Systematics and palaeobiogeography of Mesozoic amphibians in Thailand

Thanit Nonsrirach

A Thesis Submitted in Partial Fulfillment of Requirements for
degree of Doctor of Philosophy in Palaeontology (International Program)
May 2022

ซิสเต็มมาติกส์และบรรพชีวภูมิศาสตร์ของสัตว์สะเทินน้ำสะเทินบก มหายุคมีโซโซอิกในประเทศไทย

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May 2022

The examining committee has unanimously approved this Thesis, submitted by Mr. Thanit Nonsrirach , as a partial fulfillment of the requirements for the Doctor of Philosophy Palaeontology (International Program) at Mahasarakham University

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ABSTRACT

The non-marine Mesozoic sedimentary rocks of Thailand, which consist of the Indochina block and the Sibumasu block, have yielded several terrestrial and aquatic vertebrate fossils, but only a few amphibian remains have been reported. Here, we present an overview of the Thai amphibian palaeo-diversity based on the literature, re-examination of published material, new findings, and unpublished material. Thai amphibian fossil remains are assigned to Temnospondyls (*Cyclotosaurus* cf. *posthumus*, Plagiosauridae, Metoposauroidea, and Brachyopoidea) and Anura and were discovered from four formations (Huai Hin Lat Formation, Khlong Min Formation, Phu Kradung Formation, and Sao Khua Formation), ranging from the Upper Triassic to the Lower Cretaceous of Thailand. The Thai amphibian fossils show the most diverse Mesozoic amphibian record in Southeast Asia. The occurrence of Brachyopidae in Thailand, which are related to Chinese forms, supports the previous hypothesis of physical connections between the Indochina blocks and the Sibumasu block during the Mesozoic era.

Keyword : fossil, Mesozoic, amphibian, palaeo-diversity

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CHAPTER 1
INTRODUCTION

1.1 Background

The amphibians of the Paleozoic and the Mesozoic can be divided into three major clades: the Seymouriamorpha, the Lepospondyli, and the Temnospondyli (Vitt and Caldwell, 2014). Basal members of temnospondyls were the most diverse and most successful group of amphibians in the Paleozoic Era, which lived during the Mesozoic Era (Damiani and Rubidge, 2003; Schoch, 2014; Vitt and Caldwell, 2014). Temnospondyls are commonly retrieved in the tetrapod assemblages from Triassic continental deposits such as fluvial and lacustrine environments (Dias-Da-Silva and Dias, 2013).

Several vertebrate fossils from the Mesozoic sediment have been found in both Sibumasu and Indochina blocks of Thailand. These fossils assemblages show an important and high diversity, including; freshwater sharks, actinopterygian fishes, lungfish, amphibians, turtles, crocodilians, dinosaurs, and pterosaurs (Buffetaut and Suteethorn, 1998; Buffetaut et al., 1994a, b; Cuny et al., 2014; Tong et al., 2009). However, few number of amphibian remains have been reported. The first discovery of an amphibian in Thailand was a partial skull from the Huai Hin Lat Formation (Upper Triassic). It was reported by Ingavat and Janvier, (1981), and allowed an assignment to *Cyclotosaurus*. The other postcranial remains are a plagiosauroid dermal bone and temnospondyl intercentrum (Buffetaut et al., 1994a, b; Suteethorn et al., 1988).

Recently, new amphibian specimens (intercentra and a posterior part of a skull) were collected from new Mesozoic localities in Thailand (Chanthasit et al., 2019; Laojumpon et al., 2014). Most of these specimens have never been studied in detail. In order to understand the diversity and biogeography of Thai Mesozoic amphibians, the description and re-check the taxonomic status of all amphibian remains housed in the collections of the Sirindhorn Museum (SDM, Kalasin Province) and The Palaeontological Research and Education Centre of Mahasarakham

University (PRC, Mahasarakham Province). The relationships between these amphibians and their Asian relatives are used in a palaeobiogeographical framework for a better reconstruction of the physical connections in Southeast Asia.

1.2 Objective of the research

1.2.1 To study the taxonomic status and the phylogeny of Mesozoic amphibians in Thailand.

1.2.2 To study the paleobiogeography of Mesozoic amphibians in Southeast Asia.

1.3 Scope of the Research

The study concerns the morphology, systematics, taxonomic status, and palaeobiogeography of amphibian remains found in the Mesozoic rocks of Thailand. The materials, which are kept in the Sirindhorn Museum (SDM) and the Palaeontological Research and Education Centre of Mahasarakham University (PRC) were obtained from the excavation at Mesozoic localities in Thailand. Description, comparison, and determination of the specimens were conducted at the Department of Biology, Faculty of Science, Mahasarakham University.

