises, *Megalochelys*, Neogene, Tha Chang, Thailand

Introduction

Extinct giant tortoises are known from the southern part of Asia since the 19th century. The first described species, *Megalochelys sivalensis* Falconer and Cautley 1837, was reported from the Plio-Pleistocene of Siwaliks, India. Later, Falconer and Cautley (1844) studied more material of the giant tortoises from the same region and referred them to *Colossochelys atlas* Falconer and Cautley, 1844. Other names such as *Testudo atlas* or *Geochelone atlas* have also been used later for these giant tortoises from India (Loveridge and Williams, 1957; Hooijer, 1971a,b; Sahni and Khan 1988; Lydekker, 1989). According to a recent review (Setiyabudi, 2009), *Megalochelys sivalensis* has the priority and is thus considered is as valid.

Megalochelys sivalensis Falconer and Cautley, 1837 is considered as being the largest land tortoise (Lapparent de Broin, 2002). In South and Southeast Asia, two additional giant tortoise taxa were also identified from the Plio-Pleistocene of the Siwalik Hills *Megalochelys cautleyi* Lydekker 1886 and *Megalochelys punjabiensis* Lydekker, 1886 which were diagnosed by the epiplastral projection (Lydekker, 1989; Sahni and Khan, 1988). Giant tortoises are also known from several localities in Indonesia including Java, Sulawesi, and Flores islands and in Timor (Setiyabudi, 2009). An Early Pleistocene giant tortoise from the Bumiayu area, Central Java has been recently reexamined by Setiyabudi (2009) and was identified as *M.* cf. *sivalensis*. Finally large tortoises were recently reported from the Irrawaddy Group, Myanmar; dated from the latest Middle Miocene to Early Pleistocene. These tortoises were also referred to *Megalochelys* (Sonoda *et al*, 2010; Sonoda *et al.*, 2011).

Remains of giant testudinid turtles, together with a rich vertebrate fauna, have been reported from the Neogene of Thailand, in the area of Tha Chang, Chalerm Phrakiet District, Nakhon Ratchasima Province (Tong *et al.*, 2006; Claude *et al.*, 2011) but were not described in detail. The material consists of articulated shells (now mostly destroyed), fragmentary shell elements and isolated limb bones. The systematic study of these giant tortoises is presented in this paper. Geographical distribution of giant tortoises in Asia are assessed and discussed.

Materials and geological context

Nine sand pits have yielded fossil vertebrates in Tha Chang area, especially mammals (Thasod, 2007). The sands, conglomerates, or mud composing the layers in which pits were dug were deposited in a fluvial context. The sediments were accumulated and preserved around the present Mun River and overlie Cretaceous Khok Kruat or Mahasarakham formations (Claude *et al.*, 2011). The pits were dug by water jets for mining purpose during the extraction of sands, and fossils are washed out from time to time and fell down at the bottom of the sand pits. Because of the way to extract sediment, the vertebrate remains were mostly fragmentary material and mix together from several layers (see Claude *et al.*, 2011).

The age of the sand pits are established based on the correlation of the mammal assemblages; ranging from the Middle or Late Miocene to the Pleistocene (Department of Mineral Resources, 2005; Hanta *et al.*, 2008). Most pits are now flooded. Giant tortoise material principally comes from the sand pit no 8 (Somsak sand pit) and the sand pit no 9 (Siam sand pit). The most spectacular material was a nearly complete shell with articulated carapace and plastron collected by Department of Mineral Resources (DMR) in June 2003. The specimen was found *in situ* in the Siam sand pit in a sand layer below conglomeratic levels, some 13 meters below the surface. This layer belongs to the reducing subunit of the quarry (see Claude *et al.*, 2011). Unfortunately during preparation and transportation of this very heavy fossil to The Research Center and Dinosaur Museum (PM) in Wiang Kao district, the specimen collapsed and only parts of it could be restored. In addition isolated but often fragmentary shell plates and limb bones have been collected in Tha Chang, they are housed in Northeastern Research Institute of Petrified Wood and Mineral Resources (RIN), Nakhon Ratchasima Province in the Sirindhorn Musuem (SM), Kalasin Province; and part of them were also examined in the private collection at the Chavalit Vidthayanon Collection of Zoology (CCZ), Bangkok.

Systematic Palaeontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
? Genus *Megalochelys* Falconer and Cautley, 1837
?Megalochelys sp.
Figs. 1-8

Referred specimens: PM 2012-1-001, a nearly complete shell; RIN 906, RIN 630, RIN 232, and RIN 543, four nuchal plates; RIN 533, a portion of carapace with several neurals connected with proximal part of costals; RIN 402, a nearly complete left seventh costal plate; RIN 865, a portion of carapace with proximal part of several articulated costals; RIN 489, a nearly complete left first peripheral plate; RIN 917, three complete epiplastron projections; RIN 861 and SM11-1-234, two left portions of epiplastron projection; posterior part of the left epiplastron and the anterior portion of the hyoplastron; RIN 847, a fragmentary left hypoplastron; RIN 930, an incomplete left xiphiplastron; RIN 654, a left humerus; RIN 658, RIN 243, RIN 507, and RIN 496, RIN 531, five right humerus; RIN 862, CCZ 399 and CCZ 400.

Description

Articulated material (PM2012-1-001):

PM2012-1-001 is an articulated carapace and plastron that was partially destroyed during transportation. The carapace retains essentially the original shape, although the top was slightly sinking and collapsed during fossilization; the anterior part of both plastron and carapace is damaged. The right half and part of the posterior portion of the carapace are missing. Most of the plastron has been destroyed during the transportation, but some interesting features can be observed on the cast that was made for the transportation and on fragmentary plastral remains. The cast of the plastron shows that it was nearly complete except the anterior part (on the left side, the part anterior to the humeral scute is missing, while on the right side, the portion anterior to the abdominal scute is not preserved). Sulci are deeply impressed but sutures are unfortunately not discernible on the cast.

Carapace (Fig. 1, A1-A3)

The carapace of PM2012-1-001is dome shaped with a smooth surface, of about 1.5 meter in length. There is no midline keel on the carapace. The posterior and anterior margins of the carapace are smooth. The nuchal is not preserved. Most of the neural plates are difficult to observe because bones are partly fused in this region. The fourth neural contacts the third, fourth and fifth costal plates on its right side, which indicates that this plate was certainly octagonal in shape. The seventh and eighth neurals are hexagonal with short anterolateral sides. Only the left lateral oblique suture of the first suprapygal plate is preserved, this plate is likely trapezoid in shape. The anterior part of the pygal is missing while its posterior end is present. Its lateral oblique suture at the right side indicates that it was trapezoid in shape with lateral margins convergent backward. Costal plates are preserved only on the left side from distal part of the second to the anterior part of the eight costal plate. The distal end of the fifth costal plate is longer than both distal end of the second and third costal plates. The distal end of the seven costal plate is shorter than that of the sixth. The seventh costal plate is shorter than the sixth costal plate. This plate contacts the ninth and probably the tenth peripherals. The right tenth peripheral plate and the left third to eleventh peripheral plates are preserved. They are all mesiolaterally elongated. The fourth to seventh peripheral plates contribute to the bridge, which bears a curved lateral keel. They are parallelograms which are higher than wide. The sixth and seventh peripherals are longer than others. From the posterior part of the eighth peripheral backwards, the peripherals are curved internally. The slender ninth peripheral plate is incomplete, only its proximal part is preserved. It is wider than the eighth peripheral plate. The tenth peripheral is rather short and wider than the ninth peripheral.

The medial portions of the second to fourth pleural scutes are well impressed but their distal parts are more difficult to observe. They are longer than wide. The fourth pleural is the widest. The second pleural contacts the fifth and sixth marginals. The third pleural scute contacts the sixth to eighth marginal scutes. The fourth pleural scute contacts the eight to tenth marginal scutes. The fourth to seventh left marginal scutes are elongated mesiolaterally. The tenth and eleventh marginal scutes, preserved on the right side, are slender. The tenth marginal scute is shorter than the eleventh. There is a single supracaudal scute (as attested by the absence of midline sulcus on the pygal plate). The pleuro-marginal sulcus matches the costo-peripheral suture.

Plastron (Fig. 1, B1)

Based on the cast, the plastron is elongated. The posterior lobe is narrower than the anterior lobe. There is a deep and wide triangular anal notch. Lateral margins of the posterior lobe are straight and convergent backward. The xiphiplastron processes are rather rounded. The midline humeral length is longer than the interpectoral sulcus. The humeropectoral sulcus is parallel to the pectoroabdominal sulcus. The pectoral scutes are the shortest. Abdominal scutes are longer than posterior lobe. The femoroanal sulcus is convex anteriorly. Anal scutes are short but they are longer than pectoral scutes. The abominofemoral sulcus is deeply impressed on the partially preserved right hypoplastron (Fig. 4C), it is curved at the lateral border.

