รายงานวิจัยฉบับสมบูรณ์

โครงการ นิเวศวิทยาบรรพกาลของปลากระดูกแข็งน้ำจืดในมหายุคมีโซโซอิกของไทย

โดย

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พฤษภาคม 2563

สัญญาเลขที่ MRG6180086

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สนับสนุนโดยสำนักงานกองทุนสนับสนุนการวิจัย

Abstract

Project Code: MRG6180086

Project Title: Palaeoecology of Thai Mesozoic freshwater bony fishes

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Project Period: 2 year

The study of the Mesozoic fish record of Thailand is still in its infancy. This project aims at continuing the discovery of new bony fish material by excavating old (Phu Nam Jun, Phu Noi, Chong Chat, ect.) and new (Triassic sites, Early Cretaceous of Laos, ect.) fossil sites and to continuing the osteological and phylogenetic studies of the new Thai ginglymodian taxa. The bony fish diversity is growing years after years thanks to new discoveries but, strangely enough, most of the taxa belong to only few clades, notably the ginglymodians and the halecomorphs. This situation might be due to taphonomical reasons, but we cannot exclude that South East Asia was a center of diversification for these fishes at that time. The palaeobiogeographical signal of the fish assemblages is not yet very clear. In the Late Jurassic, affinities with Central Asia are detected, then in the Early Cretaceous the affinities moved towards Eastern Asia. Strangely enough, several taxa also show links with fishes from Africa. More detailed analyses, however, are necessary to get a better image of the evolutionary history of these groups, but it is already established that the fossil record of Thailand plays an important role to understand the evolution of freshwater bony fishes during the Mesozoic worldwide.

Keywords :ginglymodians, phylogenetic studies, taphonomical, palaeobiogeographical, evolutionary history

บทคัดย่อ

รหัสโครงการ : MRG6180086

ชื่อโครงการ : นิเวศวิทยาบรรพกาลของปลากระดูกแข็งน้ำจืดในมหายุคมีโซโซอิกของไทย

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การศึกษาซากดึกดำบรรพ์ปลากระดูกแข็งในช่วงมหายุคมีโซโซอิกของไทยยังอยู่ในระยะเริ่มต้น ซึ่งโครงงานวิจัยนี้มีวัตถุประสงค์เพื่อสำรวจแหล่งขุดค้นและเก็บตัวอย่างซากดึกดำบรรพ์ปลากระดูกแข็งเพิ่มเติม ทั้งในแหล่งเดิมที่เคยมีการขุดค้น และในแหล่งใหม่ที่มีกระจายในช่วงยุคไทรแอสสิกไปจนถึงยุคครีเทเชียสทั้งในประเทศไทยเองและในประเทศใกล้เคียงอย่างประเทศลาว เพื่อทำการศึกษาตัวอย่างที่ได้จากการออกสำรวจและตรวจสอบความสัมพันธ์ใกล้ชิดของตัวอย่างใหม่ดังกล่าว โดยความหลากหลายของปลากระดูกแข็งในช่วงเวลาหลังแสดงความหลากหลายเพิ่มมากขึ้นเรื่อย ๆ แต่อย่างไรก็ตามกลับพบว่าสมาชิกส่วนใหญ่จัดอยู่ในกลุ่มใหญ่เพียงไม่กี่กลุ่ม หลัก ๆ ได้แก่ สาย ginglymodians และสาย halecomorphs ซึ่งคาดว่าเกิดจากกระบวนการเกิดซากดึกดำบรรพ์ (taphonomical reasons) แต่เราไม่สามารถยกเว้นได้ว่าเอเชียตะวันออกเฉียงใต้เป็นศูนย์กลางความหลากหลายของปลาเหล่านี้ในช่วงเวลามีโซโซอิก ซึ่งในแง่การกระจายตัวทางภูมิศาสตร์โบราณของกลุ่มปลานี้ยังไม่ชัดเจน ในช่วงปลายยุคจูแรสสิกความสัมพันธ์ระหว่างเผ่าพันธุ์ทั้งหมดเกิดขึ้นภายในเอเชียกลาง จากนั้นเมื่อเข้าสู่ต้นยุคครีเทเชียสความสัมพันธ์ระหว่างเผ่าพันธุ์มีการย้ายการกระจายไปยังเอเชียตะวันออก ยิ่งไปกว่านั้นหลาย ๆ ชนิดที่กระจายในเอเชียยังแสดงความสัมพันธ์เชื่อมโยงกับกลุ่มปลาในแอฟริกา ดังนั้นการศึกษามากยิ่งขึ้นยิ่งเป็นการเพิ่มความเข้าใจเรื่องของวิวัฒนาการของกลุ่มนี้ได้มากยิ่งขึ้น ซึ่งจากข้อมูลด้านซากดึกดำบรรพ์ของปลากระดูกแข็งในไทยถือได้ว่าเป็นตัวแทนหลักใหญ่ที่แสดงบทบาทวิวัฒนาการของปลาน้ำจืดในช่วงมหายุคมีโซโซอิกทั่วโลก

คำหลัก : ginglymodians, phylogenetic studies, taphonomical, palaeobiogeographical, evolutionary history

บทสรุปผู้บริหาร

1. **ชื่อโครงการ : นิเวศวิทยาบรรพกาลของปลากระดูกแข็งน้ำจืดในมหายุคมีโซโซอิกของไทย**
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3. **สาขาวิชาที่ทำการวิจัย** : Palaeontology
4. **ระยะเวลาโครงการ: 2 ปี**
5. **ความเป็นมาและความสำคัญของงานวิจัย**

เอเชียตะวันออกเฉียงใต้จัดเป็นพื้นที่หลักที่แสดงความหลาหลายของปลาปัจจุบันอย่างปลาในอันดับ Cypriniforms ซึ่งเป็นกลุ่มที่พบมากในสภาพแวดล้อมน้ำจืด จัดเป็นกลุ่มที่เรียกว่า Otophysan fishes โดยการศึกษาระดับยีนนั้นบ่งบอกได้ว่าจุดกำเนิดและการแตกแขนงของปลาในอันนี้น่าจะเกิดที่เอเชียตะวันออกเฉียงใต้ในระหว่างช่วงอายุยุคจูแรสสิกตอนปลายหรือครีเทเชียสตอนต้น (Saitoh et al. 2011, Chen et al. 2013) แต่ที่แปลกไปกว่านั้นคือข้อมูลด้านซากดึกดำบรรพ์ของกลุ่มนี้ในไทยยังค่อนข้างมีน้อยเมื่อเทียบกับการแพร่กระจายพันธุ์ของปลาน้ำจืดอีกกลุ่มที่เรียกว่า ginglymodians ซึ่งปลาในอันดับ Cypriniforms ในช่วงมหายุคมีโซโซอิกยังไม่มีการค้นพบหลักฐานซากดึกดำบรรพ์ ยกเว้นในแอ่งไมโอซีนบริเวณทะเลสาบเพชรบูรณ์ทางตอนเหนือของประเทศไทยที่มีรายงานการค้นพบ (Robert and Jumnongthai, 1999) แต่อย่างไรก็ตาม เมื่อเทียบกับปลา ginglymodians ในปัจจุบันเป็นกลุ่มที่มีการกระจายจำกัดแค่บริเวณอเมริกาเหนือและอเมริกากลาง โดยปัจจุบันกลุ่มนี้เหลือเพียง 2 สกุล (the gars *Lepisosteus* and *Atractosteus*) 7 สปีชีส์ เท่านั้น ซึ่งวิวัฒนาการของปลาในเคลดนี้ยังคงเป็นปริศนามาอย่างยาวนาน แต่ข้อมูลการศึกษาเมื่อเร็ว ๆ นี้เผยให้เห็นถึงวิวัฒนาการในแต่ละวงศ์ (Grande, 2010) และยังเผยถึงความสัมพันธ์กับ holosteans อื่น ๆ อีกด้วย (Cavin, 2010; López-Arbarello, 2012)

ภายใต้ความร่วมมือในการทำงานวิจัยด้านบรรพชีวินวิทยาระหว่างนักวิจัยไทยและต่างชาติทำให้ทราบถึงความหลากหลายของปลาจิงกลีโมเดียนในช่วงปลายยุคจูแรสสิกและต้นยุคครีเทเชียสของกลุ่มหินโคราชที่ครอบคลุมพื้นที่ภาคตะวันออกเฉียงเหนือของไทย (Cavin et al., 2003; Cavin & Suteethorn, 2006; Cavin et al., 2009; Cavin et al., 2013; Cavin et al., 2014; Cavin et al., 2019; Deesri et al., 2014a and b; Deesri et al., 2016; Deesri et al., 2017) ซึ่งงานวิจัยหลาย ๆ งานนี้ มีทั้งที่ศึกษาความสัมพันธ์ทางสายวิวัฒนาการ แม้ว่าข้อมูลบางส่วนหรือสายวิวัฒนาการบางต้น (phylogenetic trees) ยังคงไม่แน่นอน แต่สายหลัก ๆ ระหว่างกลุ่มปลาจิงกลีโมเดียนที่พบบ่อย

เป็นประจำและค่อนข้างแน่นอน เช่น งานวิจัยของ Gibson, 2013 and Bermúdez-Rochas & Poyato-Ariza, 2015

ปลาจิงกลีโมเดียนช่วงระหว่างปลายยุคจูแรสสิกและต้นยุคครีเทเชียสของไทยและพื้นที่อื่น ๆ ของโลก แสดงการปรับตัวทางระบบนิเวศวิทยา เห็นได้ชัดจากความหลากหลายของรูปร่างและสัดส่วน รวมถึงรูปแบบของฟัน ตัวอย่างชิ้นแรกที่มีการสำรวจ บ่งชี้ว่าเป็นกลุ่มปลานักล่าปลา (piscivorous predators) และ เป็นปลาที่กินอาหารแข็ง (durophagous fishes) โดยอาศัยฟันบดเดี่ยว ๆ ที่หลุดมา (isolated crushing teeth) และกลุ่มที่กินพืชด้วยการครูดส่วนยอดของพืชน้ำ (grazer fish) สิ่งที่ซึ่งการค้นพบความหลากหลายของปลาจิงกลีโมเดียนพบว่าสอดคล้องกับความหลากหลายของปลาในอันดับ cypriniforms ปัจจุบัน อย่างน่าประหลาด นั่นแสดงว่าการกระจายพันธุ์ของทั้งสองกลุ่มเกิดขึ้นทั่วโลกในช่วงเวลาที่ค่อนข้างแน่นอน ยิ่งไปกว่านั้น การเข้าใจถึงความหลากหลายของปลาจิงกลีโมเดียนในเอเชียตะวันออกเฉียงใต้ และความหลากหลายของปลา cyprinids ปัจจุบันซึ่งอยู่ในแหล่งระบบนิเวศเดียวกันนี้ยังได้รับการสนับสนุนจากการศึกษาระดับยีนอีกด้วย (Bohlen et al., 2011) ซึ่งงานวิจัยดังกล่าวนำความสนใจให้กับนักบรรพชีวินวิทยา เนื่องจากทั้งนักชีววิทยาและนักนิเวศวิทยาต่างก็ทำงานเกี่ยวกับความสัมพันธ์ทางสายวิวัฒนาการของปลาในระบบแวดล้อมที่อยู่อาศัย โดยเฉพาะในเอเชียตะวันออกเฉียงใต้

ดังนั้นจุดมุ่งหมายของงานวิจัยนี้คือเพื่อศึกษาและอธิบายตัวอย่างใหม่ที่ได้จากการสำรวจและเก็บจากงานภาคสนามเพื่อตรวจสอบความสัมพันธ์ทางสายวิวัฒนาการ โดยใช้การวิเคราะห์ความใกล้ชิดของสายวิวัฒนาการ (cladistics method) รวมไปถึงการศึกษาโครงสร้างขนาดเล็กบนผิวเกล็ดของปลาจิงกลีโมเดียนด้วยการถ่ายภาพใต้กล้องกำลังขยายสูง (scanning electron microscope) รวมไปถึงการวิเคราะห์ลักษณะสัดส่วนรูปร่างของกระดูกและฟัน (morphometric analyses) ของตัวอย่างจากหลาย ๆ เช่น แหล่งภูน้ำจั้น และแหล่งภูน้อย ซึ่งเป็นแหล่งที่มีอายุอยู่ในหมวดหินภูกระดึง ยุคจูแรสสิกตอนปลายถึงต้นยุคครีเทเชียส รวมไปถึงเพื่อตรวจสอบนิเวศวิทยาบรรพกาลของปลาน้ำจืดไทยในช่วงมหายุคมีโซโซอิก โดยอาศัยการเปรียบเทียบระหว่างความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียนกับปลา cyprinids ปัจจุบัน เพื่อให้ได้มาซึ่งความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียนในมหายุคมีโซโซอิกและปลา cypriniforms อาจจำเป็นต้องมีการวิเคราะห์ลำดับยีนของปลา ปัจจุบันเข้าไปด้วย

ผลงานวิชาการที่ได้จากโครงการ

จากผลงานที่ได้นี้มีงานวิจัยที่ส่งตีพิมพ์ไปแล้ว 1 เรื่อง และที่กำลังเตรียมร่างงานวิจัยเพื่อส่งตีพิมพ์ในวารสารนานาชาติ ISI จำนวน 2 เรื่อง

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กิตติกรรมประกาศ

คณะผู้วิจัยโครงการ นิเวศวิทยาบรรพกาลของปลากระดูกแข็งน้ำจืดในมหายุคมีโซโซอิกของไทย ขอขอบพระคุณทุนพัฒนาศักยภาพในการทำงานวิจัยของอาจารย์รุ่นใหม่ที่ฝ่ายวิชาการสกวและสำนักงานคณะกรรมการการอุดมศึกษา (สกอ.) ได้สนับสนุน

ขอขอบพระคุณมหาวิทยาลัยมหาสารคาม ภาควิชาชีววิทยา คณะวิทยาศาสตร์ และศูนย์วิจัยและการศึกษาบรรพชีวินวิทยา ที่ได้สนับสนุนให้ทำวิจัยพร้อมเครื่องมือและสถานที่ได้อย่างเต็มที่

สารบัญ

สารบัญภาพ

ภาพที่ **หน้า**

บทที่ 1

1. บทนำ

1.1 ความสำคัญและที่มาของงานวิจัย

เอเชียตะวันออกเฉียงใต้จัดเป็นพื้นที่หลักที่แสดงความหลาหลายของปลาปัจจุบันอย่างปลาในอันดับ Cypriniforms ซึ่งเป็นกลุ่มที่พบมากในสภาพแวดล้อมน้ำจืด จัดเป็นกลุ่มที่เรียกว่า Otophysan fishes โดยการศึกษาระดับยีนนั้นบ่งบอกได้ว่าจุดกำเนิดและการแตกแขนงของปลาในอันนี้น่าจะเกิดที่เอเชียตะวันออกเฉียงใต้ในระหว่างช่วงอายุยุคจูแรสสิกตอนปลายหรือครีเทเชียสตอนต้น (Saitoh et al. 2011, Chen et al. 2013) แต่ที่แปลกไปกว่านั้นคือข้อมูลด้านซากดึกดำบรรพ์ของกลุ่มนี้ในไทยยังค่อนข้างมีน้อยเมื่อเทียบกับการแพร่กระจายพันธุ์ของปลาน้ำจืดอีกกลุ่มที่เรียกว่า ginglymodians ซึ่งปลาในอันดับ Cypriniforms ในช่วงมหายุคมีโซโซอิกยังไม่มีการค้นพบหลักฐานซากดึกดำบรรพ์ ยกเว้นในแอ่งไมโอซีนบริเวณทะเลสาบเพชรบูรณ์ทางตอนเหนือของประเทศไทยที่มีรายงานการค้นพบ (Robert and Jumnongthai, 1999) แต่อย่างไรก็ตาม เมื่อเทียบกับปลา ginglymodians ในปัจจุบันเป็นกลุ่มที่มีการกระจายจำกัดแค่บริเวณอเมริกาเหนือและอเมริกากลาง โดยปัจจุบันกลุ่มนี้เหลือเพียง 2 สกุล (the gars *Lepisosteus* and *Atractosteus*) 7 สปีชีส์ เท่านั้น ซึ่งวิวัฒนาการของปลาในเคลดนี้ยังคงเป็นปริศนามาอย่างยาวนาน แต่ข้อมูลการศึกษาเมื่อเร็ว ๆ นี้เผยให้เห็นถึงวิวัฒนาการในแต่ละวงศ์ (Grande, 2010) และยังเผยถึงความสัมพันธ์กับ holosteans อื่น ๆ อีกด้วย (Cavin, 2010; López-Arbarello, 2012)

ภายใต้ความร่วมมือในการทำงานวิจัยด้านบรรพชีวินวิทยาระหว่างนักวิจัยไทยและต่างชาติทำให้ทราบถึงความหลากหลายของปลาจิงกลีโมเดียนในช่วงปลายยุคจูแรสสิกและต้นยุคครีเทเชียสของกลุ่มหินโคราชที่ครอบคลุมพื้นที่ภาคตะวันออกเฉียงเหนือของไทย (Cavin et al., 2003; Cavin & Suteethorn, 2006; Cavin et al., 2009; Cavin et al., 2013; Cavin et al., 2014; Cavin et al., 2019; Deesri et al., 2014a and b; Deesri et al., 2016; Deesri et al., 2017) ซึ่งงานวิจัยหลาย ๆ งานนี้ มีทั้งที่ศึกษาความสัมพันธ์ทางสายวิวัฒนาการ แม้ว่าข้อมูลบางส่วนหรือสายวิวัฒนาการบางต้น (phylogenetic trees) ยังคงไม่แน่นอน แต่สายหลัก ๆ ระหว่างกลุ่มปลาจิงกลีโมเดียนที่พบบ่อยเป็นประจำและค่อนข้างแน่นอน เช่น งานวิจัยของ Gibson, 2013 and Bermúdez-Rochas & Poyato-Ariza, 2015

ปลาจิงกลีโมเดียนช่วงระหว่างปลายยุคจูแรสสิกและต้นยุคครีเทเชียสของไทยและพื้นที่อื่น ๆ ของโลก แสดงการปรับตัวทางระบบนิเวศวิทยา เห็นได้ชัดจากความหลากหลายของรูปร่างและสัดส่วน รวมถึงรูปแบบของฟัน ตัวอย่างชิ้นแรกที่มีการสำรวจ บ่งชี้ว่าเป็นกลุ่มปลานักล่าปลา (piscivorous predators) และ เป็นปลาที่กินอาหารแข็ง (durophagous fishes) โดยอาศัยฟันบดเดี่ยว ๆ ที่หลุด

มา (isolated crushing teeth) และกลุ่มที่กินพืชด้วยการครูดส่วนยอดของพืชน้ำ (grazer fish) สิ่งที่ซึ่งการค้นพบความหลากหลายของปลาจิงกลีโมเดียนพบว่าสอดคล้องกับความหลากหลายของปลาในอันดับ cypriniforms ปัจจุบัน อย่างน่าประหลาด นั่นแสดงว่าการกระจายพันธุ์ของทั้งสองกลุ่มเกิดขึ้นทั่วโลกในช่วงเวลาที่ค่อนข้างแน่นอน ยิ่งไปกว่านั้น การเข้าใจถึงความหลากหลายของปลาจิงกลีโมเดียนในเอเชียตะวันออกเฉียงใต้ และความหลากหลายของปลา cyprinids ปัจจุบันซึ่งอยู่ในแหล่งระบบนิเวศเดียวกันนี้ยังได้รับการสนับสนุนจากการศึกษาระดับยีนอีกด้วย (Bohlen et al., 2011) ซึ่งงานวิจัยดังกล่าวนำความสนใจให้กับนักบรรพชีวินวิทยา เนื่องจากทั้งนักชีววิทยาและนักนิเวศวิทยาต่างก็ทำงานเกี่ยวกับความสัมพันธ์ทางสายวิวัฒนาการของปลาในระบบแวดล้อมที่อยู่อาศัยโดยเฉพาะในเอเชียตะวันออกเฉียงใต้

ดังนั้นจุดมุ่งหมายของงานวิจัยนี้คือเพื่อศึกษาและอธิบายตัวอย่างใหม่ที่ได้จากการสำรวจและเก็บจากงานภาคสนามเพื่อตรวจสอบความสัมพันธ์ทางสายวิวัฒนาการ โดยใช้การวิเคราะห์ความใกล้ชิดของสายวิวัฒนาการ (cladistics method) รวมไปถึงการศึกษาโครงสร้างขนาดเล็กบนผิวเกล็ดของปลาจิงกลีโมเดียนด้วยการถ่ายภาพใต้กล้องกำลังขยายสูง (scanning electron microscope) รวมไปถึงการวิเคราะห์ลักษณะสัดส่วนรูปร่างของกระดูกและฟัน (morphometric analyses) ของตัวอย่างจากหลาย ๆ เช่น แหล่งภูน้ำจั้น และแหล่งภูน้อย ซึ่งเป็นแหล่งที่มีอายุอยู่ในหมวดหินภูกระดึงยุคจูแรสสิกตอนปลายถึงต้นยุคครีเทเชียส รวมไปถึงเพื่อตรวจสอบนิเวศวิทยาบรรพกาลของปลาน้ำจืดไทยในช่วงมหายุคมีโซโซอิก โดยอาศัยการเปรียบเทียบระหว่างความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียนกับปลา cyprinids ปัจจุบัน เพื่อให้ได้มาซึ่งความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียนในมหายุคมีโซโซอิกและปลา cypriniforms อาจจำเป็นต้องมีการวิเคราะห์ลำดับยีนของปลา ปัจจุบันเข้าไปด้วย

1.2 วัตถุประสงค์

1.2.1. เพื่อสำรวจการค้นพบตัวอย่างปลาชนิดใหม่ จากการขุดสำรวจในแหล่งเดิม เช่น ภูน้ำจั้น ภูน้อย ช่องชาด และแหล่งอื่น ๆ รวมทั้งการสำรวจและขุดในแหล่งใหม่จากแหล่งต่าง ๆ ในยุคไทรแอสสิก และยุคครีเทเชียสอื่น ๆ ทั้งใน ไทย และในประเทศลาว เป็นต้น

1.2.2. เพื่อศึกษาลักษณะทางสัณฐานวิทยากระดูกและตรวจสอบความสัมพันธ์ทางสายวิวัฒนาการของปลาจิงกลีโมเดียนชนิดใหม่ในไทย

1.2.3. เพื่อให้เกิดองค์ความรู้ใหม่ ๆ เกี่ยวกับสภาพนิเวศถิ่นอาศัยของปลาจิงกลีโมเดียนในไทยเปรียบเทียบกับสภาพนิเวศถิ่นอาศัยของปลา cypriniforms ปัจจุบัน

1.3 ระเบียบวิธีวิจัย

1.3.1. ศึกษางานวิจัยที่เกี่ยวข้อง

1.3.2. ศึกษาหรือบรรยายลักษณะของตัวอย่างใหม่โดยอาศัยการเปรียบเทียบลักษณะสัณฐานวิทยาภายนอก

1.3.3. ศึกษาหรือวิเคราะห์ความสัมพันธ์ใกล้ชิดทางสายวิวัฒนาการด้วยวิธี cladistics methods

1.3.4. ศึกษาโครงสร้างขนาดเล็กบนผิวเกล็ด (MEB) กรณีตัวอย่างใหม่ที่ได้จากการเก็บใหม่ไม่สมบูรณ์เพียงพอให้ทำการเปรียบเทียบลักษณะโครงสร้างภายนอกได้ อาจใช้เฉพาะส่วนของเกล็ดมาทำการตรวจสอบแทน

1.3.5. ศึกษาและวิเคราะห์ลักษณะสัดส่วนรูปร่างและรูปแบบของฟัน โดยอาศัยการนับฟัน (morphometric analyses)

บทที่ 2

2. แหล่งสำรวจตัวอย่างในช่วงมหายุคมีโซโซอิก

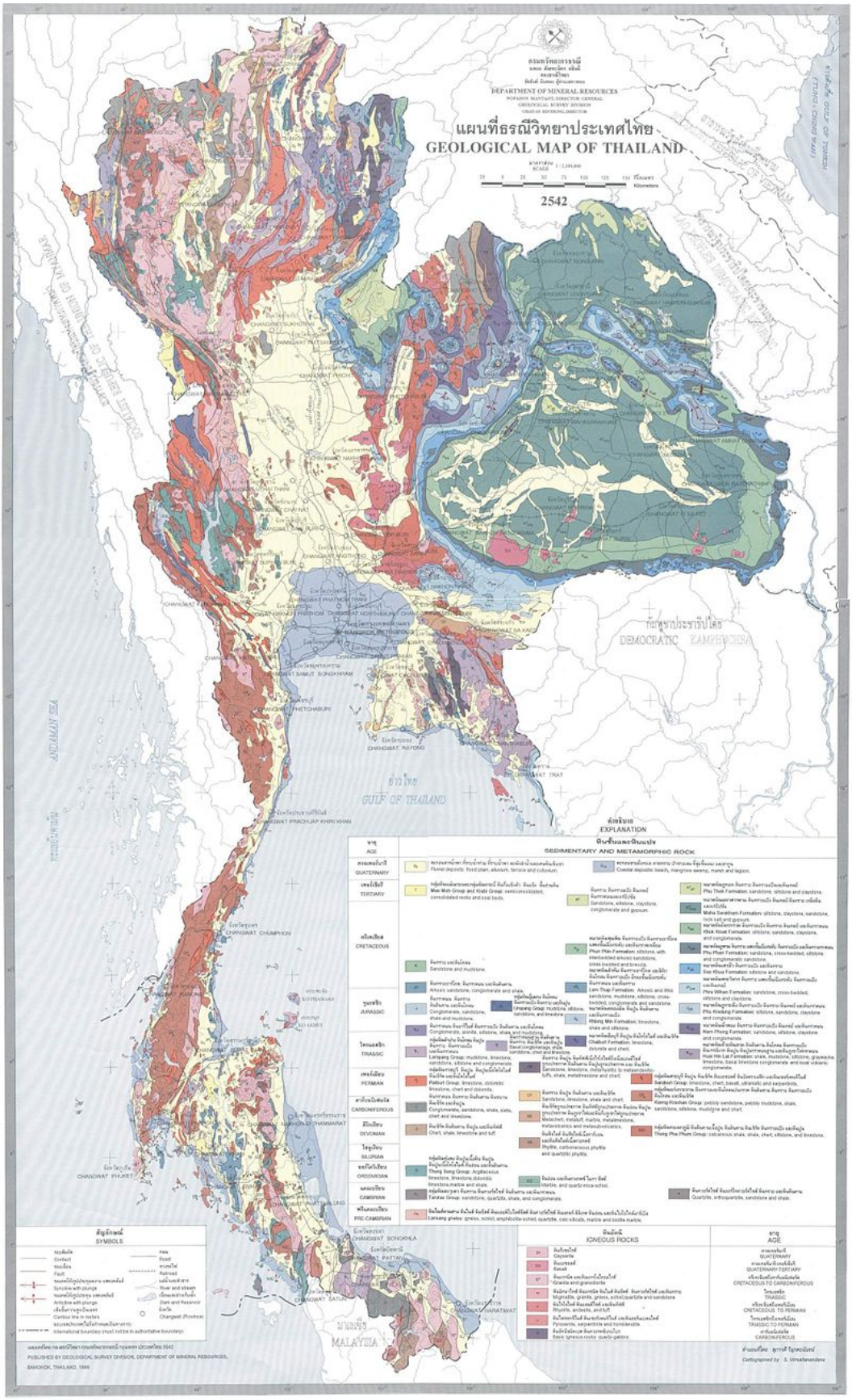
เนื่องจากพื้นที่ส่วนใหญ่ในประเทศไทยที่มีการสะสมตัวของตะกอนหรือชุดหินในมหายุคมีโซโซอิกนั้นพบมากบริเวณภาคตะวันออกเฉียงเหนือ ดังแสดงในภาพที่ 2-1 ในแผนที่ธรณีวิทยาประเทศไทย จะพบว่ามีพื้นที่สีเขียว (แทนหมวดหินที่มีอายุในยุคครีเทเชียส) กินพื้นที่บริเวณภาคตะวันออกเฉียงเหนือ หรือ ที่เรียกว่า กลุ่มหินโคราชเกือบทั้งหมด ในขณะที่บริเวณขอบด้านทิศตะวันตกของที่ราบสูงโคราชนั้นจะมีสีม่วง (แทนหมวดหินห้วยหินลาด และหมวดหินน้ำพอง ซึ่งจัดอยู่ในยุคไทรแอสสิก) และสีฟ้า (แทนหมวดหินภูกระดึงซึ่งจัดอยู่ในยุคจูแรสสิก) สำหรับการสะสมตัวของตะกอนในช่วงเวลานี้จะพบซากดึกดำบรรพ์ของสัตว์ในช่วงมหายุคมีโซโซอิก ได้แก่ สัตว์เลื้อยคลานและสัตว์ร่วมยุค อย่าง ปลากระดูกแข็ง ปลากระดูกอ่อน เป็นจำนวนมาก และค่อนข้างหลากหลาย ในขณะที่มหายุคซีโนโซอิกซึ่งพบกระจายบริเวณแอ่งสะสมตะกอนซีโนโซอิกตามภาคเหนือและภาคใต้ พบซากดึกดำบรรพ์ของสัตว์เลี้ยงลูกด้วยน้ำนมเป็นส่วนใหญ่ ร่วมกับสัตว์เลื้อยคลาน และปลาที่มีความใกล้เคียงกับปลาปัจจุบันมากขึ้นแทน ดังนั้น เพื่อให้ได้มาซึ่งตัวอย่างในช่วงมหายุคมีโซโซอิก จึงจำเป็นต้องมีการออกสำรวจและเก็บรวบรวมตัวอย่างจากแหล่งต่าง ๆ ในจังหวัดต่าง ๆ ที่แสดงลักษณะชั้นหินในหมวดหินต่าง ๆ ตามอายุที่กำหนดโดยนักธรณีวิทยา ซึ่งตัวอย่างที่ได้จากการออกสำรวจ จะมีการจากแหล่งเดิมที่เคยทำการสำรวจหรือขุดค้นไว้อยู่แล้ว และจากแหล่งใหม่ที่ต้องออกสำรวจเพิ่มเติม เพื่อให้ได้มาซึ่งตัวอย่างที่ฝังตัวอยู่ในชั้นหิน

2.1 การลำดับชั้นหิน

หมวดหินต่าง ๆ ในกลุ่มหินโคราช เรียงลำดับจากอายุเก่าไปอ่อน ประกอบด้วย

หมวดหินห้วยหินลาด (Huai Hin Lat Formation) เป็นหมวดหินล่างสุดของชั้นตะกอนบนภาคพื้นทวีปวางตัวไม่ต่อเนื่องกับหมวดหินน้ำดุกและชั้นหินปูนเพอร์เมียนตอนบน ลักษณะทางกายภาพของหินแบ่งออกได้เป็น 2 ส่วน คือ ส่วนล่างหนา 200 เมตร ประกอบด้วยหินกรวดมนพื้นฐานโดยมีหินปูนสลับอยู่ด้านบนเล็กน้อย ส่วนบนหนา 50 เมตร ประกอบด้วยหินทรายและหินโคลน สีเทาสลับกัน มีหินปูนปนโคลน สีเทาแกมดำแทรก ซึ่งเมื่อผุมีสีขาว

หมวดหินน้ำพอง (Nam Phong Formation) เป็นหมวดหินที่มีอายุตะกอนสะสมอยู่ในยุคแรกของมหายุคมีโซโซอิก นั่นคือยุคไทรแอสสิก พบแผ่กระจายตัวทางด้านตะวันออกเฉียงใต้ ของพื้นที่จังหวัดขอนแก่น และเพชรบูรณ์ ได้จัดแบ่งลำดับชั้นของหมวดหินนี้ออกเป็น 3 ส่วน คือ ในส่วนล่างเป็นการสะสมตะกอนหินทรายแป้ง หินทราย และหินโคลน สีน้ำตาลแกมแดง สีม่วงแกมแดงมีความคงทนต่อ



ภาพที่ 2-1 แผนที่ธรณีวิทยาประเทศไทย

การทำลายน้อย ลำดับชั้นหินบริเวณส่วนกลางประกอบด้วยหินทรายและหินกรวดมนชั้นหนา ซึ่งมีกรวดขนาดประมาณ 5 เซนติเมตร ของแร่ควอตซ์ หินเชิร์ต หินทรายแป้ง สีน้ำตาลแกมแดงและหินอัคนี ลำดับชั้นหินบริเวณส่วนบน ประกอบด้วยหินดินดาน หินโคลนและหินทรายแป้ง สีน้ำตาลแกมแดง ลักษณะคล้ายคลึงกับลำดับชั้นด้านล่าง ความหนาของหมวดหินน้ำพองมีความแปรเปลี่ยนอยู่ในช่วงประมาณ 100 - 1,500 เมตร สภาพแวดล้อมของการสะสมตัวของตะกอนเกิดจากการสะสมตัวของตะกอนในที่ราบเชิงเขาในระยะแรก และแปรเปลี่ยนไปเป็นการตกตะกอนในแม่น้ำที่มีกระแสน้ำรุนแรงโดยจะพบชั้นหินกรวดมนตามร่องน้ำและหลังจากนั้นเป็นการตกตะกอนบริเวณสองฝั่งของที่ราบลุ่มแม่น้ำในสภาวะภูมิอากาศที่ค่อนข้างกึ่งแห้งแล้ง ทำให้เกิดการสะสมตะกอนเม็ดละเอียด จากหลักฐานซากดึกดำบรรพ์ที่พบในหลายพื้นที่สามารถบ่งชี้ได้ว่าหมวดหินน้ำพองมีอายุในยุคไทรแอสซิกตอนปลาย