1.4 Significance of the research

This study would provide a significant result on taxonomy, diversity, and palaeobiogeography of amphibians in Thailand during the Mesozoic as well as allow a better understanding of the physical connection between the Indochina block and Laurasia.

1.5 Abbreviations

acr: acetabulum rim, **act**: acetabulum, **ap**: ascending process, **cap**: capitulum, **Ch.D**: Chulabhorn Dam, **CY-HN**: Chaiyaphum– Huai Nam Aun, **D.M.R.**:

Department of Mineral Resources, **dc**: deltoidei crest, **ect**: ectepicondyle, **ent**: entepicondyle, **exo**: exoccipital, **int**: interpalatal vacuities, **isc**: ischium, **KS**: Kalasin, **nc**: notochordal pit, **ob**: orbit, **oc**: occipital condyles, **p**: parietal, **PN**: Phu Noi, **pp**: parapophysis, **ppt**: postparietal, **PRC**: Palaeontological Research and Education Centre, **ps**: polygonal sculpture, **psp**: parasphenoid, **pt**: pterygoid, **pu**: pubis, **q**: quadrate, **rc**: radial crest, **rs**: sculpture, **SDM**: Sirindhorn Museum, **SHM-HY**: Srisuk's House Museum – Huai Lao Yang, **SHM-PT**: Srisuk's House Museum –Phu Phan Thong, **st**: supratemporal, **sub**: subtemporal fossa, **t**: tabular, **TF**: Thai Fossil.

CHAPTER 2
LITERATURE REVIEW

2.1 General geology of the Mesozoic sedimentary rock of the northeastern and southern Thailand

The continental Mesozoic rocks of Thailand consist of two sub-continent blocks. The western part, called “Shan-Thai block” or “Sibumasu block” includes the eastern part of Myanmar along with northern, western, and southern parts of Thailand as well as the western part of peninsula Malaysia (Fig. 1). The eastern part is the Indochina block, which includes; northeastern and eastern parts of Thailand, southern parts of Laos and Cambodia, and the western part of Vietnam (Buffetaut and Suteethorn, 1998; Metcalfe, 1996; Racey, 2009).

The red bed Mesozoic rocks in the northeastern part of Thailand, which belong to the Indochina block, consist of a non-marine red bed sequence deposited in a continental environment (Racey, 2009b; Racey and Goodall, 2009; Racey et al., 1996). This block consists of seven formations considered Upper Triassic to Cretaceous in age based on invertebrate and vertebrate remains as well as palynomorphs (Meesook et al., 1995; Racey et al., 1996) which are as follows.

The Huai Hin Lat Formation is the lowermost Mesozoic continental formation, unconformably overlies the Upper Permian rock. This formation is about 250 meters thick at its type section which is mainly formed by lacustrine bituminous limestone and shales (Buffetaut and Suteethorn, 1998). It is considered Upper Triassic based on palynomorphs, plant macro-remains, conchostracans, and vertebrate remains (Buffetaut and Suteethorn, 1998b; Department of Mineral Resources, 2014; Kobayashi, 1975; Racey et al., 1996). The vertebrate assemblages from the Huai Hin Lat Formation consist of actinopterygian fishes (Martin, 1984), lungfish (Martin and Ingavat, 1982), temnospondyls (Ingavat and Janvier, 1981; Suteethorn et al., 1988), and phytosaurs (Buffetaut and Ingavat, 1982). The lithology and fossils found in the Huai Hin Lat Formation indicate deposition in an environment of flat rolling at foot of mountains or a lacustrine environment (Chonglakmani and Sattayarak, 1978; Department of Mineral Resources, 2014).