Isolated and fragmentary material:

Nuchal (Fig. 2, A1-D2 and Fig. 3, A'1-D'2)

Four incomplete isolated nuchal plates are known. The nuchal is longer than wide. The anterior margin of the nuchal is clearly emarginated, as preserved in RIN 534. The cervical scute is around twice to three times as long as it is wide, with a straight to convex posterior sulcus. The anterior margin of the first vertebral is convex anteriorly. On the visceral side, the impression of the cervical scute is wider posteriorly than anteriorly.

Neurals (Fig. 2, H1,2 and Fig. 3, H'1,2)

The seventh and eighth neural plates are preserved in RIN 533. These neurals are hexagonal with short anterolateral sides. The seventh neural is wider than long while the eight neural is longer than wide. The eighth neural plate is crossed by the posterior sulcus of fourth vertebral scute.

Pygal (Fig. 4, E1,2 and Fig. 5, E'1,2)

The pygal plate (CCZ 398) is longer than wide, although its anterior end is damaged. The lateral borders are convergent backward. The midline marginal sulcus is absent which indicates the presence of a single supracaudal scute. In visceral view of the plate, scute impression is high and becomes short in lateral sides (Figure 4, E2).

Costals (Fig. 2, E1-F2 and Fig. 3, E'1-F'2)

RIN 402 is a nearly complete left seventh costal plate, lacking the proximal end (Figure 2, E1). The proximal portion is narrower than the distal end. The lateral sulcus of the fourth vertebral scute is visible on the proximal part of the plate. No sulcus is observable on the distal part, which indicates that the pleuro-marginal sulci were probably concurrent with the costo-peripheral suture. In visceral view, the rib head is visible. RIN 865 (F1,2) consists of proximal parts of articulated right fifth to seventh costal plates in contact with the parts of sixth and seventh neurals. The fourth vertebral scute should have a rectangular shape according to the relatively straight vertebral sulcus. The posterior part of the scute is narrower than the anterior one which is common for the fourth vertebral scute. The middle of the sixth costal plate is crossed by the interpleural sulcus.

Peripheral (Fig. 2, G1,2 and Fig. 3, G'1,2)
RIN 489 is a nearly complete right first peripheral plate, with slightly damaged posterior margin. It is mediolaterally expanded, with slightly undulated anterior margin and devoid of any scute sulci.

Epiplastron (Fig. 4, A1,2 and Fig. 5, A'1,2)

All epiplastra from Tha Chang sandpits are incomplete. RIN 917 consists of the posterior part of the left epiplastron and the anterior part of the hyoplastron. The lateral margin is convex. The suture of the epiplastron and the hyoplastron is oblique, directed anterolaterally. Five additional epiplastra display different morphology on the epiplastral projection. Based on the shape and thickness, three morphotypes are recognized:

Morphotype I (Fig. 6, A1- B3). RIN 862 is a complete epiplastral projection while RIN 861 presents only the left half. The size from the base of the projection to the tip is 21 cm and 13 cm respectively. The projection is thick and elongated with rounded borders. The thickness increases posteriorly. The right and left epiplastra contacts each other along a clear suture. Anteriorly, the epiplastra bifurcate and form a triangular notch, with an angle of 90 degrees. The lateral borders of the projection are straight and roughly parallel one another. A median ridge is absent on both dorsal and ventral sides but the ventral surface bears a groove running along the midline. The cross section of the projection at the base is roughly square in shape.

Morphotype II (Fig. 6, C1-4)
SM11-1-234 is the left side of epiplastral projection preserved together with the anterior part of the epiplastron. The preserved fragment is 18.8 cm long. The epiplastral projection is short, rather flat, triangular in shape as seen from above with a short

bifurcation at the tip, with an angle of 90 degrees. The ventral surface is flat, without a median ridge.

Morphotype III (Fig. 6, D1-E3)

CCZ 399 and CCZ 400 are preserved as complete anterior epiplastral projection with right and left epiplastra. The projection is short, wider than long and rather thick. The outline is trapezoidal as seen from above with a straight anterior margin and forward convergent lateral borders. There is no bifurcation at the tip and no median ridge on the ventral surface. The cross section of the projection at the base has a wider than high oval shape.

Hypoplastron (Fig. 4, B1,2 and Fig. 5, B'1,2)

RIN 847 is a fragmentary left hypoplastron, lacking the lateral, medial, and anterior parts and the inguinal buttress. The hypo-xiphiplastral suture, probably straight for all its length but curved backward laterally, is situated posterior to the inguinal process.

Xiphiplastron (Fig. 4, D1,2 and Fig. 5, D'1,2)

RIN 930 is a left xiphiplatron lacking the anterior and medial parts. The xiphiplastron process is rounded. The anal notch is probably deep and has a wide triangular shape.

Humerus (Fig. 7, A1-F4)

There are five right humeri (RIN 243, RIN 496, RIN 507, RIN 531 and RIN 658) and one left humerus (RIN 654). The humerus has the well expanded proximal and distal ends and curved shaft. The caput humeri is short and rounded. A thick medial crest extends on the diaphysis below the caput humeri. The medial and lateral processes are well developed and parallel one another as seen from above. The intertubercular fossa is deep. The entepicondylar foramen is enclosed in an elongated groove and penetrates beside the capitellum. The latissimus dorsi scar is well impressed on dorsal surface of the distal part of the lateral process.

The reconstruction of Thai giant tortoise is shown in Fig. 8.

Discussion

The giant tortoises from Tha Chang sandpits consist of an articulated shell, isolated plates and limb bones. All specimens have a huge size, thick shell and smooth surface. Based on five right humeri and five epiplastral projections, these giant tortoises are represented at least by five individuals. The presence of a single supracaudal scute and epiplastral projection and curved humeral shaft are typical of the family Testudinidae. Within this family the concurrence of the marginal-pleural sulcus with the peripheral-costal suture is present in most species except in *Manouria impressa* and *Achilemys*.

In South and Southeast Asia, all Plio-Pleistocene tortoises of very large size have been assigned to the genus *Megalochelys*, however this genus is not well defined because the holotype of the type species is based on fragmentary material (Auffenberg, 1974; Setiyabudi, 2009). The genus *Megalochelys* includes three species which are distinguished one another on the morphology of the epiplastral projection (see below). Setiyabudi (2009) proposed to restrict *Megalochelys* to giant tortoises with a “Y” epiplastral projection, therefore restricting the genus to the type species. If we follow Setiyabudi, several large tortoises defined in the Indo-Pakistanese region are therefore excluded from that genus (*Megalochelys cautleyi* and *Megalochelys punjabiensis*) and do not have proper generic names. Based on the restricted concept of *Megalochelys*, Thai specimens should also be excluded from that genus, because none of the epiplastral morphotype displays the “Y” epiplastral projection. However, it is uncertain whether this character may be used as diagnostic feature because it may be present in only one of the two sexes. In the former reconstructions and speculation about the carapace morphology of *Megalochelys*, two characters at least are also uncertain: the presence of the cervical scute and the fusion of the twelfth marginals; because of these uncertainties Thai and Indo-Pakistanese taxa could fit in one or several distinct lineage.

We therefore followed a conservative approach in assigning our specimens to ?*Megalochelys* based on the large size and geographical facts. All specimens from Thailand could likely belong to a single species (or lineage), because we did not noticed large differences on the morphology of the nuchal plates nor the humeri. In that case, there is a high degree of polymorphism in the shape of epiplastral projection; which can be explained, at least partially, by sexual dimorphism, ontogeny (or uncertainties linked with the precise location of most of the specimen in the pit section).