หมวดหินภูกระดึง (Phu Kradung Formation) จัดเป็นตะกอนที่สะสมตัวในยุคจูแรสสิก พบแผ่กระจายตัวอยู่รอบที่ราบสูงโคราช โดยมากล้อมรอบตะกอนหินครีเทเชียส ประกอบด้วยหินทรายแป้งสีแดงแกมม่วง สีน้ำตาลแกมแดง และสีเทาแกมเขียว มีกมีแร่ไมกาปน บางบริเวณมีชั้นหินปูนบางๆ สลับ ตอนกลางของหมวดหินเป็นหินทรายแป้ง หินโคลน สีน้ำตาลแกมแดง มีเม็ดปูนและชั้นเม็ดปูน โดยมีหินทรายเนื้อไมกาและหินกรวดมนเม็ดปูนสลับบ้าง ตอนบนของหมวดหินเป็นหินทรายแป้งสลับชั้นหินทราย หินโคลนและหินกรวดมนเนื้อปูน สีแดงแกมเทา และสีเทาแกมเขียว ชั้นบนสุดพบโผล่เป็นหน้าผาหินทราย สีน้ำตาลแกมแดง และมีชั้นหินทรายแป้งสลับบ้าง หินเหล่านี้แสดงถึงสภาพแวดล้อมของการสะสมตัวของตะกอนในบริเวณทางน้ำโค้งตวัดที่มีกระแสน้ำรุนแรง บริเวณสองฝั่งที่ราบลุ่มแม่น้ำ หนอง และบึง ถายใต้สภาวะภูมิอากาศกึ่งแห้งแล้ง

หมวดหินพระวิหาร (Pha Wihan Formation) จัดเป็นหมวดหินในยุคครีเทเชียสตอนต้น พบตะกอนหินแผ่กระจายตัวบริเวณภูเขาสูง วงแหวนรอบนอก ประกอบด้วยหินทราย สีขาว สีเทา สีน้ำตาล เม็ดละเอียดถึงหยาบ มีการคัดขนาดและความมนดี ประกอบด้วยเม็ด ควอรตซ์เป็นส่วนใหญ่ แสดงชั้นหนาถึงไม่แสดงชั้น พบแนวชั้นเฉียงระดับขนาดใหญ่ อยู่ทั่วไป นอกจากนี้ยังมีหินทรายแป้ง หินโคลน ชั้นบางๆ และหินกรวดมน มีความคงทนต่อการพุพังทำลายสูง ดังนั้นจึงมักจะเห็นหมวดหินนี้แสดงลักษณะเป็นสันเขาแนวยาวเป็นรูปเควสต้า หรือรูปอีโต้ มีความหนาของชั้นหินประมาณ 50 - 250 เมตร สภาพแวดล้อมของการตกตะกอนเกิดจากการสะสมตะกอนจากแม่น้ำชนิด ธารน้ำประสานสาย และมีแม่น้ำโค้งตวัดเป็นบางครั้ง ในสภาพภูมิอากาศที่ค่อนข้างกึ่งแห้งแล้งและร้อนชื้น จากข้อมูลด้านซากดึกดำบรรพ์ ยังไม่ปรากฏชิ้นส่วนเศษกระดูก พบเฉพาะที่เป็นร่อยรอยทางเดินของไดโนเสาร์ เช่น แหล่งรอยตีนไดโนเสาร์ในเขตอุทยานแห่งชาติภูเวียง จ. ขอนแก่น เป็นต้น

หมวดหินเสาขัว (Sao Khua Formation) เป็นหมวดหินที่พบกระจายตัวตามเนินเขาวงแหวนรอบใน เป็นเนินเขาไม่สูงมากนัก มักเป็นเขาลูกโดด อยู่ในช่วงชั้นความสูงประมาณ 240 - 465 เมตร เหนือ

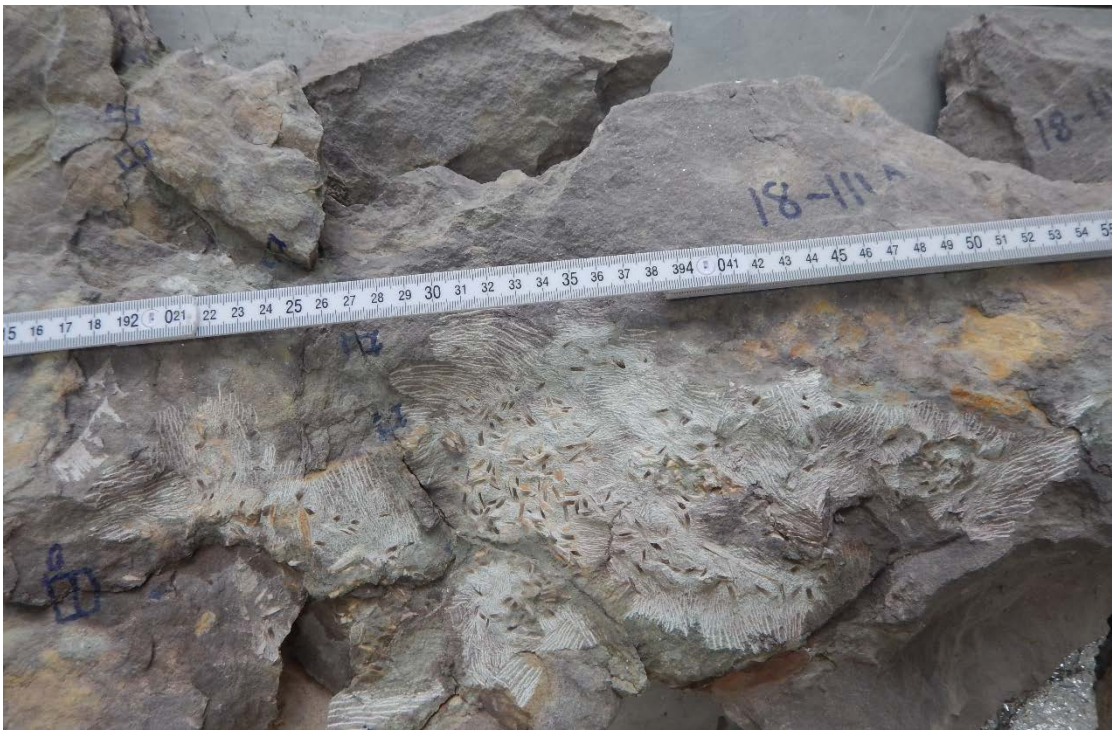
ระดับทะเลปานกลาง หมวดหินเสาขัวประกอบด้วยชั้นหินสลับกันเป็นแบบ cycle ของหินโคลนหินทราย สีน้ำตาลแกมแดง สลับกับหินทรายแป้ง หินทราย เม็ดละเอียดถึงเม็ดปานกลาง และหินกรวดมนกับชั้นของ caliches, calcrete nodules และ thin- bedded and nodular silicrete โดยทั่วไปชั้นหินของหมวดหินเสาขัวมีสีน้ำตาลแกมแดง และมี calcrete และ silcrete หนาและเด่นกว่าที่พบในหมวดหินภูกระดึงและหมวดหินโคกกรวด ชั้นหินมีความหนาระหว่าง 200 - 760 เมตร โดยวางตัวต่อเนื่องจากหมวดหินพระวิหาร และเกิดจากการสะสมตะกอนจากแม่น้ำโค้งตวัด ที่พบว่ามีการตกตะกอนในร่องน้ำทั้งหินกรวดมน หินทราย และตะกอนที่สะสมตัวในที่ราบน้ำท่วมขัง ในสภาพภูมิอากาศที่เป็นแบบกึ่งแห้งแล้ง แต่พบว่าเป็นหมวดหินที่พบซากดึกดำบรรพ์สะสมเป็นจำนวนมากและค่อนข้างหลากชนิด

หมวดหินภูพาน (Phu Phan Formation) พบแผ่กระจายตัวไม่มากนักโดยหมวดหินชุดนี้จะพบเป็นเนินที่ไม่สูงมากนักต่อเนื่องจากเนินเขาของหมวดหินเสาขัว ประกอบด้วยหินทราย สีเทาแกมขาว มีขนาดเม็ดตะกอนปานกลางถึงเม็ดหยาบ หินกรวดมน เป็นชั้นหนาและมีชั้นเฉียงระดับขนาดใหญ่ทั้งแบบ planar และ แบบ trough cross-bedding โดยมีส่วนประกอบเป็นพวกควอตซ์สีขาว หินภูเขาไฟ หินเชิร์ตสีเทา เทาดำ น้ำตาล แดง ดำ และเขียว เม็ดตะกอนมีความมนดีแต่มีการคัดขนาดไม่ค่อยดี ในบางแห่งมีชั้นหินดินดาน สีเทาแกมดำสลับอยู่มีลักษณ์เป็นเลนส์ ลักษณะเด่นของหมวดหินภูพาน คือ เป็นหินทรายและหินกรวดมน สีน้ำตาลแกมเหลือง ส้มอ่อน ชมพู และขาว บางชั้นของหินทรายมีกรวดปน แสดงลักษณะเด่นของชั้นเฉียงระดับขนาดกลาง ถึงขนาดใหญ่ หมวดหินภูพานมีความหนาระหว่าง 80 - 140 เมตร วางตัวต่อเนื่องกับหมวดหินเสาขัวที่วางตัวอยู่ล่าง เกิดจากการสะสมตัวและตะกอนจากแม่น้ำชนิดธารประสานสาย และแม่น้ำโค้งตวัดเป็นบางครั้งบางคราว ในสภาพภูมิอากาศที่ค่อนข้างร้อนชื้นถึงกึ่งแห้งแล้ง จากข้อมูลด้านซากดึกดำบรรพ์พบว่าในหมวดหินนี้ ยังไม่ปรากฏเศษชิ้นส่วนของซากดึกดำบรรพ์เช่นเดียวกันกับหมวดหินพระวิหาร พบเฉพาะแหล่งรอยตีนของไดโนเสาร์

หมวดหินโคกกรวด (Khok Kruat Formation) หมวดหินนี้พบกระจายตัวไม่มาก ตามเนินดินที่สูงหรือตามท้องนา ที่ลุ่ม ประกอบด้วยหินทราย สีแดงอ่อน แดงแกมเทา สีน้ำตาลแกมแดง ขาวแกมน้ำตาล ชั้นบางถึงปานกลาง เม็ดตะกอนขนาดละเอียด บางชั้นมีการปนของเม็ดกรวด หินทรายแป้ง หินโคลนและหินกรวดมน สีน้ำตาลแกมแดง สีแดงแกมม่วง นอกจากนี้ยังพบชั้น caliches และ calcrete nodules อยู่ในชั้นหินโคลน ชั้นหินหมวดนี้วางตัวต่อเนื่องจากหมวดหินภูพาน มีความหนาแปรเปลี่ยนประมาณ 30 - 150 เมตร เกิดจากการสะสมตัวและตะกอนจากแม่น้ำแบบโค้งตวัด ในสภาพภูมิอากาศที่ค่อนข้างกึ่งแห้งแล้งและในช่วงปลายของหมวดหินเป็นแบบแห้งแล้ง

อย่างไรก็ตามแหล่งสำรวจในแต่ละแหล่งจะมีสภาพการเก็บรักษาตัวอย่างและลักษณะของตะกอนแตกต่างกัน อาจขึ้นอยู่กับสภาพแวดล้อม ณ ขณะนั้นแตกต่างกัน เช่น ในแหล่งภูน้อย อ.คำ

ม่วง จ. กาฬสินธุ์ ตะกอนส่วนใหญ่เป็นตะกอนหินทราย ทรายแป้ง และหินโคลน บ่งชี้ว่าเกิดในสภาพแวดล้อมที่เป็นน้ำนิ่ง หรือไหลเอื่อย ๆ ในขณะที่ในแหล่งบ้านโกรกเดือนห้า อ.เมือง จ. นครราชสีมา ตะกอนมีลักษณะค่อนข้างเฉพาะตัว นั่นคือประกอบด้วยหินกรวด หินทรายเม็ดหยาบและขนาดใหญ่ แทรกปนอยู่กับก้อนหินโคลน (mud nodule) ซึ่งตัวอย่างมักแทรกฝังตัวอยู่ในก้อนหินโคลนดังกล่าว ดังแสดงในภาพที่ และ ภาพที่ 2-



ภาพที่ 2-2 ตัวอย่างในแหล่งภูน้อย อ.คำม่วง จ. กาฬสินธุ์ ฝังตัวในตะกอนหินทรายปนโคลน

ภาพที่ 2-3 ตัวอย่างในแหล่งบ้านโกรกเดือนห้า อ.เมือง จ. นครราชสีมา ฝังตัวในตะกอนมีลักษณะค่อนข้างเฉพาะตัว นั่นคือประกอบด้วยหินกรวด หินทรายเม็ดหยาบและขนาดใหญ่

บทที่ 3

3.1 ความหลากหลายของซากดึกดำบรรพ์ปลากระดูกแข็งในประเทศไทย

ตัวอย่างที่ได้จากการเก็บสำรวจเพิ่มเติมเพื่อนำมาศึกษาและจากการตรวจสอบเอกสารนั้น พบว่าค่อนข้างหลากหลายกลุ่ม ซึ่งปลากระดูกแข็งแบ่งออกเป็น 2 subclass ได้แก่ subclass Actinopterygii ซึ่งเป็นซับคลาสของปลากลุ่มที่มีก้านครีบแข็ง ดังนี้

“Palaeonisciformes”

ปลาในอันดับ Palaeonisciforms เป็นสายที่ไม่จัดว่าเป็น monophyletic group ซึ่งเป็นกลุ่มที่ค่อนข้างมีปรากฏน้อยในเมืองไทย และแม้กระทั่งปัจจุบันเองยังพบตัวอย่างเพียงไม่กี่ตัวอย่าง ซึ่งคาดว่าจัดอยู่ใน cf. *Ptycholepis* sp. โดยพบในแหล่งบ้านโคกสนาม (แหล่งเดิม) และล่าสุดพบในแหล่งภูน้อย ซึ่งทั้งสองแหล่งตั้งอยู่ในเขต อ.คำม่วง จ. กาฬสินธุ์ ซึ่งสกุลนี้แสดงลักษณะค่อนข้างเฉพาะ นั่นคือ เกล็ดที่ปรากฏมีลักษณะเป็นทรงสี่เหลี่ยม (ganoid scale) แคบ ยาว และมีสันยาววางเรียงขนานไปกับแนวยาวของเกล็ด แสดงดังใน**Error! Reference source not found.** และ 3-2

ภาพที่ 3-1 ตัวอย่างเกล็ดและกระดูกของปลาในอันดับ Palaeonisciforms ในแหล่งภูน้อย (แหล่งใหม่)

ภาพที่ 3-2 ตัวอย่างเกล็ดของปลาในอันดับ Palaeonisciforms ในแหล่งบ้านโคกสนาม (แหล่งเดิม)

Pycnodontiformes

เป็นอันดับของกลุ่มปลาที่สูญพันธุ์ไปแล้วซึ่งมีลักษณะรูปร่างที่แปลกประหลาด และพบปรากฏน้อย ส่วนใหญ่พบปรากฏในตะกอนน้ำเค็ม แต่ก็มีบ้างที่ปรากฏในตะกอนแหล่งน้ำจืดช่วงยุคจูแรสสิกตอนกลางหรือตอนปลายทางตอนใต้ของประเทศไทย ในหมวดหินมาบชิง (Mab Ching Formation) และในหลาย ๆ แหล่งช่วงยุคครีเทเชียสตอนต้นประมาณอายุ Hauterivian ถึง Barremian ในหมวดหินเสาขัว (Sao Khua Formation) เช่น แหล่งภูพานทอง จ.หนองบัวลำภู โดยซากดึกดำบรรพ์ที่พบ มีลักษณะเป็นเศษฟันขนาดเล็ก ที่น่าสนใจเนื่องจากค่อนข้างน้อยที่พบในแหล่งน้ำจืด จัดเป็นตัวแทนเดียวที่พบปรากฏในฝั่งตะวันออกของโลกโบราณ

Ginglymodi

ปลาในสายนี้จัดอยู่ร่วมกับกลุ่ม Halecomorphi เรียกเป็นชื่อใหม่ว่า Holostei ซึ่งยังคงมีสมาชิกเหลือรอดอยู่ในปัจจุบันจัดอยู่ในอันดับของปลาการ์ (living gars) โดยพบกระจายพันธุ์ในแถบอเมริกาเหนือ ซากดึกดำบรรพ์ของปลาจิงกลีโมเดียนจัดเป็นกลุ่มที่พบมากสุดในประเทศไทย ประกอบด้วย

จิงกลีโมเดียนที่พบปรากฏเก่าแก่ที่สุดในช่วงปลายยุคไทรแอสสิกของหมวดหินห้วยหินลาด ในแหล่งห้วยผาผึ้ง อ.คอนสาร จ. ชัยภูมิ ซึ่งการศึกษาเบื้องต้นเป็นการอธิบายลักษณะตัวอย่างไว้แล้ว แต่ยังไม่สามารถส่งตีพิมพ์ลงในวารสารเนื่องจากเนื้อหารายละเอียดยังไม่สมบูรณ์ต้องอาศัยตัวอย่างเพิ่มเติม

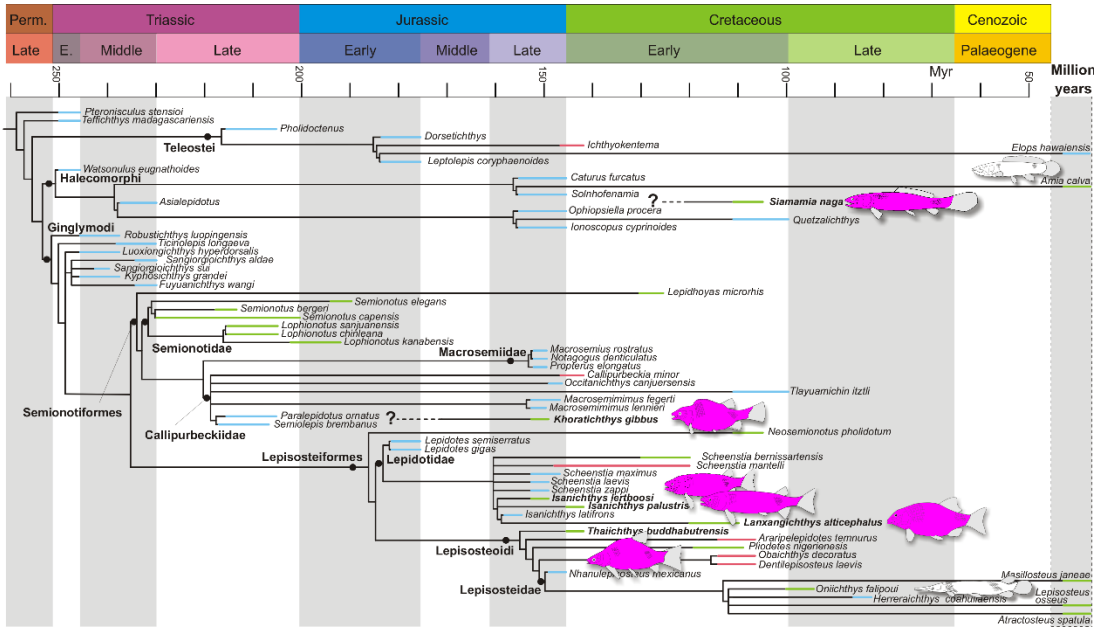
ในหมวดหินภูกระดึง จัดอยู่ในช่วงกลางถึงปลายยุคจูแรสสิก เป็นหมวดหินที่พบความหลากชนิดของปลาจิงกลีโมเดียนมากที่สุด ในแหล่งเขาภูหลวง อ.วังน้ำเขียว จ. นครราชสีมา จัดเป็นชนิดที่โบราณที่สุด คือ *Khoratichthys gibbus* (Deesri et al., 2016) และชนิดต่อมาคือ *Isanichthys lertboosi* (Deesri et al., 2014) ในแหล่งภูน้อย อ.คำม่วง จ. กาฬสินธุ์ ชนิดถัดมาคือ *Thaiichthys buddhabutrensis* พบในแหล่งภูน้ำจั้น ซึ่งวางตัวอยู่บนสุดของหมวดหิน คาดว่ามีอายุอยู่ในช่วงต้นยุคครีเทเชียส (Berriasian) และจัดเป็นสกุลที่พบค่อนข้างมาก โดยเฉพาะในแหล่งภูน้ำจั้น อ.กุฉินารายณ์ จ. กาฬสินธุ์ สามารถศึกษารายละเอียดสัณฐานวิทยาภายนอก กายวิภาค และกระบวนการเกิดซากดึกดำบรรพ์ได้เป็นอย่างดี เนื่องจากพบเป็นจำนวนมาก นอกจากนี้แล้วยังพบในแหล่งช่องชาด อ.โนนสัง จ. หนองบัวลำภู แหล่งบ้านคำพอก จ. มุกดาหาร ปลาจิงกลีโมเดียนในแหล่งภูน้ำจั้นนอกจาก *Thaiichthys* ซึ่งพบเป็นจำนวนมากในแหล่งภูน้ำจั้นแล้ว ยังพบตัวอย่างต้นแบบของ *Isanichthys palustris* (Cavin & Suteethorn, 2006) ซึ่งเป็นสกุลเดียวกับที่พบในแหล่งภูน้อยด้วยเช่นกัน

ปลาจิงกลีโมเดียนในหมวดหินเสาขัว (Sao Khua Formation) พบค่อนข้างน้อย และตัวอย่างที่พบส่วนใหญ่แตกหักเป็นเศษ ชิ้นส่วนของฟัน และเกล็ด

จิงกลีโมเดียนในหมวดหินโคกกรวด (Khok Kruat Formation) อายุประมาณ Aptian-Albian ส่วนใหญ่ก็มีลักษณะแตกหักเป็นเศษชิ้นเล็กไม่สมบูรณ์เช่นเดียวกันกับหมวดหินเสาขัว ยกเว้นในแหล่งบ้านสะพานหิน อ.เมือง จ. นครราชสีมา พบเศษกระดูกส่วนหัวร่วมกับเศษเกล็ดที่ยังคงเรียงกันบ้าง แต่ไม่สมบูรณ์ทั้งตัว และถึงแม้จะพบแค่เศษกระดูกส่วนหัว แต่ลักษณะที่พบกลับพบกระดูกชิ้นที่เป็นลักษณะเฉพาะที่คล้ายกับส่วนหัวของปลาที่พบในหมวดหิน ของประเทศลาว ซึ่งเป็นหมวดหินที่เทียบเคียงได้กับหมวดหินโคกกรวดของไทย จึงระบุชนิดใหม่ชนิดเดียวกันกับ *Lanxangichthys alticephalus* ที่พบในหมวดหิน ของประเทศลาว (Cavin et al., 2019)

Halecomorphi

ปลาในสายนี้ปัจจุบันเหลือเพียงชนิดเดียวคือ ปลา bowfin (*Amia calva*) ซึ่งกระจายพันธุ์อยู่ในแหล่งน้ำจืดในประเทศอเมริกาเหนือเท่านั้น อย่างไรก็ตาม ข้อมูลซากดึกดำบรรพ์ปลาในสายนี้ยังไม่มีปรากฏในแหล่งใดในช่วงยุคไทรแอสสิกและยุคจูแรสสิกของไทย พบปรากฏเฉพาะในหมวดหินเสาขัวและหมวดหินโคกกรวดเท่านั้น ชนิดแรกที่เป็นที่รู้จักในประเทศไทยไทยคือ *Siamamia naga* (Cavin et al., 2007a) จัดอยู่วงศ์ Siamamiidae ซึ่งเป็นวงศ์ที่พบในยุคครีเทเชียส และจัดว่าเป็นกลุ่มสัตว์เฉพาะถิ่นในเอเชียตะวันออก เช่น จีน ญี่ปุ่น และในประเทศไทย โดยในประเทศไทยค้นพบในแหล่งภูพอก อ.เต่างอย จ. สกลนคร ถือเป็นที่แรกที่เป็นที่รู้จัก จากนั้นก็มีปรากฏเศษชิ้นส่วนในแหล่งอื่น ๆ เช่น แหล่งหนองสูง จ. มุกดาหาร แหล่งภูพานทอง จ. หนองบัวลำภู แหล่งภูดินแดง อ.นาแก จ. นครพนม ซึ่งในแหล่งภูดินแดงนี้ นอกจากปรากฏลักษณะของเกล็ดที่เรียบ บาง คล้าย cf. *Siamamia* แล้ว ยังพบเกล็ดที่ค่อนข้างประหลาดและแตกต่างแหล่งอื่น ๆ นั่นคือ บริเวณผิวเกล็ดไม่เรียบ แต่ปรากฏลักษณะเป็นหนามแหลมคล้ายฟันที่ผิวเกล็ด (Tong et al., 2019) ซึ่งเบื้องต้นคาดว่าอยู่ในวงศ์ย่อย Vidalamiinae นั่นคือ ฟันที่ขากรรไกรล่างมีลักษณะยอดฟันที่แหลมคล้ายหัวหอก ในขณะที่ตัวฟันค่อนข้างยาว ร่วมกับลักษณะของเกล็ดที่เป็นหนามแหลมบนผิวเกล็ด ทำให้จัดจำแนกแตกต่างไปจาก *Siamamia* ในหมวดหินโคกกรวด เศษซากของปลาในวงศ์ sinamiids เป็นที่รู้จักและพบกระจายอยู่เป็นจำนวนมากในแหล่งโคกฝาส้วม อ.ศรีเมืองใหม่ จ. อุบลราชธานี และอีกตัวอย่างที่มีการเก็บรักษา (preservation) ค่อนข้างดี ถูกค้นพบเมื่อไม่นานมานี้ ในแหล่งบ้านโกรกเดือนห้า อ. เมือง จ. นครราชสีมา และยังอยู่ระหว่างการศึกษาวิจัย เตรียมร่างเอกสารวิจัยส่งตีพิมพ์นี้ คาดว่าเป็น sinamiids ชนิดใหม่ (Deesri et al., underprepared)



ภาพที่ 3-3 ภาพแสดงสายวิวัฒนาการและความสัมพันธุ์ของปลากระดูกแข็งในกลุ่มก้านครีบแข็ง (Actinopterygian) ในมหายุคมีโซโซอิกของไทย

Subclass Sarcopterygii ประกอบด้วยปลาที่มีครีบเป็นพูเนื้อ (lobe finned fishes) ได้แก่ กลุ่มปลาปอดและปลาซีลาแคนธ์ที่ยังเหลือรอดอยู่ในปัจจุบัน ในประเทศไทยข้อมูลด้านซากดึกดำบรรพ์พบปรากฏเฉพาะ Dipnoi หรือกลุ่มปลาปอด (lungfish)

ปัจจุบันปลาปอด พบกระจายพันธุ์เฉพาะถิ่นในเขตทวีปแอฟริกา (*Protopterus annectens*) เขตทวีปอเมริกาใต้ (*Lepidosiren paradoxa*) และในทวีปออสเตรเลีย (*Neoceratodus forsteri*) ทั้งสามสกุลนี้เป็นปลาที่สามารถหายใจได้ทั้งในน้ำและบนบก เนื่องจากมีปอดช่วยในการหายใจนอกเหนือจากการใช้เหงือก ภายในปากของปลาปอดจะมีฟันมีลักษณะเป็นแผ่นฟันหนา และแข็งแรง เมื่อเกิดการกลายสภาพเป็นซากดึกดำบรรพ์ส่วนของแผ่นฟันนี้จะถูกแทนที่ด้วยแร่ธาตุต่าง ๆ จึงพบเห็นได้ทั่วไป ซึ่งซากดึกดำบรรพ์ของแผ่นฟันปลาปอดพบครั้งแรกในหมวดหินห้วยหินลาด (Martin & Ingavat 1982) และจากนั้นพบในแหล่งมาบชิง (Martin et al. 1997) ซึ่งจัดอยู่ในหมวดหินภูกระดึงทางภาคใต้ของไทย และในแหล่งช่องชาด จ. หนองบัวลำภู จัดอยู่ในหมวดหินภูกระดึงเช่นเดียวกัน โดยในหมวดหินภูกระดึงนี้เอง ในแหล่งภูน้ำจั้น อ.กุฉินารายณ์ จ. กาฬสินธุ์ ที่มีการค้นพบเศษกระดูกส่วนกะโหลกร่วมกับแผ่นฟันติดบนขากรรไกรบนและล่าง จนสามารถตั้งเป็นสกุลใหม่ ชนิดใหม่ ได้ว่า *Ferganoceratodus martini* (Cavin et al. 2007b) เมื่อไม่นานมานี้ได้มีการค้นพบเศษชิ้นส่วนของกระดูกกะโหลกศรีษะเพิ่มเติม ในแหล่งภูน้อย อ.คำม่วง จ. กาฬสินธุ์ ซึ่งอยู่ในหมวดหินภูกระดึงเช่นกัน โดยตัวอย่างนี้กำลังอยู่ในขั้นตอนการเตรียมร่างเพื่อตีพิมพ์ในวารสารนานาชาติต่อไป (Cavin et al., underprepared

3.2 ตัวอย่าง KT181

A.

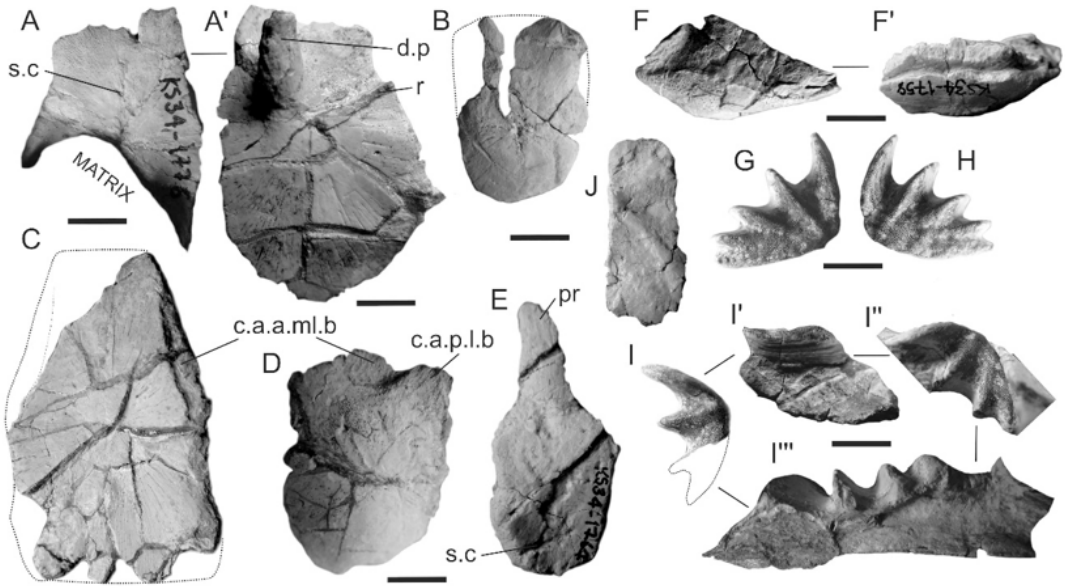
B.

C.

ภาพที่ 3-4 ตัวอย่างเกล็ดและกระดูกของปลาในอันดับ Amiiforms ในแหล่งบ้านโกรกเดือนห้า A. ตัวอย่างต้นแบบ KT181 B. ภาพขยายส่วนหัวมุมมองด้านหลัง C. ภาพขยายส่วนหัวมุมมองด้านซ้าย

เป็นตัวอย่างที่อยู่ระหว่างการเตรียมร่าง manuscript เป็นตัวอย่างที่ค้นพบในแหล่งใหม่ แหล่งบ้านโกรกเดือนห้า ต.สุรนารี อ.เมือง จ. นครราชสีมา ฝังตัวในตะกอนหินทรายปนกรวดของหมวดหินโคกกรวด ยุคครีเทเชียสตอนต้น ตัวอย่างต้นแบบ (holotype specimen) KT181 แสดงรายละเอียดส่วนหัว กระดูกส่วนหัวเรียงต่อกันสมบูรณ์ ส่วนลำตัวช่วงท้ายขาดหายไป คาดว่าความเสียหายเกิดขึ้นในขณะเก็บตัวอย่าง โดยเบื้องต้นคาดว่าเป็นชนิดใหม่ จัดอยู่ในอันดับของปลา Amiiformes (ดูท้ายเล่มในภาคผนวก หน้า 34-40)

3.3 ตัวอย่าง KS34 – 1785



ภาพที่ 3-5 ตัวอย่างกระดูกและแผ่นฟัน (KS34 – 1785) ของปลาปอดในอันดับ Dipnoi ในแหล่งภูน้อย จ.กาฬสินธุ์ A, anterior bone of the mediolateral series in dorsal (A) and ventral (A') views; B, anterior bone of the medial series; C, posterior bone of the mediane series in ventral view; D, posterior bone of the mediolateral series in dorsal view; E, posterior bone of the lateral series (YZ bone) in dorsal view; F, ?lingual bone (angular) in ?lateral (F) and ?oblique (F') views; G, H, right (G) and left (H) dorsal tooth plates; I, left ventral tooth plate in occlusal view with the posterior part reconstructed

เป็นตัวอย่างที่อยู่ระหว่างการเตรียมร่าง manuscript เป็นตัวอย่างของปลาปอดที่ค้นพบในแหล่งภูน้อย อ.คำม่วง จ. กาฬสินธุ์ ฝังตัวอยู่ในตะกอนหินทรายปนโคลนของหมวดหินภูกระดึง ยุคจูแรสสิกตอนปลายถึงต้นยุคครีเทเชียส ตัวอย่างที่พบ (study materials) และใช้ในการอธิบายลักษณะ มีลักษณะแยกหลุดเป็นหลายชิ้น ไม่ได้เรียงต่อกัน แต่แสดงรายละเอียดส่วนหัวค่อนข้างชัด และสามารถศึกษาเปรียบเทียบกับตัวอย่างต้นแบบ FERGANOCERATODUS JURASSICUS Kaznyshkin & Nessov, 1985 และตรวจสอบความสัมพันธุ์ทางวิวัฒนาการได้ (ดูในภาคผนวกท้ายเล่ม หน้า 41-43)

บทที่ 4

4. บทสรุปและข้อเสนอแนะ

4.1 บทสรุป

โครงงานนี้มีวัตถุประสงค์เพื่อศึกษาและอธิบายตัวอย่างใหม่ที่ได้จากการสำรวจและเก็บจากงานภาคสนามเพื่อตรวจสอบความสัมพันธ์ทางสายวิวัฒนาการ โดยใช้การวิเคราะห์ความใกล้ชิดของสายวิวัฒนาการ (cladistics method) ของตัวอย่างจากหลาย ๆ เช่น แหล่งภูน้ำจั้น และแหล่งภูน้อย และแหล่งอื่น ๆ ซึ่งเป็นแหล่งที่มีอายุอยู่ในช่วงยุคไทรแอสสิก หมวดหินห้วยหินลาด หมวดหินภูกระดึง ยุคจูแรสสิกตอนปลายถึงต้นยุคครีเทเชียส และหมวดหินโคกกรวด อายุครีเทเชียสตอนต้น รวมไปถึงเพื่อตรวจสอบนิเวศวิทยาบรรพกาลของปลาน้ำจืดไทยในช่วงมหายุคมีโซโซอิก โดยอาศัยการเปรียบเทียบระหว่างความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียน และปลาดึกดำบรรพ์อื่น ๆ กับทั่วโลกจากข้อมูลที่ปรากฏในการตีพิมพ์ที่มีความทันสมัย เพื่อให้ได้มาซึ่งความหลากหลายของสภาพแวดล้อมปลาจิงกลีโมเดียน และปลาดึกดำบรรพ์อื่น ๆ ในมหายุคมีโซโซอิก

ในขั้นต้นพบว่ามีตัวอย่างที่ได้จากการออกภาคสนามสำรวจและเก็บเพิ่มเติม แบ่งออกได้เป็น 2 กลุ่ม ได้แก่ กลุ่มปลาก้านครีบแข็ง ได้แก่ ปลาชนิดใหม่ในอันดับ Amiiformes ในยุคครีเทเชียสตอนต้นของหมวดหินโคกกรวด และกลุ่มปลาครีบเป็นพูเนื้อ ได้แก่ ปลาปอดชนิดใหม่ ในยุคจูแรสสิกของหมวดหินภูกระดึง เพิ่มเติมจากเดิมที่พบและจัดจำแนกไว้ในปี 2007 จะเห็นได้ว่าซากดึกดำบรรพ์ปลาแสดงความหลากหลายเพิ่มมากขึ้นเรื่อย ๆ ในรอบสิบปีที่ผ่านมา และในอนาคตข้อมูลในส่วนของความหลากชนิด ระบบนิเวศวิทยาบรรพกาล และการกระจายพันธุ์ทางชีวภูมิศาสตร์โบราณจะเติมองค์ความรู้ได้สมบูรณ์มากขึ้น

แต่อย่างไรก็ตามข้อมูลด้านซากดึกดำบรรพ์มีข้อจำกัดหลายอย่าง ทั้งความสมบูรณ์ของตัวอย่างและระยะเวลาที่ใช้ในการเก็บตัวอย่างขณะออกภาคสนาม และเวลาที่ใช้ไปกับการเตรียมและอนุรักษ์ตัวอย่าง

4.2 ข้อเสนอแนะสำหรับงานวิจัยในอนาคต

ข้อมูลพื้นฐานที่ได้จากการจัดจำแนกลำดับอนุกรมวิธานปลากระดูกแข็งนี้สามารถนำไปเพื่อต่อยอดการศึกษาด้านต่าง ๆ ที่มีการใช้เทคนิควิจัยขั้นสูงได้อีก เช่น การศึกษาโครงสร้างอ่อนนุ่มภายในกะโหลก โดยอาศัยเทคนิคการถ่ายภาพแสกน 3 มิติ และการวิเคราะห์ตรวจสอบปริมาณแร่ธาตุต่าง ๆ เช่น ออกซิเจนไอโซโทป เป็นต้น ในการตรวจสอบระบบนิเวศถิ่นที่อยู่อาศัย ดังนั้น ข้อมูลพื้นฐานที่ได้จากการศึกษาอธิบายลักษณะสัณฐานวิทยาเปรียบเทียบเพื่อจัดจำแนกนี้จึงยังคงเป็นงานวิจัยที่จำเป็นและสำคัญ

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Output จากโครงการวิจัยที่ได้รับทุนจาก สกว.