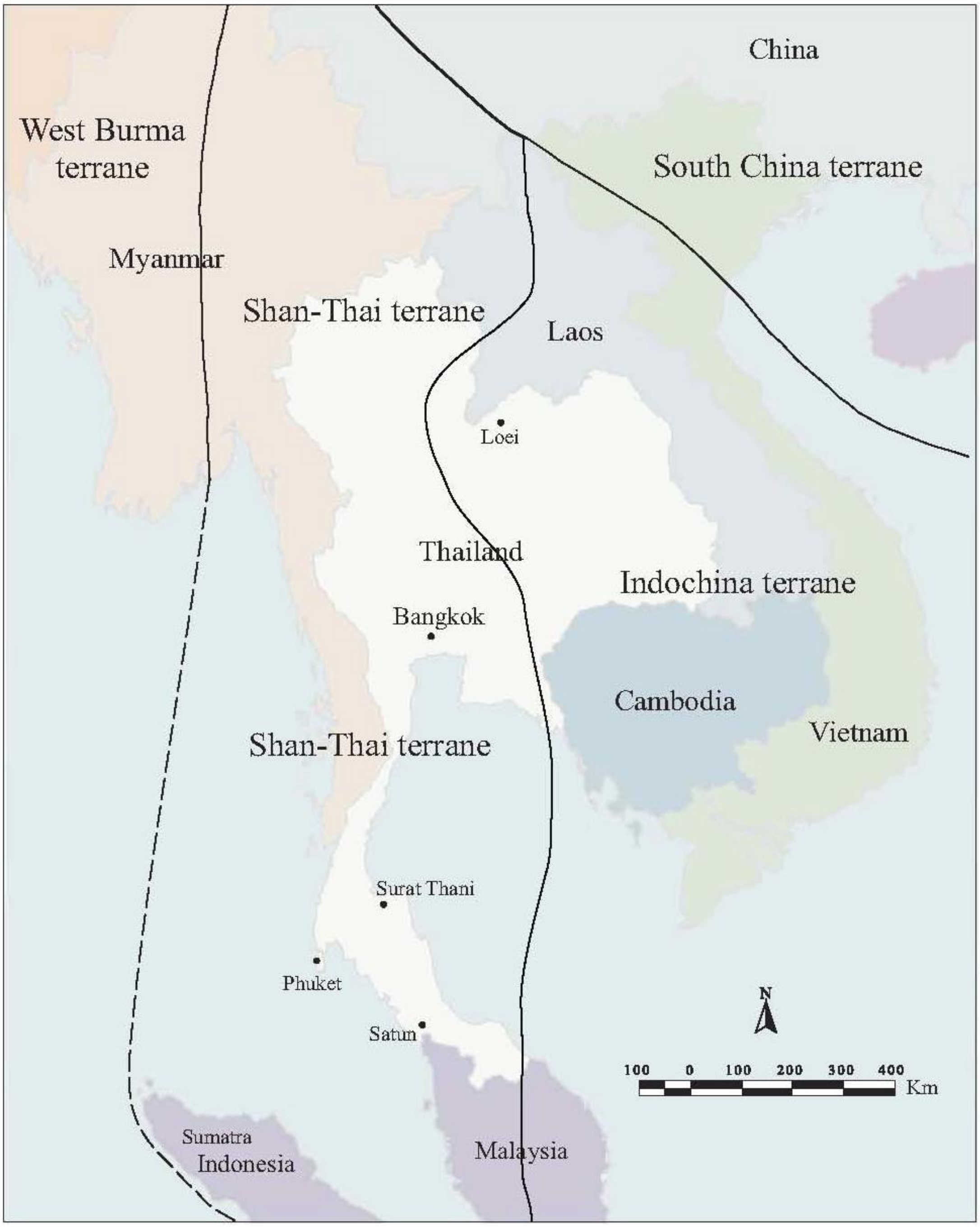

Figure 1 Map shows the boundary of tectonic terranes in Thailand (Department of Mineral Resources, 2014)

The Nam Phong Formation unconformably overlies on the Huai Hin Lat Formation. This formation is about 1,465 meters thick at its type of section, which is composed of sandstones, mudstones, and conglomerate containing pebbles of vein quartz, chert, reddish-brown siltstone, and igneous. The lithology indicated depositional environment as alluvial fan and flood plains in semi-arid paleoclimate (Department of Mineral Resources, 2014). The age of this formation is not younger than Rhaetian based on the study of the palynomorphs (Racey et al., 1996) and the evidence of vertebrates (Buffetaut et al., 2000; Laojumpon et al., 2017).