The allocation of Thai materials to *?Megalochelys* is further supported by the well developed epiplastral projection although it is never clearly forked as in *M. sivalensis*. In its old version, *Megalochelys* consists of several taxa as suggested by Lyddeker (1889) on the basis of skull, plastral and carapacial morphology. A cervical scute is present in the giant tortoise from Thailand, while this scute is apparently absent in *M. sivalensis* in Falconer's reconstruction (Lydkker, 1889). Another large nuchal with a cervical scute from Siwaliks, housed in the British Museum, may belong to a distinct species, according to Lyddeker (1889). Identification at the species level is difficult because specimens are mostly fragmentary and the articulated shell lacks important character for species assignment since the species of *Megalochelys* are distinct one another only by the shape of the epiplastral projection. Based on the shape of the epiplastral projection, *Megalochelys* from Siwaliks, India have been assigned to three species: *M. sivalensis* which has a large and elongate Y-shaped projection; *M. punjabiensis* which has a triangular projection and *M. cautleyi* with a quadrangular projection (Lydekker, 1889). While Sonoda (2011) considered the different morphotypes of the epiplastral projection of the Myanmar *Megalochelys* as result of sexual dimorphism or growth stages. The variation in Myanmar specimen is much smaller than the variation among the Indo-paksitanese or Thai morphotypes. According to Sonoda *et al.* (2011), based on the comparisons with the extant testudinids, the adult male has more developed epiplastral projection, the adult female has a shorter and smaller epiplastral projection and the projection is much less developed in juvenile than in adult. Consequently *M. sivalensis* is considered as male, *M. cautleyi* as female and *M. punjabiensis* as juvenile.

Similar to giant tortoise from India, those from Thailand present great variation in the morphology of the epiplastral projection. There are three morphotypes of epiplastral projection in specimens from Thailand. The morphotype I is similar to *M. sivalensis* from Siwaliks, India and *M.* cf. *sivalensis* from Bumiayu area, Central Java in development, while the morphology differs (Lydekker, 1889; Setiyabudi, 2009). In specimens from Thailand, the projection has parallel lateral borders and the Y-shaped ridge is absent on the ventral surface. While *M. sivalensis* has a Y-shaped projection which is reinforced by a Y-shaped ridge on the ventral surface. In addition, although the projection is bifurcated on the tip in both cases, the angle formed by the bifurcation is acute (90 degrees) in Thai specimens instead of obtuse in *M. sivalensis*. Two specimens of the morphotype I (RIN 861 and RIN 862) have the same shape but differs one another by the size, which indicate that the morphology of the projection could remain unchanged during the ontogeny.

The morphotype II from Thailand is comparable to *M. punjabiensis* from Siwaliks in the triangular shape and flat, but differs in the presence of the bifurcation (Lydekker, 1889). The difference on presence or absence of the bifurcation on the tip is possibly due to the sexual dimorphism because the size and general outline are similar between Thai and Indian specimens.

The morphotype III is similar to *M. cautleyi* from Siwaliks in the quadrangular shape which is wider than long and slightly narrowed anteriorly with almost straight anterior rim (Lydekker, 1889). It resembles also that of *Manouria emys*, but is more elongate and more massive than the latter. As *M. penjabiensis* and *M. cautleyi* are known only by the epiplastral projection, more complete material are requested to confirm the systematic position of these giant tortoises.

Conclusion

The giant tortoises from Tha Chang Sand pits, Thailand are identified as ?*Megalochelys* sp. based on the huge size and large epiplastron projection. While other part of the carapace and limb morphology seems rather constant, variation in the morphology of the epiplastron projection allows to define three morphotypes depending on the shape, presence of bifurcation, the degree of development and angle of the bifurcation, and thickness. Such a variation of epiplastral projection are not only found in Thailand but also present in the giant fossil tortoises from India, Myanmar and also Indonesia. . This variation is also found in modern species exhibiting important sexual dimorphism (*Astrochelys yniphora*). More complete material, well positioned in the stratigraphy is needed in Indo-Pakistan and Thailand to further establish the systematics of the Asian giant tortoise.

Up to now, fossil giant tortoises have been reported from India, Indonesia (Java, Sulawesi, and Flores Islands), Timor, Myanmar. The discovery of giant tortoises in Thailand provides new evidence that their distribution was not only on island but also in mainland.

Acknowledgments

This work was granted by the Thai Science Scholar Project and Mahasarakham University grant, the TRF/BIOTEC Special Program for Biodiversity Research and Training grant BRT T_148022 and Mahasarakham University fiscal year 2012. We are grateful to Northeastern Research Institute of Petrified Wood and Mineral Resources, The Research Center and Dinosaur Museum, Sirindhorn Museum, Chavalit Vidthayanon Collection of Zoology and Senckenberg Museum, Frankfurt. We express our thanks to Jeremy Martin for correction manuscript and giving advice and Ren Hirayama and Teppei Sonoda for providing and discuss useful information. We also deeply thank to Chotima Yamee, Kamonlak Wongko, Nareerat Boonchai, Yupa Thasod, Rattanaporn Hunta, Suravech Suteethorn and Jaroon Duangkrayom, Stephan Shaal and Linda Acker for their helps and everybody whom concerned this work.

Figure and table captions:

Figure 1. Shell of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand (PM2012-1-001); A, carapace 1.5 meter in length in anterior (1), lateral (2,3), posterior (4), and dorsal (5) views; B, a cast of plastron. Scale bar of plastron is 12 cm.

Figure 2. Isolated plates of *?Megalochelys* sp. carapace from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Nuchal plates, A (RIN 906), B (RIN 630), C (RIN 232), D (RIN 543); costal plates, E (RIN 402), F (RIN 865); a peripheral plate, G (RIN 489) ; neural plates associated with costal plates, H (RIN 533) in external (1) and visceral (2) views. Scale bars are 5 cm.

Figure 3. Isolated plates drawing of *?Megalochelys* sp. carapace from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Nuchal plates, A' (RIN 906), B' (RIN 630), C' (RIN 232), D' (RIN 543); costal plates, E' (RIN 402), F' (RIN 865); a

peripheral plate, G' (RIN 489) ; neural plates associated with costal plates, H' (RIN 533) in external (1) and visceral (2) views. Scale bars are 5 cm.

Figure 4. Isolated plates of plastron and carapace of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A (RIN 917), epiplastron; B (RIN 847), fragmentary hypoplastron and xiphiplastron; C (PM2012-1-001), fragment of hypoplastron; D (RIN 930), left xiphiplastron; E (CCZ 398), pygal in external (1) and visceral (2) views. Scale bars are 5 cm.

Figure 5. Isolated plates of plastron and carapace drawing of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A' (RIN 917), epiplastron; B' (RIN 847), fragmentary hypoplastron and xiphiplastron; C' (PM2012-1-001), fragment of hypoplastron; D' (RIN 930), left xiphiplastron; E' (CCZ 398), pygal in external (1) and visceral (2) views. Scale bars are 5 cm.

Figure 6. Isolated epiplastron projections of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A (RIN 862), B (RIN 861), C (SM11-1-234), D (CCZ 399) and E (CCZ 400) in dorsal (1), ventral (2), lateral (3), anterior (4) and posterior (5) views. Scale bars are 5 cm.

Figure 7. Humeri of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. A left humerus, A (RIN 654); Right humeri, B (RIN 658), C (RIN 243), D (RIN 507), E (RIN 496), F (RIN 531) in dorsal (1), posterior (2), anterior (3), ventral (4), proximal (5) and distal (6) views. Scale bars are 5 cm.

Figure 8. Reconstruction of the shell of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Scale bar is 12 cm.

References

Auffenberg, W. (1974) Checklist of fossil land tortoise (Testudinidae). Bulletin of the Florida State Museum, Biological Sciences 18, 121-251.

Brown, B. (1931) The largest known land tortoise. American Museum of Natural History, New York. 31(2), 183-187.

Claude, J., Naksri, W., Boonchai, N., Buffetaut, E., Duangkrayom, J., Laojumpon, C., Jintasakul, P., Lauprasert, K., Martin, J., Suteethorn, V., Tong, H. (2011) Neogene reptiles of northeastern Thailand and their paleogeographical significance. *Annales de Paléontologie* 97, 113-131.

Claude, J. and Tong, H. (2004) Early Eocene Testudinoid Turtles from Saint-Papoul, France, with comments on the Origin of modern Testudinoidea. Oryctos 5, 71-113.

Falconer, H. and Cautley, P.T. (1837) On additional fossil species of the order Quadrumona from Siwaliks Hill. *Journal Asiatic Society Bengal* **6**, 354-360.

Falconer, H., and Cautley, P.T. (1844) On the osteological characters and paleontological history of the *Colossochelys atlas*, a fossil tortoise of enormous size from the Tertiary strata of the Siwalik Hill in the north of India. *Proceedings Zoology Society London* **12**, 54—55 and p. 84. (communication continued through two issues).

Hooijer, D.A. (1971a) A Giant land tortoise, *Geochelone atlas* (Falconer & Cautley), from the Pleistocene of Timor I. *Konikl. Nederl. Akad. van Wetens.-Amsterdam. Reprint from Proc. Series B* 74, 504—517.

Hooijer, D.A. (1971b) A Giant land tortoise, *Geochelone atlas* (Falconer & Cautley), from the Pleistocene of Timor II. *Konikl. Nederl. Akad. van Wetens.-Amsterdam. Reprint from Proc. Series B* 74, 518—525.