1. Tong, T., Buffetaut, E., Suteethorn, V., Suteethorn, S., Cuny, G., Cavin, L., Deesri, U., Martin, J., Wongko, K., Naksri, W., Claude, J. (2019). Phu Din Daeng, a new Early Cretaceous vertebrate locality on the Khorat Plateau, NE Thailand. Annales de Paléontologie, 105, 223–237. doi.org/10.1016/j.annpal.2019.04.004

ร่าง manuscript เพื่อตีพิมพ์ในวารสารระดับนานาชาติ

1. Uthumporn Deesri a, b *, Varavudh Suteethorn b, Wilailuck naksri c, Pratueng Jintasakul c, Yoshikazu Noda d, Hirokazu Yukawa d, and Lionel Cavin e. XXX, a new amiiform fish (Holostei, Halecomorpha) from the Early Cretaceous Khok Kruat Formation, northeastern Thailand. In Cretaceous research.
2. Lionel CAVIN*1, Uthumporn DEESRI2,3, Phornphen CHANTHASIT4. A new lungfish from the Jurassic of Thailand. In Journal of Vertebrate Paleontology.

Tong, T., Buffetaut, E., Suteethorn, V., Suteethorn, S., Cuny, G., Cavin, L., Deesri, U., Martin, J., Wongko, K., Naksri, W., Claude, J. (2019). Phu Din Daeng, a new Early Cretaceous vertebrate locality on the Khorat Plateau, NE Thailand. Annales de Paléontologie, 105, 223–237. doi.org/10.1016/j.annpal.2019.04.004

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Original article

Phu Din Daeng, a new Early Cretaceous vertebrate locality on the Khorat Plateau, NE Thailand

Phu Din Daeng, un nouveau site à vertébrés fossiles du Crétacé inférieur sur le plateau de Khorat, NE de la Thaïlande

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ARTICLE INFO

Article history:
Available online 27 May 2019

Keywords:
Vertebrates
Early Cretaceous
Khorat Group
Sao Khua Formation
NE Thailand

Mots clés :
Vertébrés fossiles
Crétacé inférieur
Groupe de Khorat
Formation Sao Khua
NE Thaïlande

ABSTRACT

In this paper, we report on a new Early Cretaceous vertebrate locality, Phu Din Daeng, in Nakhon Phanom Province, NE Thailand. The Phu Din Daeng site has yielded a diverse vertebrate assemblage, including sharks (*Heteroptychodus steinmanni*), bony fishes (Pycnodontiformes; Sinamiidae cf. *Stamamia* and ?Vidalamiinae, and Ginglymodi), adocid turtles, indeterminate neosuchian crocodiles, pterosaurs and dinosaurs (spinosaurids and indeterminate theropods). A new adocid turtle, *Protoshachemys rubra* n. g. n. sp. is described on the basis of shell material. Field investigations on the geology and comparisons with other vertebrate faunas place Phu Din Daeng in the Sao Khua Formation (Barremian) of the Khorat Group.

RÉSUMÉ

Phu Din Daeng, un nouveau site à vertébrés fossiles d'âge Crétacé inférieur dans la province de Nakhon Phanom, NE de la Thaïlande, est signalé. Le site de Phu Din Daeng a livré une faune de vertébrés fossiles diversifiée, comprenant des requins (*Heteroptychodus steinmanni*), des poissons osseux (Pycnodontiformes; Sinamiidae cf. *Stamamia* et ? Vidalamiinae, ainsi que Ginglymodi), des tortues adocidés, des crocodiles néosuchiens indéterminés, des ptérosaures et des dinosaures (spinosauridés et théropodes indéterminés). Une nouvelle tortue, *Protoshachemys rubra* n. g. n. sp., est décrite sur la base d'éléments de carapace. Les investigations géologiques sur le terrain et la comparaison avec les faunes de vertébrés du Groupe de Khorat placent Phu Din Daeng dans la Formation Sao Khua (Barrémien).

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https://doi.org/10.1016/j.annpal.2019.04.004
0753-3969/

1. Introduction

The Mesozoic non-marine deposits of the Khorat Group (Late Jurassic–Early Cretaceous) in NE Thailand are rich in vertebrate fossils. Among the five formations included in the Khorat Group (from bottom to top: Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations), numerous localities in the Phu Kradung, Sao Khua and Khok Kruat formations have yielded abundant vertebrate body remains (see Buffetaut et al., 2009 and references therein). In this paper, we report on a new vertebrate locality, Phu Din Daeng, in Nakhon Phanom Province. Recently discovered by local people, the site has been visited regularly by the Palaeontological Research and Education Centre (PRC), Mahasarakham University, since 2012. The material was collected on the surface or by systematic excavations to extract apparently partially associated fish or turtle skeletons; and the sediments were screen-sieved. The Phu Din Daeng site has yielded a diverse and somewhat peculiar vertebrate assemblage including sharks, bony fishes, turtles, crocodiles, pterosaurs and theropod dinosaurs. The geology of the site is investigated and the stratigraphical significance of the assemblage is discussed. A new species of turtle, yet unique to this locality is described.

2. Geological setting

The Phu Din Daeng site is located in Tambon (sub-District) Si Chompu, Amphoe (District) Na Kae, Changwat (Province) Nakhon Phanom, NE Thailand (Fig. 1). The outcrop where fossils were discovered corresponds to a small erosional area at the northeastern end of the anticline of the Phu Phan Range, on the Khorat Plateau. Stratigraphically, the Phu Din Daeng site is located at the top of the Sao Khua Formation, a few metres below the Phu Phan Formation. Next to the site is a hill that is topped by hard layers of medium to coarse-grained sandstones and conglomerates typical of the Phu Phan Formation. The fossiliferous deposits correspond to a thin layer of siltstone of a few centimetres thick, itself interbedded in layers of red mudstones, siltstones and sandstones. Vertebrate fossils are relatively abundant, including sharks, bony fishes, crocodiles, turtles, pterosaurs and theropod dinosaurs; bivalves have also been collected. Large bones are very rare, fish and turtle remains are by far the most abundant vertebrates at Phu Din Daeng, but often represented by fragmentary and isolated elements or by loosely associated sets of plates or scales. The generally disarticulated nature of the material may indicate that carcasses were partially or totally decayed and disarticulated before burial. Most fossils consist of relatively small elements suggesting a possible winnowing. It does not appear that there are important concentrations of fossils, indicating that the bone bed is probably the result of a single flooding event occurring at some distance from the main water bodies somewhere in the flood plain. Some turtle elements belonging to a single individual, although disarticulated, have been collected over a small area, suggesting an *in situ* preservation or short transportation.

Based on palynology and vertebrate palaeontology, the Sao Khua Formation is considered to be Early Cretaceous (Buffetaut et al., 2006; Racey, 2009; Racey et al., 1996), and more precisely Barremian in age based on the study of bivalves (Tumpeesuwan et al., 2010). Located stratigraphically at the top of the formation, the Phu Din Daeng site seems to be younger than some other fossiliferous outcrops in the Sao Khua Formation, such as Phu Kum Khao (Kalasin Province) and Phu Wat (Nong Bua Lamphu Province), and indeed displays a slightly different fossil assemblage.

3. Vertebrate fauna from Phu Din Daeng

3.1. *Chondrichthyes Huxley, 1880*

Hybodontiformes Patterson, 1966

Heteroptychodus steinmanni Yabe & Obata, 1930

Material: Three teeth with the root preserved (**PRC34-PRC36**) and three fragments of tooth crown (Fig. 2).

Description: The three teeth are flat, roughly parallelogram-shaped in apical view with a sigmoid curvature in labial or lingual view. **PRC34**, the most complete one (Fig. 2A-B), measures 19 mm mesiodistally, 14 mm labiolingually and is 7 mm high, including the root. Its apical surface shows 25 closely packed mesiodistal ridges. **PRC35** (Fig. 2E–F) measures 15 mm mesiodistally, but is incomplete and 17 mm labiolingually. It shows 31 mesiodistal ridges. **PRC36**, the largest one, has been found in three parts that have been glued back together (Fig. 2C–D). It measures 21 mm mesiodistally and 15 mm labiolingually and displays 30 mesiodistal ridges. Each mesiodistal ridge bears fine perpendicular ridges on its lingual side. A marginal area is visible on the lingual part of the apical side of the crown, ornamented with anastomosed ridges roughly oriented perpendicularly to the lingual edge of the crown. On the labial, mesial and distal extremities, this marginal area is strongly reduced. The labial, lingual, mesial and distal faces of the crown are ornamented with fine, irregular, anastomosed ridges. The root is thicker than the crown, up to twice so, and is very porous, showing a multitude of small pores on all its faces. On the labial and lingual sides, at roughly mid-height of the root, there is a row of enlarged foramina.

Discussion: The presence on these teeth of several mesiodistal ridges, each bearing numerous short perpendicular ridges together with a reduced marginal area around the crown is characteristic of the genus *Heteroptychodus* (Yabe and Obata, 1930). Three species of *Heteroptychodus* are currently recognized. *H. chuvalovi* is easily separated from the Phu Din Daeng teeth by its chevron-shaped mesiodistal ridges (Cuny et al., 2008). *Heteroptychodus kokutensis* is also easily separated from the Phu Din Daeng teeth as its teeth are more elongated mesiodistally and its labiolingual ridges between the main ridges are not as regular and thin as in the teeth from Phu Din Daeng (Cuny et al., 2010). The latter character, as well as the labiolingual width of the teeth from Phu Din Daeng allow attributing them to *H. steinmanni* (Cuny et al., 2003; Yabe and Obata, 1930). This species was originally described from the Hauterivian Tatsukawa Formation in Japan (Kozai et al., 2005; Yabe and Obata, 1930). In Japan, *H. steinmanni* is restricted to the Hauterivian-Barremian interval (Okazaki, 2016). The species is also known from the Aptian of southern China (Mo et al., 2016) and in Thailand, it has been reported in the Sao Khua (see Cuny et al., 2007, Fig. 2B) and Khok Kruat formations.

3.2. *Actinopterygii Cope, 1887*

Pycnodontiformes Berg, 1937

Genus and species indet.

Material: PRC84, fragment of a vomer

Description: PRC84 is an isolated fragmentary tooth-bearing bone. It is referred with caution to a piece of a vomer of a pycnodontiform (Fig. 3). The molariform and oval shaped teeth without pedicel but with an apical papilla are typical of the teeth of some pycnodontiforms. The symmetry observed in the bone indicates an unpaired toothed bone, i.e. a vomer.

Discussion: Rather similar teeth from Phu Phan Thong, in the Sao Khua Formation, have been referred to cf. *Anomoeodus* by

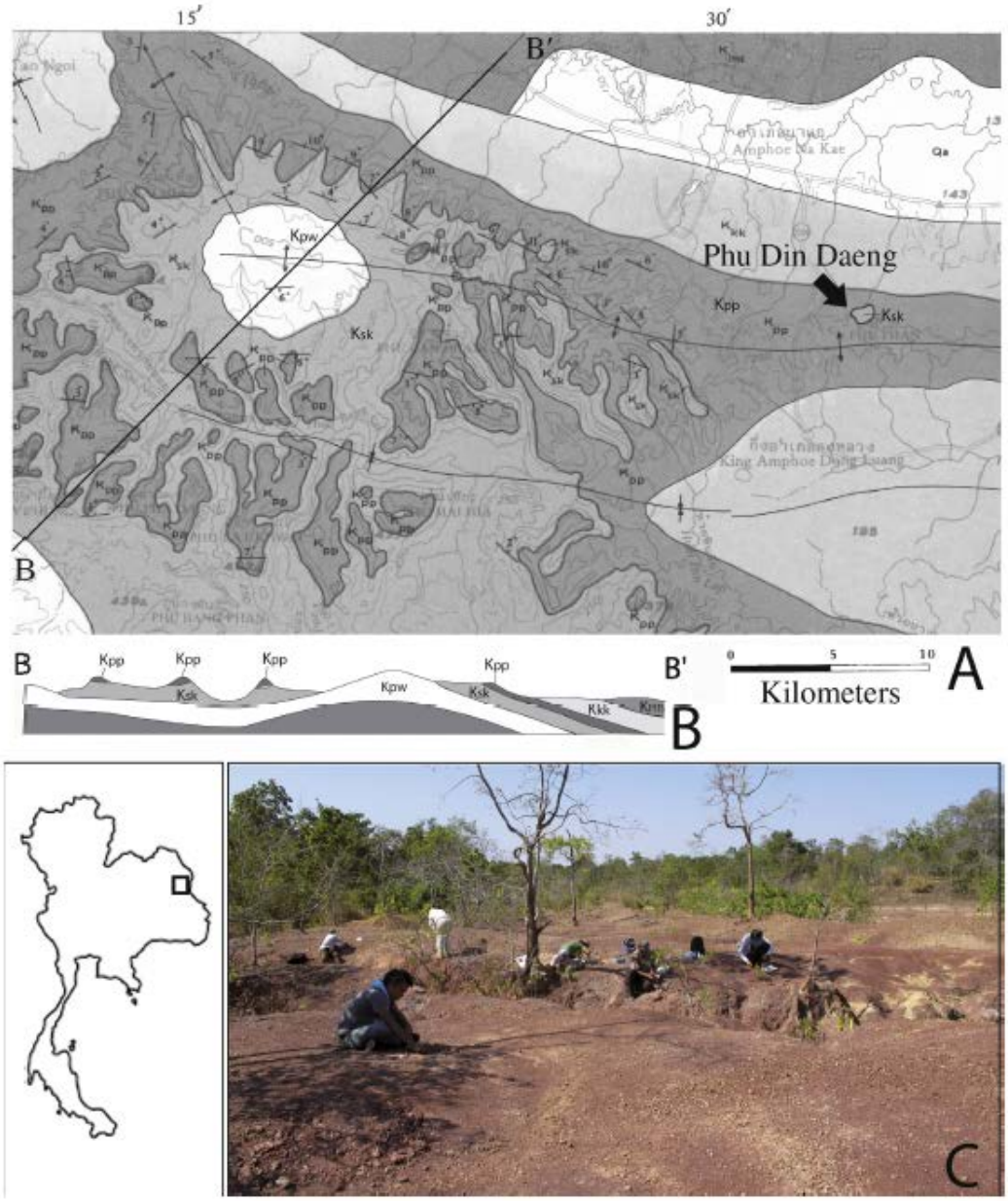

Fig. 1. Map showing the location and geology of the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, geological map and B, section (modified from Suteethorn and Jarnyahran, 1980); C, excavation at Phu Din Daeng. Abbreviations: K_{kk}, Khok Kruat Formation; K_{mr}, Marasahakham Formation; K_{pp}, Phu Phan Formation; K_{pw}, Phra Wihan Formation; K_{sk}, Sao Khua Formation.

Carte montrant la localisation et géologie du site de Phu Din Deang (Crétacé inférieur, NE de la Thaïlande). A, Carte géologique et B, Coupe (modifié d'après Suteethorn and Jarnyahran, 1980) ; C, Fouilles à Phu Din Deang. Abbréviations : K_{kk}, Formation Khok Kruat ; K_{mr}, Formation Marasahakham ; K_{pp}, Formation Phu Phan ; K_{pw}, Formation Phra Wihan ; Ksk, Formation Sao Khua.

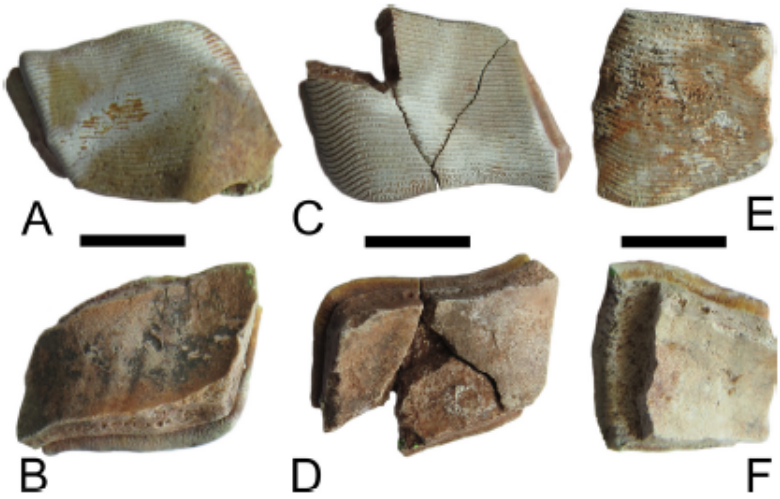

Fig. 2. Teeth of *Heteroptychodus steinmanni* from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A–B, (PRC34) in apical (A) and basal (B) views; C–D, (PRC36) in apical (C) and basal (D) views; E–F, (PRC35) in apical (E) and basal (F) views. Scale bars = 1 cm.
*Dents d'*Heteroptychodus steinmanni *provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–B, (PRC34) en vues apicale (A) et basale (B) ; C–D, (PRC36) en vues apicale (C) et basale (D) ; E–F, (PRC35) en vues apicale (E) et basal (F). Barre d'échelle = 1 cm.*

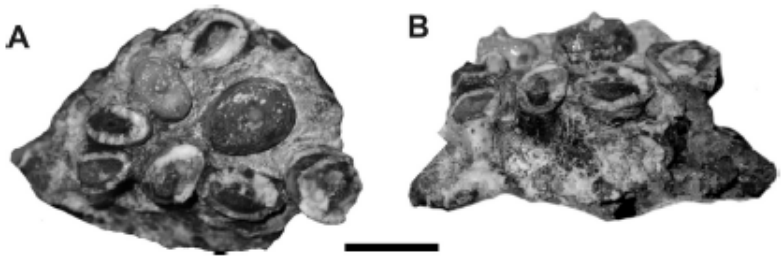

Fig. 3. Pycnodontiformes indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). PRC84, fragment of a vomer in occlusal (A) and lateral (B) views. Scale bar = 5 mm.
Pycnodontiformes indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). PRC84, fragment de vomer en vues occlusale (A) et latérale (B). Barre d'échelle = 5 mm.

Cavin et al. (2009). Pending new and more complete material, the material from Phu Din Daeng is referred to an indeterminate pycnodontiform taxon.

Amiiformes sensu Grande and Bemis, 1998
Sinamiidae Berg, 1940**cf. *Stamamia***
Cavin et al., 2007

Material: **PRC92**, dermopterotic; **PRC93**, basioccipital; **PRC90**, fragment of a left maxilla; **PRC91**, posterior extremity of a maxilla; **PRC89**, right premaxilla; **PRC87**, left dentary; **PRC88**, fragment of a right dentary with a coronoid; **PRC85**, anterior vertebral centrum; **PRC86**, posterior vertebral centrum.

Description: Isolated fragments referable to sinamiids are common at Phu Din Daeng (Fig. 4). Most of the preserved bones are the same as bones of sinamiids from other localities that have yielded this taxon (Phu Phok, Khok Pha Suam, etc.), indicating that these ossifications are the most resistant in the skeleton of these fishes. These bones are vertebral centra, jaw bones (premaxillae, maxillae and dentaries), basioccipitals, dermopterotics and scales. Most of these bones show characters of sinamiids.

A more or less complete, but distorted left dentary is preserved (Fig. 4G). It bears on its lateral side a row of irregular in size oval pores corresponding to the mandibular sensory canal. Twenty large and slightly compressed conical teeth strongly inwardly curved and irregular in size can be counted along a single row. Most of the teeth are broken but fine ridges at their bases are still visible. The acrodine caps are only imperfectly preserved, but it is visible that the sections of the caps were oval and their outline was likely conical. A fragment of a dentary with a coronoid still in situ shows labially elongated pores for the mandibular sensory canal, and lingually a deep groove for the Meckelian cartilage (Fig. 4B). The sockets corresponding to compressed dentary teeth, together with fragments of teeth are visible on the dentary. A patch of small, thin and slightly recurved teeth, smaller than the dentary teeth, are associated with the coronoid still attached to the dentary.

An almost complete right premaxilla (Fig. 4E) has a typical triangular shape with a large ovoid concavity on the labial face of the nasal process. The locations of about ten compressed teeth are visible. A large posterior tooth is still present, as well as a smaller tooth at the mid-length of the bone. The base of the teeth indicates that the anterior teeth were smaller than the posterior ones.

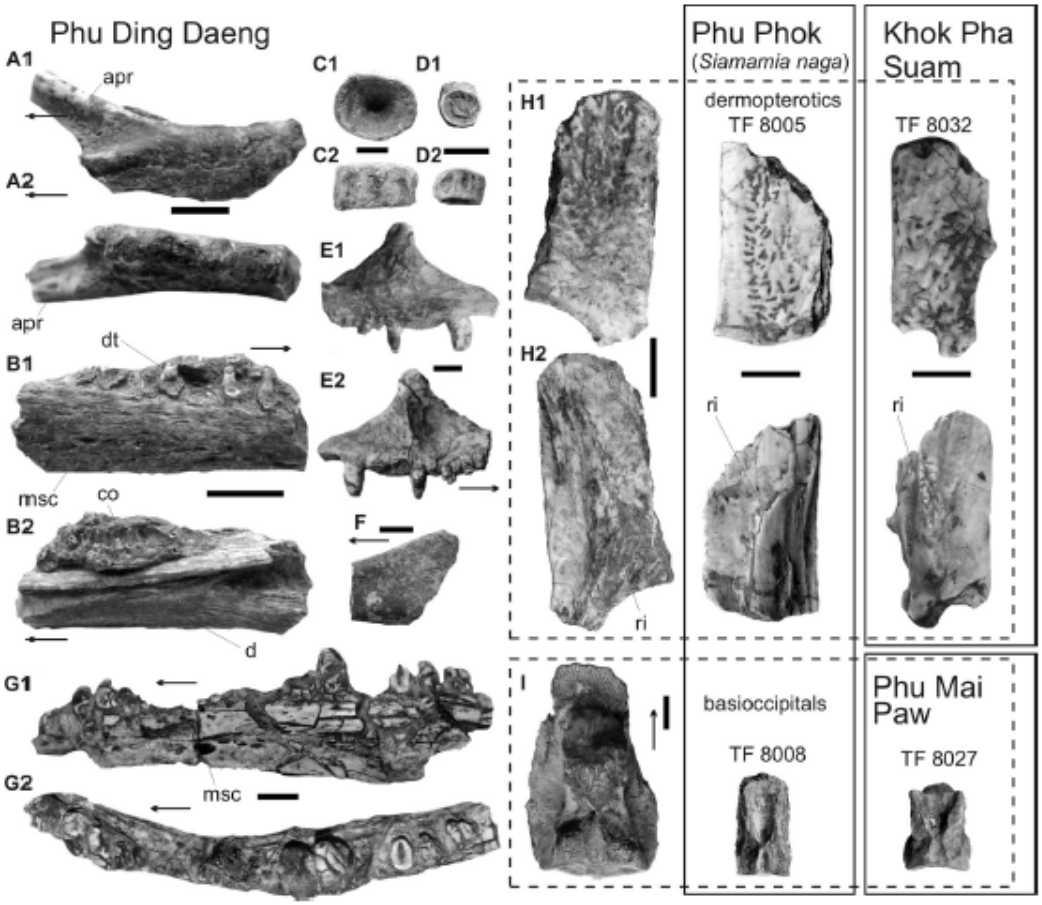

Fig. 4. cf. Sinamiidae from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, fragment of the anterior part of a maxilla (**PRC90**) in medial (A1) and occlusal (A2) views; B, fragment of a right dentary (**PRC88**) with a coronoid in labial (B1) and lingual (B2) views; C, anterior vertebral centrum (**PRC85**) in median (C1) and lateral (C2) views; D, posterior vertebral centrum (**PRC86**) in anterior (D1) and lateral (D2) views; E, right premaxilla (**PRC89**) in internal (E1) and external (E2) views; F, posterior extremity of a maxilla (**PRC91**) in lateral view; G, left dentary (**PRC87**) in labial view (G1) and occlusal (G2) views; H, dermopterotic (**PRC92**) in external (H1) and internal (H2) views; I, basioccipital (**PRC93**) in dorsal view. Scale bars = 5 mm. Upper box, comparisons with dermopterotics from other localities; lower box, Comparison with basioccipitals form other localities. Abbreviations: apr, articular process; co, coronoid; d, dentary; dt, dentary tooth; msc, mandibular sensory canal; ri, ridge.

*cf. Sinamiidae provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, fragment de la partie antérieure d'un maxillaire (**PRC90**) en vues médiale (A1) et occlusale (A2) ; B, fragment de dentaire droit (**PRC88**) avec coronoïde en vues labiale (B1) et linguale (B2) ; C, centrum de vertèbre antérieure (**PRC85**) en vues médiane (C1) et latérale (C2) ; D, centrum de vertèbre postérieure (**PRC86**) en vue antérieure (D1) et latérale (D2) ; E, prémaxillaire droit (**PRC89**) en vues interne (E1) et externe (E2) ; F, extremité postérieure du maxillaire (PRC91) en vue latérale ; G, dentaire gauche (**PRC87**) en vues labiale (G1) et occlusale (G2) ; H, dermoptérotique (**PRC92**) en vues externe (H1) et interne (H2) ; I, basioccipitale (**PRC93**) en vue dorsale. Barres d'échelle = 5 mm. Cadre en haut, comparisons avec dermoptérotiques provenants des autres sites ; Cadre en bas, comparison avec basioccipitales provenants des autres sites. Abbréviations : apr, processus articulaire ; co, coronoïde ; d, dentaire ; dt, dent dentaire ; msc, canal sensoriel mandibulaire ; ri, crête.*

A fragment of an anterior part of a left maxilla (Fig. 4A) shows the base of a large articular process and the sockets for teeth with a round section. Another fragment (Fig. 4F) corresponds to the triangular posterior extremity of the maxilla with an extended posterodorsal corner reminiscent of *Siamamia*.

An ornamented skull roof bone, bearing internally a shallow crest, is identified as a dermopterotic (Fig. 4H).

A bone bearing an ovoid articular facet, with excavated lateral sides and sutural surfaces dorsally (for the exoccipitals) is identified as a basioccipital (Fig. 4I).

Thin rhomboidal ganoid scales with a smooth surface are present and assigned with caution to *Siamamia*.

The commonest elements are vertebral centra, which are generally found isolated but which also occurred as sets of two to three centra still partly articulated. The shape of vertebral centra ranges from short centra with an ovoid compressed section, corresponding to anterior vertebrae, to longer centra round in section corresponding to posterior vertebrae (Fig. 4C–D).

Discussion: These isolated bones are very similar to isolated bones of *Siamamia naga* described from the type-locality of Phu Phok, in the Sao Khua Formation. In particular, the premaxilla shows the typical triangular outline of *S. naga*, with a nasal process broad at its base and extending posteriorly to a blunt process. The only difference with the figured premaxilla of *S. naga* (Cavin et al.,

2007, fig. 5E–G) is the proportionally smaller size of the nasal process. However, because the specimen from Phu Din Daeng is about 1.5 times larger than the specimen from Phu Phok, we cannot exclude that this difference is caused by allometric growth. The maxillae, with the departure of a well-developed articular process (PRC90) and with a deep and triangular posterodorsal corner (PRC91), are also similar to the maxillae of *S. naga* from Phu Phok. The general shape of the dentary PRC87, the shape of its preserved teeth and the arrangement of the mandibular sensory pores is reminiscent of *S. naga*. The second dentary associated to the coronoid (PRC88) is referred here with caution to this taxon. Both dentaries, although incomplete, seem to have had symphyses proportionally deeper than the very shallow symphysis of the sinamiids from Khok Pha Suam in the Khok Kruat Formation, but reminiscent of *S. naga* (compare Fig. 4B and G with fig. 7 in Cavin et al., 2009). The basioccipital of the Phu Din Daeng sinamiid is more similar to that from the Phu Mai Paw locality, in the Sao Khua Formation, than to the one of *S. naga* from Phu Phok because in the first two the articular facet is more flattened than in the type material, and the dorsal suturing surfaces form an X-shape, while they are almost parallel in *S. naga* (lower box in Fig. 4). The bone identified with caution as a dermopterotic bears an ornamentation more similar to the ornamentation of this bone from Khok Pha Suam, but the shallow crest is more reminiscent to the condition present in *Siamamia naga* from Phu Phok (upper box in Fig. 4).

?Vidalamiinae Grande & Bemis, 1998

Genus and species indet.

Material: PRC94, right dentary; **PRC95**, anterior extremity of a right dentary; **PRC96**, piece of a semi-articulated specimen with unidentified bones, toothed scales and vertebral centra in connection; **PRC97**, piece of a semi-articulated specimen with scales and fin rays; **PRC98**, accumulation of scales in articulation; **PRC99**, accumulation of bones, scales and fragments of fin rays.

Description: A right dentary, smaller in size than the dentary referred to cf. *Siamamia naga*, presents other features differing from *S. naga* (Fig. 5A). The irregular in size, thin and tall teeth are arranged in one row along the labial margin of the bone. They are gently curved lingually and their base is separated from the crown by a well-developed constriction (Fig. 5A'). The crown of each tooth is topped by an acrodine cap that is labiolingually compressed and shows very well-developed mesial and distal carinae forming a triangular outline. The shaft of each tooth has a rounded cross section at its base then the labial face is slightly flat while the lingual face is gently convex. A second specimen (not figured) corresponding to the anterior portion of a right dentary bears teeth similar in shape to the specimen described above. The symphyseal region appears to be very shallow.

Several accumulations of bones associated with scales with a very peculiar morphology, corresponding to strongly disarticulated fish individuals, are referred here with caution to a probable vidalamiin. This assignation rests on a specimen (PRC96), which displays scales bearing well developed spines associated with vertebral centra of amioid type (Fig. 5B). This association of bones indicates that this fish is likely a halecomorph, but different from the sinamiid cf. *Siamamia* from the same locality because the latter possesses supposedly smooth scales without any kind of ornamentation. The scales in PRC96 are deep, with a vertical pointed articular process (peg) at the anterior extremity of the dorsal margin. Three spines arranged along the depth of the scale extend posteriorly. Another specimen (PRC97) consists of an accumulation of scales together with fin rays (Fig. 5C). The scales are deeper than long (although proportionally less deep than in PRC96); a large triangular process is present dorsally and two very elongated spines extend posteriorly (Fig. 5C'). A specimen (PRC99) with scales still in articulation shows that each scale bears a pair of spines extending posteriorly and covering the following row of scales (Fig. 5D). The fin rays on PRC97 are formed by slightly deeper than wide elements, each one bearing a spine (Fig. 5C''). Another specimen (PRC99) shows a fragment of fin ray with a dermal segment covered with ridges of ganoin (Fig. 5E). Because of the disarticulated state of preservation of the material, we cannot reconstruct the organisation of the fin, with the respective location of the spines and ganoin patches on the rays.