Lapparent de Broin (2002) A giant tortoise from the Late Pliocene of Lesvos Island (Greece) and its possible relationships. *Annales Géologiques Des Pays Helléniques*. 1, 99-130.

Loveridge, A., and Williams, E.E. (1957) Revision of the African Tortoise and Turtles of the Suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology* 115, 163-557.

Lydekker, B.A. (1889) On the land tortoises of Siwaliks. The records, Geological survey of India, Vol XXII. Pp. 209-214.

Lydekker, R. (1885) Indian Tertiary and Post-Tertiary Vertebrata. *Siwalik and Narbada Chelonia Serie X Volume* **3**, pp. 155-208.

Sahni, M.R., Khan, E. (1988) Pleistocene vertebrate fossil & prehistory of India. Books & Books; New Delhi, India. P. 119.

Setiyabudi, E. (2009) An Early Pleistocene giant tortoise (Reptilia; Testudines; Testudinidae) from Bumiayu area, Central Java, Indonesia. Journal of Fossil Research, 42(1), 1-11.

Sonoda, T., Hirayama, R., Takai, M., Htike, T., Ando, H. (2010) A preliminary of fossil turtles from the Irrawaddy Group (the Latest middle Miocene to Early Pleistocene) in Myanmar (abstract). The 2nd International Conference on Palaeontology of Southeast Asia (ICPSEA 2010), 1-5 November 2010, Mahasarakham University, Thailand. Pp.54.

Sonoda, T., Hirayama, R., Takai, M., Htike, T., Thein, Z.M.M., Ando, H. (2011) The morphological variation in Giantic tortoises (Testudnididae; Testudines) from the Irrawaddy sediments in Central Myanmar. Program and abstracts; World conference on Paleontology and stratigraphy, To honor his Majesty the King's 84th Anniversary, 28 November -2 December, 2011 Nakhon Ratchasima, Thailand. Pp. 47-48.

Thasod, Y., Jintasakul, P., Ratanasthien, B. 2012. Proboscidean fossil from the Tha Chang sand pits, Nakhon Ratchasima Province, Thailand. *Journal of Scinece and Technology Mahasarakham University* 31(1), 33-44.

Thasod, Y. 2007. Miocene mastodont in Thailand and palaeoevironment. Ph.D thesis, Department of Geological Science, Chiang Mai University, Thailand. Published thesis.

Tong, H., Claude, J., Buffetaut, E., Suteethorn, V., Naksri, W., Chitsing, S. (2006) Fossil turtles of Thailand,": an updated review. In Lu, J.C., Kobayashi, Y., Huang, D & Lee, Y.-N (eds). Papers from the 2005 Heyuan International Dinosaur Symposium. Geological Publishing House, Beijing. 183-184.

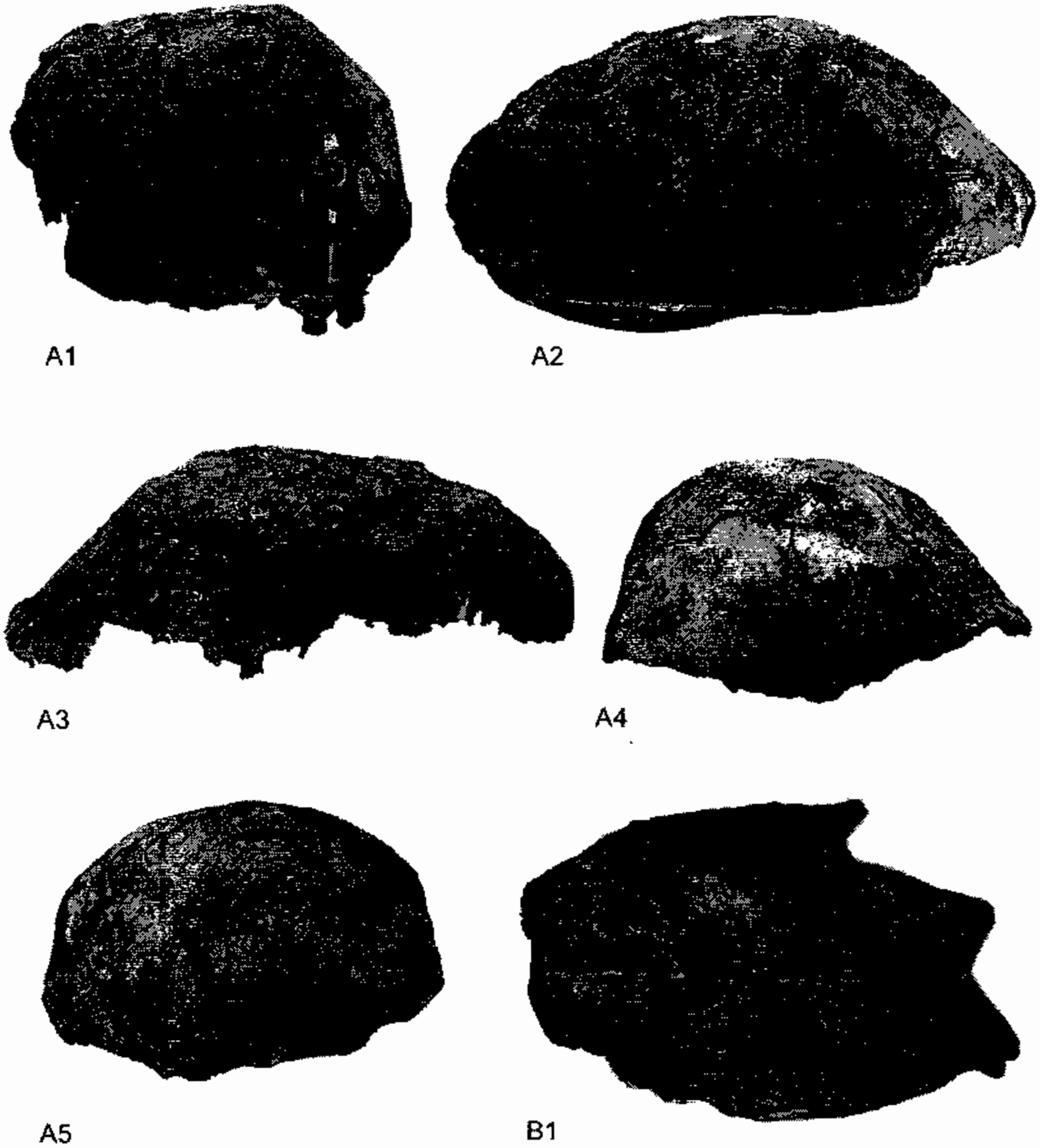

Figure 1. Shell of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand (PM2012-1-001); A, carapace 1.5 meter in length in anterior (1), plastron is 12 cm.

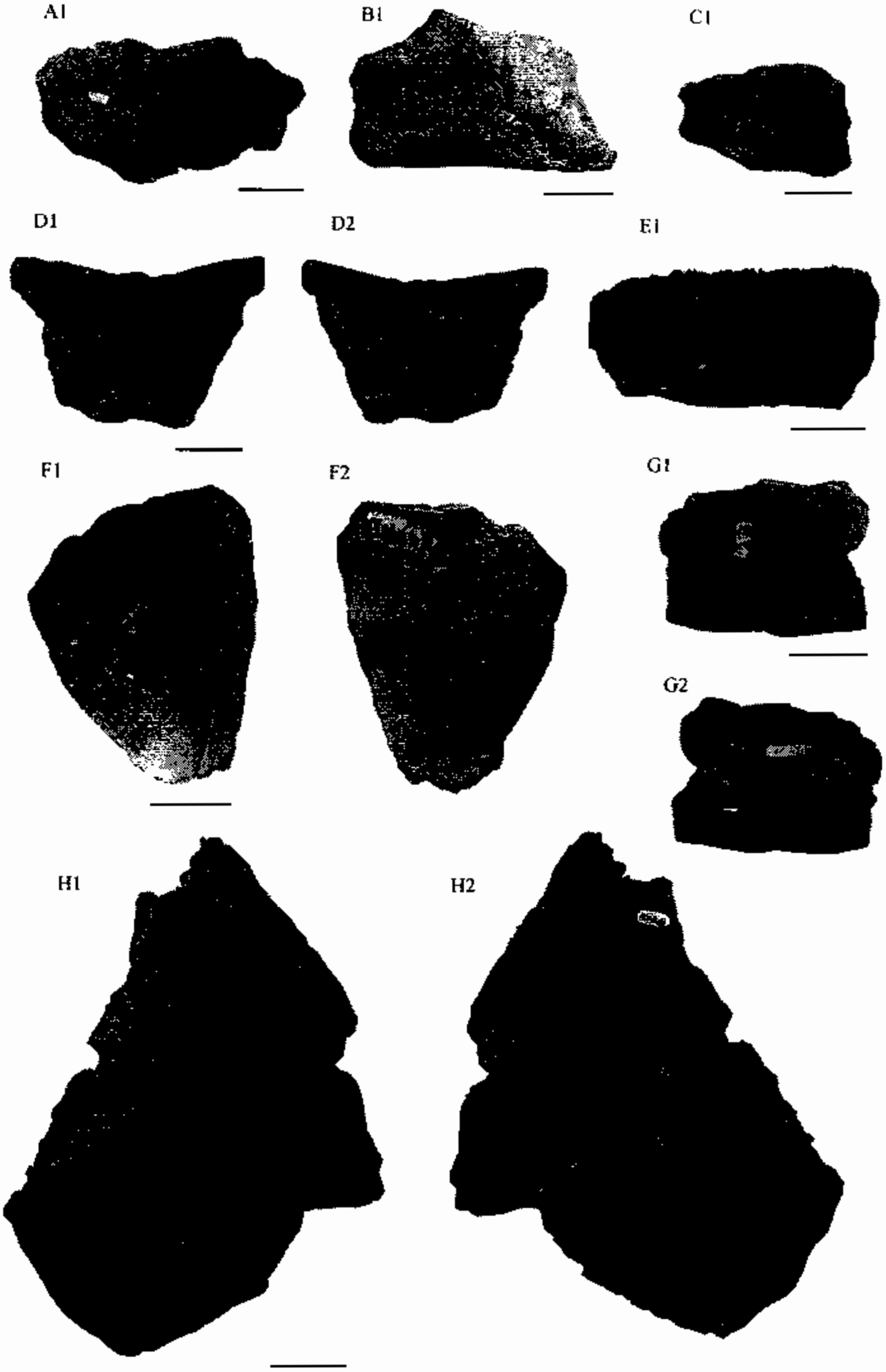

Figure 2. Isolated plates of *?Megalochelys* sp. carapace from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Nuchal plates, A (RIN 906), B (RIN 630), C (RIN 232), D (RIN 543); costal plates, E (RIN 402); , F (RIN 865); a peripheral plate, G (RIN 489); neural plates associated with costal plates, H (RIN 533) in external (1) and visceral (2) views. Scale bars are 5 cm.

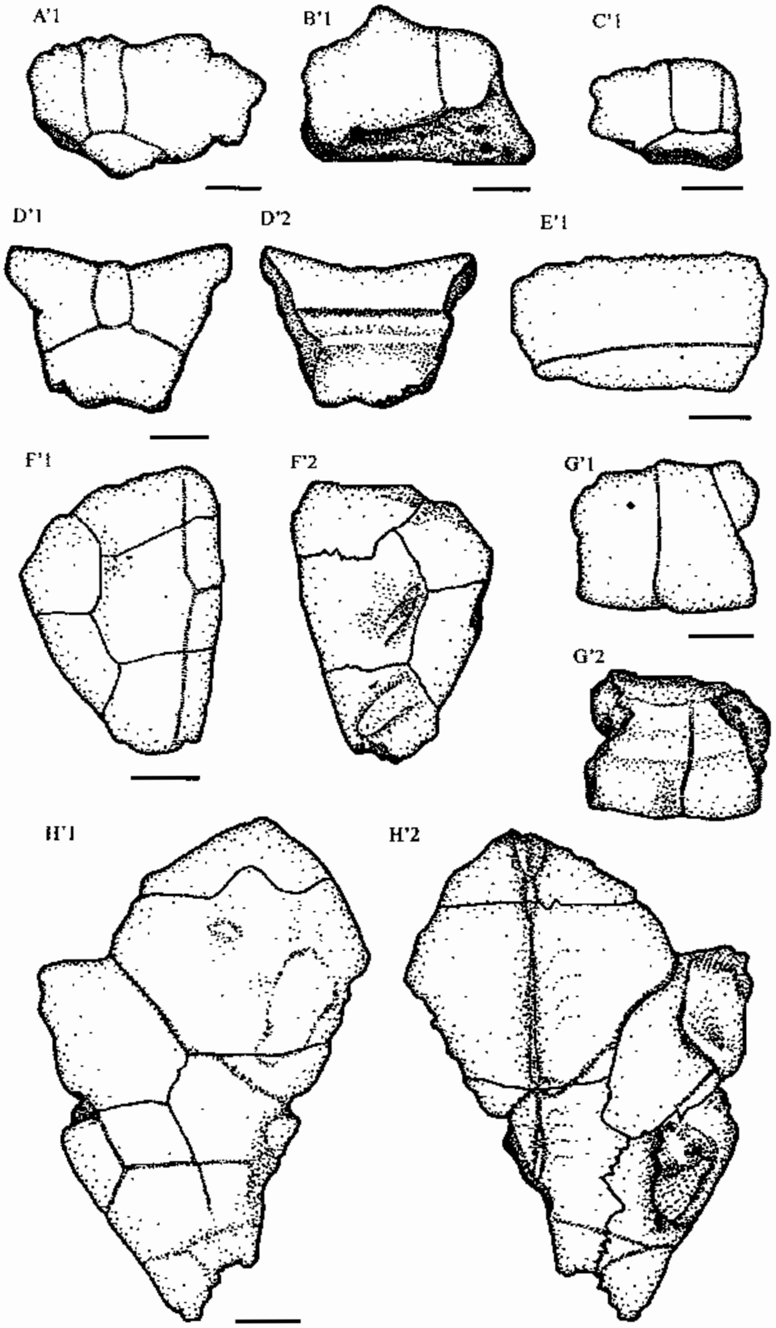

Figure 3. Isolated plates drawing of *?Megalochelys* sp. carapace from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Nuchal plates, A' (RIN 906), B' (RIN 630), C' (RIN 232), D' (RIN 543); costal plates, E' (RIN 402), F' (RIN 865); a peripheral plate, G' (RIN 489) ; neural plates associated with costal plates, H' (RIN 533) in external (1) and visceral (2) views. Scale bars are 5 cm.