Discussion: The general morphology of the dentary and especially of the carinate acrodine tooth caps are diagnostic features of some halecomorphs. Carinate teeth in halecomorphs have been regarded as independently acquired in Caturidae and Vidalamiinae (Grande and Bemis, 1998: 341). There are no morphological features visible on the material from Phu Din Daeng that allow assignation to either the caturids or the vidalamiins. The caturids are mostly marine fishes from the Late Jurassic, while vidalamiins are represented by some marine (*Pachyamia*), but mostly brackish or freshwater fishes (*Calamopleurus*, *Vidalamia*) from the Early Cretaceous. For these environmental and stratigraphical reasons, we assign with caution this kind of teeth from Phu Din Daeng to a Vidalamiinae, pending that new material will allow a better supported identification. The teeth referred to *Caturus* from Phu Phan Tong (Cuny et al., 2006) and Nong Sung (Cuny et al., 2009), both situated in the Sao Khua Formation, can also be referred to this taxon. While no spined scales are associated with carinate teeth, we temporarily associated these teeth and scales to the same taxon, although vidalamiins usually have elasmoid scales rather than thin ganoid scales (Grande and Bemis, 1998). We cannot exclude also that this material belongs to a sinamiids different from *Siamamia*, based on the scale morphology with carinate tooth caps convergent with vidalamiins and caturids. Here again, more material will be necessary to confirm or refute this identification.

Ginglymodi *sensu* Grande, 2010

Genus and species indet.

Material: a large number of unnumbered thick ganoid scales.

Description:

The occurrence of ginglymodians at Phu Din Daeng is attested by the presence of thick ganoid scales (Fig. 6). The shape of the scales differ depending of their position on the body: A large elongate rhombic scale was located in front of the anal fin, a more narrow rhomboid scale was located close to the caudal part, rectangular scales were located in the anterior part of the body, scales with small pores were situated along the lateral line and a symmetrical scale with a concave anterior margin and a posterior spine corresponds to a scale from the dorsal mid-line. Some scales show an ornamentation with faint parallel ridges on their external surface. The anterior peg and socket articulation is present. The posterior margins of all scales are smooth with no serrations.

Discussion

Ginglymodian remains are the commonest fish fossils within the Khorat Group, which ranges from the Late Jurassic to the Aptian. The taxic diversity is relatively high in each formation (Cavin et al., 2009, 2014; Deesri et al., 2017). However, a more precise identification of the scales from Phu Din Daeng is difficult. The only observation we can do here is that the scales differ from scales from most of the described taxa, which are smooth except some scales from Khok Pha Suam, in the Khok Kruat Formation (Ginglymodi indet.

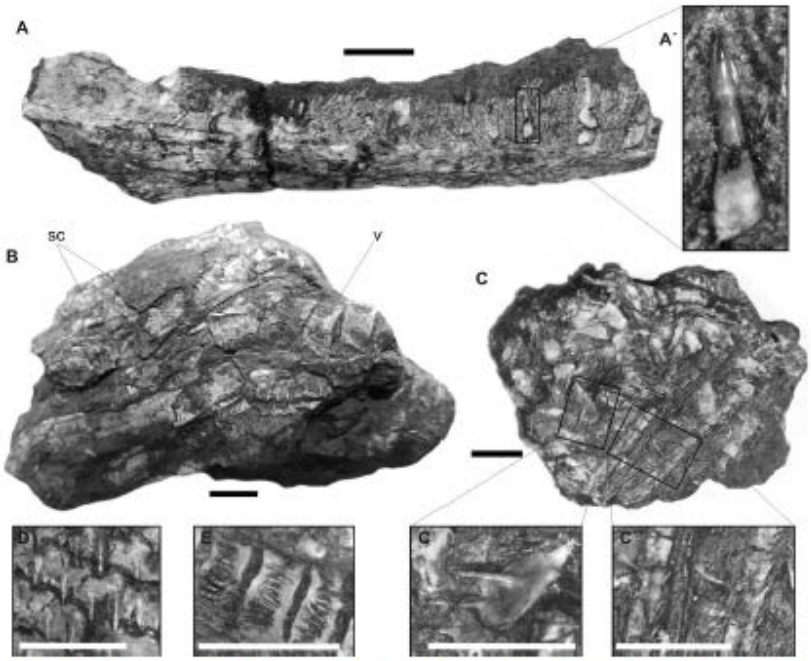

Fig. 5. ?Vidalamiinae indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, right dentary (**PRC94**) in labial view with close up of a tooth (A'), B, piece of a semi-articulated specimen (**PRC96**) showing unidentified bones, toothed scales and vertebral centra in connection; C, piece of a semi-articulated specimen (**PRC97**) showing toothed-scales (C') and fin rays with denticulated segment (C''); D, detail of toothed scales (**PRC98**); E, detail of fin-ray segments with patches of ganoine (**PRC99**). Scale bars = 5 mm. Abbreviations: sc, scales; v, vertebra.

*?Vidalamiinae indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, dentaire droit (**PRC94**) en vue labiale ; A', gros plan d'une dent ; B, spécimen semi-articulé (**PRC96**) montrant des os non identifiés, des écailles denticulées et centrums vertébraux en connection ; C, spécimen semi-articulé (**PRC97**) montrant des écailles denticulées (C') et rayons avec segment denticulé (C'') ; D, détail des écailles denticulées (**PRC98**) ; E, détail des segments de rayons avec ganoïne (**PRC99**). Barres d'échelle = 5 mm. Abbréviations : sc, écailles ; v, vertèbre.*

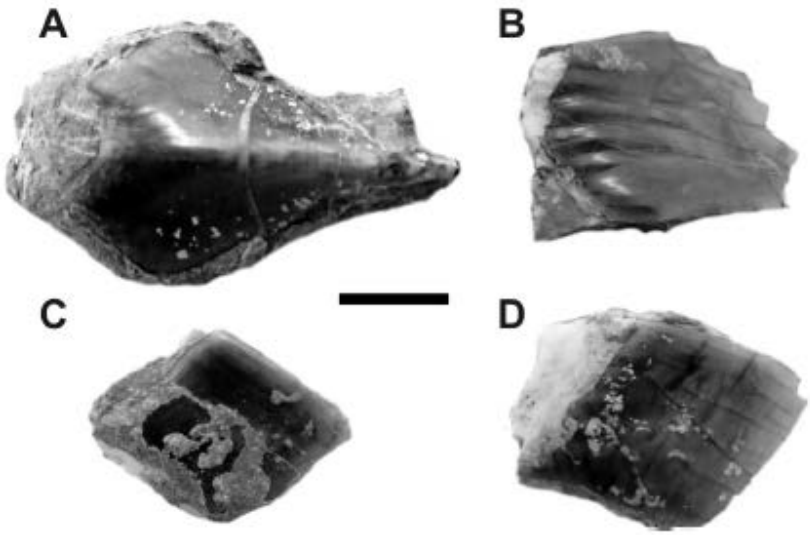

Fig. 6. Ginglymodi indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). Ganoid scales (no number). Scale bar = 5 mm.

Ginglymodi indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). Ecailles ganoïdes (sans numéro). Barre d'échelle = 5 mm.

4 in Cavin et al. (2014: Table I)). But the latter bear ridges that are stronger than in the material from Phu Din Daeng.

3.3. *Testudines*

Cryptodira Cope, 1868
Trionychoidae Fitzinger, 1826
Adocidae Cope, 1870
Shachemydinae Khosatzky, 1977

***Protoshachemys rubra* n. gen. n. sp.**
(Fig. 7A–L and Fig. 8)

Etymology: Genus name from Greek 'protos' first, primitive to denote that the taxon is more primitive than *Shachemys*; species name from the name of the locality: Phu Din Daeng (ภูดินแดง) in Thai, red rock mountain or hill.

Holotype: PRC81 (Fig. 7A–D), a nearly complete but disarticulated shell, including complete nuchal, one neural, suprapygal 1 (incomplete), suprapygal 2, pygal (lacking posterior portion), right costal 1, left costal 2, the distal portion of the left costal 3, right costal 4 (lacking proximal end), left costal 5 and distal end of the right costal 5, left costal 6 (lacking the proximal end), left and right costal 7 (the right one lacking the proximal end), right costal 8, left peripherals 1–2, 4–6 and 8–11, right peripherals 8 and 10–11; nearly complete left epiplastron and right hyoplastron, and incomplete right hypoplastron. All these elements were unearthed within one square metre and in all likelihood belong to the same individual.

Referred material: PRC54, nuchal (Fig. 7E–F); **PRC55, PRC56, PRC57**, suprapygal 2; **PRC58**, pygal (Fig. 7K–L); **PRC59**, left costal 6 (Fig. 7I–J); **PRC60**, right costal 3 (Fig. 7G–H); **PRC61**, right peripheral 1; **PRC62**, left and right peripheral 2 of same individual; **PRC67**, right epiplastron;

Type locality and horizon: Phu Din Daeng, Sakhon Nakhon Province, NE Thailand. Top of the Sao Khua Formation, Lower Cretaceous (see Geological setting).

Diagnosis: a genus of Adocidae; with a combination of primitive and derived characters that differ from all other members of that family, as follows: shell surface smooth with sparse pores; carapace flat with a serrated posterior margin; nuchal roughly as long as wide; neural series reduced, narrow neurals with a tetragonal neural 1 followed by a hexagonal neural 2; two suprapygals, the first one much smaller than the second; cervical scute narrow; vertebral 1 not extending to the peripheral 2; lateral marginals extending onto the costals 1–5, marginal 11 and 12 elongate and greatly overlapping the suprapygal 2 and also slightly the costal 8; plastron with truncated anterior margin, entoplastron shortened anteriorly, a hinge between epiplastra and entoplastron/hyoplastra absent.

Description: Shell surface ornamentation: The surface of both carapace and plastron is smooth, with sparse tiny pores.

Carapace: When reconstructed, the carapace is flat with an oval outline. The anterior margin of the carapace is straight or slightly emarginated. The anterolateral margin of the carapace, from the posterior end of the peripheral 2 to the peripheral 6, is blunt and slightly upturned, but not forming a clear gutter. The posterolateral margin, from peripheral 8 to 11, is sharp. The posterior margin of the peripherals 10 and 11 presents sharp serrations. The posterior margin of the pygal has a small triangular caudal notch. A light ridge is present on the suprapygal 1, whereas the suprapygal 2 is convex dorsally. The peripherals are sutured to the costals, without a carapacial fontanelle. A large free rib end is developed on the distal end of the costals; they are wide and flat on the costal 2 to 5, and slender and long on the costal 7 and 8. The inner surface of the costals is perfectly flat, without rib swelling. As partly preserved on costal 2, the rib head is large and flat.

The nuchal in the holotype is slightly longer than wide, trapezoidal in shape with a straight anterior margin; its lateral margins are straight and convergent forward. PRC54 has a slightly emarginated anterior margin. In the holotype, the neurals are mostly missing, except one that is stuck on the inner surface of the suprapygal 2 and presented in ventral view. It is hexagonal, longer than wide and relatively narrow, but its precise position cannot be determined. The morphology of the neural series is indicated by the intact medial edges of the costals 1, 2, 5, 7 and 8 of the holotype and that of the isolated right costal 3 (PRC60) and left costal 6 (PRC59). There are likely six neurals, the neural 1 is tetragonal, followed by a hexagonal neural 2 with short anterolateral sides. Damaged on its posterior end, the suprapygal 1 remains articulated with the costal 8 in the holotype. When reconstructed, the suprapygal 1 is triangular, longer than wide and much smaller than the suprapygal 2, with a smooth and concave inner surface. The suprapygal 2 is trapezoidal. It contacts anteriorly the small suprapygal 1, anterolaterally the costal 8, and posteriorly the peripherals 10–11 and the pygal. This plate is greatly thickened posteriorly, especially the contact region with the pygal. The pygal is elongate, expanded posteriorly; with straight lateral borders and a very thick anterior contact with the suprapygal 2. The size of this plate is similar to that of the peripheral 11. An isolated pygal (PRC58) shows a small triangular caudal notch. The costal 1 is long as in advanced turtles. It is in contact with the nuchal, the neurals 1–2 and the peripherals 1–3. The costal 7 and the anterior part of the costal 8 meet their counterpart at the midline. As indicated by the isolated costal 6, this plate has also the posterior part meeting its counterpart at the midline. The inner surface of the costal 8 bears a large process to articulate with the ilium. The peripheral 1 is triangular and relatively narrow, with a short contact with the costal 1. The peripheral 2 is roughly square. The peripherals 4 to 11 are mesiolaterally elongate.

The scute sulci are lightly imprinted. The cervical scute is elongate and narrow. It is very narrow, with roughly parallel and slightly convex lateral sulci in the holotype, but slightly wider in PRC54. The vertebral 1 is wider than the nuchal, covering the posteromedial part of the peripheral 1 and contacting the marginal 2. The anterior sulcus of the vertebral 1 presents an anterior convexity at the level of the cervical scute. The sulcus between the cervical and the vertebral 1 is convex forward. The vertebrals 2 to 4 are narrow, being clearly longer than wide. The vertebral 5 is triangular and wider than the vertebral 4; it contacts the full width of the marginal 11 and 12, but is not in contact with the marginal 10. The contact between the vertebral 5 and the marginal 12 is straight. The pleural scutes are wider than the vertebral scutes. The marginal scutes 1 to 3 are short and restricted in the peripherals, with the marginal/pleural sulcus located far from the peripheral/costal suture on the peripherals 1 and 2. The marginals 4 to 7 extend onto the costal plates 2 to 4, and cover also the posterolateral corner of the costal 1 and the anterolateral corner of the costal 5. The marginals 8 to 10 are restricted in the peripherals again. The marginals 11 and 12 are greatly elongated and much longer than the marginal 10, overlapping the posterior half of the suprapygal 2, as well as the posteromedial corner of the costal 8.

Plastron: The plastron is well developed with wide anterior and posterior lobes. The bridge appears to be long and narrow. The anterior lobe of the plastron is truncated, with a straight or slightly emarginated front border, as in *Isanemys* and *Ferganemys* spp. The epiplastron has its anterior margin almost as long as its lateral free edge and these two edges form together a clear angle. The epiplastron is slightly thickened at its anterolateral corner, as well as its lateral edge. The intact sutural margin of the epiplastron and hyoplastron shows that no hinge is present between the epiplastra and entoplastron/hyoplastra, and the entoplastron is pentagonal in shape and shortened anteriorly, with its anterior margin shorter

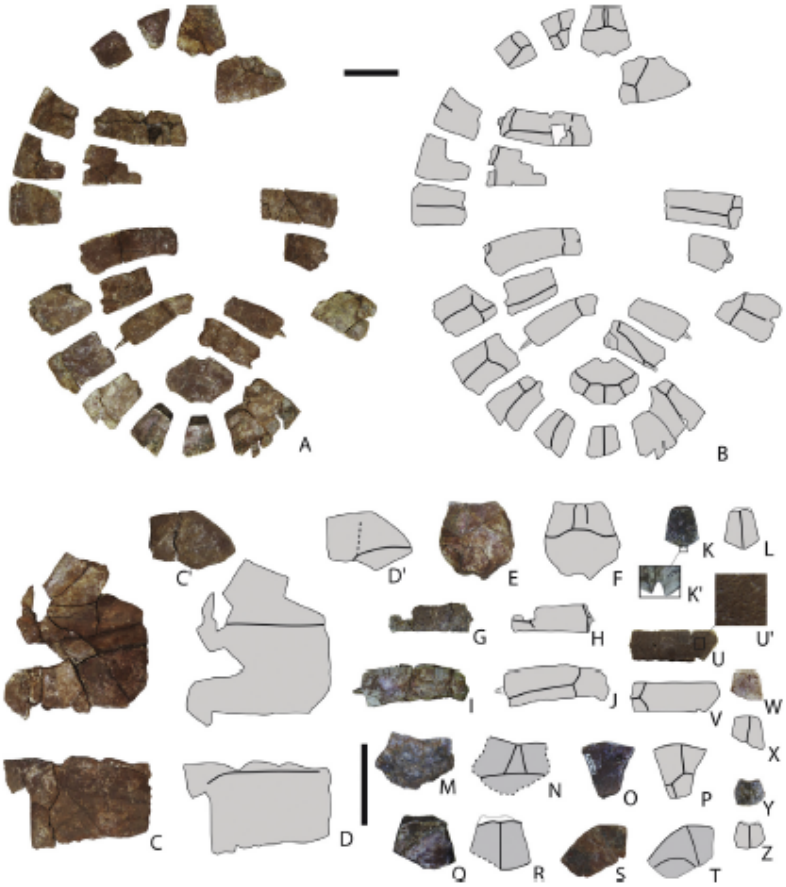

Fig. 7. Adocid turtles from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A–L, *Protoshachemys rubra* n. g. n. sp. A–D, holotype (**PRC81**), carapace in dorsal view (A–B) and plastron in ventral view (C–D); E–F, nuchal (**PRC54**); G–H, costal 3 (**PRC60**); I–J, costal 6 (**PRC59**); K–L, pygal (**PRC58**), K', close-up showing the caudal notch. M–T, *Protoshachemys* sp., M–N, nuchal (**PRC69**); O–P, left peripheral 1 (**PRC70**); Q–R, pygal (**PRC73**); S–T, right epiplastron (**PRC76**). U–Z, Adocidae indet. U–V, costal (**PRC77**), U', close-up showing the surface ornamentation; W–X, pygal (PRC82); Y–Z, peripheral 11 (**PRC78**). Scale bar = 5 cm (horizontal scale bar for A–D; vertical scale bar for E–Z).
*Tortues adocidés provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–L, Protoshachemys rubra n. g. n. sp. A–D, holotype (**PRC81**), carapace en vue dorsale (A–B) et plastron en vue ventrale (C–D) ; E–F, nuchale (**PRC54**) ; G–H, costale 3 (**PRC60**) ; I–J, costale 6 (**PRC59**) ; K–L, pygale (**PRC58**), K', gros plan montrant l'échancrure caudale. M–T, Protoshachemys sp., M–N, nuchale (**PRC69**) ; O–P, périphérique 1 gauche (**PRC70**) ; Q–R, pygale (**PRC73**) ; S–T, épiplastron droit (PRC76). U–Z, Adocidae indet. U–V, costale (**PRC77**), U', gros plan montrant l'ornementation sur la surface ; W–X, pygale (**PRC82**) ; Y–Z, périphérique 11 (**PRC78**). Barre d'échelle = 5 cm (barre d'échelle horizontale pour A–D ; barre d'échelle verticale pour E–Z).*

than the posterior one. The hypoplastron contacts the xiphiplastron with a nearly straight suture.

The scute sulci are poorly preserved on the plastron. The intergulars extend onto the entoplastron, but not the gulars. The intergular/gular sulci are nearly parallel to one another. The intergular/gular sulcus meets the gular/humeral sulcus on the epiplastron. The gular/humeral sulcus runs from the posterolateral corner of the epiplastron to the mid-length of the epi/entoplastral suture. The humeropectoral sulcus is straight and located posterior to the entoplastron as in *Isanemys*, but different from *Adocus* spp. and *Ferganemys* spp. in which the humeropectoral sulcus overlaps the posterior end of the entoplastron. The abdominofemoral sulcus is located anterior to the base of the posterior lobe. The inframarginal scutes are not discernible on the bridge region.

Comparisons and discussion: The reduction of the posterior neurals and the suprapygal 1, with the costals 7 and 8 meeting their counterpart at the midline; the suprapygal 1 much smaller than the suprapygal 2; a greatly reduced cervical scute that is much longer than wide and the marginal 11–12 greatly overlapping the suprapygal 2 indicate that the turtle specimens described above belong to trionychoid Adocidae. They are assigned to the sub-family Shachemydinae based on the smooth shell surface with sparse pores and an anteriorly truncated entoplastron.

Shachemydinae is a group of freshwater turtles endemic in the Cretaceous of Asia. The subfamily contains two genera, *Shachemys* Kuznetsov, 1976 and *Ferganemys* Nessov and Khosatzky, 1977 (Danilov et al., 2013; Lapparent de Broin, 2004; Syromyatnikova, 2011; Syromyatnikova et al., 2013, 2012; Syromyatnikova and Danilov, 2013). *Shachemys* is known from three species: *Shachemys baibolatica* Kuznetsov, 1976 and *Sh. ancestralis* Nessov, 1984 from the Late Cretaceous of Kazakhstan, Tajikistan and Uzbekistan; and *Sh. laosiana* Lapparent de Broin, 2004 from the Early Cretaceous of Laos (Danilov et al., 2007; Kuznetsov, 1976; Lapparent de Broin, 2004; Nessov and Krasovskaya, 1984). Fragmentary shell

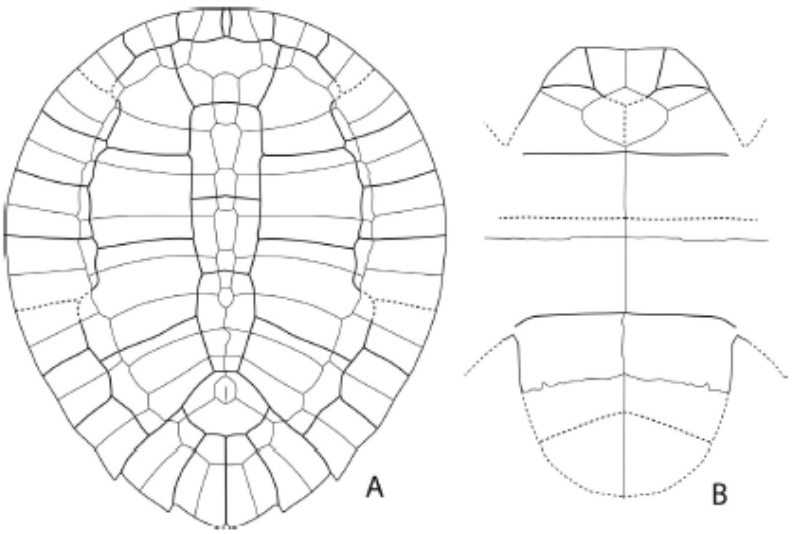

Fig. 8. Reconstruction of the shell of *Protoshachemys rubra* n. g. n. sp. from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). A, carapace in dorsal view; B, plastron in ventral view.
Reconstruction de carapace de Protoshachemys rubra *n. g. n. sp. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, carapace en vue dorsale ; B, plastron en vue ventrale.*

remains of *Shachemys* sp. are also recorded from the Early Cretaceous Khok Kruat Formation (Aptian) of Thailand (Tong et al., 2005, 2009,). *Ferganemys* is known from two species: *F. verzilini* from the Early Cretaceous (Albian) of Kirgizstan and *F. itemirensis* from the Late Cretaceous (Cenomanian) of Uzbekistan (Nessov, 1981; Nessov and Khosatzky, 1977; Syromyatnikova, 2011). Lapparent de Broin et al. (2004) assigned *Sinaspideretes wimani* (Young and Chow, 1953) from the Late Jurassic of Sichuan Basin, China to Shachemydinae, but the subsequent review of that taxon placed it at a more basal position among Trionychoidae (Tong et al., 2014).

Most trionychoid turtles have a sculptured shell surface. In the family Adocidae, the shell surface has a pitted ornamentation, such as in *Isanemys srisuki* from the Early Cretaceous Sao Khua Formation of NE Thailand (Tong et al., 2006), *Ferganemys* spp. and *Adocus* spp. from the Late Cretaceous and Palaeogene of Asia and North America (Hay, 1908; Sonoda et al., 2015; Syromyatnikova et al., 2013, 2012; Syromyatnikova and Danilov, 2013), except for *Shachemys*. *Shachemys* has a smooth shell surface (*Sh. laosiana*) or with fine wrinkles (*Sh. baibolatica* and *Sh. ancestralis* as figured in Danilov et al. (2007)), with numerous marked pores, corresponding to a well-developed reticular system of vascular canals (Scheyer et al., 2017). Some turtles referred to *Adocus* have a weaker shell surface sculpture with small dots, such as in cf. '*Adocus*' *orientalis* from the Late Eocene of Inner Mongolia, China and *Adocus* sp. from the Palaeocene of Montana, USA that Danilov et al. (2013) considered different from the sculpture with small grooves and pits of 'true' *Adocus*. These sculptures, which give the shell surface a 'rugose' aspect, appear however to be more pronounced than that seen in our specimens. The shell surface of the specimens from Phu Din Daeng is smooth, pores are variably developed. They are not obvious on PRC81 and on the specimens from Phu Din Daeng of a dark colour, but in some specimens of pale colour, marked pores are more easily observed.

Although an epiplastra-entoplastron/hyoplastra hinge is absent, *Protoshachemys* shares with *Isanemys*, *Ferganemys* and *Shachemys* an anteriorly shortened entoplastron. In these taxa, the anterior margin of the entoplastron (the epiplastron/entoplastron suture) is clearly shorter than its posterior margin (the entoplastron/hyoplastron suture); in contrast to *Adocus* spp. which have a diamond-shaped entoplastron, with the length of the anterior margin roughly equal to that of its posterior margin. In *Shachemys* spp., the anterior margin of the entoplastron is straight and a hinge is developed between epiplastra and entoplastron/hyoplastra (Danilov et al., 2007; Lapparent de Broin, 2004). Such a hinge is also present in some juveniles of *Ferganemys* (Syromyatnikova, 2011).

Like *Shachemys*, *Protoshachemys* has a relatively narrow nuchal that is roughly as long as wide; while in *Ferganemys* spp. and *Isanemys*, the nuchal is clearly wider than long. However, *Shachemys* is characterized by a series of autapomorphic features in addition to pores on the shell surface and a plastral hinge. These include absence of all or nearly all neurals, only one suprapygal, absence of a cervical scute and the vertebral 1 overlapping the peripheral 2. *Protoshachemys* is obviously more primitive than *Shachemys* spp. in having more neurals (up to six), two suprapygals, a narrow cervical scute and the vertebral 1 overlapping the peripheral 1.

Protoshachemys shares with *Isanemys* a tetragonal neural 1 and a straight humeropectoral sulcus that is located posterior to the entoplastron. It is, however, more derived than *Isanemys* and *Ferganemys* in having greatly elongated lateral and posterior peripherals and lateral marginals extending onto the costals. These characters are shared with *Adocus* spp. and might be plesiomorphic at the level of Shachemydinae. Detailed comparisons between *Protoshachemys* and other adocids are shown in Table 1. On the basis of these comparisons, the turtle remains from Phu Din Daeng described above appear to be distinct from other adocids and are therefore considered as belonging to a new genus and new species. The combination of shell characters of this new taxon supports its basal position in Shachemydinae.

***Protoshachemys* sp.**

(Fig. 7M–T)

Referred material: PRC68 and **PRC69** (Fig. 7M–N), nuchals; **PRC70** (Fig. 7O–P) and **PRC71**, left peripheral 1, **PRC72**, right peripheral 1; **PRC73** (Fig. 7Q–R) and **PRC74**, pygals; **PRC75**, left

Table 1
Comparisons of shell characters between *Protoshachemys rubra* n. g. n. sp. and other adocids.
Comparaisons des caractères de carapace entre Protoshachemys rubra *n. g. n. sp. et d'autres Adocidés.*

Characters	*Protoshachemys rubra*	*Shachemys* spp.	*Isanemys srisuki*	*Fergunemys* spp.	*Adocus* spp.
Shell surface ornamentation	Smooth with sparse pores	Smooth with marked pores	Pitted	Pitted	Pitted
Cervical notch	Absent or very shallow	Present or absent	Present	Present or absent	Present or absent
Serrated posterior margin	Yes	No	No	No	No
Nuchal	Roughly as long as wide	As long as wide	Wider than long	Wider than long	Wider than long
Number of neural	6	Absent or only the first	6 or 7	7	6
Neural formula	4>6>6>6>6>5	–	4>6>6>6>6>5	6<4>6>6>6>6>5	6<4>6>6>6>5
Number of suprapygal	2	1	2	2	2
Cervical scute	Present, Narrow	Absent	Present, Wide	Present, Narrow	Present, Narrow
Vertebral 1	Overlapping peripheral 1	Overlapping peripheral 2	Overlapping peripheral 1	Overlapping peripheral 1	Overlapping peripheral 1
Vertebral 2–3	Clearly longer than wide	Longer than wide or wider than long	As long as wide	Longer than wide	Longer than wide or wider than long
Marginals 4–8 extending onto costals	Yes	No	No	No	Yes
Marginal 10 shorter than marginal 11	Yes	Yes or no	No	Yes	No
Entoplastron anteriorly truncated	Yes	Yes	Yes	Yes	No
Hinge between epiplastra and entoplastron/hyoplastra	Absent	Present	Absent	Present in juveniles	Absent

epiplastron, **PRC76** (Fig. 7S–T), right epiplastron and other shell elements.

Remarks: Turtle shell remains are relatively abundant at Phu Din Daeng locality, most of them are isolated elements or fragments. Most shell elements have a smooth outer surface and when well preserved, tiny pores are apparent. These elements are therefore tentatively referred to *Protoshachemys*. Some diagnostic plates, such as nuchal, peripheral 1, pygal and epiplastron, show a different morphology as compared with *Protoshachemys rubra*. These include the presence of a large nuchal emargination, a wider than long pygal, a larger and triangular cervical scute, a rounded anterior edge of the plastron and the gular extending onto the entoplastron. These differences may correspond to an important inter-individual variation that could be due to sexual dimorphism or may indicate distinct species. More complete material is needed to make sure of the association of the characters and estimate intraspecific variation.

Adocidae genus and species indet.
(Fig. 7U–Z)

Referred material: PRC77 (Fig. 7U–V), a costal; **PRC82** (Fig. 7W–X), a pygal and **PRC78** (Fig. 7Y–Z), a peripheral 11.

Remarks: These plates have a slightly pitted outer surface, similar to that of *Isanemys srisuki* (Tong et al., 2006). The pygal is wider than long, in contrast to the elongate pygal of *Protoshachemys rubra*. The marginals 11 and 12 extend onto the suprapygal 2. The material is too fragmentary to warrant a more precise systematic assignment beyond Adocidae indet.

3.4. *Crocodilia Gmelin, 1789*

Neosuchia Benton & Clarck, 1988

Genus and species indet.

Crocodilians are poorly represented at Phu Din Daeng and consist of a single mandibular element as well as isolated tooth crowns, the latter being the most abundant type of material recovered (Fig. 9).

Description: A single left articular (PRC144) is about 4 cm long and preserves the glenoid surface as well as the retroarticular process. As seen in lateral view (Fig. 9A), the articular preserves a sutural area for the surangular and angular, which extends toward the posteriormost level of the articular. The retroarticular process projects posteriorly; its tip is not projecting dorsally as is observed in derived eusuchians (Iordansky, 1973). As observed in dorsal view (Fig. 9B), the retroarticular process is faintly concave and is narrower than the glenoid fossa. This is different from eusuchians where the retroarticular process is concave and medially expanded to provide attachment for M. pterygoideus posterius (Iordansky, 1973). As seen in ventral view (Fig. 9D), the retroarticular process is straight and narrow and shows a groove that may correspond to the suture with the angular. The glenoid fossa is divided into lateral and medial articular surfaces of equal widths to accommodate the craniomandibular joint. In eusuchians, the lateral hemicondyle is wider than the medial one. The foramen aëreum is placed on the medial edge of the articular (Fig. 9B).

Subconical, slightly curved tooth crowns are often missing enamel and possess distinct apicobasal ridges, which are about the same strength as the mesiodistal carinae (PRC145, Fig. 9E).

Discussion: Although the material is limited, the morphology of PRC144 does not match that of a derived eusuchian. The mandible of a probable eusuchian has recently been described from the Aptian-Albian Khok Kruat Formation (Kubo et al., 2018) and is not comparable with the Phu Din Daeng specimen. Further identification is presently not possible because the Phu Din Daeng articular differs in morphology from those of pholidosaurids such as *Chalawan thailandicus* from the Phu Kradung Formation (Buffetaut and Ingavat, 1980; Martin et al., 2014) or is unknown in other crocodilians described from the early Cretaceous of Thailand (Lauprasert et al., 2007, 2009). As such, the mandible is unknown in the derived neosuchian *Khoratosuchus jintasakuli* from the Aptian-Albian Khok Kruat Formation (Lauprasert et al., 2007) and in the goniopholidid *Siamosuchus phuphokensis* from the ante-Aptian Sao Khua Formation (Lauprasert et al., 2007). The posterior region of the mandible is also unknown in the diminutive atoposaurid *Theriosuchus grandinaris* from the ante-Aptian Sao Khua Formation (Lauprasert et al., 2011). More complete discoveries are required to assess the identity of the Phu Din Daeng crocodilian beyond Neosuchia indet.

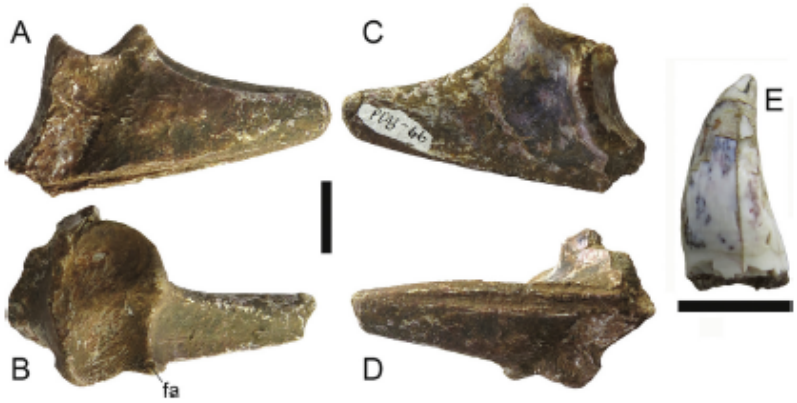

Fig. 9. Neosuchia indet. from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). Left articular (PRC144) in A, lateral; B, dorsal; C, medial and D, ventral views. E, isolated tooth (PRC145). Scale bar = 1 cm. Abbreviations: fa, foramen aëreum.
Neosuchia indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–D, Articulaire gauche (PRC144) en vues latérale (A), dorsale (B) ; mediale (C) et ventrale (D). E, dent isolée (PRC145). Barre d'échelle = 1 cm. Abbréviations : fa, foramen aëreum.

3.5. *Pterosauria Kaup, 1834*

Genus and species indet.

A few long, slender and more or less tubular teeth (PRC146, Fig. 10C) apparently belong to pterosaurs, although their enamel is too poorly preserved to clearly show the distinguishing features of pterosaur teeth. Pterosaurs have been reported from the Sao Khua Formation (Buffetaut et al., 2003) and also occur in the Khok Kruat Formation. The putative pterosaur teeth from Phu Din Daeng provide no stratigraphic indications.

3.6. *Dinosauria Owen, 1842*

Theropoda Marsh, 1881
Spinosauridae Stromer, 1915

Genus and species indet.