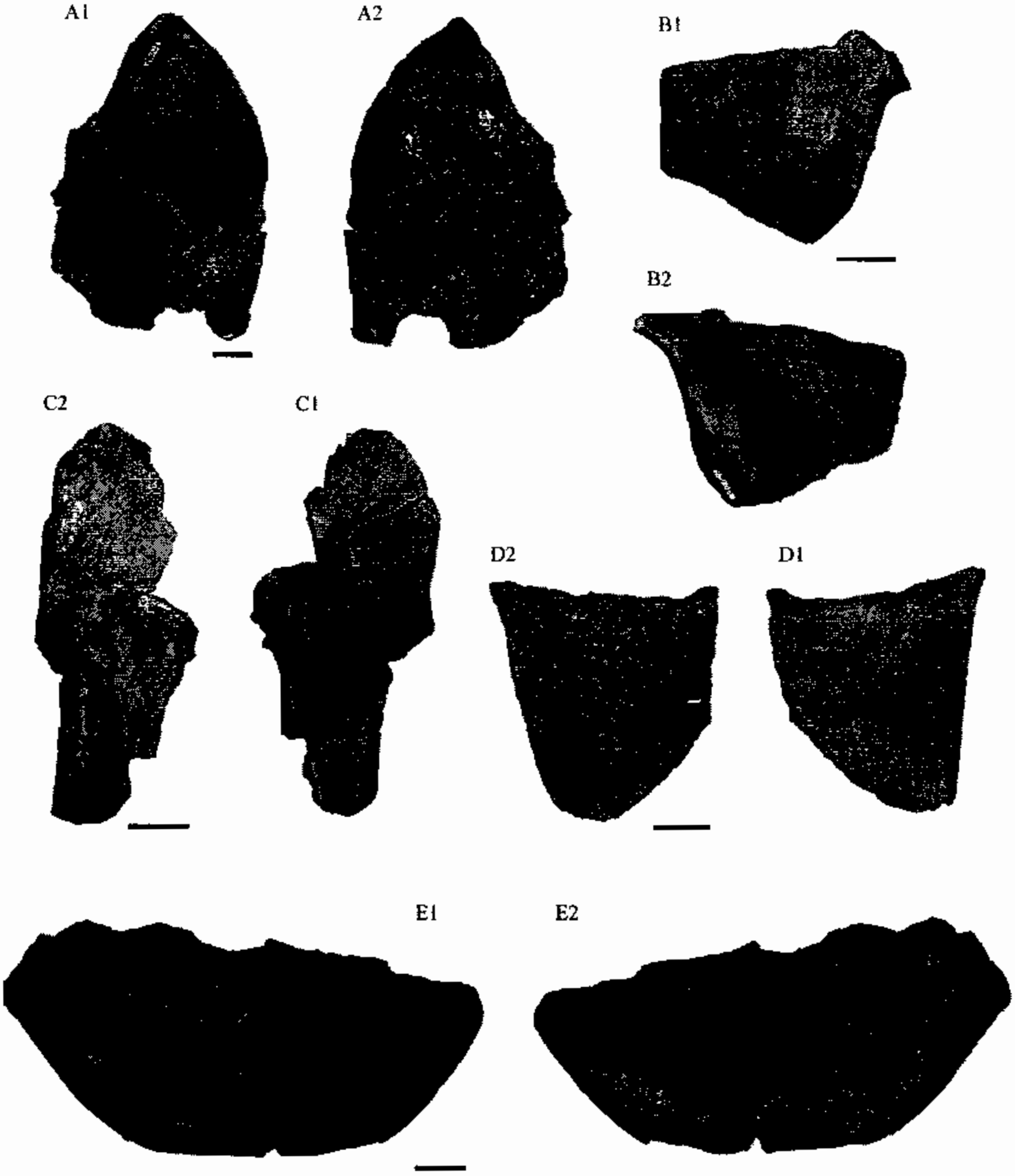

Figure 4. Isolated plates of plastron and carapace of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A (RIN 917), epiplastron; B (RIN 847), fragmentary hypoplastron and xiphiplastron; C (PM2012-1-001), fragment of hypoplastron; D (RIN 930), left xiphiplastron; E (CCZ 398), pygal in external (1) and visceral (2) views. Scale bars are 5 cm.

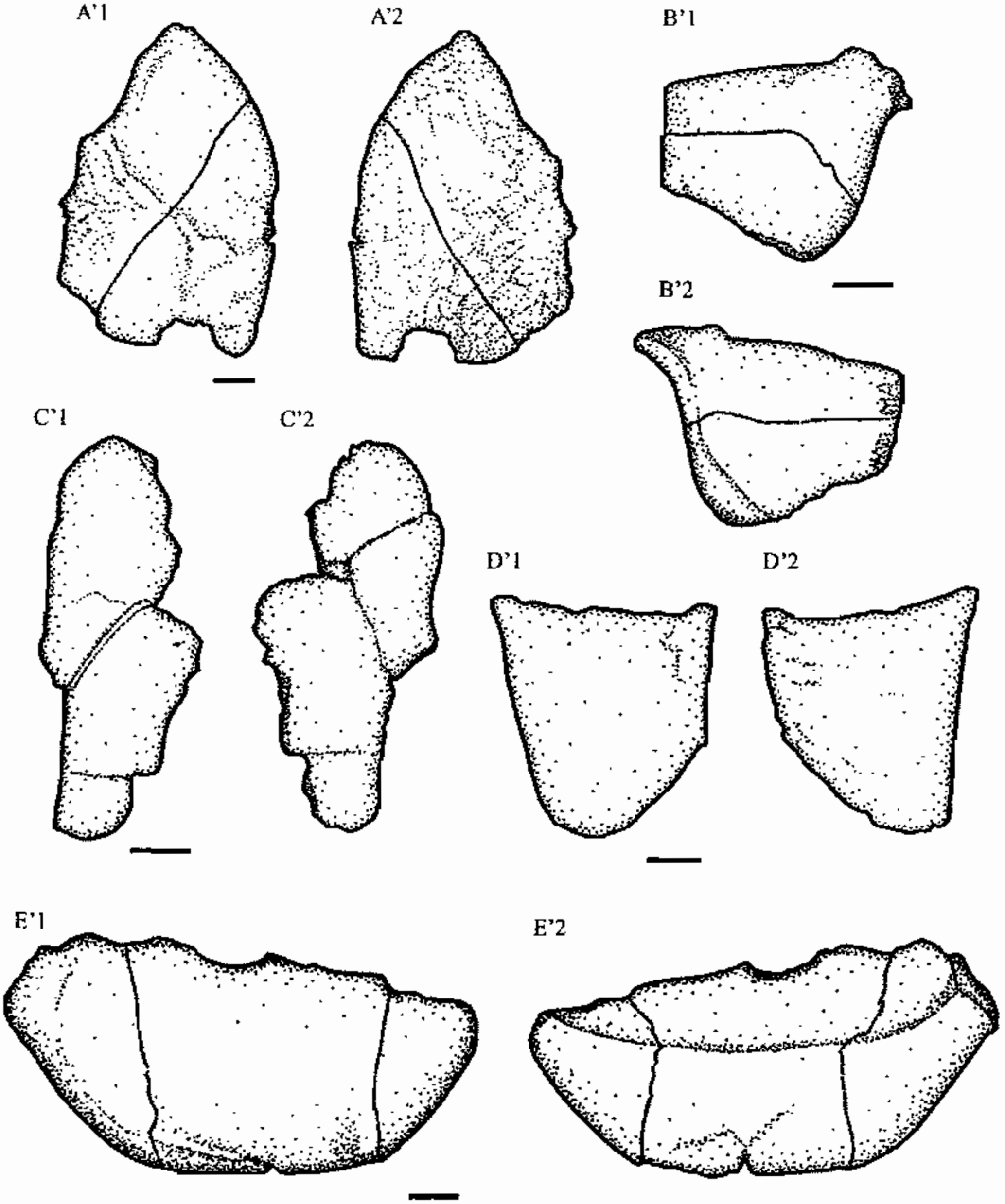

Figure 5. Isolated plates of plastron and carapace drawing of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A' (RIN 917), epiplastron; B' (RIN 847), fragmentary hypoplastron and xiphiplastron; C' (PM2012-1-001), fragment of hypoplastron; D' (RIN 930), left xiphiplastron; E' (CCZ 398), pygal in external (1) and visceral (2) views. Scale bars are 5 cm.

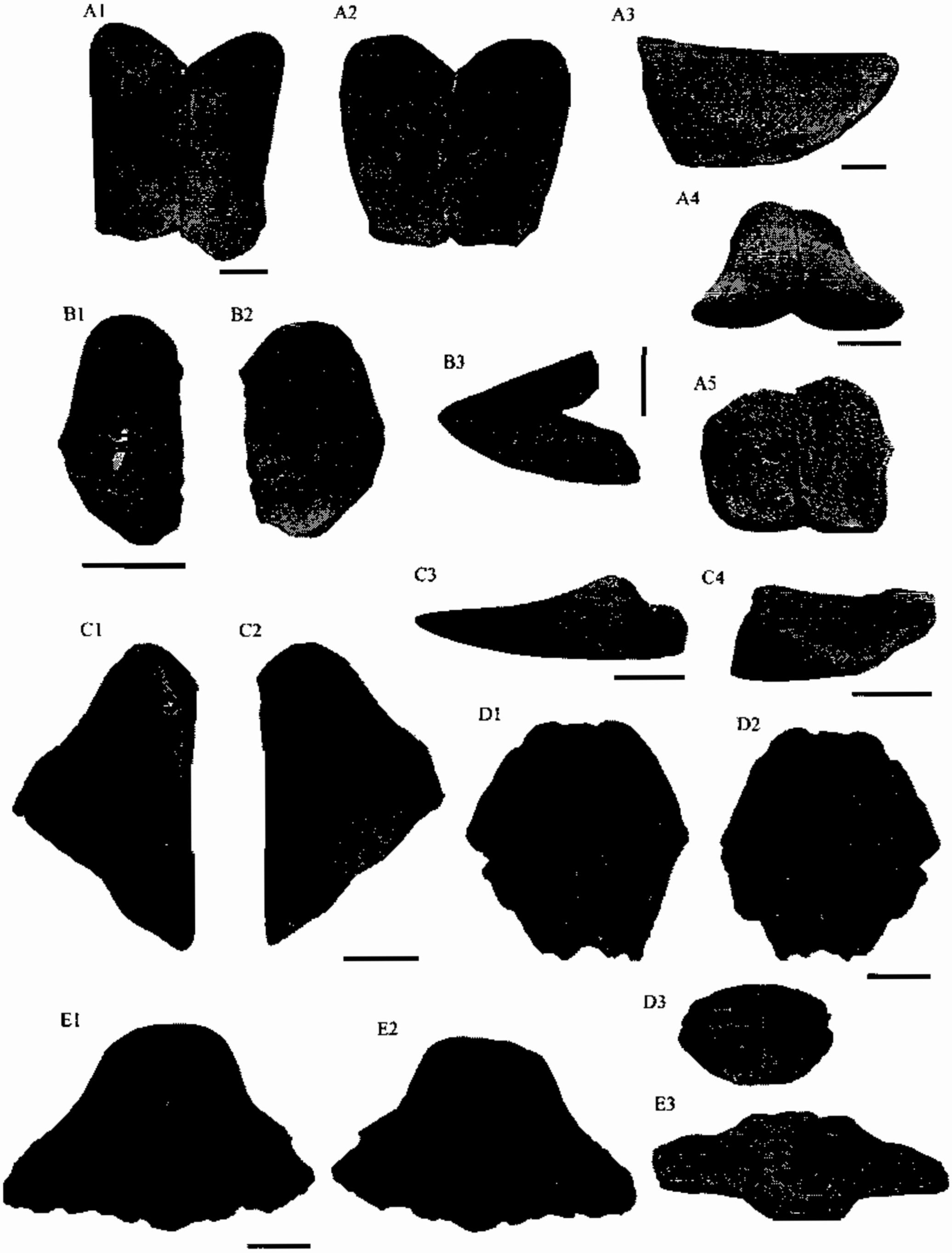

Figure 6. Isolated epiplastron projections of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand; A (RIN 862), B (RIN 861), C (SM11-1-234), D (CCZ 399) and E (CCZ 400) in dorsal (1), ventral (2), lateral (3), anterior (4) and posterior (5) views. Scale bars are 5 cm.

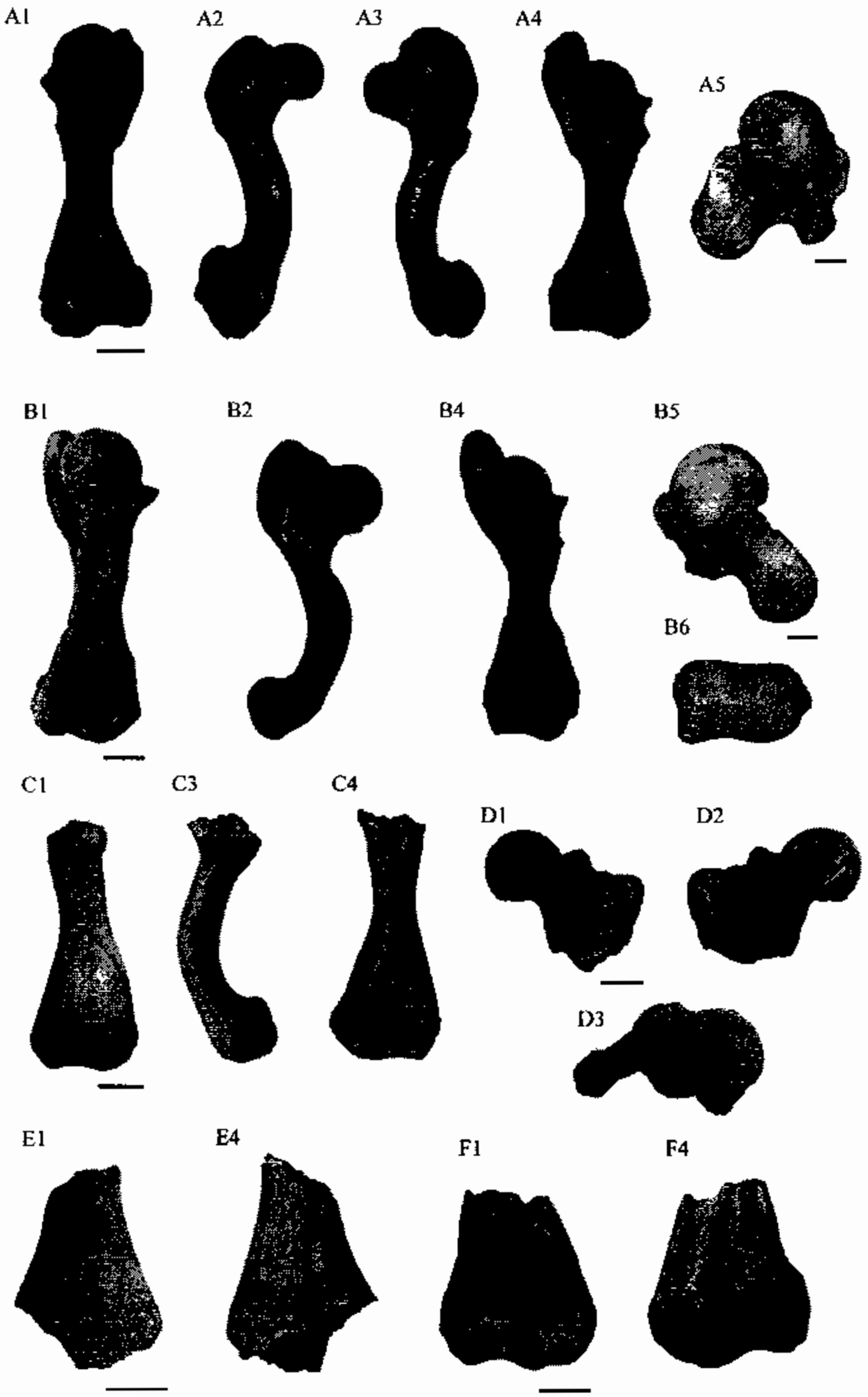

Figure 7. Humeri of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. A left humerus, A (RIN 654); Right humeri, B (RIN 658), C (RIN 243), D (RIN 507), E (RIN 496), F (RIN 531) in dorsal (1), posterior (2), anterior (3), ventral (4), proximal (5) and distal (6) views. Scale bars are 5 cm.

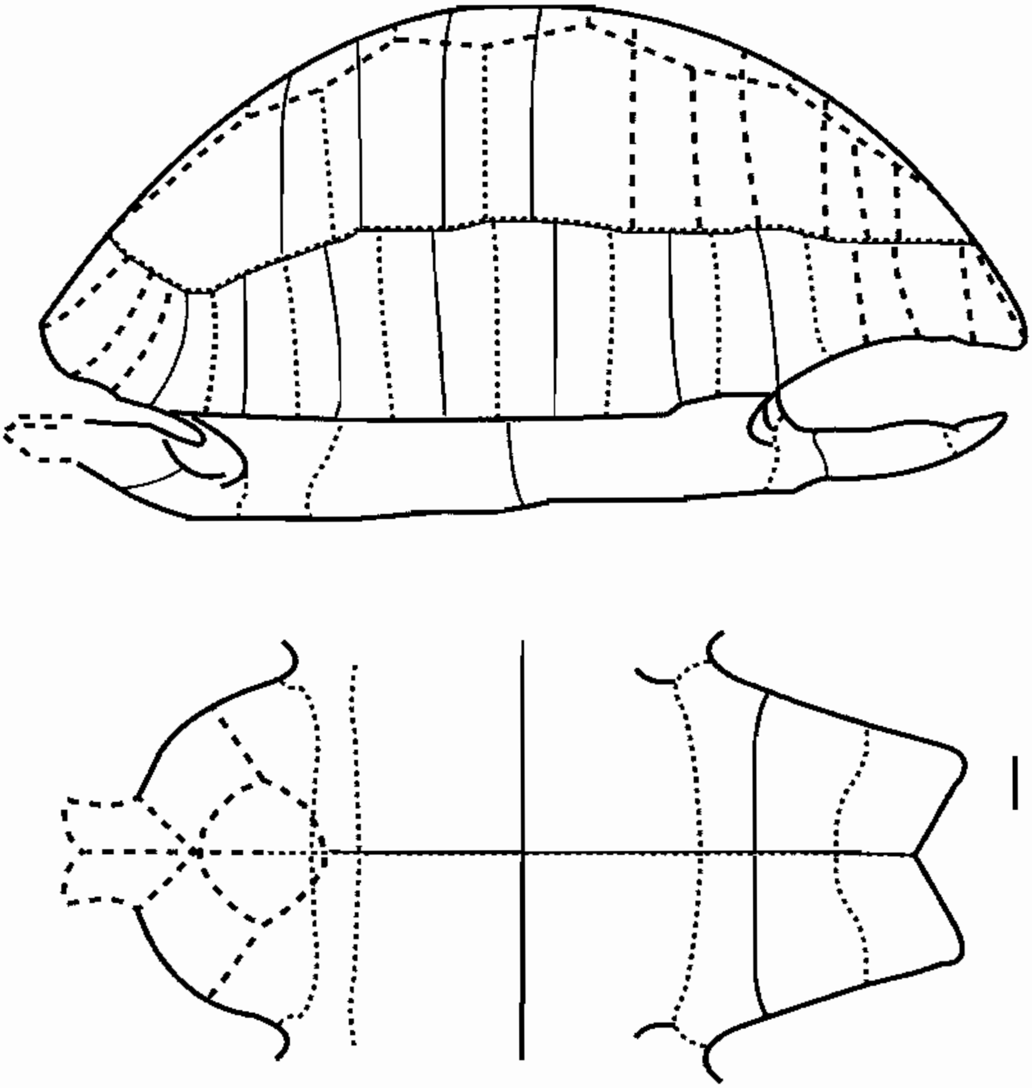

Figure 8. Reconstruction of the shell of *?Megalochelys* sp. from Tha Chang sandpits, Nakhon Ratchasima Province, Thailand. Scale bar is 12 cm.