Spinosaurid teeth are relatively common at Phu Din Daeng, but mostly poorly preserved. They show the usual characters of the teeth of Asian spinosaurids: a crown that is only slightly compressed laterally and covered with strong apicobasal ridges (PRC147, Fig. 10A). Spinosaurid teeth occur in abundance in both the Sao Khua and Khok Kruat Formations, and several morphotypes, which may correspond to distinct taxa, are present in both (Suteethorn et al., 2018; Wongko et al., 2019). Because of this morphological variability, at the moment it is not really possible to clearly distinguish spinosaurid teeth from the Sao Khua and Khok Kruat Formations on the basis of their shape or ornamentation.

Theropoda genus and species indet.

Apart from a large caudal vertebra lacking the neural spine, which may belong to a theropod, this group of dinosaurs is mainly represented by isolated teeth. Several blade-shaped, laterally compressed teeth with serrated carinae have been found (PRC148, Fig. 10B). Their poor preservation makes it impossible to identify them beyond Theropoda indet. and they provide no stratigraphic information.

4. Discussion and conclusion

The Phu Din Daeng site has yielded a diverse vertebrate assemblage. Although it has some elements in common with the vertebrate fauna from the Khok Kruat Formation, this assemblage seems to be more comparable with those from the Sao Khua Formation. The stratigraphical significance of the assemblage is discussed below.

The shark fauna is represented by a single species, *Heteroptychodus steinmanni*. This taxon has mainly been recovered from the Khok Kruat Formation in Thailand (Cappetta et al., 2006; Cuny et al., 2008), but has also been reported from several sites in the Sao Khua Formation, like for example Ban Huai Dua (Cuny et al., 2008) and Phu Wat (specimens PWAI 499, 537–550 from the collection of the PRC) in Nong Bua Lamphu Province. However, *H. kokutensis* appears to be more common than *H. steinmanni* in the Sao Khua Formation, even though the separation between the two species is not yet clear and a revision of *Heteroptychodus* is warranted (Teng et al., 2017), but beyond the scope of the present work. On the other hand, *H. kokutensis* has never been recovered from the Khok Kruat Formation. The absence of *H. kokutensis* in Phu Din Daeng could therefore be linked to the younger age of the site compared to the other sites known in the Sao Khua Formation, or to the scarcity of shark remains in this locality that may be linked to taphonomical or environmental factors. It is difficult to decide which explanation is the most likely in the current stage of our knowledge.

Among bony fishes, pycnodont remains are rare in the Early Cretaceous continental localities in north-eastern Thailand. Until now, their fossils are only known in the Sao Khua Formation including teeth with morphology close to the morphology of teeth from Phu Din Daeng. Halecomorph remains corresponding to sinamiids and to vidalamiins, are the commonest fish remains in Phu Din Daeng. Sinamiids have been recognized in several localities from two Early Cretaceous formations of the Khorat Group in northeastern Thailand. *Siamamia naga* was identified on the basis of material from Phu Phok (Sakhon Nakhon Province) in the Sao Khua Formation (Cavin et al., 2007). Then, *Siamamia* sp. was recorded in several localities in the Sao Khua Fm., viz. Nong Sung (Mukdahan Province), Phu Phan Tong (Nong Bua Lamphu Province) and Phu Mai Paw (Kalasin Province), but also in one locality in the Khok Kruat Formation, viz. Khok Pha Suam locality (Ubon Ratchathani Province) (Cavin et al., 2009; Deesri et al., 2017). Except a few articulated specimens from Phu Phok, all the material consists of isolated and often fragmentary remains. The sinamiid from Phu Din Daeng appears to be closer to *Siamamia naga* than to the other sinamiids, in particular the sinamiid from Khok Pha Suam, and thus would support the inclusion of Phu Din Daeng in the Sao Khua Formation.

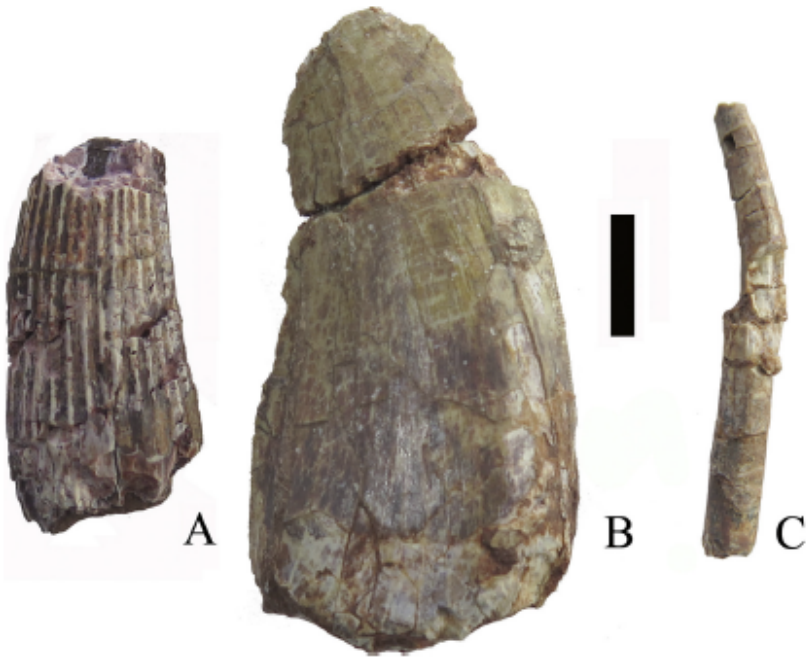

Fig. 10. Dinosaur and pterosaur teeth from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). A, spinosaurid theropod (PRC147). B, indeterminate theropod (PRC148). C, indeterminate pterosaur (PRC146). Scale bar = 1 cm.
Dents de dinosaure et ptérosaure provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, théropode spinosauridé (PRC147). B, théropode indéterminé (PRC148). C, ptérosaure indéterminé (PRC146). Barre d'échelle = 1 cm.

However, more complete material is necessary to test this hypothesis. The possible presence of a vidalamiin in Phu Din Daeng is the first record of this subfamily in the Early Cretaceous of Thailand, and actually of East Asia in general. This identification, if confirmed, will have strong biogeographical implications because the vidalamiins are known so far from Western Gondwana with *Calamopleurus*, and from Europe (including the Near-East) and North America with several genera. The presence of elongated spines on the scales of this taxon will deserve to be studied in detail. A superficial examination indicates that these denticles may have a histology similar to that of oral teeth. Such a tooth-like structure has been described among actinopterygians in the obaichthyids from the Early Cretaceous of Western Gondwana (Grande, 2010) and in the extant loricarioidei siluriforms form South America (Rivera-Rivera and Montoya-Burgos, 2017), both clades being phylogenetically remote from the vidalamiins. The occurrence of carinate teeth at Phu Phan Thong and Nong Sung also reinforces the placement of Phu Din Daeng in the Sao Khua Formation.

All turtle remains hitherto collected from Phu Din Daeng are referred to Adocidae (Cryptodira: Trionychoidea). *Protoshachemys rubra* n. g. n. sp., a primitive Shachemydinae, is the oldest known representative of that group. A more advanced form, *Shachemys*, has been reported from the Khok Kruat Formation in Thailand and its lateral equivalent the Grès Supérieurs Formation in Laos (Lapparent de Broin, 2004; Tong et al., 2005). The remains of Adocidae indet., although fragmentary, seem to be close to *Isanemys srisuki* from the Phu Khum Khao and Phu Wat localities of the Sao Khua Formation (Tong et al., 2006). Therefore, the general aspect of the turtle fauna from Phu Din Daeng is clearly more primitive than that of turtle fauna from the Khok Kruat Formation and supports the inclusion of the site in the Sao Khua Formation. The presence of *Protoshachemys* as the dominant component of the turtle fauna from Phu Din Daeng makes this assemblage distinct from other turtle faunas from the Sao Khua Formation. This may be due to an environmental or chronological difference. The absence of the carettochelyid turtle *Kizylkumemys* at Phu Din Daeng seems to be related to environmental factors. Present in both Sao Khua and Khok Kruat formations (also in the Grès Supérieurs Formation in Laos) (Lapparent de Broin, 2004; Tong et al., 2009), *Kizylkumemys* remains are found in the localities with higher energy palaeoenvironments.

As noted above, the dinosaur remains from Phu Din Daeng are too fragmentary and too poorly preserved to yield much stratigraphic information. However, the absence of ornithischian remains is worth noting, as it suggests that the locality belongs to the Sao Khua Formation rather than to the Khok Kruat Formation. Although the Sao Khua Formation has yielded thousands of dinosaur bones and teeth, so far they all belong to sauropods and theropods, no ornithischian remains have been reported (Buffetaut et al., 2006; Buffetaut and Suteethorn, 1999). By contrast, ornithischians are well represented in the Khok Kruat Formation, by both ceratopsians (*Psittacosaurus*) and various iguanodontians (Buffetaut et al., 2005). The shed teeth of the latter are very common at some Khok Kruat localities, such as Khok Pha Suam (Ubon Ratchathani Province). Although it is negative evidence, the lack of ornithischian remains at Phu Din Daeng is in line with an attribution to the Sao Khua Formation.

In conclusion, based on the geology and vertebrate assemblage, Phu Din Daeng can be confidently placed in the Sao Khua Formation. The difference in the faunal composition compared with those from other localities of the formation may reflect a difference in age (the locality being at the top of the Sao Khua Formation), or in the environmental or taphonomic conditions.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgments

This research is supported by the International Research Group PalBioDivASE (GDRI) grant of CNRS; PHC "Evolution des réseaux trophiques mésozoïques en Thaïlande et son impact sur la biodiversité"; the Mahasarakham University Development Fund and the National Research Council of Thailand (NRCT) of the fiscal years 2017 and 2018. The research of UD is further supported by TRF Grant for new researcher (MRG 6180086). We thank the members and students of Palaeontological Research and Education Centre (PRC), Mahasarakham University and Department of Mineral Resources (DMR) who took part the field work at Phu Din Daeng; Adán Pérez-García and Attila Ősi for reviewing the manuscript.

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ร่าง manuscript เพื่อตีพิมพ์ในวารสารระดับนานาชาติ

1. Uthumporn Deesri a, b *, Varavudh Suteethorn b, Wilailuck naksri c, Pratueng Jintasakul c, Yoshikazu Noda d, Hirokazu Yukawa d, and Lionel Cavin e. XXX, a new amiiform fish (Holostei, Halecomorpha) from the Early Cretaceous Khok Kruat Formation, northeastern Thailand. In Cretaceous research.

xxxx, a new amiiform fish (Holostei, Halecomorpha) from the Early Cretaceous Khok Kruat Formation, northeastern Thailand

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Abstract

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1. Introduction

Amiiformes fishes have been the subject of much study, because they occupy a position as one of position living sister groups to the Teleostei. Amiid fishes are represented today by only one species, *Amia calva*, a taxon restricted in freshwaters of eastern North America. In Thailand the cionellid, *Siamia ozoa* (Cavin et al., 2007) has been described base on partly articulated skulls and many isolated ossifications from the older stratigraphic age of the Sao Khua Formation of the Khorat series in the northeastern part of the country. During the collaborate field work between Thai-Japanese at Ban Krok Dusun Ha, Nakhorn Ratchasima province, Thailand led to the discovery of the nearly complete fish preserved together with xxxx. We here describe the nearly complete fish as a new name.

2. Geological settings

The Khorat Group crops out across the Khorat Plateau of NE Thailand, and extends eastwards into Laos and southwards into Kampuchea. The Khorat Group is normally considered to comprise six formations which the Khok Kruat Formation is the uppermost. Traditionally, an Aptian-Albian age is propose for the formation based on the occurrence of the peculiar freshwater hybodont shark *Thaiodus ruchae*, which is also known from the Aptian-Albian Takena Formation of Tibet (Cappetta et al., 1990). In addition, palynomorphs indicating an Aptian age have been reported from its upper part (Sattayarak et al., 1991; Racey et al., 1996). An Aptian age is therefore, well supported. This formation is predominantly fluvial in origin (Racey, 2009). Vertebrate remains from this formation have been well known such as hybodont sharks (Cappetta et al., 1990, 2006; Cuny et al., 2008), fishes and turtle (Cavin et al., 2019; Tong et al., 2005, 2019), a neosuchian crocodyliform (Lauprasert et al., 2009), pterosaur and dinosaurs (Buffetaut and Suteethorn, 1992, 2011; Shibata et al., 2011, 2015). The Study area is located in Suranaree subdistrict of Nakhon Ratchasima Province, northeastern Thailand (Fig.1). The Lower Cretaceous Khok Kruat Formation is distributed in

this area. Since 2017 Northeastern Research Institute of Petrified Wood and Mineral Resources Rajabhat University and Fukui Prefectural Dinosaur Museum excavated at this dinosaur site (KDH). The excavation site is originally a field of cone and/or cassava. The strata are covered by soil about several ten centimeters in thickness. Outcrops appeared as the soil was removed. The strata were eroded and were separated as "islands". Many vertebrate fossils including the dinosaur, pterosaur, fish, crocodile and turtle are preserved at this excavation site. Coprolites and bivalves are preserved too. The sedimentary succession of the Krok Dusun Ha site is composed of medium- to coarse-grained sandstone and conglomerate but rarely mudstones. The conglomerate mainly comprises clasts of clay rip-up pebble and rounded calcareous nodule granule. Planar cross stratified well sorted medium- to coarse-grained sandstone with nodule granule bed, trough cross stratified medium- to coarse-grained sandstone with nodule granule bed, not clear parallel stratified relatively well sorted coarse-grained sandstone with clay rip-up pebble and nodule granule bed, massive relatively well sorted medium- to coarse-grained sandstone with clay rip-up pebble and nodule granule bed and cross laminated well sorted medium-grained sandstone bed are observed. It was found that some beds eroded lower sediments. These features indicated to be deposited in channel and bar. The fish specimen is found in the not clear parallel stratified relatively well sorted coarse-grained sandstone with clay rip-up pebble and nodule granule bed (Fig. 1).

3. Material and method

The material described here has been found in the locality of Ban Krok Dusun Ha, Nakorn Ratchasima Province (Fig.1), during a Thai –Japan joint excavation in 2018. The holotype (NRRU-F01020023), paratype (NRRU-F01020024) and an isolated element (NRRU-F01020025) are housed at the Northeastern Research Institute of Petrified Wood and Mineral Resources. The holotype, NRRU-F01020023 is the anterior half of an individual with details

of the skull visible from both sides. The holotype was broken during the field collection and glued in the laboratory. The paratype (NRRU-F01020024) is preserved as a partly articulated posteranial skeleton including the squamation and part of the vertebral column, but with the fin missing because of preservation. The paratype is a bigger specimen than the holotype by comparison with scales dimension. The other material (NRRU-F01020025) is portion of a body with articulated scales. During the field excavation the specimens were extracted using hammer to break down the rock. As a consequence, the material consists of isolated pieces, which are glued afterward. The preparation was performed using an air pen in the laboratory of the Palaeontological Research and Education Centre, Mahasarakham University. An air-pen xx size was used for operating the sediment far from the fossil, then a needlepoint xx size with lower pressure was used to free the surface of the fossil. The time-consuming preparation was done under the binocular. The nomenclature used in the anatomical description follows Grande (1998).

4. Systematic palaeontology

Order AMIIFORMES Hay, 1929

Superfamily AMIOIDEA Bonaparte, 1838

Family SINAMIIDAE Berg, 1940

Genus *Sinamia* Stensiö, 1935

Type species: Sinamia zdanskyi Stensiö, 1935.

New sinamia sp. nov.

(Figs 2-6)

Derivation of name. The species is proposed in memory to the King Rama XI Bhumipol, honoring his important contribution to the systematic excavation at the Phu Noi locality in Kam Muang district, Kalasin province, northeastern Thailand.

Holotype. NRRU-F01020023, anterior haft fish with the dermal bones preserved.

Paratype. NRRU-F01020024, portion of a body with articulated scales, with a series of vertebral centra wedged in between both flanks of the specimen.

Other material. NRRU-F01020025, portion of a body with articulated scales.

Locality and horizon. Ban Krok Duean Ha, Tambon Krok Kruat, Amphoe Muang Nakhorn Ratchasima, Nakhorn Ratchasima Province, NE Thailand. Krok Kruat Formation, Early Cretaceous, Aptian.

Diagnosis: This species is distinguished from other species in the genus by the following combination of characters: crescent preopercular with dorsal and ventral ends broader; four paired of extrascapulars with the six median ones rectangular in shape and the lateral most ones elongate and triangular in shape; interdigitate suture between the quadrate and metapterygoid; pyriform shaped gular plate with a smooth undulate posterior margin; high cylindrical teeth with conical enamel stalk marked by fine ridges and with an arrow head shaped acrodin cap with cutting carinae ; rhombic scales with serrated posterior margins; no peg and socket articulation of the scales with a keel on the internal surface at the center of the scales.

Abbreviations: **ang**, angular; **ao**, antorbital; **br**, branchiostegal rays; **c**, centrum; **cha**, anterior ceratohyal; **chp**, posterior ceratohyal: **cl**, cleithrum; **d**, dentary; **dpt**, dermopterotic; **dsp**, dermosphenotic; **ecptp**, ectopterygoid tooth patch; **enp**, entopterygoid; es, extrascapular; **exo**, exoccipital; **fm**, foramen magnum; **fr**, frontal; **g**, gular; **h**, hyomandibula; **hh**, hypohyal; **hmf**, foramen and groove for the hyomandibular trunk, a mixed nerve containing fibers from

cranial nerve VII plus the anteroventral lateral line nerve; **iocn**, infraorbital sensory canal; **iop**, interopercle; **l**, lacrimal, anteriormost infraorbital=io1; **le**, lateral ethmoid; **mpt**, metapterygoid; **mptp**, metapterygoid process; **mx**, maxilla; **mxp**, anterior articular process of maxilla; **n**, nasal; **nop**, posterior nostril; **of**, olfactory foren; **op**, opercle; **pa**, parietal; **pcl**, postcleithrum; **pmx**, premaxilla; **pmxnp**, nasal process of premaxilla; **po**, postinfraorbitals, used here to refer to the infraorbital bone posterior to the orbit = io4 and io5; **pop**, preopercle; **popcn**, preopercular sensory canal; **pro**, prootic; **pt**, posttemporal; **q**, quadrate; **qc**, condyle of quadrate; **ro**, rostral bone; **roc**, opening to rostral sensory canal; **sag**, supraangular; **scl**, supracleithrum; **sclcn**, sensory canal of supracleithrum which connects to the main trunk lateral line; **smx**, supramaxilla; **so**, subinfraorbital, used here to refer to the small infraorbitals between the lacrimal and the postinfraorbital = io2 and io3; **socn**, supraorbital sensory canal; **sop**, subopercle; **spo**, sphenotic; **stcn**, supratemporal sensory canal; **su**, supraorbital bones.

Description

The material at hand is not complete and only the head and part of the trunk can be described. The general feature of the fish is an elongated and cylindrical body shape based on the holotype. The head length is 45 mm (including the opercular series), and approximately 25 mm in depth. The ossifications of the head have no ganoin cover. Bones of the skull roof bear a faint rugose ornamentation. The body is covered by rhombic scales with their posterior margin serrated. The base of the anterior part of the dorsal fin is visible on the right side of the holotype, whereas as well as elements of the paired fins on the left side of the same specimen.

Skull roof (Fig. xx). The frontals are the longest ossification of the dermal skull roof. Each frontal is slightly narrower anteriorly than posteriorly, and marks a regular curvature at the level of the orbit. The posterior margin of the pair of frontals is W-shaped and is firmly

sutured with the dermopterotics and a single unpaired parietal. The anterior margin of the right frontal is notched. This notch is filled with a bone, which extends ventrally underneath the antorbital, identified as the tip of the nasal process of the premaxilla. The lateral branch of the notch extends ventrally as a small process, with a concave surface that probably accommodated the dorsal extremity of the lacrimal (slightly shifted on the holotype). We cannot observe the suture between the left and right frontals on most of their length because of the presence of a crack along the mid-way of the skull roof. Only a short posterior portion of the suture presents a straight line towards the point extremity of the median parietal. The dorsal surface of the frontal bears a faint rugose ornamentation forming a reticulated pattern from the center of ossification. The frontal is twice as long as broad at its broadest posterior level. The parietal is a flat large median ossification as in other sinamiids. It is longer than wide (12 vs. 8 mm), with a sharp and pointed extremity wedged in the reversed V of the W-shaped margin of both frontals anteriorly. The right lateral margin is slightly undulate whereas the left lateral margin is straight. Both lateral margins mark a narrowing at the level of the posterior fourth of their length, thus forming a spearhead-shaped parietal. The dorsal surface of the parietal bears ridges radiating from the center of the bone. The dermopterotic borders laterally the parietal and extends anteriorly as a lateral pointed process with a slightly undulate suture along the posterolateral margin of the frontal. The dermopterotic is nearly three times longer than broad (14 vs. 5 mm), and as long but narrower than the parietal. Unlike the frontal and parietal, the dermopterotic is slightly convex in lateral view. Ridges radiating from the center of bone are present. The dermosphenotic is a small roughly rectangular bone wedged laterally between the right anterior extremity of the dermopterotic, and to the posterolateral margin of the frontal. It forms part of the skull roof. Its surface bears ornamentation similar to the rest of the skull roof bones. Posterior to the parietal and dermopterotics is a series of four pairs of extrascapulars. The six median extrascapulars are

Lionel Cavin
I cannot really see a difference between both sides (only slightly more slightly undulate…)

Lionel Cavin
Not very clear for me. Or 'concave in transversal section ' ?

rectangular in shape and the two most lateral ones are triangular with a blunt spine extending posteriorly. The external surface of the extrascapulars has no ornamentation, but small pores for the extrascapular commissure. The anteriormost preserved bone of the skull roof is the nasal, visible on the right side. The nasal is a plate like ossification laying on the ascending process of the premaxilla. It articulates with frontal posteriorly.

Lionel Cavin
Rather in the circumorbital section.

Braincase. Nothing is visible of the braincase, except the lateral extremity of the sphenotic wedged between the dermosphenotic and the dermopterotic, and fragments of ethmoid bones. The lateral ethmoid is visible on the right side as a vertical piece of bone held vertically under the anterolateral corner of the frontal, which forms a small ventral process (see above). On the left side, this region is not well preserved, and only a fragment of the lateral ethmoid is visible posterior to the nasal process of the premaxilla, which is almost vertical.

Circumorbital Ring. The circumorbital ring is well preserved on the right side. It consists of a dermosphenotic, two supraorbitals, three postinfraorbitals with the largest one located posteroventrally to the orbit, a lacrimal and an antorbital. Ventral to the orbit is a gap between the ventral most postinfraorbital and the lacrimal, in which lay probably a subinfraorbital. The entopterygoid is visible in this gap. The dermosphenotic ossification has no contact with the orbit, because anteriorly is a tiny element corresponding likely to the third postinfraorbital. The shape of dermosphenotic is roughly rectangular, except at the anterordorsal corner of the bone marked by a notch. The external surface of the bone is not smooth and bears several pores located mostly along the dorsal edge. Two supraorbitals are present above the orbit. They are firmly sutured to each other and form a narrow crescent shape with their convex dorsal margin fitting well the deep curvature of the frontal. Anterior to the orbit is the lacrimal, which is slightly shifted unveiling the lateral ethmoid underneath. It is boomerang

shaped, with the length of dorsal arm equal to ventral arm. Its concave dorsal margin forms the anteroventral border of the orbit. The antorbital, without contact with the orbit, is roughly triangular in shape with pore openings for the sensory canal at each summits of the triangle. A space delimitated by the antorbital, lacrimal, frontal and nasal corresponds to the posterior nostril. The lacrimal is separated by a small gap from the massive ventral postinfraorbital indicating that a small subinfraorbital was probably present on the living fish. The ventral postinfraorbital (=po1), situated at the posteroventral corner to the orbit, is the largest and more massive bone of the circumorbital ring. It bears strong ornamentation with strong knobs and grooves, even stronger than on the dermal roof bones. The shape is very peculiar, somewhat conch shell shaped, with the anterior portion protruding as a blunt process, with a broad mid-length area and with the posterior extremity tapering. The margins of the bone are smooth except the ventral one, which is undulate in correspondence to the ridges and grooves lying on the lateral surface. There are two small postinfraorbitals dorsally to the massive postinfraorbital. The second postinfraorbital, po2 is deeply sunk from its normal position. It is trapezoidal in shape with the ventral edge forming an oblique line contacting a curvature of the massive postinfraorbital. Its dorsal edge is indented at the mid length for the path of the sensory canal The third postinfraorbital is the smallest. It is rectangular in shape, and its surface bears a pore opening.

Lionel Cavin
Better in the sensory canal system ("There are pores located at the center of the outer surface of the lacrimal bone.")

Jaws. The premaxilla is incomplete being located in the most destroyed region of the skull. Therefore, its outline cannot be precisely described but the nasal process is apparently triangular in shape and held almost vertically. The extremity of the nasal process extends posteriorly as a spiny process fitting a notch on the frontal. The exposure of the nasal process on the skull roof is, as far as we know, unique within halecomorphs but present in lepisosteoidei among holosteans. On the right premaxilla one broken tooth is visible on the

oral margin of the bone, but the total number of teeth cannot be estimate. A large excavation marking the path of the olfactory nerve, with the non-visible olfactory foramen located in the bottom is present on the left premaxilla. The maxillae are visible on both sides of the head. On the left side, the posterodorsal part of the bone is visible as an imprint only, but it clearly shows the concave margin that forms a deep notch. On the right side the posterior extremity of the maxilla appears distinctive convex, but the posteroventral part of the ossification is not preserved.

The oral margin of the maxilla is better preserved on the left side. It is straight or very slightly concave. There are about thirty-three teeth in total, each has a long conical base. The acrodine cap is very peculiar being proportionally small with an arrow-head shape with cutting carinae. There are some pits on the lateral surface of the right maxilla. A supramaxilla is preserved on the right side just above the posterior part of the maxilla. It is narrow and elongate, ca 8.5 mm in long and 2 mm in depth at the posterior part, and gradually tapering towards its anterior extremity. The length of the bone is about half length of the maxilla.

The mandibles are low and their ventral margins expand horizontally. The visible part of the lower jaw comprises a dentary that bears a single row of conical teeth, an angular, a supraangular and a retroarticular visible as a tiny ossification at the posteroventral tip of the right mandible. The angular forms most of the posterior part of the mandible. It contacts the dentary along a zigzag suture anteriorly and the supraangular dorsally, which is partly visible on both sides. The dentary is long and anteriorly very shallow in lateral view with the posterior part of the bone increasing in depth to form the coronoid process. The dentary bears about 20 conical teeth with pointed arrow-head carinate acrodine caps. The teeth vary in size: the largest ones are located at the mid length while the ones on the posterior and anterior portions of the bone are smaller. Each tooth is composed of a high cylindrical base and extends with conical enamel stalk marked by fine ridges. Its acrodine cap forms a rounded

base and gradually tapers at the tip. Along the lateral edges of acrodine tip are strongly sharp carinae. All teeth are curve inwardly into the mouth.

Suspensorium. The well preserved suspensorium on the right side of the holotype shows the hyomandibula, the metapterygoid, and the quadrate whereas fragments of these bones plus a piece of ectopterygoid with small teeth is present on the left side. The right hyomandibula exposes its lateral side. The main axis of the bone is only slightly inclined posteriorly from the horizontal axis, and only part of the rounded articular head, of the concave posterior margin and of a fragment of the concave anterior margin are visible. The foramen and groove for the hyomandibular trunk, a mixed nerve containing fibers from cranial nerve VII plus the anteroventral lateral line nerve, opens near the anterior concave margin of the bone. The general shape of the hyomandibula is discussed in the section 'comparisons'. Anterior to the hyomandibula is the metapterygoid, which is roughly sub rectangular, with a posterior portion slightly expanding over the hyomandibula and an anterior portion narrowing. Its anterior margin has a deep notch for the path of the trigeminal nerve (Grande & Bemis, 1998), between the basal and otic processes, according to Stensiö (1935) nomenclature. Ventrally it connects the quadrate through an interdigitate suture. The otic process of the metapterygoid is twisted while the basal process is blunted. The lateral surface of the ossification is totally concave. On the left side, the ectopterygoid is visible as a poorly preserved rod of bone with tiny recurved teeth. The quadrate is a large fan-shaped ossification. Its lateral surface shows a concavity extending the concavity on the metapterygoid. The convex ventral end forms the jaw articulation with the lower jaw. Along the posteroventral border of the bone runs a strong crest starting from the condyle. The symplectic is not visible. the right entopterygoid is exposed between the ventral postinfraorbital and the lacrimal.

Opercular series, branchiostegal rays, and gular. The opercular series is complete, formed by the preoperculum, operculum, suboperculum and interoperculum.

The preoperculum is a narrow crescent shaped bone with its extremities distinctly widening both ventrally and dorsally. The anterior and posterior margins are regularly curved, while the dorsal margin is straight. The preopercle is lying along the anterior edges of the opercle, subopercle and interopercle. The dorsoposterior edge of the bone forms a plan which marks an angle with the rest of the ossification and completely fit the space with the opercle. This feature seems to be peculiar to *Khoratamia* among halecomorphs. The anteroventral margin of the bone rests against the strong crest of quadrate which runs along the upper arm. The operculum is roughly trapezoid in shape and deeper than long (12 x 8 mm). The dorsal and anterior borders are rather straight, while the posterior and ventral borders are slightly curved. The nearly upper half part of the posterior edge is smooth whereas the lower part has strongly serrations corresponding to the fine grooves present on its venteroposterior surface area. The shape of the subopercle, lying between the opercle and interopercle, is somewhat the miniature of opercle in overturn position. The dorsal border of the bone tightly contacts the ventral border of the opercle. The subopercle reaches the half depth of the opercle. The posterior edge of the subopercle is entirely serrated and no anterior ascending process is visible. The interopercle is visible as a triangular bone wedged between the subopercle and the posteroventral edge of the preopercle. Its anterior tip is pointed and it runs toward the ventral tip of the preopercle. The ventral margin of the bone is gently convex.

Eleventh elongated branchiostegal rays are well preserved on the holotype, NRRU-F01020023; the posteriormost one is the shortest but the widest. The branchiostegal rays are rather closely packed to each other. Each ray is narrow proximally and much broader distally. The anterolateral surface of each ray bears a crest, which is pronounced at the articulated point and gradually decrease and becomes complete flat at the half length of the bone.

Anterior to the branchiostegals is a median pyriform-shaped gular plate. The anterior portion is longer and narrower than the posterior portion. On the midline of the ventral surface is a ridge that nearly reaches the center of the bone. The ventral surface of the expended posterior portion shows faint ridges and grooves of regular size extending to the posterior margin, which forms a slightly undulate edge. In the central portion of the gular are small pits randomly distributed. The ceratohyal is partly exposed between the left dentary and the gular plate, but its shape is hard to precise. A thin element anterior to the ceratohyal is regard as hyohyal.

Pectoral girdle and fin. The large posttemporal lies posteriorly to the extrascapulars. It is visible as large trapezoidal to ovoid shaped ossification with a notch along its posterior margin for the path of the sensory canal. Its external surface bears a faint rugose ornamentation forming a reticulated pattern from the center of ossification. The anteroventral edge is strongly convex whereas its dorsal edge is almost straight with slight undulation. Because of the posterior extension of the lateral most extrascapulars, the posttemporals do not reach the lateral margin of the skull roof and have no direct contact with the opercle. The supracleithrum is proportionally very large, with an elongated general rectangular shape, an expended ventral extremity and a dorsal border firmly applied against the notch at the posterior margin of the posttemporal. Along the dorsal margin of the supracleithrum runs a short and curved ridge, which lies against a notch at the posterior margin of the posttemporal. The cleithrum is well visible on the left side. It is crescent in shape with the anterior part is narrow where the posterior wider. Base on the right cleithrum is twist thus its provide us that the lateral surface of the anterior narrow part is convex while posterior part become flat. The lateral face of the cleithrum is marked by smooth ridges which converge to the center of the expanding posterior area. The ventral margin of the cleithrum is convex. Two postcleithra are

original place on the right side while on the left side both of them are shifted to place underneath the suborbital. The upper postcleithrum is larger and deeper and is prominently convex dorsally and becomes thinner in its ventral part, which is flattened. The lowest postcleithrum is small and less convex, but it is not complete, making the estimate of its shape impossible. The posterior edges of the postcleithra have serration extending as compact grooves on the surface of the bone. A saddle-shaped ossified scapulocoracoid is partly visible on the left side.

Eleven fin rays are visible, but more were likely present., The preserved portion of the rays, ca 25 mm long are unsegmented, indicating that the total length of the fin was proportionally long because about half of the rays are unsegmented in the pectoral fin of *Anoia calva*.

Cephalic sensory canals (Fig xx). The numerous pores at the surface of the bones indicate the general pattern of the sensory canal system. In some parts of the head, the path of the canals can be seen through the very thin bone. The supraorbital sensory canal opens via numerous pores on the dermopterotic and frontal. The dermopterotic bears a douzaine of irregularly arranged pores on its dorsal surface. Moreover, tiny pores also open along the thin lateral margin of the dermopterotic, as previously observed in other sinamiids. The connection with the preopercular canal is not visible and it is possible that it occurred on the ventral surface of the bone. On the frontal, the pores are irregularly arranged and more concentrated above the posterior level of the orbit and in the anterior portion of the bone. The main supraorbital canal apparently forms an angle in the center of the frontal and gives off tubuli medially and laterally that reach the openings spread over the surface. The dermosphenotic, which is part of the skull roof, bears ca 6 foramens irregularly arranged. The path of the canal in the nasal is unclear, but a large pore is present on the anterior margin of the bone. The supratemporal commissure is clearly visible by transparency along the mid length of the extrascapulars. The

lateral most extrascapular, which extends posteriorly, bears ca 6 openings along its lateral border in alignment with the series on the dermopterotic. On the postemporal, two openings for the sensory canal are present on the lateral margin of the posterior prominent knob of bone, and a third smaller foramen opens between the two on the dorsal surface. The pores on the lateral margin of the bone correspond to the entry and exit of the canal, which thus forms a short loop in the posttemporal. This pattern implies that a section of the canal is not bone-enclosed between the exit of the extrascapular and the entry in the posttemporal. The sensory canal runs posteroventrally from the knob on the posterior extremity of the posttemporal to the mid-depth of the bone posteriorly. The preopercular sensory canal runs along the center of the bone. It gives off posterior tubuli that open via a few pores in the depressed posterodorsal corner, at least one pore in the mid-depth of the bone and at least four pores along the ventral part of the preopercle. The infraorbital sensory canal crosses both small dorsal postinfraorbitals as indicates the presence of pores and notch. We cannot follow the path of the canal within the large ventral postinfraorbital, in particular the potential presence of tubuli extending posteriorly as in *Sinamia zdanskyi* (Stensiö, 1935) because of the presence of strong ornamentation. There are pores located at the center of the lacrimal indicating the path of the canal that reach the antorbital anteriorly. The three pores in the antorbital indicates the path of a canal that crosses the bone and reaches the rostral (not preserved), and an opening dorsally close to the posterior nostril. The mandibular sensory canal runs along the ventral horizontal lamina of bone formed by the angular and dentary. Small foramens along the medial margin of the angular, which are followed anteriorly by a larger pore at the limit between this bone and the dentary, and by another medium-size foramen aligned in the dentary. Along most of the length of the dentary, the ca 10 large oval pores are shifted laterally compared to the posterior alignment, and located at the limit between the ventral and lateral sides of the

mandible. At the anterior extremity of the mandible, five large oval foramens are located again along the medial margin.