BIOGRAPHY

BIOGRAPHY

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PUBLICATIONS

Naksri, W., Tong, H., Lauprasert, K., Suteethorn, V. & Claude, J. A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance. Geological Magazine, 150, 908-922. doi:10.1017/S0016756812001082.

Martin, J., Buffetaut, E., **Naksri, W.**, Lauprasert, K. & Claude, J. 2012. *Gavialis* from the Pleistocene of Thailand and its relevance for drainage connections from India to Java. PLoS ONE. 7(9): e44541. doi:10.1371/journal.pone.0044541 (In press)

Claude, J., **Naksri, W.**, Boonchai, N., Buffetaut, E., Duangkrayom, J., Laojumpon, C., Jintasakul, P., Lauprasert, L., Martin, J., Suteethorn, V. &Tong, H. 2011.Neogene reptiles of northeastern Thailand and their paleogeographical significance. Annales de Paléontologie. 97(3-4), 113-131.

Tong, H., Claude, J., **Naksri, W.**, Suteethorn, V., Buffetaut, E., Khansubha, S., Wongo, K. & Yuangdetkal, P. 2009a. *Basilochelys macrobios* n. gen. and n. and sp., a large crptodiran turtle from the Phu Kradung Formation (latest Jurassic-earliest Cretaceous) of the Khorat Plateau, NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., & Suteethorn, V. (eds.) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London, Geological Society, Special Publication, 315, 153-173.

Tong, H., Claude, J., Suteethorn, V., **Naksri, W.** & Buffetaut, E. 2009b. Turtle assemblages of the Khorat Group (Late Jurassic-Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In: Buffetaut, E., Cuny, G., Le Loeuff, J., & Suteethorn, V. (eds.) *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London, Geological Society, Special Publication, 315, 141-152.

CONFERENCES

Naksri, W., Tong, H., Lauprasert, K., Suteethorn, V., Srisuk, P. & Claude, J. 2012. The Late Oligocene Turtle Assemblage from Nong Ya Plong, Petchaburi Province, Thailand. Symposium on turtle evolution, University of Tübingen, Germany, 2-4 June 2012. p. 31. (Oral presentation)

Naksri, W., Tong, H., Thirakhupt, K., Lauprasert, K., Suteethorn, V. & Claude, J. A new fossil of *Cuora* from the Miocene of Thailand sheds new light on the origin of Asian box turtles. The 9th Annual Meeting of the European Association of Vertebrate Palaeontologists Heraklion, Crete, 14-19 June 2011.
(Oral presentation)

Lauprasert, K. , Wattanapituksakul, A. , Laojumpon, C., Buffetaut, E. , Cuny, G., Tong, H., Martin, J., Le Loeuff, J., Claude, J., Wongko, K., Cavin, L., Srisuk, P., Khamha, S., Suteethorn, S., Deesri, U., **Naksri, W.** & Suteethorn, V. Dinosaur Valley of Thailand: The spectacular vertebrate fossil sites in Southeast Asia. The 9th Annual Meeting of the European Association of Vertebrate Palaeontologists Heraklion, Crete, 14-19 June 2011. (Oral presentation)

Naksri, W., Tong, H., Thirakhupt, K., Lauprasert, K., Suteethorn, V. & Claude, J. 2011. Continental Miocene Turtle Assemblages from Northern Thailand. World Conference on Paleontology and Stratigraphy 2011 (WCPS2011), 28 Nov-2 Dec, 2011. p. 32. (Oral presentation)

Tong, H., Danilov, I., Ye, Y., Ouyan, H., Peng G-Z., Li, K., **Naksri, W.**, Claude, J., Buffetaut, E. & Suteethorn, V. 2011. Revision of turtle assemblages from the Jurassic of Sichuan Basin, China and comparison with Thai faunas. World Conference on Paleontology and Stratigraphy 2011 (WCPS2011), 28 Nov-2 Dec, 2011. p. 17-18. (Oral presentation)

Claude, J., **Naksri, W.**, Lauprasert, K., Jintasakul, P., Boonchai, N., Buffetaut, E., Suteethorn, V. & Tong, H. 2010. Tertiary reptiles of the paleo-Mun river valley in Northeastern Thailand. The 2nd International Conference on Palaeontology of Southeast Asia at Mahasarakham University, November 1-5, 2010. (Oral presentation)

Lauprasert, K., Wattanapituksakul, A., Laojumpon, C., Buffetaut, E., Cuny, G., Tong, H., Le Loeuff, J., Claude, J., Wongko, K., Cavin, L., Cheychiw, O., Srisuk, P., Suteethorn, S., Deesri, U., Saenphala, W., **Naksri, W.**, Saman, R. & Suteethorn, V. 2010. Dinosuar valle the miracle of Isan. The 14th Biodiversity Research and Training Program (BRT) at Sunee Grand Hotel, Ubon Ratchathani, October 10-12, 2010. (Oral presentation)

Naksri, W., Lauprasert, K. & Claude, J. 2010. Diversity of Neogene and Quaternary turtles in Thailand. Abstracts of The 5th Conference on Science and Technology for Youths, 19-20 March, 2010. Bangkok, Thailand. (Poster presentation)

Naksri, W., Thirakhupt, K, Lauprasert, K., Suteethorn, V., Jintasakul, P., Tong, H., & Claude, J. 2010. Neogene giant tortoise from Tha Chang sandpit, Nakhon Ratchasima Province, Thailand. The 2nd International Conference on Palaeontology of Southeast Asia at Mahasarakham University, November 1-5, 2010. (Oral presentation)

Naksri, W., Lauprasert, K. & Claude, J. 2010. Presence of *Cuora* in the Middle Miocene of Northern of Thailand. Abstracts of The 6th Conference on Science and Technology for Youths, 19-20 March, 2011. Bangkok, Thailand. (Poster presentation)

Naksri, W., Claude, J., Thirakhupt, K. & Talubmook, C. 2008. Appraisal of the evolution of testudinoid turtle diversity from the Late Palaeogene and Neogene of Thailand. Abstracts: Research and thesis 2008. 12th BRT Annual Conference October 10-13, 2008 Diamond Plaza, Suraj Thani. p. 160. (Poster presentation)

Tong, H., Claude, J., Suteethorn, V., **Naksri, W.**, Buffetaut, E. 2008. Turtle assemblages of the Khorat Group (Late Jurassic-Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. Abstract of Mid-Mesozoic life and environments Congnac (France), June 24th-28th 2008. Docum. Lab. Geol. Lyon, ก 164. p.85.

Tong, H., Claude, J., Buffetaut, E., Suteethorn, V., **Naksri, W.** & Chitsing, S. 2006. Fossil turtles of Thailand: an updated review. In: Lu, J.C., Kobayashi, Y., Huang, D & Lee, Y.-N (eds.) *Papers from the 2005 Heyuan International Dinosaur Symposium*. Beijing, Geological Publishing House. pp. 183-184.

Naksri, W., Thirakhupt, K., Talabmook, C. & Claude, J. 2006. The illustrated osteology of living testudinoid turtles from Thailand. 10th BRT annual Meeting, Krabi, 8-11 October 2006. (Poster presentation)

Naksri, W., Thirakhupt, K., Talabmook, C., Suteethorn, V., Jintasakul, P., Tong, H. & Claude, J. 2006. Neogene giant tortoise from Tha Chang sandpit, Nakorn Ratchasima Province, Thailand. Abstracts of the 11th Biological Sciences Graduate Congress. 15-17 December 2006 Chulalongkorn University, Bangkok.p. 18. (Oral presentation)

Claude J., Tong, H., **Naksri, W.**, P. Jintasakul, S. Paladej & V. Suteethorn (2004): Fossil turtles of Thailand. 8th BRT annual Meeting, Surathanee, 14-17 October. (Poster presentation)