Vertebral column –A series of vertebrae is visible on the paratype (NRRU-F01020024). Five articulated centra are preserved wedged between the left and right scales covering of the body. The length is shorter than width in lateral side (ca. 6 mm long and 11 mm, respectively). Thanks to both posterior centra broken at their middle part, the sandglass shape of the centrum is visible and indicates that the anterior and posterior articular surfaces are deeply concave. The lateral surface present trace of grooves and ridges. Each centrum has the same proportion.

Dorsal fin. Although this area was destroyed, the origin of the dorsal fin can however be located. It is placed at the 5/8 distance of the pelvic fin.

Pelvic girdle and fins. The pelvic fins are apparently very small based on the pelvic fin rays partly preserved on the left side, which are small and short. The basipterygium is visible as a long rod of bone with an enlarged posterior extremity (char. 29 on G & B). Three pairs of lepidotriches can be count.

Squamation – The whole body is covered by thick rhombic scales covered with a ganoin layer. The scales of the dorsal region are small, as long as deep, whereas the scales of the lateral or the ventral regions of the trunk are distinctly longer than deep (about 3 mm long and 1.5 mm deep). In addition, their lateral surface presents a ridge on the ventral edge in the holotype, but in other material such as NRRU-F01020025 there are two ridges located closed to the dorsal and ventral margins. The posterior margin of all scales is serrated, with about 11

tiny denticulations in maximum (the number varies from 2-11 depending of the position on the body). The lateral line scales are not visible on the anterior part of the preserved body. At the level of the beginning of the dorsal fin, one scale every two or three scale (with a gap of four consecutive scales) are marked with a sensory pore, which has the shape of a vertical elongate groove dug in the middle of the scale. No peg and socket articulation has been observed in the overlapped area where scales are destroyed. The imprints of scales indicate that the internal surface of the scales is protruded like a strong keel or ridge at its center. The keel is visible on scales preserved in internal view behind the dorsal fin of the holotype.

5. Discussion

Hyomandibula. The orientation of the hyomandibula in *Khoratamia* is very inclined, probably in connection with the elongated and shallow head of this fish, but its complete shape is unclear because part of the bone is hidden under the preopercle. Stensiö (1935) observed a hyomandibula with an elongated opercular process in S. zdanskyi. Peng et al. (2015) described on an articulated specimen of *Sinamia lanzhouensis* a hyomandibula composed of two portions: one articulating with the dermopterotic dorsally and one going along the anterior margin of the preopercle. They cannot decide if a preopercular process is present on this bone, because this part is obscured or not preserved. However, they also figured (Peng et al., 2015: fig. 9J), but not described, an isolated hyomandibula referred to *Sinamia lanzhouensis*, which has a large double-headed ventral extremity. The posterior articular head is likely a poorly opercular process, while the anterior expansion applied against the posterodorsal margin of the quadrate. It is difficult to understand how such a short opercular process could reach the articular facet of the opercle, and we suggest that the isolated

hyomandibula figured by Peng et al. (2015) is either uncomplete or do not belong to the species, and that *Khoratamia* has a long opercular process under the preopercle, with almost the same proportion as the one of *Calamopleurus* (Grande & Bemis, 1998: fig. 305).

Jaws. Several features of the jaws are shared with the vidalamiinae: the short premaxilla, with a vertically held nasal process and a large excavation for the olfactory foramen are reminiscent of *Calamopleurus*, the deep posterior margin of the maxilla very concave is reminiscent of vidalamiini (*Vidalamia* and *Pachyamia*), although the ventral process below the notch is not as elongated, and eventually the carinate acrodine tips of the teeth is a feature shared with all vidalamiins.

Preopercle. The preopercule of the Khorat specimen has narrow crescent shape, approximately similar to the preopercle of other sinamiid fish but that differs by its distinctive broader both ventrally and dorsally ends. The preopercle of *Sinamia lanzhouensis* (Peng et al., 2015) shows a similar general shape, but the extremities are less wide compare with Thai fish. In addition, the curvature of the anterior border of the preopercle of yyy is more deeply concave. This strong curvature of the anterior border is similar to *Sinamia zdanskyi* (Stensiö, E. A. 1935) but, however, the dorsal and ventral ends of *S. zdanskyi* are not as wide as in the Thai specimen. The posterodorsal corner of the preopercle that forms a triangular area arranged at an angle with the rest of the body of the bone appears to be restricted to *Khoratamia*.

Parietal. In yyy, the median parietal has a spearhead-shaped with its sharp pointed anterior extremity and its lateral margins curved inward at the posterior fourth, while in *S. zdanskyi* the anterior portion of the bone is blunt and the lateral margins present a broad obtuse processes fitting into the median margin of the dermopterotic. One such process is visible on the right lateral margin of the Khorat specimen, whereas the lateral margins are straight in Siamamia naga (Cavin et al., 2007). The large ventral postorbital located at the posteroventral corner to

the orbit of the Khorat material is similar to the fifth infraorbital of *S. liaoningensis* (Zhang, 2012) and to the fourth infraorbital of the *S. zdanskyi*. But yyy has very somewhat peculiar conch shell shape contrary to the trapezoidal shape in the *S. zdanskyi* and to the rectangular shape in the *S. liaoningensis*. The presence of interdigitate suture between the quadrate and metapterygoid is different from other Sinamia. *Gular*. The pyriform shaped gular shape has been described from two isolated ossifications of *Sinamia kukurihime* by Yabumoto, 2014, which is reminiscent to the Khorat yyy except the smooth posterior margin. The Japanese specimens, however, are not complete preserved and the comparison between both taxa is still uncertain. Compare to the *S. zdanskyi*, the gular shape of yyy is clearly different by the deeper posterior portion than in *S. zdanskyi*. The posterior margin of the gular of most amioids is straight except the strongly denticulation present in *Calamopleurus cylindricus*, which differs from the smooth undulate margin of the Khorat one.

Lionel Cavin
[illegible] is no suture [illegible]

YYY is characterized by the absence of peg and socket articulation on the scales, by denticulations along its posterior margin and by its internal face marked with a strong keel and its external side by one or two ridges, features that differ from *Siamamia*, which lacks the denticulation on the posterior margin, its dorsal surface is smooth and no strong ridge or keel is apparent on its interior surface.

Sensory canal system. The density of pores for the exits of the sensory canals in *Khoratamia* is higher than in *Amia*. A typical feature is the presence of a series of pores aligned along the lateral margin of the dermoperotic and the lateral most extrascapular. The pores in the extrascapulars are apparently connected to a canal that branches from the supratemporal canal close to its exit from the extrascapular. It is not clear how the lateral openings on the dermopterotic are connected to the main supraorbital canal. On the left side, a broken part of the lateral margin of the frontal shows a cluster of three openings leading to a single small canal reaching the main supraorbital canal. In *Sinamia zdanskyi*, a series of pores along these

two bones are also present, and Stensiö suggested that the pores along the lateral edge of the dermopterotic are connected to the main canal via clusters of two or three tubuli (1935: fig. 18). In *Siamamia*, a similar series of pores also open along the lateral margin of the dermpoterotic. In both Thai species, the supratemporal sensory canal open equally on the surface of the pterotic, while such openings are apparently absent in *A. calva* and *S. zdanskyi*. In *Sinamia liaoningensis*, there is a high density of openings of the sensory canal along the lateral margin of the dermopterotic, and especially along the lateral extrascapular, but few on the dorsal surface of the dermopterotic (Zhang, 2012). This feature, when visible, seems to be restricted to the sinamiids among the halecomorphs.

6. Conclusions

Acknowledgments

This work was supported by Thailand-Japan Dinosaur Excavation Project, a collaboration research project between Northeastern research institute of petrified wood and mineral resources, Thailand and Fukui Prefectural Dinosaur Museum, Japan and We would like to thanks all the members of the project who took part in field work and prepared specimens. We express our thanks to Masateru Shibata, Teppei Sonoda, Duangsuda Chokchaloemwong for their supports. This work was also supported in part by the Office of the Higher Education Commission and the Office of Research Fund- developing the potential for research work of new generation teacher Fiscal year 2018 (MRG 6180086) to UD.

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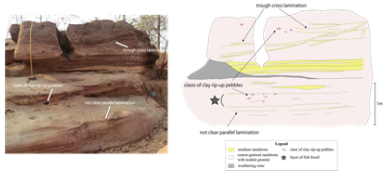
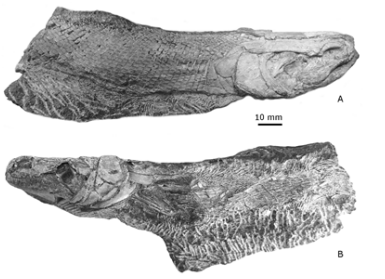
Figures



Text-fig. 1

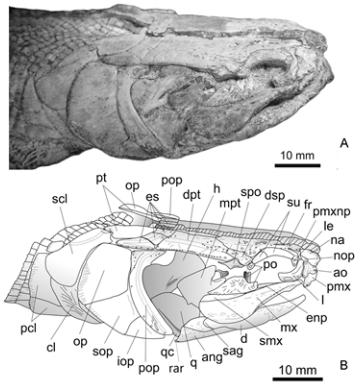
Study area at the dinosaur excavation site in KDH. Star mark is the layer of fish. The layer with some vertebrate assemblages preserved in clay rip-up pebbles.



Text-fig. 2

25

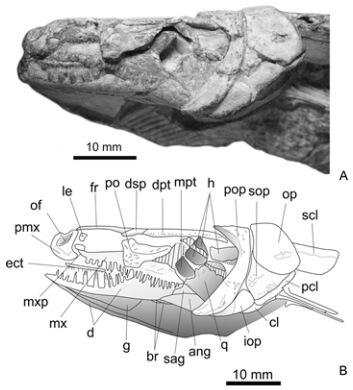
xxx sp. nov. NRRU-F01020023 (holotype). A, preserved in right lateral view. B, preserved in left lateral view. Scale bars = 10 mm.



Text-fig. 3

xxx, skull roof of holotype (NRRU-F01020023) in right lateral views. A, detail in photograph; B, line drawing. Scale bars = 10 mm.

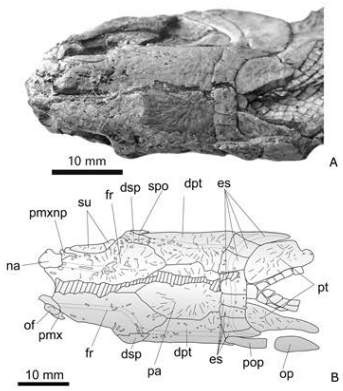
26



Text-fig. 4

xxx, skull roof of holotype (NRRU-F01020023) in left lateral views. A, detail in photograph; B, line drawing. Scale bars = 10 mm.

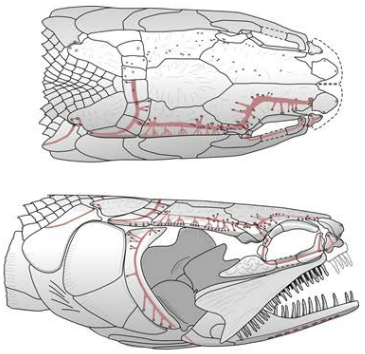
27



Text-fig. 5

xxx, skull roof of holotype (NRRU-F01020023) in dorsal views. A, detail in photograph; B, line drawing. Scale bars = 10 mm.

28



Text-fig. 6

xxx, skull roof of holotype (NRRU-F01020023) in dorsal views. A, detail in photograph; B, line drawing. Scale bars = 10 mm.

2. LIONEL CAVIN*1, UTHUMPORN DEESRI2,3, PHORNPHEN CHANTHASIT4 A NEW LUNGFISH FROM THE JURASSIC OF THAILAND. In JOURNAL OF VERTEBRATE PALAEONTOLOGY.

A NEW LUNGFISH FROM THE JURASSIC OF THAILAND

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RH: CAVIN ET AL.-NEW LUNGFISH FROM THAILAND

The lungfishes, or Dipnoi, form a depauperate clade of sarcopterygian fishes living today in freshwaters of eastern Australia, Africa and South America. Lungfishes were mostly marine in the Devonian, then typically freshwater since the Carboniferous (Challands et al., 2019). An evolutionary trend observed in this lineage is a reduction of ossification of the skeleton associated to an increasing mineralization of the oral teeth. As a consequence, the Mesozoic fossil record of lungfishes, especially in post-Triassic deposits, is made in large part of isolated tooth plates and cranial elements are rarely found. Isolated tooth plates bear diagnostic features for identification at the specific and generic levels, but only cranial bones bring characters allowing to draw the general frame of the lungfish evolution.

Here we describe a new species of the lungfish *Ferganoceratodus* based on cranial elements with associated tooth plates found in the fossiliferous site of Phu Noi located in the lower or middle part of the Late Jurassic – Early Cretaceous Phu Kradung Formation in northeastern

Thailand (Fig. 1). This Formation has already yielded a separate species of *Ferganoceratodus* in a site located in the upper part of the series. The new discovery sheds a new light on the biogeographical relationships and stratigraphical succession of Eastern Asian lungfishes during the Jurassic and Early Cretaceous.

SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Order DIPNOI Müller, 1844

NEODIPNOI Agnolin, 2010 *sensu* Kemp et al. 2017

Suborder CERATODONTOIDEI Nikolski, 1954 *sensu* Kemp et al. 2017

Genus *FERGANOCERATODUS* Kaznyshkin & Nessov, 1985

Type species-*FERGANOCERATODUS JURASSICUS* Kaznyshkin & Nessov, 1985

Other species: *F. szechuanensis* (Young, 1942), *F. martini* Cavin, Suteethorn, Buffetaut, Tong, 2007

FERGANOCERATODUS XXX sp. nov.

Holotype: KS34 – 1785 (Fig. 2)

Etymology: yyy

Diagnosis: *Ferganoceratodus* distinguished from the other Asian species of that genus by the following combination of characters: posterolateral bone (YZ bone) with a process for

articulation with the mandible longer than in *F. jurassicus* (unknown in the other two species); widest level of the anterolateral bone in its mid-length (similar in *F. jurassicus*; the whole anterior half of the bone is wide in *F. martini*; situation unknown in *F. szechuanensis*); inner angle of upper and lower tooth plates poorly marked (in the three other species, this angle is sharper); mesial margin of upper and lower tooth plates slightly shorter than the lingual margin (significantly shorter in the three other species); lower tooth plate with a first notch significantly deeper than the following ones (as in *F. jurassicus* but to the contrary of *F. szechuanensis* and *F. martini*).

Type locality: Phu Noi, Tambon Din Chi, Kam Muang district, Kalasin province, northeastern Thailand.

Type horizon: Lower part of the Phu Kradung Formation, probably Late Jurassic in age.

Anatomical Description

For synonymies between the names of the bones used here and in other publication, see Cavin et al., 2007, table I and Criswell, 2015).

The skull roof is disarticulated but all bones are concentrated on a little space and obviously belong to the same individual. As far as the skull bones pattern can be reconstructed, it is close to those of *Ferganoceratodus jurassicus* and *F. martini* (Fig. 3). The external side of the bones is smooth and the internal side bears fine radiating ridges. One incomplete bone is regarded as the anterior bone of the median series (Fig. 2B). Its probable posterior extremity is rounded and although its anterior part is damaged, it appears that the bone broadens slightly anteriorly. The posterior bone of the median series (Fig. 2C) is almost complete except its right lateral margin. It was slightly more than 1.5 times longer than wide. The maximum width is situated in the mid-length of the bone. Anteriorly to this point, the lateral margins that sutured with the anterior bone of the mediolateral series are straight and slightly convergent frontward. Posteriorly to the widest point, the margin marks a concavity close. No median groove for the anchorage of the chondrocranium is visible on the internal side. The posterior margin is

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irregular in shape, but because of the thinness of the bone its precise outline is uncertain. The posterior bone of the mediolateral series (Fig. 2D) is approximately oval with a short broad quadrangular expansion on one corner that we regard as the anterolateral corner, which rested underneath the posterior bone of the lateral series (YZ bone). Another sutural surface located nearly the quadrangular expansion is regarded as an area underlying the posterior margin of the anterior bone of the lateromedial series (Fig. 3). The left anteromedial bone is present (Fig. 2A). It is reminiscent of the same bone in *F. martini*, except that in the latter the anterior portion of the ossification corresponds to the widest part of the bone while in the new species the anterior portion is significantly narrower than the posterior portion. The posterior margin is regularly curved and marks no angle with the medial margin. The contour of the orbit is visible as a concavity at the anterior extremity of the lateral margin. Traces of the sensory canal is visible on the dorsal face of the bone in its mid-width (Fig. 2A). The descending process for articulation with the ascending process of the pterygopalatine is present in the anteromedial quarter of the ventral side of the bone (Fig. 2A'). The descending process is inclined anteriorly, still more than in *F. martini*, but we cannot exclude that this arrangement was caused by deformation due to fossilization. The extremity of the descending process shows no details because of preservation. On the internal face of the bone, a ridge runs from the anterior corner of the base of the descending process towards the anterolateral corner of the bone (Fig. 2A'). The olfactory cartilage anchored on this ridge (Kemp, 1998). An isolated bone has an ovoid shape with an elongated and slightly curved process (Fig. 2E). Pits and short grooves dug in the plate-like portion of the bone are related to the sensory canal. This ossification is regarded here as the posterior bone of the lateral series (YZ bone). In the holotype of *F. martini*, only a fragment of the posterior bone of the lateral series is preserved and the complete ossification was reconstructed as a single ovoid bone without a process for articulation based on comparison with a reconstruction of *F. jurassicus* by Kaznyshkin (1993). In this model, this bone shows no anteroventral extension and it is unclear how the mandible articulates with the skull. In Neoceratodus, the quadrate is cartilaginous and occurs as an outgrowth from the process of the posterior lateral bone (also named YZ or XYZ bone or squamosal), and the situation was likely similar in most extinct lungfishes (Kemp, 1998). The original description of *F. jurassicus* by Nessov & Kaznyshkin (1985) shows that the YZ bone

actually bears a small process, that can be regarded as a reduced articular process for the mandible (Nessov & Kaznyshkin, 1985, fig. 1:5). Our reconstruction of the skull roof of *F. jurassicus* shows this bone oriented with the process facing anterolaterally (Fig. 3). This reconstruction is also supported by the presence of two sutural surfaces that likely rested under both bones of the mediolateral series. A similar re-interpretation of the posterior bone of the lateral series was made by Kemp (1998) for *Argenodus* (*Asiatoceratodus* according to Kemp) *atlantis* initially reconstructed by Martin (1981). The discovery of the complete ossification in *F. xxx* indicates that the situation was somehow likely similar in *F. martini*, although it is unknow if the extension of the process was as long as in the new species or reduced as in *F. jurassicus*. Because the paths of the sensory canal are not visible on this bone, it is unclear if an independent dermosphenotic bone was present, as in *F. martini* (Cavin et al., 2007). In *F. jurassicus*, Kaznyshkin (1993) reconstructed the skull roof with an independent X (dermosphenotic) bone, but this bone is apparently not preserved. We suspect that this reconstruction rested on a supposition based on the absence of a triple junction of the sensory canal in the posterior bone of the lateral series. In *Argenodus atlantis*, there is a single bone on the lateral series corresponding to the fusion of both ossifications (XYZ bone) (Kemp, 1998). An ovoid bone forming a right angle, very incomplete, with a fragment of another bone located in its concavity (Fig. 2F) is provisionally identified as a piece of the labial bone (angular) of the mandible, with possibly a fragment of the labial bone (prearticular) inside. An elongated rectangular bone, with a ridge possibly corresponding to the path of a sensory canal, is not identified (Fig. 2E).

Both upper tooth plates and the left lower tooth plate are preserved. The rather thick upper tooth plates bear five ridges (Fig, G, H). The anteriormost two ridges are sharp and the posterior three are blunt. The surface of the plates shows a fine pattern of pits. The inner angle is slightly less than 90° (approximately 86°). The left lower tooth plate is still attached to its supporting bone (Fig. I). It bears four ridges, the anteriormost one being significantly longer than the posterior ones. The anteriormost two ridges are sharper than the posterior two. The tooth plate is thick and bears the similar pitted pattern than the upper tooth plates. Its inner angle equals approximately 98°. Based on the presence of a lamina of bone of the supporting

ossification situated anteromedially to the lower tooth plate, it is assumed that both tooth plates were not in contact.

Discussion

Figure 3 show a comparison of *F. xxx* with *F. jurassicus* and *F. martini*. The most distinctive differences between *F. martini* and *F. xxx*, both found in the same formation, such as the shape of the anterior bone of the lateral series, which narrows anteriorly in the new species (as in *F. jurassicus*) and remains wide in *F. martini*. Other differences are visible in the shape and size proportions of the skull roof bones between the three species, but we are reluctant to use these features as diagnostic characters because 1) these are weakly pronounced and 2) we cannot assess the intraspecific variations. Moreover, the reconstruction of the skull roof of *F. xxx* is still uncertain, such as the identification and orientation of the posterior bone of the mediolateral series. If correctly reconstructed, *F. jurassicus*, from the Middle Jurassic of Kyrgyzstan, differs from *F. xxx* by its much-reduced articular process of the posterior bone of the lateral series (YZ bone). Diagnostic characters are present on the tooth plates, such as the inner angle of upper and lower tooth plates more poorly marked and the mesial margin of upper and lower tooth plates only slightly shorter than the lingual margin in the new species, while the inner angle is more marked and the mesial margin is significantly shorter in other species of *Ferganoceratodus*, including *F. czechuanensis*. The latter species, known by isolated tooth plates only, was identified in the Late Jurassic or Early Jurassic of South China, then recorded in Thailand in the Late Triassic Huai Hin Lat Formation (Martin & Ingavat, 1982), and in the Middle Jurassic Khlong Min Formation and in the Late Jurassic Phu Kradung Formation (lower part) (Martin et al., 1997). In *F. xxx* the first notch of the lower tooth plates is deeper than the other ones, as in *F. jurassicus* but to the contrary of *F. czechuanensis*, and *F. martini*. As a result, the general pattern of the lower tooth plates shows sharp cutting ridges in *F. xxx* and a broader crushing surface in other *Ferganoceratodus* species.

Recently found lungfish tooth plates from the Middle Jurassic of the Xintiangou Formation, Chongqing, China, currently under study share features with *F. xxx*, but also with *F. jurassicus* (Buffetaut et al. in progress).

Cranial and tooth plates characteristics of the new lungfish specimens clearly point to a distinctive species than *F. martini*, which is nevertheless found in the same formation (Fig. 1). *F. martini* was found in Phu Nam ~~jumjun~~. This site has yielded several hundreds of articulated specimens of ginglymodian fishes (*Thaiichthys* and *Isanichthys*), which have likely died following the drying up of a pond. *F. xxx* was found in the rich assemblage of the Phu Noi site, which has yielded a diversified fish and tetrapod assemblage partly articulated, probably transported before burial. Lungfish are usually a rare component of vertebrate assemblages, although their tooth plates may be rather common in some Formation. In the Early Cretaceous of Tunisia, for instance, a relatively high diversity of lungfishes has been recognized (Fanti et al., 2016), but in this deposit the lungfishes belong to different lungfish lineages. Both species found in the Phu Kradung Formation are closely related species, and they rather correspond to distinct species from the same lineage separate in time, potentially the result of a anagenetic evolution. This result also supports the hypothesis that the Phu Kradung Formation has deposited during a long-time span, with *F. xxx* located in the lower - middle part dated to the Late Jurassic, and *F. martini* located in the upper part dated to the basal Cretaceous.

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Caption

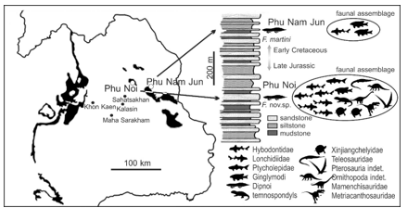

Figure 1

Left, geographical location of the Phu Noi site that yielded the holotype of *F. xxx*, and of Phu Nam Jun, that has yielded the holotype of *F. martini*. The former locality is likely Late Jurassic in age and the later locality is Early Cretaceous in age. Right, Simplified series of the Phu Kradung Formation with the position of the Phu Noi and Phu Nam Jun locality, together with an overview of their vertebrate assemblages. Phu Noi has yielded a diversified assemblage of fish and tetrapod assemblage, probably the result of an accumulation after some transportation, while the Phu Nam jun assemblage has yielded an almost monospecific assemblage of several hundreds of specimens of the ginglymodian *Thaiichthys*, plus a couple of specimen of the ginglymodian *Isanichthys*, a single(?) tooth of hybodontids and the single specimen of the lungfish *F. martini*. The stratigraphical section was modified from Martin et al. (2016).

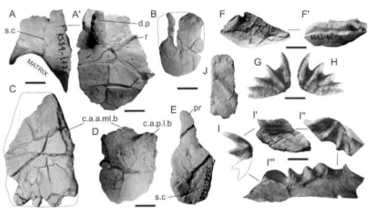

Figure 2

Holotype of *F. xxx* (KS34 – 1785), Late Jurassic of Phu Noi, Tambon Din Chi, Kam Muang district, Kalasin province, northeastern Thailand. A, anterior bone of the mediolateral series in dorsal (A) and ventral (A') views; B, anterior bone of the medial series; C, posterior bone of the mediane series in ventral view; D, posterior bone of the mediolateral series in dorsal view; E, posterior bone of the lateral series (YZ bone) in dorsal view; F, ?lingual bone (angular) in ?lateral (F) and ?oblique (F') views; G, H, right (G) and left (H) dorsal tooth plates; I, left ventral tooth plate in occlusal view with the posterior part reconstructed (I) (the plate is not fully visible in occlusal view), in labial (I') and lingual (I''') views, with a piece of the lingual bone (prearticular) still attached; E, indeterminate bone. Abbreviations: c.a.a.ml.b, contact area with the anterior bone of the mediolateral series; c.a.p.l, contact area with the posterior bone of the lateral series; dp, descending process; pr, process; s.c, sensory canal.

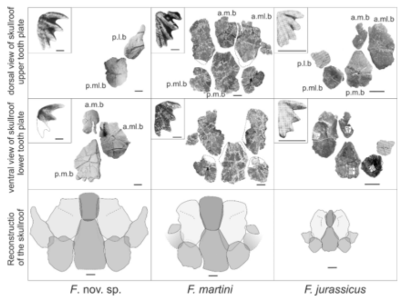

Figure 3

Comparison of the skull roofs and tooth plates of three species of *Ferganoceratodus*. *F. martini* was found articulated while the other two species are reconstructed. Abbreviations: a.m.b, anterior bone of the medial series; a.ml.b, anterior bone of the mediolateral series; p.l.b, posterior bone of the lateral series; p.m.b, posterior bone of the medial series; p.ml.b, posterior bone of the mediolateral series. Scale bars for the calvaria: 10 mm; Scale bars for the tooth plates: 5 mm.

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Annales de Paléontologie 105 (2019) 223–237

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Original article

Phu Din Daeng, a new Early Cretaceous vertebrate locality on the Khorat Plateau, NE Thailand

Phu Din Daeng, un nouveau site à vertébrés fossiles du Crétacé inférieur sur le plateau de Khorat, NE de la Thaïlande

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ARTICLE INFO

Article history:
Available online 27 May 2019

Keywords:
Vertebrates
Early Cretaceous
Khorat Group
Sao Khua Formation
NE Thailand

Mots clés :
Vertébrés fossiles
Crétacé inférieur
Groupe de Khorat
Formation Sao Khua
NE Thaïlande

ABSTRACT

In this paper, we report on a new Early Cretaceous vertebrate locality, Phu Din Daeng, in Nakhon Phanom Province, NE Thailand. The Phu Din Daeng site has yielded a diverse vertebrate assemblage, including sharks (*Heteroptychodus steinmanni*), bony fishes (Pycnodontiformes; Sinamiidae cf. *Siamamia* and ?Vidalamiinae, and Ginglymodi), adocid turtles, indeterminate neosuchian crocodiles, pterosaurs and dinosaurs (spinosaurids and indeterminate theropods). A new adocid turtle, *Protoshachemys rubra* n. g. n. sp. is described on the basis of shell material. Field investigations on the geology and comparisons with other vertebrate faunas place Phu Din Daeng in the Sao Khua Formation (Barremian) of the Khorat Group.

RÉSUMÉ

Phu Din Daeng, un nouveau site à vertébrés fossiles d'âge Crétacé inférieur dans la province de Nakhon Phanom, NE de la Thaïlande, est signalé. Le site de Phu Din Daeng a livré une faune de vertébrés fossiles diversifiée, comprenant des requins (*Heteroptychodus steinmanni*), des poissons osseux (Pycnodontiformes; Sinamiidae cf. *Siamamia* et ? Vidalamiinae, ainsi que Ginglymodi), des tortues adocidés, des crocodiles néosuchiens indéterminés, des ptérosaures et des dinosaures (spinosauridés et théropodes indéterminés). Une nouvelle tortue, *Protoshachemys rubra* n. g. n. sp., est décrite sur la base d' éléments de carapace. Les investigations géologiques sur le terrain et la comparaison avec les faunes de vertébrés du Groupe de Khorat placent Phu Din Daeng dans la Formation Sao Khua (Barrémien).

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https://doi.org/10.1016/j.annpal.2019.04.004
0753-3969/

1. Introduction

The Mesozoic non-marine deposits of the Khorat Group (Late Jurassic–Early Cretaceous) in NE Thailand are rich in vertebrate fossils. Among the five formations included in the Khorat Group (from bottom to top: Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations), numerous localities in the Phu Kradung, Sao Khua and Khok Kruat formations have yielded abundant vertebrate body remains (see Buffetaut et al., 2009 and references therein). In this paper, we report on a new vertebrate locality, Phu Din Daeng, in Nakhon Phanom Province. Recently discovered by local people, the site has been visited regularly by the Palaeontological Research and Education Centre (PRC), Mahasarakham University, since 2012. The material was collected on the surface or by systematic excavations to extract apparently partially associated fish or turtle skeletons; and the sediments were screen-sieved. The Phu Din Daeng site has yielded a diverse and somewhat peculiar vertebrate assemblage including sharks, bony fishes, turtles, crocodiles, pterosaurs and theropod dinosaurs. The geology of the site is investigated and the stratigraphical significance of the assemblage is discussed. A new species of turtle, yet unique to this locality is described.

2. Geological setting

The Phu Din Daeng site is located in Tambon (sub-District) Si Chompu, Amphoe (District) Na Kae, Changwat (Province) Nakhon Phanom, NE Thailand (Fig. 1). The outcrop where fossils were discovered corresponds to a small erosional area at the northeastern end of the anticline of the Phu Phan Range, on the Khorat Plateau. Stratigraphically, the Phu Din Daeng site is located at the top of the Sao Khua Formation, a few metres below the Phu Phan Formation. Next to the site is a hill that is topped by hard layers of medium to coarse-grained sandstones and conglomerates typical of the Phu Phan Formation. The fossiliferous deposits correspond to a thin layer of siltstone of a few centimetres thick, itself interbedded in layers of red mudstones, siltstones and sandstones. Vertebrate fossils are relatively abundant, including sharks, bony fishes, crocodiles, turtles, pterosaurs and theropod dinosaurs; bivalves have also been collected. Large bones are very rare, fish and turtle remains are by far the most abundant vertebrates at Phu Din Daeng, but often represented by fragmentary and isolated elements or by loosely associated sets of plates or scales. The generally disarticulated nature of the material may indicate that carcasses were partially or totally decayed and disarticulated before burial. Most fossils consist of relatively small elements suggesting a possible winnowing. It does not appear that there are important concentrations of fossils, indicating that the bone bed is probably the result of a single flooding event occurring at some distance from the main water bodies somewhere in the flood plain. Some turtle elements belonging to a single individual, although disarticulated, have been collected over a small area, suggesting an *in situ* preservation or short transportation.

Based on palynology and vertebrate palaeontology, the Sao Khua Formation is considered to be Early Cretaceous (Buffetaut et al., 2006; Racey, 2009; Racey et al., 1996), and more precisely Barremian in age based on the study of bivalves (Tumpeesuwan et al., 2010). Located stratigraphically at the top of the formation, the Phu Din Daeng site seems to be younger than some other fossiliferous outcrops in the Sao Khua Formation, such as Phu Kum Khao (Kalasin Province) and Phu Wat (Nong Bua Lamphu Province), and indeed displays a slightly different fossil assemblage.

3. Vertebrate fauna from Phu Din Daeng

3.1. *Chondrichthyes Huxley, 1880*

Hybodontiformes Patterson, 1966

Heteroptychodus steinmanni Yabe & Obata, 1930

Material: Three teeth with the root preserved (**PRC34-PRC36**) and three fragments of tooth crown (Fig. 2).

Description: The three teeth are flat, roughly parallelogram-shaped in apical view with a sigmoid curvature in labial or lingual view. **PRC34**, the most complete one (Fig. 2A-B), measures 19 mm mesiodistally, 14 mm labiolingually and is 7 mm high, including the root. Its apical surface shows 25 closely packed mesiodistal ridges. **PRC35** (Fig. 2E–F) measures 15 mm mesiodistally, but is incomplete and 17 mm labiolingually. It shows 31 mesiodistal ridges. **PRC36**, the largest one, has been found in three parts that have been glued back together (Fig. 2C–D). It measures 21 mm mesiodistally and 15 mm labiolingually and displays 30 mesiodistal ridges. Each mesiodistal ridge bears fine perpendicular ridges on its lingual side. A marginal area is visible on the lingual part of the apical side of the crown, ornamented with anastomosed ridges roughly oriented perpendicularly to the lingual edge of the crown. On the labial, mesial and distal extremities, this marginal area is strongly reduced. The labial, lingual, mesial and distal faces of the crown are ornamented with fine, irregular, anastomosed ridges. The root is thicker than the crown, up to twice so, and is very porous, showing a multitude of small pores on all its faces. On the labial and lingual sides, at roughly mid-height of the root, there is a row of enlarged foramina.

Discussion: The presence on these teeth of several mesiodistal ridges, each bearing numerous short perpendicular ridges together with a reduced marginal area around the crown is characteristic of the genus *Heteroptychodus* (Yabe and Obata, 1930). Three species of *Heteroptychodus* are currently recognized. *H. chuvalovi* is easily separated from the Phu Din Daeng teeth by its chevron-shaped mesiodistal ridges (Cuny et al., 2008). *Heteroptychodus kokutensis* is also easily separated from the Phu Din Daeng teeth as its teeth are more elongated mesiodistally and its labiolingual ridges between the main ridges are not as regular and thin as in the teeth from Phu Din Daeng (Cuny et al., 2010). The latter character, as well as the labiolingual width of the teeth from Phu Din Daeng allow attributing them to *H. steinmanni* (Cuny et al., 2003; Yabe and Obata, 1930). This species was originally described from the Hauterivian Tatsukawa Formation in Japan (Kozai et al., 2005; Yabe and Obata, 1930). In Japan, *H. steinmanni* is restricted to the Hauterivian-Barremian interval (Okazaki, 2016). The species is also known from the Aptian of southern China (Mo et al., 2016) and in Thailand, it has been reported in the Sao Khua (see Cuny et al., 2007, Fig. 2B) and Khok Kruat formations.

3.2. *Actinopterygii Cope, 1887*

Pycnodontiformes Berg, 1937

Genus and species indet.

Material: PRC84, fragment of a vomer

Description: PRC84 is an isolated fragmentary tooth-bearing bone. It is referred with caution to a piece of a vomer of a pycnodontiform (Fig. 3). The molariform and oval shaped teeth without pedicel but with an apical papilla are typical of the teeth of some pycnodontiforms. The symmetry observed in the bone indicates an unpaired toothed bone, i.e. a vomer.

Discussion: Rather similar teeth from Phu Phan Thong, in the Sao Khua Formation, have been referred to cf. *Anomoeodus* by

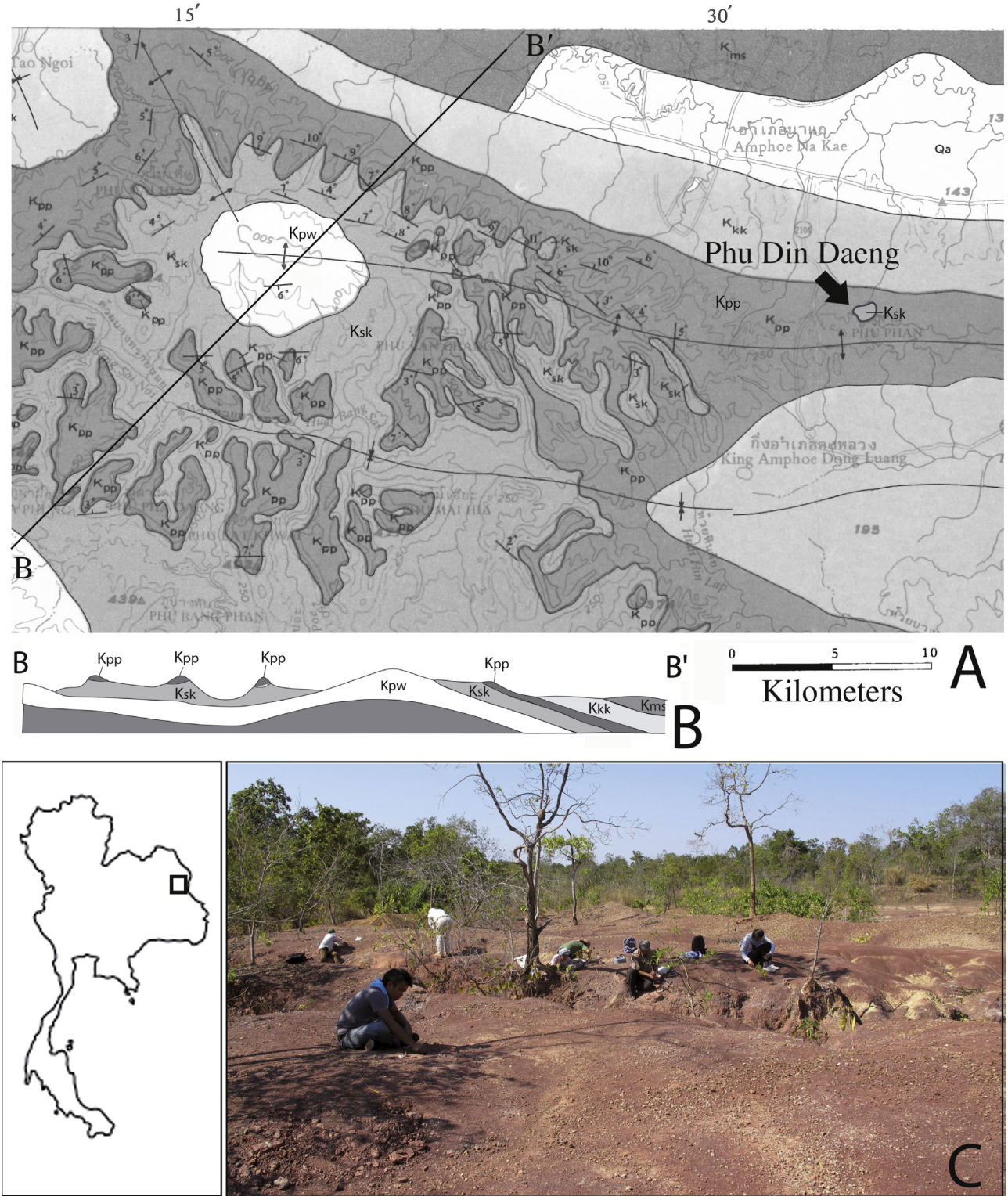

Fig. 1. Map showing the location and geology of the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, geological map and B, section (modified from Suteethorn and Jarnyahran, 1980); C, excavation at Phu Din Daeng. Abbreviations: K_{kk}, Khok Kruat Formation; K_{ms}, Marasahakham Formation; K_{pp}, Phu Phan Formation; K_{pw}, Phra Wihan Formation; K_{sk}, Sao Khua Formation.

Carte montrant la localisation et géologie du site de Phu Din Deang (Crétacé inférieur, NE de la Thaïlande). A, Carte géologique et B, Coupe (modifié d'après Suteethorn and Jarnyahran, 1980) ; C, Fouilles à Phu Din Deang. Abbréviations : K_{kk}, Formation Khok Kruat ; K_{ms}, Formation Marasahakham ; K_{pp}, Formation Phu Phan ; K_{pw}, Formation Phra Wihan ; Ksk, Formation Sao Khua.

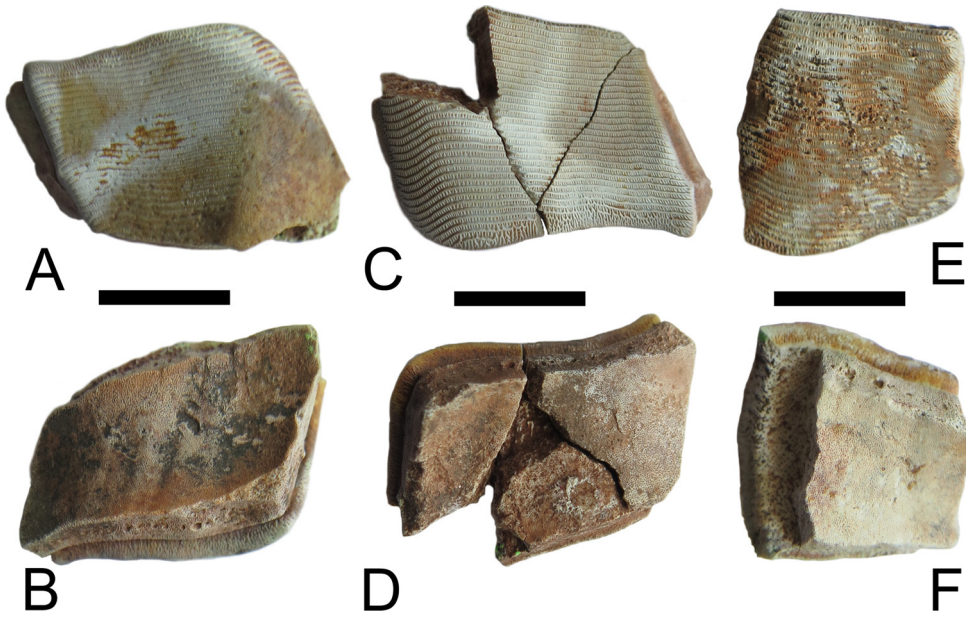

Fig. 2. Teeth of *Heteroptychodus steinmanni* from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A–B, (PRC34) in apical (A) and basal (B) views; C–D, (PRC36) in apical (C) and basal (D) views; E–F, (PRC35) in apical (E) and basal (F) views. Scale bars = 1 cm.
*Dents d'*Heteroptychodus steinmanni *provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–B, (PRC34) en vues apicale (A) et basale (B) ; C–D, (PRC36) en vues apicale (C) et basale (D) ; E–F, (PRC35) en vues apicale (E) et basal (F). Barre d'échelle = 1 cm.*

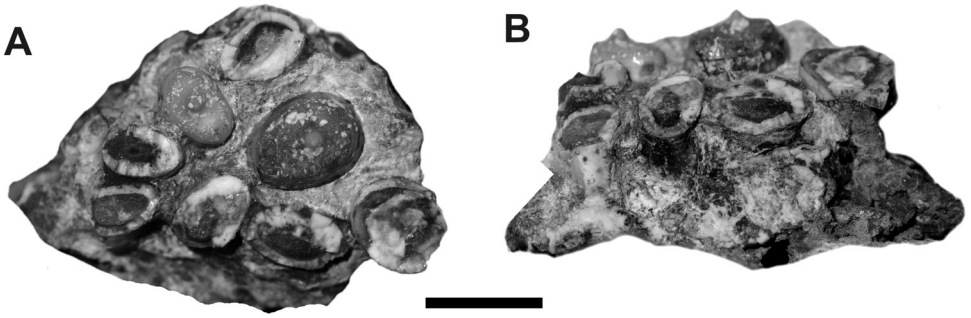

Fig. 3. Pycnodontiformes indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). PRC84, fragment of a vomer in occlusal (A) and lateral (B) views. Scale bar = 5 mm.
Pycnodontiformes indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). PRC84, fragment de vomer en vues occlusale (A) et latérale (B). Barre d'échelle = 5 mm.

Cavin et al. (2009). Pending new and more complete material, the material from Phu Din Daeng is referred to an indeterminate pycnodontiform taxon.

Amiiformes sensu Grande and Bemis, 1998
Sinamiidae Berg, 1940**cf. *Siamamia***
Cavin et al., 2007

Material: PRC92, dermopterotic; **PRC93**, basioccipital; **PRC90**, fragment of a left maxilla; **PRC91**, posterior extremity of a maxilla; **PRC89**, right premaxilla; **PRC87**, left dentary; **PRC88**, fragment of a right dentary with a coronoid; **PRC85**, anterior vertebral centrum; **PRC86**, posterior vertebral centrum.

Description: Isolated fragments referable to sinamiids are common at Phu Din Daeng (Fig. 4). Most of the preserved bones are the same as bones of sinamiids from other localities that have yielded this taxon (Phu Phok, Khok Pha Suam, etc.), indicating that these ossifications are the most resistant in the skeleton of these fishes. These bones are vertebral centra, jaw bones (premaxillae, maxillae and dentaries), basioccipitals, dermopterotics and scales. Most of these bones show characters of sinamiids.

A more or less complete, but distorted left dentary is preserved (Fig. 4G). It bears on its lateral side a row of irregular in size oval pores corresponding to the mandibular sensory canal. Twenty large and slightly compressed conical teeth strongly inwardly curved and irregular in size can be counted along a single row. Most of the teeth are broken but fine ridges at their bases are still visible. The acrodine caps are only imperfectly preserved, but it is visible that the sections of the caps were oval and their outline was likely conical. A fragment of a dentary with a coronoid still in situ shows labially elongated pores for the mandibular sensory canal, and lingually a deep groove for the Meckelian cartilage (Fig. 4B). The sockets corresponding to compressed dentary teeth, together with fragments of teeth are visible on the dentary. A patch of small, thin and slightly recurved teeth, smaller than the dentary teeth, are associated with the coronoid still attached to the dentary.

An almost complete right premaxilla (Fig. 4E) has a typical triangular shape with a large ovoid concavity on the labial face of the nasal process. The locations of about ten compressed teeth are visible. A large posterior tooth is still present, as well as a smaller tooth at the mid-length of the bone. The base of the teeth indicates that the anterior teeth were smaller than the posterior ones.

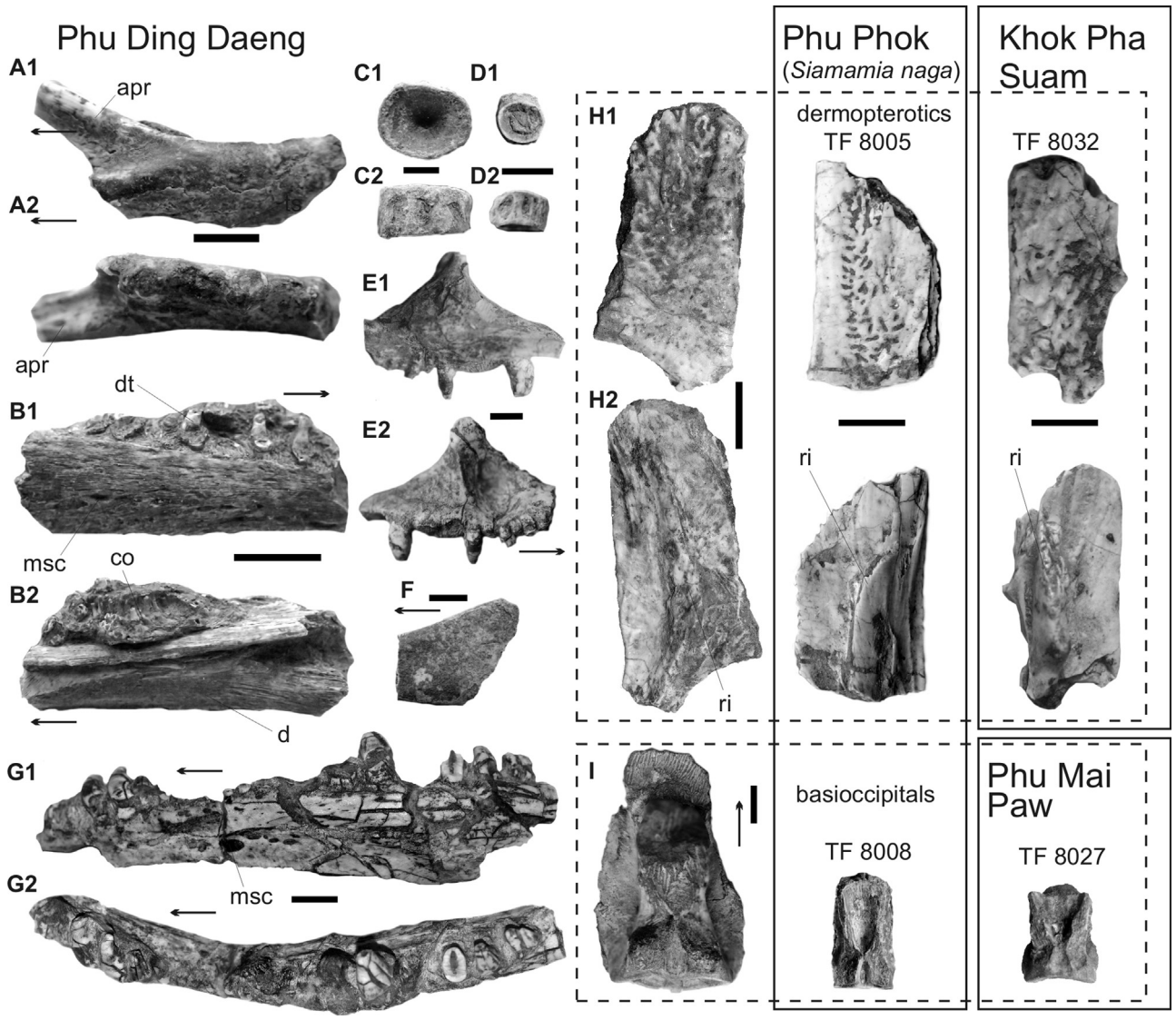

Fig. 4. cf. Sinamiidae from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, fragment of the anterior part of a maxilla (**PRC90**) in medial (A1) and occlusal (A2) views; B, fragment of a right dentary (**PRC88**) with a coronoid in labial (B1) and lingual (B2) views; C, anterior vertebral centrum (**PRC85**) in median (C1) and lateral (C2) views; D, posterior vertebral centrum (**PRC86**) in anterior (D1) and lateral (D2) views; E, right premaxilla (**PRC89**) in internal (E1) and external (E2) views; F, posterior extremity of a maxilla (**PRC91**) in lateral view; G, left dentary (**PRC87**) in labial view (G1) and occlusal (G2) views; H, dermopterotic (**PRC92**) in external (H1) and internal (H2) views; I, basioccipital (**PRC93**) in dorsal view. Scale bars = 5 mm. Upper box, comparisons with dermopterotics from other localities; lower box, Comparison with basioccipitals form other localities. Abbreviations: apr, articular process; co, coronoid; d, dentary; dt, dentary tooth; msc, mandibular sensory canal; ri, ridge.

*cf. Sinamiidae provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, fragment de la partie antérieure d'un maxillaire (***PRC90***) en vues médiale (A1) et occlusale (A2) ; B, fragment de dentaire droit (***PRC88***) avec coronoïde en vues labiale (B1) et linguale (B2) ; C, centrum de vertèbre antérieure (***PRC85***) en vues médiane (C1) et latérale (C2) ; D, centrum de vertèbre postérieure (***PRC86***) en vue antérieure (D1) et latérale (D2) ; E, prémaxillaire droit (***PRC89***) en vues interne (E1) et externe (E2) ; F, extremité postérieure du maxillaire (PRC91) en vue latérale ; G, dentaire gauche (***PRC87***) en vues labiale (G1) et occlusale (G2) ; H, dermoptérotique (***PRC92***) en vues externe (H1) et interne (H2) ; I, basioccipitale (***PRC93***) en vue dorsale. Barres d'échelle = 5 mm. Cadre en haut, comparisons avec dermoptérotiques provenants des autres sites ; Cadre en bas, comparison avec basioccipitales provenants des autres sites. Abbréviations : apr, processus articulaire ; co, coronoïde ; d, dentaire ; dt, dent dentaire ; msc, canal sensoriel mandibulaire ; ri, crête.*

A fragment of an anterior part of a left maxilla (Fig. 4A) shows the base of a large articular process and the sockets for teeth with a round section. Another fragment (Fig. 4F) corresponds to the triangular posterior extremity of the maxilla with an extended posterodorsal corner reminiscent of *Siamamia*.

An ornamented skull roof bone, bearing internally a shallow crest, is identified as a dermopterotic (Fig. 4H).

A bone bearing an ovoid articular facet, with excavated lateral sides and sutural surfaces dorsally (for the exoccipitals) is identified as a basioccipital (Fig. 4I).

Thin rhomboidal ganoid scales with a smooth surface are present and assigned with caution to *Siamamia*.

The commonest elements are vertebral centra, which are generally found isolated but which also occurred as sets of two to three centra still partly articulated. The shape of vertebral centra ranges from short centra with an ovoid compressed section, corresponding to anterior vertebrae, to longer centra round in section corresponding to posterior vertebrae (Fig. 4C–D).

Discussion: These isolated bones are very similar to isolated bones of *Siamamia naga* described from the type-locality of Phu Phok, in the Sao Khua Formation. In particular, the premaxilla shows the typical triangular outline of *S. naga*, with a nasal process broad at its base and extending posteriorly to a blunt process. The only difference with the figured premaxilla of *S. naga* (Cavin et al.,

2007, fig. 5E–G) is the proportionally smaller size of the nasal process. However, because the specimen from Phu Din Daeng is about 1.5 times larger than the specimen from Phu Phok, we cannot exclude that this difference is caused by allometric growth. The maxillae, with the departure of a well-developed articular process (PRC90) and with a deep and triangular posterodorsal corner (PRC91), are also similar to the maxillae of *S. naga* from Phu Phok. The general shape of the dentary PRC87, the shape of its preserved teeth and the arrangement of the mandibular sensory pores is reminiscent of *S. naga*. The second dentary associated to the coronoid (PRC88) is referred here with caution to this taxon. Both dentaries, although incomplete, seem to have had symphyses proportionally deeper than the very shallow symphysis of the sinamiids from Khok Pha Suam in the Khok Kruat Formation, but reminiscent of *S. naga* (compare Fig. 4B and G with fig. 7 in Cavin et al., 2009). The basioccipital of the Phu Din Daeng sinamiid is more similar to that from the Phu Mai Paw locality, in the Sao Khua Formation, than to the one of *S. naga* from Phu Phok because in the first two the articular facet is more flattened than in the type material, and the dorsal suturing surfaces form an X-shape, while they are almost parallel in *S. naga* (lower box in Fig. 4). The bone identified with caution as a dermopterotic bears an ornamentation more similar to the ornamentation of this bone from Khok Pha Suam, but the shallow crest is more reminiscent to the condition present in *Siamamia naga* from Phu Phok (upper box in Fig. 4).

?Vidalamiinae Grande & Bemis, 1998

Genus and species indet.

Material: PRC94, right dentary; **PRC95**, anterior extremity of a right dentary; **PRC96**, piece of a semi-articulated specimen with unidentified bones, toothed scales and vertebral centra in connection; **PRC97**, piece of a semi-articulated specimen with scales and fin rays; **PRC98**, accumulation of scales in articulation; **PRC99**, accumulation of bones, scales and fragments of fin rays.

Description: A right dentary, smaller in size than the dentary referred to cf. *Siamamia naga*, presents other features differing from *S. naga* (Fig. 5A). The irregular in size, thin and tall teeth are arranged in one row along the labial margin of the bone. They are gently curved lingually and their base is separated from the crown by a well-developed constriction (Fig. 5A'). The crown of each tooth is topped by an acrodine cap that is labiolingually compressed and shows very well-developed mesial and distal carinae forming a triangular outline. The shaft of each tooth has a rounded cross section at its base then the labial face is slightly flat while the lingual face is gently convex. A second specimen (not figured) corresponding to the anterior portion of a right dentary bears teeth similar in shape to the specimen described above. The symphyseal region appears to be very shallow.

Several accumulations of bones associated with scales with a very peculiar morphology, corresponding to strongly disarticulated fish individuals, are referred here with caution to a probable vidalamiin. This assignation rests on a specimen (PRC96), which displays scales bearing well developed spines associated with vertebral centra of amioid type (Fig. 5B). This association of bones indicates that this fish is likely a halecomorph, but different from the sinamiid cf. *Siamamia* from the same locality because the latter possesses supposedly smooth scales without any kind of ornamentation. The scales in PRC96 are deep, with a vertical pointed articular process (peg) at the anterior extremity of the dorsal margin. Three spines arranged along the depth of the scale extend posteriorly. Another specimen (PRC97) consists of an accumulation of scales together with fin rays (Fig. 5C). The scales are deeper than long (although proportionally less deep than in PRC96); a large triangular process is present dorsally and two very elongated spines extend posteriorly (Fig. 5C'). A specimen (PRC99) with scales still in articulation shows that each scale bears a pair of spines extending posteriorly and covering the following row of scales (Fig. 5D). The fin rays on PRC97 are formed by slightly deeper than wide elements, each one bearing a spine (Fig. 5C"). Another specimen (PRC99) shows a fragment of fin ray with a dermal segment covered with ridges of ganoin (Fig. 5E). Because of the disarticulated state of preservation of the material, we cannot reconstruct the organisation of the fin, with the respective location of the spines and ganoin patches on the rays.

Discussion: The general morphology of the dentary and especially of the carinate acrodine tooth caps are diagnostic features of some halecomorphs. Carinate teeth in halecomorphs have been regarded as independently acquired in Caturidae and Vidalamiinae (Grande and Bemis, 1998: 341). There are no morphological features visible on the material from Phu Din Daeng that allow assignation to either the caturids or the vidalamiins. The caturids are mostly marine fishes from the Late Jurassic, while vidalamiins are represented by some marine (*Pachyamia*), but mostly brackish or freshwater fishes (*Calamopleurus, Vidalamia*) from the Early Cretaceous. For these environmental and stratigraphical reasons, we assign with caution this kind of teeth from Phu Din Daeng to a Vidalamiinae, pending that new material will allow a better supported identification. The teeth referred to *Caturus* from Phu Phan Tong (Cuny et al., 2006) and Nong Sung (Cuny et al., 2009), both situated in the Sao Khua Formation, can also be referred to this taxon. While no spined scales are associated with carinate teeth, we temporarily associated these teeth and scales to the same taxon, although vidalamiins usually have elasmoid scales rather than thin ganoid scales (Grande and Bemis, 1998). We cannot exclude also that this material belongs to a sinamiids different from *Siamamia*, based on the scale morphology with carinate tooth caps convergent with vidalamiins and caturids. Here again, more material will be necessary to confirm or refute this identification.

Ginglymodi *sensu* Grande, 2010

Genus and species indet.

Material: a large number of unnumbered thick ganoid scales.

Description:

The occurrence of ginglymodians at Phu Din Daeng is attested by the presence of thick ganoid scales (Fig. 6). The shape of the scales differ depending of their position on the body: A large elongate rhombic scale was located in front of the anal fin, a more narrow rhomboid scale was located close to the caudal part, rectangular scales were located in the anterior part of the body, scales with small pores were situated along the lateral line and a symmetrical scale with a concave anterior margin and a posterior spine corresponds to a scale from the dorsal mid-line. Some scales show an ornamentation with faint parallel ridges on their external surface. The anterior peg and socket articulation is present. The posterior margins of all scales are smooth with no serrations.

Discussion

Ginglymodian remains are the commonest fish fossils within the Khorat Group, which ranges from the Late Jurassic to the Aptian. The taxic diversity is relatively high in each formation (Cavin et al., 2009, 2014; Deesri et al., 2017). However, a more precise identification of the scales from Phu Din Daeng is difficult. The only observation we can do here is that the scales differ from scales from most of the described taxa, which are smooth except some scales from Khok Pha Suam, in the Khok Kruat Formation (Ginglymodi indet.

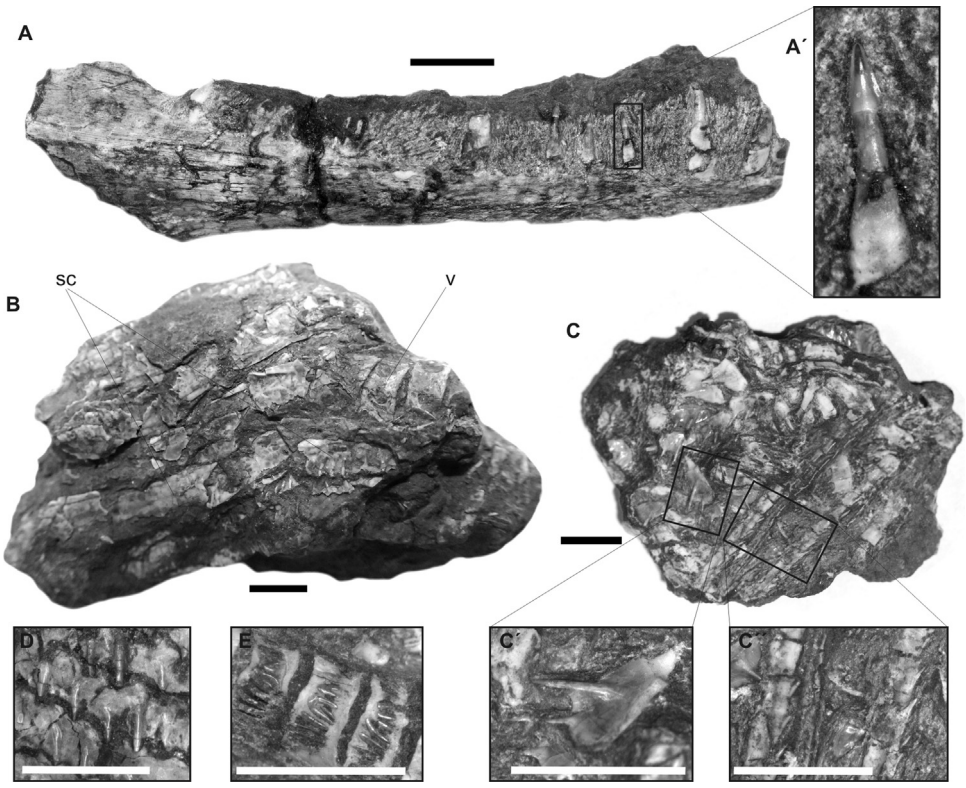

Fig. 5. ?Vidalamiinae indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A, right dentary (**PRC94**) in labial view with close up of a tooth (A'), B, piece of a semi-articulated specimen (**PRC96**) showing unidentified bones, toothed scales and vertebral centra in connection; C, piece of a semi-articulated specimen (**PRC97**) showing toothed-scales (C') and fin rays with denticulated segment (C"); D, detail of toothed scales (**PRC98**); E, detail of fin-ray segments with patches of ganoine (**PRC99**). Scale bars = 5 mm. Abbreviations: sc, scales; v, vertebra.

*?Vidalamiinae indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, dentaire droit (***PRC94***) en vue labiale ; A', gros plan d'une dent ; B, spécimen semi-articulaté (***PRC96***) montrant des os non identifiés, des écailles denticulées et centrums vertébraux en connection ; C, spécimen semi-articulaté (***PRC97***) montrant des écailles denticulées (C') et rayons avec segment denticulé (C") ; D, détail des écailles denticulées (***PRC98***) ; E, détail des segments de rayons avec ganoïne (***PRC99***). Barres d'échelle = 5 mm. Abbréviations : sc, écailles ; v, vertèbre.*

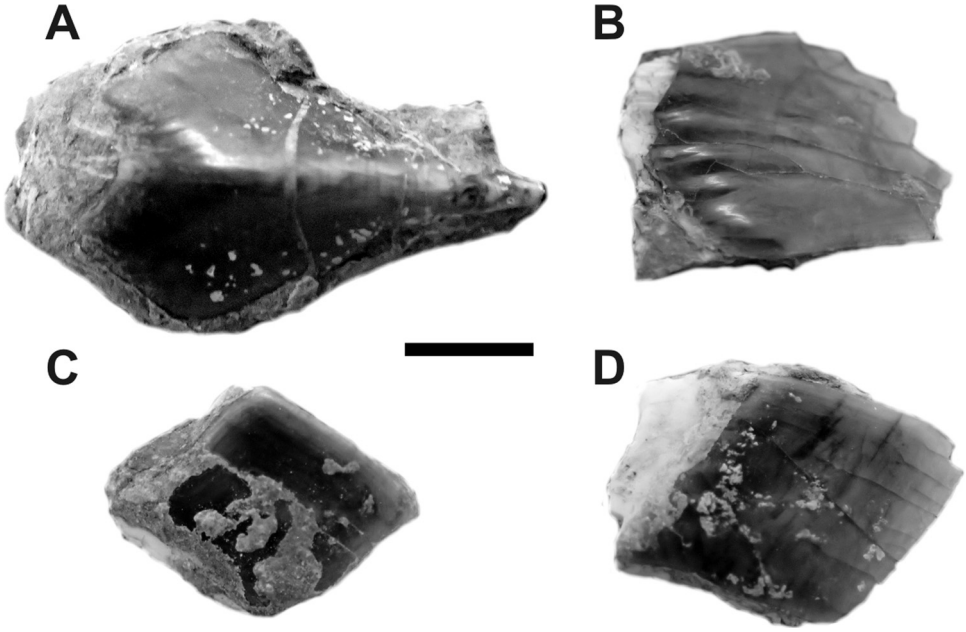

Fig. 6. Ginglymodi indet. from the Lower Cretaceous Phu Din Daeng site (NE Thailand). Ganoid scales (no number). Scale bar = 5 mm.

Ginglymodi indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). Ecailles ganoïdes (sans numéro). Barre d'échelle = 5 mm.

4 in Cavin et al. (2014: Table I)). But the latter bear ridges that are stronger than in the material from Phu Din Daeng.

3.3. Testudines

Cryptodira Cope, 1868
Trionychoidae Fitzinger, 1826
Adocidae Cope, 1870
Shachemydinae Khosatzky, 1977

***Protoshachemys rubra* n. gen. n. sp.**
(Fig. 7A–L and Fig. 8)

Etymology: Genus name from Greek 'protos' first, primitive to denote that the taxon is more primitive than *Shachemys*; species name from the name of the locality: Phu Din Daeng ((ภู ดิน แดง)) in Thai, red rock mountain or hill.

Holotype: PRC81 (Fig. 7A–D), a nearly complete but disarticulated shell, including complete nuchal, one neural, suprapygal 1 (incomplete), suprapygal 2, pygal (lacking posterior portion), right costal 1, left costal 2, the distal portion of the left costal 3, right costal 4 (lacking proximal end), left costal 5 and distal end of the right costal 5, left costal 6 (lacking the proximal end), left and right costal 7 (the right one lacking the proximal end), right costal 8, left peripherals 1–2, 4–6 and 8–11, right peripherals 8 and 10–11; nearly complete left epiplastron and right hyoplastron, and incomplete right hypoplastron. All these elements were unearthed within one square metre and in all likelihood belong to the same individual.

Referred material: PRC54, nuchal (Fig. 7E–F); **PRC55, PRC56, PRC57**, suprapygal 2; **PRC58**, pygal (Fig. 7K–L); **PRC59**, left costal 6 (Fig. 7I–J); **PRC60**, right costal 3 (Fig. 7G–H); **PRC61**, right peripheral 1; **PRC62**, left and right peripheral 2 of same individual; **PRC67**, right epiplastron;

Type locality and horizon: Phu Din Daeng, Sakhon Nakhon Province, NE Thailand. Top of the Sao Khua Formation, Lower Cretaceous (see Geological setting).

Diagnosis: a genus of Adocidae; with a combination of primitive and derived characters that differ from all other members of that family, as follows: shell surface smooth with sparse pores; carapace flat with a serrated posterior margin; nuchal roughly as long as wide; neural series reduced, narrow neurals with a tetragonal neural 1 followed by a hexagonal neural 2; two suprapygals, the first one much smaller than the second; cervical scute narrow; vertebral 1 not extending to the peripheral 2; lateral marginals extending onto the costals 1–5, marginal 11 and 12 elongate and greatly overlapping the suprapygal 2 and also slightly the costal 8; plastron with truncated anterior margin, entoplastron shortened anteriorly, a hinge between epiplastra and entoplastron/hyoplastra absent.

Description: Shell surface ornamentation: The surface of both carapace and plastron is smooth, with sparse tiny pores.

Carapace: When reconstructed, the carapace is flat with an oval outline. The anterior margin of the carapace is straight or slightly emarginated. The anterolateral margin of the carapace, from the posterior end of the peripheral 2 to the peripheral 6, is blunt and slightly upturned, but not forming a clear gutter. The posterolateral margin, from peripheral 8 to 11, is sharp. The posterior margin of the peripherals 10 and 11 presents sharp serrations. The posterior margin of the pygal has a small triangular caudal notch. A light ridge is present on the suprapygal 1, whereas the suprapygal 2 is convex dorsally. The peripherals are sutured to the costals, without a carapacial fontanelle. A large free rib end is developed on the distal end of the costals; they are wide and flat on the costal 2 to 5, and slender and long on the costal 7 and 8. The inner surface of the costals is perfectly flat, without rib swelling. As partly preserved on costal 2, the rib head is large and flat.

The nuchal in the holotype is slightly longer than wide, trapezoidal in shape with a straight anterior margin; its lateral margins are straight and convergent forward. PRC54 has a slightly emarginated anterior margin. In the holotype, the neurals are mostly missing, except one that is stuck on the inner surface of the suprapygal 2 and presented in ventral view. It is hexagonal, longer than wide and relatively narrow, but its precise position cannot be determined. The morphology of the neural series is indicated by the intact medial edges of the costals 1, 2, 5, 7 and 8 of the holotype and that of the isolated right costal 3 (PRC60) and left costal 6 (PRC59). There are likely six neurals, the neural 1 is tetragonal, followed by a hexagonal neural 2 with short anterolateral sides. Damaged on its posterior end, the suprapygal 1 remains articulated with the costal 8 in the holotype. When reconstructed, the suprapygal 1 is triangular, longer than wide and much smaller than the suprapygal 2, with a smooth and concave inner surface. The suprapygal 2 is trapezoidal. It contacts anteriorly the small suprapygal 1, anterolaterally the costal 8, and posteriorly the peripherals 10–11 and the pygal. This plate is greatly thickened posteriorly, especially the contact region with the pygal. The pygal is elongate, expanded posteriorly; with straight lateral borders and a very thick anterior contact with the suprapygal 2. The size of this plate is similar to that of the peripheral 11. An isolated pygal (PRC58) shows a small triangular caudal notch. The costal 1 is long as in advanced turtles. It is in contact with the nuchal, the neurals 1–2 and the peripherals 1–3. The costal 7 and the anterior part of the costal 8 meet their counterpart at the midline. As indicated by the isolated costal 6, this plate has also the posterior part meeting its counterpart at the midline. The inner surface of the costal 8 bears a large process to articulate with the ilium. The peripheral 1 is triangular and relatively narrow, with a short contact with the costal 1. The peripheral 2 is roughly square. The peripherals 4 to 11 are mesiolaterally elongate.

The scute sulci are lightly imprinted. The cervical scute is elongate and narrow. It is very narrow, with roughly parallel and slightly convex lateral sulci in the holotype, but slightly wider in PRC54. The vertebral 1 is wider than the nuchal, covering the posteromedial part of the peripheral 1 and contacting the marginal 2. The anterior sulcus of the vertebral 1 presents an anterior convexity at the level of the cervical scute. The sulcus between the cervical and the vertebral 1 is convex forward. The vertebrals 2 to 4 are narrow, being clearly longer than wide. The vertebral 5 is triangular and wider than the vertebral 4; it contacts the full width of the marginal 11 and 12, but is not in contact with the marginal 10. The contact between the vertebral 5 and the marginal 12 is straight. The pleural scutes are wider than the vertebral scutes. The marginal scutes 1 to 3 are short and restricted in the peripherals, with the marginal/pleural sulcus located far from the peripheral/costal suture on the peripherals 1 and 2. The marginals 4 to 7 extend onto the costal plates 2 to 4, and cover also the posterolateral corner of the costal 1 and the anterolateral corner of the costal 5. The marginals 8 to 10 are restricted in the peripherals again. The marginals 11 and 12 are greatly elongated and much longer than the marginal 10, overlapping the posterior half of the suprapygal 2, as well as the posteromedial corner of the costal 8.

Plastron: The plastron is well developed with wide anterior and posterior lobes. The bridge appears to be long and narrow. The anterior lobe of the plastron is truncated, with a straight or slightly emarginated front border, as in *Isanemys* and *Ferganemys* spp. The epiplastron has its anterior margin almost as long as its lateral free edge and these two edges form together a clear angle. The epiplastron is slightly thickened at its anterolateral corner, as well as its lateral edge. The intact sutural margin of the epiplastron and hyoplastron shows that no hinge is present between the epiplastra and entoplastron/hyoplastra, and the entoplastron is pentagonal in shape and shortened anteriorly, with its anterior margin shorter

Fig. 7. Adocid turtles from the Lower Cretaceous Phu Din Daeng site (NE Thailand). A–L, *Protoshachemys rubra* n. g. n. sp. A–D, holotype (**PRC81**), carapace in dorsal view (A–B) and plastron in ventral view (C–D); E–F, nuchal (**PRC54**); G–H, costal 3 (**PRC60**); I–J, costal 6 (**PRC59**); K–L, pygal (**PRC58**), K', close-up showing the caudal notch. M–T, *Protoshachemys* sp., M–N, nuchal (**PRC69**); O–P, left peripheral 1 (**PRC70**); Q–R, pygal (**PRC73**); S–T, right epiplastron (**PRC76**). U–Z, Adocidae indet. U–V, costal (**PRC77**), U', close-up showing the surface ornamentation; W–X, pygal (PRC82); Y–Z, peripheral 11 (**PRC78**). Scale bar = 5 cm (horizontal scale bar for A–D; vertical scale bar for E–Z).
*Tortues adocidés provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–L, Protoshachemys rubra n. g. n. sp. A–D, holotype (**PRC81**), carapace en vue dorsale (A–B) et plastron en vue ventrale (C–D) ; E–F, nuchale (**PRC54**) ; G–H, costale 3 (**PRC60**) ; I–J, costale 6 (**PRC59**) ; K–L, pygale (**PRC58**), K', gros plan montrant l'échancrure caudale. M–T, Protoshachemys sp., M–N, nuchale (**PRC69**) ; O–P, périphérique 1 gauche (**PRC70**) ; Q–R, pygale (**PRC73**) ; S–T, épiplastron droit (PRC76). U–Z, Adocidae indet. U–V, costale (**PRC77**), U', gros plan montrant l'ornementation sur la surface ; W–X, pygale (**PRC82**) ; Y–Z, périphérique 11 (**PRC78**). Barre d'échelle = 5 cm (barre d'échelle horizontale pour A–D ; barre d'échelle verticale pour E–Z).*

than the posterior one. The hypoplastron contacts the xiphiplastron with a nearly straight suture.

The scute sulci are poorly preserved on the plastron. The intergulars extend onto the entoplastron, but not the gulars. The intergular/gular sulci are nearly parallel to one another. The intergular/gular sulcus meets the gular/humeral sulcus on the epiplastron. The gular/humeral sulcus runs from the posterolateral corner of the epiplastron to the mid-length of the epi/entoplastral suture. The humeropectoral sulcus is straight and located posterior to the entoplastron as in *Isanemys*, but different from *Adocus* spp. and *Ferganemys* spp. in which the humeropectoral sulcus overlaps the posterior end of the entoplastron. The abdominofemoral sulcus is located anterior to the base of the posterior lobe. The inframarginal scutes are not discernible on the bridge region.

Comparisons and discussion: The reduction of the posterior neurals and the suprapygal 1, with the costals 7 and 8 meeting their counterpart at the midline; the suprapygal 1 much smaller than the suprapygal 2; a greatly reduced cervical scute that is much longer than wide and the marginal 11–12 greatly overlapping the suprapygal 2 indicate that the turtle specimens described above belong to trionychoid Adocidae. They are assigned to the sub-family Shachemydinae based on the smooth shell surface with sparse pores and an anteriorly truncated entoplastron.

Shachemydinae is a group of freshwater turtles endemic in the Cretaceous of Asia. The subfamily contains two genera, *Shachemys* Kuznetsov, 1976 and *Ferganemys* Nessov and Khosatzky, 1977 (Danilov et al., 2013; Lapparent de Broin, 2004; Syromyatnikova, 2011; Syromyatnikova et al., 2013, 2012; Syromyatnikova and Danilov, 2013). *Shachemys* is known from three species: *Shachemys baibolatica* Kuznetsov, 1976 and *Sh. ancestralis* Nessov, 1984 from the Late Cretaceous of Kazakhstan, Tajikistan and Uzbekistan; and *Sh. laosiana* Lapparent de Broin, 2004 from the Early Cretaceous of Laos (Danilov et al., 2007; Kuznetsov, 1976; Lapparent de Broin, 2004; Nessov and Krasovskaya, 1984). Fragmentary shell

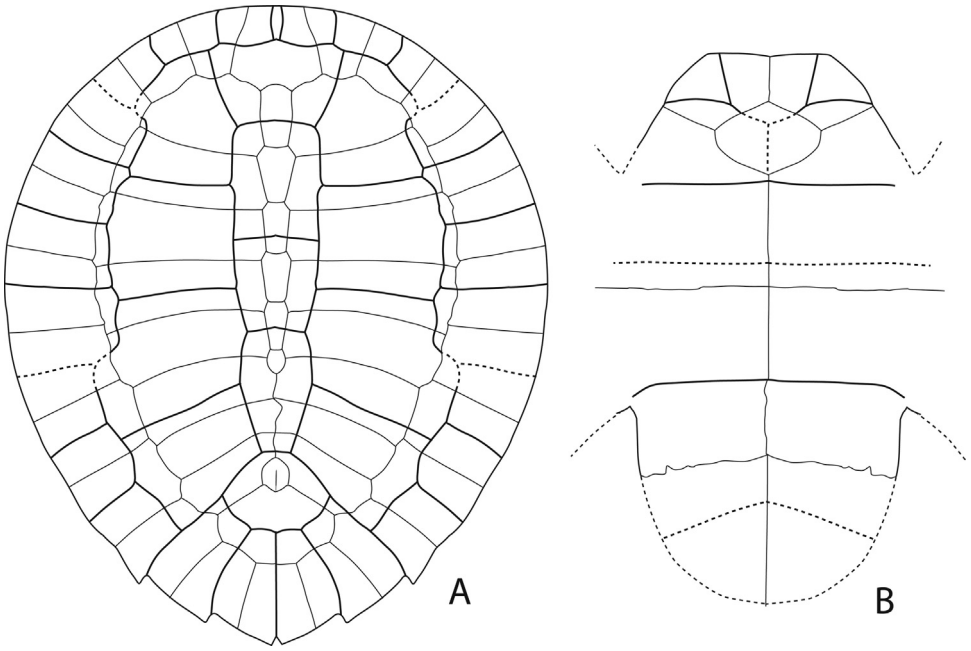

Fig. 8. Reconstruction of the shell of *Protoshachemys rubra* n. g. n. sp. from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). A, carapace in dorsal view; B, plastron in ventral view.
Reconstruction de carapace de Protoshachemys rubra *n. g. n. sp. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, carapace en vue dorsale ; B, plastron en vue ventrale.*

remains of *Shachemys* sp. are also recorded from the Early Cretaceous Khok Kruat Formation (Aptian) of Thailand (Tong et al., 2005, 2009,). *Ferganemys* is known from two species: *F. verzilini* from the Early Cretaceous (Albian) of Kirgizstan and *F. itemirensis* from the Late Cretaceous (Cenomanian) of Uzbekistan (Nessov, 1981; Nessov and Khosatzky, 1977; Syromyatnikova, 2011). Lapparent de Broin et al. (2004) assigned *Sinaspideretes wimani* (Young and Chow, 1953) from the Late Jurassic of Sichuan Basin, China to Shachemydinae, but the subsequent review of that taxon placed it at a more basal position among Trionychoidae (Tong et al., 2014).

Most trionychoid turtles have a sculptured shell surface. In the family Adocidae, the shell surface has a pitted ornamentation, such as in *Isanemys srisuki* from the Early Cretaceous Sao Khua Formation of NE Thailand (Tong et al., 2006), *Ferganemys* spp. and *Adocus* spp. from the Late Cretaceous and Palaeogene of Asia and North America (Hay, 1908; Sonoda et al., 2015; Syromyatnikova et al., 2013, 2012; Syromyatnikova and Danilov, 2013), except for *Shachemys*. *Shachemys* has a smooth shell surface (*Sh. laosiana*) or with fine wrinkles (*Sh. baibolatica* and *Sh. ancestralis* as figured in Danilov et al. (2007)), with numerous marked pores, corresponding to a well-developed reticular system of vascular canals (Scheyer et al., 2017). Some turtles referred to *Adocus* have a weaker shell surface sculpture with small dots, such as in cf. '*Adocus*' *orientalis* from the Late Eocene of Inner Mongolia, China and *Adocus* sp. from the Palaeocene of Montana, USA that Danilov et al. (2013) considered different from the sculpture with small grooves and pits of 'true' *Adocus*. These sculptures, which give the shell surface a 'rugose' aspect, appear however to be more pronounced than that seen in our specimens. The shell surface of the specimens from Phu Din Daeng is smooth, pores are variably developed. They are not obvious on PRC81 and on the specimens from Phu Din Daeng of a dark colour, but in some specimens of pale colour, marked pores are more easily observed.

Although an epiplastra-entoplastron/hyoplastra hinge is absent, *Protoshachemys* shares with *Isanemys*, *Ferganemys* and *Shachemys* an anteriorly shortened entoplastron. In these taxa, the anterior margin of the entoplastron (the epiplastron/entoplastron suture) is clearly shorter than its posterior margin (the entoplastron/hyoplastron suture); in contrast to *Adocus* spp. which have a diamond-shaped entoplastron, with the length of the anterior margin roughly equal to that of its posterior margin. In *Shachemys* spp., the anterior margin of the entoplastron is straight and a hinge is developed between epiplastra and entoplastron/hyoplastra (Danilov et al., 2007; Lapparent de Broin, 2004). Such a hinge is also present in some juveniles of *Ferganemys* (Syromyatnikova, 2011).

Like *Shachemys*, *Protoshachemys* has a relatively narrow nuchal that is roughly as long as wide; while in *Ferganemys* spp. and *Isanemys*, the nuchal is clearly wider than long. However, *Shachemys* is characterized by a series of autapomorphic features in addition to pores on the shell surface and a plastral hinge. These include absence of all or nearly all neurals, only one suprapygal, absence of a cervical scute and the vertebral 1 overlapping the peripheral 2. *Protoshachemys* is obviously more primitive than *Shachemys* spp. in having more neurals (up to six), two suprapygals, a narrow cervical scute and the vertebral 1 overlapping the peripheral 1.

Protoshachemys shares with *Isanemys* a tetragonal neural 1 and a straight humeropectoral sulcus that is located posterior to the entoplastron. It is, however, more derived than *Isanemys* and *Ferganemys* in having greatly elongated lateral and posterior peripherals and lateral marginals extending onto the costals. These characters are shared with *Adocus* spp. and might be plesiomorphic at the level of Shachemydinae. Detailed comparisons between *Protoshachemys* and other adocids are shown in Table 1. On the basis of these comparisons, the turtle remains from Phu Din Daeng described above appear to be distinct from other adocids and are therefore considered as belonging to a new genus and new species. The combination of shell characters of this new taxon supports its basal position in Shachemydinae.

***Protoshachemys* sp.**

(Fig. 7M–T)

Referred material: PRC68 and **PRC69** (Fig. 7M–N), nuchals; **PRC70** (Fig. 7O–P) and **PRC71**, left peripheral 1, **PRC72**, right peripheral 1; **PRC73** (Fig. 7Q–R) and **PRC74**, pygals; **PRC75**, left

Table 1
Comparisons of shell characters between *Protoshachemys rubra* n. g. n. sp. and other adocids.
Comparaisons des caractères de carapace entre Protoshachemys rubra *n. g. n. sp. et d'autres Adocidés.*

Characters	*Protoshachemys rubra*	*Shachemys* spp.	*Isanemys srisuki*	*Ferganemys* spp.	*Adocus* spp.
Shell surface ornamentation	Smooth with sparse pores	Smooth with marked pores	Pitted	Pitted	Pitted
Cervical notch	Absent or very shallow	Present or absent	Present	Present or absent	Present or absent
Serrated posterior margin	Yes	No	No	No	No
Nuchal	Roughly as long as wide	As long as wide	Wider than long	Wider than long	Wider than long
Number of neural	6	Absent or only the first	6 or 7	7	6
Neural formula	4 > 6 > 6 > 6 > 6 > 5	–	4 > 6 > 6 > 6 > 6 > 5	6 < 4 > 6 > 6 > 6 > 6 > 5	6 < 4 > 6 > 6 > 6 > 5
Number of suprapygal	2	1	2	2	2
Cervical scute	Present, Narrow	Absent	Present, Wide	Present, Narrow	Present, Narrow
Vertebral 1	Overlapping peripheral 1	Overlapping peripheral 2	Overlapping peripheral 1	Overlapping peripheral 1	Overlapping peripheral 1
Vertebral 2–3	Clearly longer than wide	Longer than wide or wider than long	As long as wide	Longer than wide	Longer than wide or wider than long
Marginals 4–8 extending onto costals	Yes	No	No	No	Yes
Marginal 10 shorter than marginal 11	Yes	Yes or no	No	Yes	No
Entoplastron anteriorly truncated	Yes	Yes	Yes	Yes	No
Hinge between epiplastra and entoplastron/hyoplastra	Absent	Present	Absent	Present in juveniles	Absent

epiplastron, **PRC76** (Fig. 7S–T), right epiplastron and other shell elements.

Remarks: Turtle shell remains are relatively abundant at Phu Din Daeng locality, most of them are isolated elements or fragments. Most shell elements have a smooth outer surface and when well preserved, tiny pores are apparent. These elements are therefore tentatively referred to *Protoshachemys*. Some diagnostic plates, such as nuchal, peripheral 1, pygal and epiplastron, show a different morphology as compared with *Protoshachemys rubra*. These include the presence of a large nuchal emargination, a wider than long pygal, a larger and triangular cervical scute, a rounded anterior edge of the plastron and the gular extending onto the entoplastron. These differences may correspond to an important inter-individual variation that could be due to sexual dimorphism or may indicate distinct species. More complete material is needed to make sure of the association of the characters and estimate intraspecific variation.

Adocidae genus and species indet.
(Fig. 7U–Z)

Referred material: PRC77 (Fig. 7U–V), a costal; **PRC82** (Fig. 7W–X), a pygal and **PRC78** (Fig. 7Y–Z), a peripheral 11.

Remarks: These plates have a slightly pitted outer surface, similar to that of *Isanemys srisuki* (Tong et al., 2006). The pygal is wider than long, in contrast to the elongate pygal of *Protoshachemys rubra*. The marginals 11 and 12 extend onto the suprapygal 2. The material is too fragmentary to warrant a more precise systematic assignment beyond Adocidae indet.

3.4. *Crocodilia Gmelin, 1789*

Neosuchia Benton & Clarck, 1988

Genus and species indet.

Crocodilians are poorly represented at Phu Din Daeng and consist of a single mandibular element as well as isolated tooth crowns, the latter being the most abundant type of material recovered (Fig. 9).

Description: A single left articular (PRC144) is about 4 cm long and preserves the glenoid surface as well as the retroarticular process. As seen in lateral view (Fig. 9A), the articular preserves a sutural area for the surangular and angular, which extends toward the posteriormost level of the articular. The retroarticular process projects posteriorly; its tip is not projecting dorsally as is observed in derived eusuchians (Iordansky, 1973). As observed in dorsal view (Fig. 9B), the retroarticular process is faintly concave and is narrower than the glenoid fossa. This is different from eusuchians where the retroarticular process is concave and medially expanded to provide attachment for M. pterygoideus posterius (Iordansky, 1973). As seen in ventral view (Fig. 9D), the retroarticular process is straight and narrow and shows a groove that may correspond to the suture with the angular. The glenoid fossa is divided into lateral and medial articular surfaces of equal widths to accommodate the craniomandibular joint. In eusuchians, the lateral hemicondyle is wider than the medial one. The foramen aëreum is placed on the medial edge of the articular (Fig. 9B).

Subconical, slightly curved tooth crowns are often missing enamel and possess distinct apicobasal ridges, which are about the same strength as the mesiodistal carinae (PRC145, Fig. 9E).

Discussion: Although the material is limited, the morphology of PRC144 does not match that of a derived eusuchian. The mandible of a probable eusuchian has recently been described from the Aptian-Albian Khok Kruat Formation (Kubo et al., 2018) and is not comparable with the Phu Din Daeng specimen. Further identification is presently not possible because the Phu Din Daeng articular differs in morphology from those of pholidosaurids such as *Chalawan thailandicus* from the Phu Kradung Formation (Buffetaut and Ingavat, 1980; Martin et al., 2014) or is unknown in other crocodilians described from the early Cretaceous of Thailand (Lauprasert et al., 2007, 2009). As such, the mandible is unknown in the derived neosuchian *Khoratosuchus jintasakuli* from the Aptian-Albian Khok Kruat Formation (Lauprasert et al., 2007) and in the goniopholidid *Siamosuchus phuphokensis* from the ante-Aptian Sao Khua Formation (Lauprasert et al., 2007). The posterior region of the mandible is also unknown in the diminutive atoposaurid *Theriosuchus grandinaris* from the ante-Aptian Sao Khua Formation (Lauprasert et al., 2011). More complete discoveries are required to assess the identity of the Phu Din Daeng crocodilian beyond Neosuchia indet.

Fig. 9. Neosuchia indet. from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). Left articular (PRC144) in A, lateral; B, dorsal; C, medial and D, ventral views. E, isolated tooth (PRC145). Scale bar = 1 cm. Abbreviations: fa, foramen aëreum.
Neosuchia indet. provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A–D, Articulaire gauche (PRC144) en vues latérale (A), dorsale (B) ; mediale (C) et ventrale (D). E, dent isolée (PRC145). Barre d'échelle = 1 cm. Abbréviations : fa, foramen aëreum.

3.5. *Pterosauria Kaup, 1834*

Genus and species indet.

A few long, slender and more or less tubular teeth (PRC146, Fig. 10C) apparently belong to pterosaurs, although their enamel is too poorly preserved to clearly show the distinguishing features of pterosaur teeth. Pterosaurs have been reported from the Sao Khua Formation (Buffetaut et al., 2003) and also occur in the Khok Kruat Formation. The putative pterosaur teeth from Phu Din Daeng provide no stratigraphic indications.

3.6. *Dinosauria Owen, 1842*

Theropoda Marsh, 1881
Spinosauridae Stromer, 1915

Genus and species indet.

Spinosaurid teeth are relatively common at Phu Din Daeng, but mostly poorly preserved. They show the usual characters of the teeth of Asian spinosaurids: a crown that is only slightly compressed laterally and covered with strong apicobasal ridges (PRC147, Fig. 10A). Spinosaurid teeth occur in abundance in both the Sao Khua and Khok Kruat Formations, and several morphotypes, which may correspond to distinct taxa, are present in both (Suteethorn et al., 2018; Wongko et al., 2019). Because of this morphological variability, at the moment it is not really possible to clearly distinguish spinosaurid teeth from the Sao Khua and Khok Kruat Formations on the basis of their shape or ornamentation.

Theropoda genus and species indet.

Apart from a large caudal vertebra lacking the neural spine, which may belong to a theropod, this group of dinosaurs is mainly represented by isolated teeth. Several blade-shaped, laterally compressed teeth with serrated carinae have been found (PRC148, Fig. 10B). Their poor preservation makes it impossible to identify them beyond Theropoda indet. and they provide no stratigraphic information.

4. Discussion and conclusion

The Phu Din Daeng site has yielded a diverse vertebrate assemblage. Although it has some elements in common with the vertebrate fauna from the Khok Kruat Formation, this assemblage seems to be more comparable with those from the Sao Khua Formation. The stratigraphical significance of the assemblage is discussed below.

The shark fauna is represented by a single species, *Heteroptychodus steinmanni*. This taxon has mainly been recovered from the Khok Kruat Formation in Thailand (Cappetta et al., 2006; Cuny et al., 2008), but has also been reported from several sites in the Sao Khua Formation, like for example Ban Huai Dua (Cuny et al., 2008) and Phu Wat (specimens PWAI 499, 537–550 from the collection of the PRC) in Nong Bua Lamphu Province. However, *H. kokutensis* appears to be more common than *H. steinmanni* in the Sao Khua Formation, even though the separation between the two species is not yet clear and a revision of *Heteroptychodus* is warranted (Teng et al., 2017), but beyond the scope of the present work. On the other hand, *H. kokutensis* has never been recovered from the Khok Kruat Formation. The absence of *H. kokutensis* in Phu Din Daeng could therefore be linked to the younger age of the site compared to the other sites known in the Sao Khua Formation, or to the scarcity of shark remains in this locality that may be linked to taphonomical or environmental factors. It is difficult to decide which explanation is the most likely in the current stage of our knowledge.

Among bony fishes, pycnodont remains are rare in the Early Cretaceous continental localities in north-eastern Thailand. Until now, their fossils are only known in the Sao Khua Formation including teeth with morphology close to the morphology of teeth from Phu Din Daeng. Halecomorph remains corresponding to sinamiids and to vidalamiins, are the commonest fish remains in Phu Din Daeng. Sinamiids have been recognized in several localities from two Early Cretaceous formations of the Khorat Group in northeastern Thailand. *Siamamia naga* was identified on the basis of material from Phu Phok (Sakhon Nakhon Province) in the Sao Khua Formation (Cavin et al., 2007). Then, *Siamamia* sp. was recorded in several localities in the Sao Khua Fm., viz. Nong Sung (Mukdahan Province), Phu Phan Tong (Nong Bua Lamphu Province) and Phu Mai Paw (Kalasin Province), but also in one locality in the Khok Kruat Formation, viz. Khok Pha Suam locality (Ubon Ratchathani Province) (Cavin et al., 2009; Deesri et al., 2017). Except a few articulated specimens from Phu Phok, all the material consists of isolated and often fragmentary remains. The sinamiid from Phu Din Daeng appears to be closer to *Siamamia naga* than to the other sinamiids, in particular the sinamiid from Khok Pha Suam, and thus would support the inclusion of Phu Din Daeng in the Sao Khua Formation.

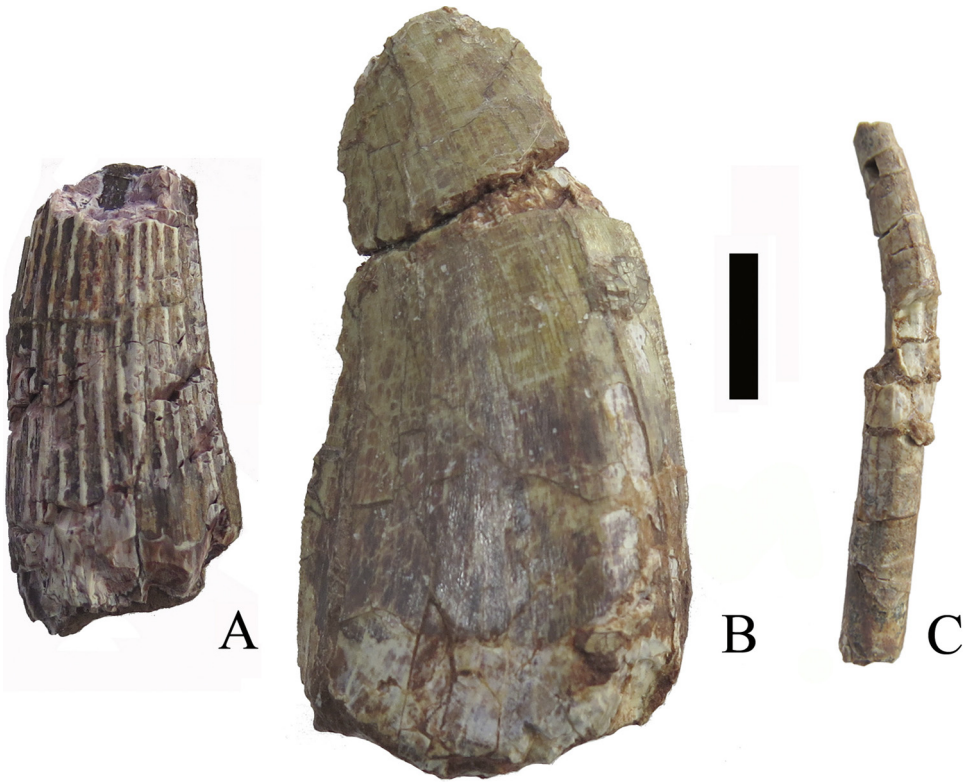

Fig. 10. Dinosaur and pterosaur teeth from the Lower Cretaceous of Phu Din Daeng site (NE Thailand). A, spinosaurid theropod (PRC147). B, indeterminate theropod (PRC148). C, indeterminate pterosaur (PRC146). Scale bar = 1 cm.
Dents de dinosaure et ptérosaure provenant du site de Phu Din Daeng (Crétacé inférieur, NE de la Thaïlande). A, théropode spinosauridé (PRC147). B, théropode indéterminé (PRC148). C, ptérosaure indéterminé (PRC146). Barre d'échelle = 1 cm.

However, more complete material is necessary to test this hypothesis. The possible presence of a vidalamiin in Phu Din Daeng is the first record of this subfamily in the Early Cretaceous of Thailand, and actually of East Asia in general. This identification, if confirmed, will have strong biogeographical implications because the vidalamiins are known so far from Western Gondwana with *Calamopleurus*, and from Europe (including the Near-East) and North America with several genera. The presence of elongated spines on the scales of this taxon will deserve to be studied in detail. A superficial examination indicates that these denticles may have a histology similar to that of oral teeth. Such a tooth-like structure has been described among actinopterygians in the obaichthyids from the Early Cretaceous of Western Gondwana (Grande, 2010) and in the extant loricarioidei siluriforms form South America (Rivera-Rivera and Montoya-Burgos, 2017), both clades being phylogenetically remote from the vidalamiins. The occurrence of carinate teeth at Phu Phan Thong and Nong Sung also reinforces the placement of Phu Din Daeng in the Sao Khua Formation.

All turtle remains hitherto collected from Phu Din Daeng are referred to Adocidae (Cryptodira: Trionychoidea). *Protoshachemys rubra* n. g. n. sp., a primitive Shachemydinae, is the oldest known representative of that group. A more advanced form, *Shachemys*, has been reported from the Khok Kruat Formation in Thailand and its lateral equivalent the Grès Supérieurs Formation in Laos (Lapparent de Broin, 2004; Tong et al., 2005). The remains of Adocidae indet., although fragmentary, seem to be close to *Isanemys srisuki* from the Phu Khum Khao and Phu Wat localities of the Sao Khua Formation (Tong et al., 2006). Therefore, the general aspect of the turtle fauna from Phu Din Daeng is clearly more primitive than that of turtle fauna from the Khok Kruat Formation and supports the inclusion of the site in the Sao Khua Formation. The presence of *Protoshachemys* as the dominant component of the turtle fauna from Phu Din Daeng makes this assemblage distinct from other turtle faunas from the Sao Khua Formation. This may be due to an environmental or chronological difference. The absence of the carettochelyid turtle *Kizylkumemys* at Phu Din Daeng seems to be related to environmental factors. Present in both Sao Khua and Khok Kruat formations (also in the Grès Supérieurs Formation in Laos) (Lapparent de Broin, 2004; Tong et al., 2009), *Kizylkumemys* remains are found in the localities with higher energy palaeoenvironments.

As noted above, the dinosaur remains from Phu Din Daeng are too fragmentary and too poorly preserved to yield much stratigraphic information. However, the absence of ornithischian remains is worth noting, as it suggests that the locality belongs to the Sao Khua Formation rather than to the Khok Kruat Formation. Although the Sao Khua Formation has yielded thousands of dinosaur bones and teeth, so far they all belong to sauropods and theropods, no ornithischian remains have been reported (Buffetaut et al., 2006; Buffetaut and Suteethorn, 1999). By contrast, ornithischians are well represented in the Khok Kruat Formation, by both ceratopsians (*Psittacosaurus*) and various iguanodontians (Buffetaut et al., 2005). The shed teeth of the latter are very common at some Khok Kruat localities, such as Khok Pha Suam (Ubon Ratchathani Province). Although it is negative evidence, the lack of ornithischian remains at Phu Din Daeng is in line with an attribution to the Sao Khua Formation.

In conclusion, based on the geology and vertebrate assemblage, Phu Din Daeng can be confidently placed in the Sao Khua Formation. The difference in the faunal composition compared with those from other localities of the formation may reflect a difference in age (the locality being at the top of the Sao Khua Formation), or in the environmental or taphonomic conditions.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgments

This research is supported by the International Research Group PalBioDivASE (GDRI) grant of CNRS; PHC "Evolution des réseaux trophiques mésozoïques en Thaïlande et son impact sur la biodiversité"; the Mahasarakham University Development Fund and the National Research Council of Thailand (NRCT) of the fiscal years 2017 and 2018. The research of UD is further supported by TRF Grant for new researcher (MRG 6180086). We thank the members and students of Palaeontological Research and Education Centre (PRC), Mahasarakham University and Department of Mineral Resources (DMR) who took part the field work at Phu Din Daeng; Adán Pérez-García and Attila Ősi for reviewing the manuscript.

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