The Phu Kradung Formation unconformably overlies on the Nam Phong Formation. This formation is about 1,001 meters thick at its type section, which is composed of sandstone, siltstone, and mudstone (Department of Mineral Resources, 2014). This formation is assigned to Upper Jurassic based on palynomorphs, bivalves (Meesook, 2000; Racey et al., 1994, 1996), and vertebrate remains which consist of hybodont sharks (Cuny et al., 2005), actinopterygians (Cavin et al., 2003; Cavin and Suteethorn, 2006), temnospondyls (Buffetaut, et al., 1994a), turtles (Tong et al., 2009), crocodiles (Buffetaut and Ingavat, 1980), and dinosaurs (Buffetaut et al., 2014). The lithology indicates the depositional environment as lacustrine-dominated alluvial floodplain environment (Meesook, 2000; Racey, 2009a).

The Phra Wihan Formation varies from 100 to 250 meters thick and overlies on the Phu Kardung Formation. This formation consists of well-sorted rounded, fine to coarse-grained, pale yellow sandstone, thin-bedded siltstone, mudstone, and conglomerate (Department of Mineral Resources, 2014). The lithology and stratigraphy indicated a depositional environment of braided streams and occasional meandering rivers (Department of Mineral Resources, 2014; Meesook, 2000). The age of this formation is regarded as Middle Jurassic to Early Cretaceous based on palynomorphs, invertebrates, and trace fossils (Heggemann et al., 1990; Le Loeuff et al., 2002; Racey et al. 1994, 1996).

The Sao Khua Formation varies from 200-760 meters thick, which consists of sequences of reddish-brown sandstone and siltstone, and claystone (Meesook, 2000). This formation is assigned to Lower Cretaceous based on palynomorphs and bivalves (Meesook, 2000; Racey et al., 1994, 1996; Tumpeesuwan et al., 2010). The vertebrate assemblages from the Sao Khua Formation consist of hybodont sharks (Cuny et al., 2007), actinopterygian fishes (Cavin et al., 2009), anurans (Srisuk, 2002, 2005), turtles (Tong et al., 2009), crocodilians (Buffetaut and Ingavat, 1980), and dinosaurs (Buffetaut and Suteethorn, 1999). Based on studies of lithology and fossil remains indicated a depositional environment of meandering rivers and swamps on the riverbank in semi-arid paleoclimate (Department of Mineral Resources, 2014; Meesook, 2000).

The Phu Phan Formation is conformable to the underlying Sao Khua Formation. This formation is about 80-140 meters thick, which consists of siltstone, shale, conglomerate with calcareous lens, and reddish-brown sandstone (Department of Mineral Resources, 2014; Meesook, 2000). The Phu Phan Formation dated as an Early Cretaceous basis on vertebrate remain and palynomorph (Buffetaut and Suteethorn, 1999; Racey et al., 1996). No vertebrate remains have been found, but the trackway of a theropod dinosaur has been found in this formation (Le Loeuff et al., 2005). The lithology indicates the depositional environment of this formation as braided streams and occasional meandering rivers (Department of Mineral Resources, 2014; Meesook, 2000b).

The Khok Kruat Formation unconformably overlies on the Phu Phan Formation. This formation is about 430-700 meters thick, which consists of sequences of reddish-brown, reddish-purple sandstone, siltstone, mudstone, and conglomerate (Department of Mineral Resources, 2014; Meesook, 2000). This formation was interpreted as deposited in a meandering river system, which dated between Aptian and Albian in the Early Cretaceous based on vertebrate fossils and sediments (Department of Mineral Resources, 2014). The vertebrate assemblages from the Khok Kruat Formation consist of freshwater sharks (Cuny et al., 2008), bonny fish (Cavin et al., 2009), turtles (Tong et al., 2009), dinosaurs (Buffetaut et al., 2005).

The Maha Sarakham Formation unconformably overlies on the Khok Kruat Formation. This formation, about 600-1,000 meters thick, consists of brick-red siltstone and sandstone, thick beds of salt, gypsum, and anhydrite (Department of Mineral Resources, 2014; Meesook, 2000). Based on studies of sediments indicated that depositional environment of the formation as salty lakes and ponds in an arid climate (Meesook, 2000). The Maha Sarakham Formation is dated as early Late Cretaceous basis on the lithology and fossil remains (Department of Mineral Resources, 2014). No vertebrate remains have been found in this formation.

The Phu Tok Formation is about 205 meters thick, which overlies on the Maha Sarakham Formation. The sediments of this formation consist of red sandstone, siltstone, and claystone (Meesook, 2000). Based on studies of sediments indicated that the formation deposited in meandering river systems (Department of Mineral Resources, 2014). This formation is presumably Late Cretaceous to Early Tertiary (Department of Mineral Resources, 2014).

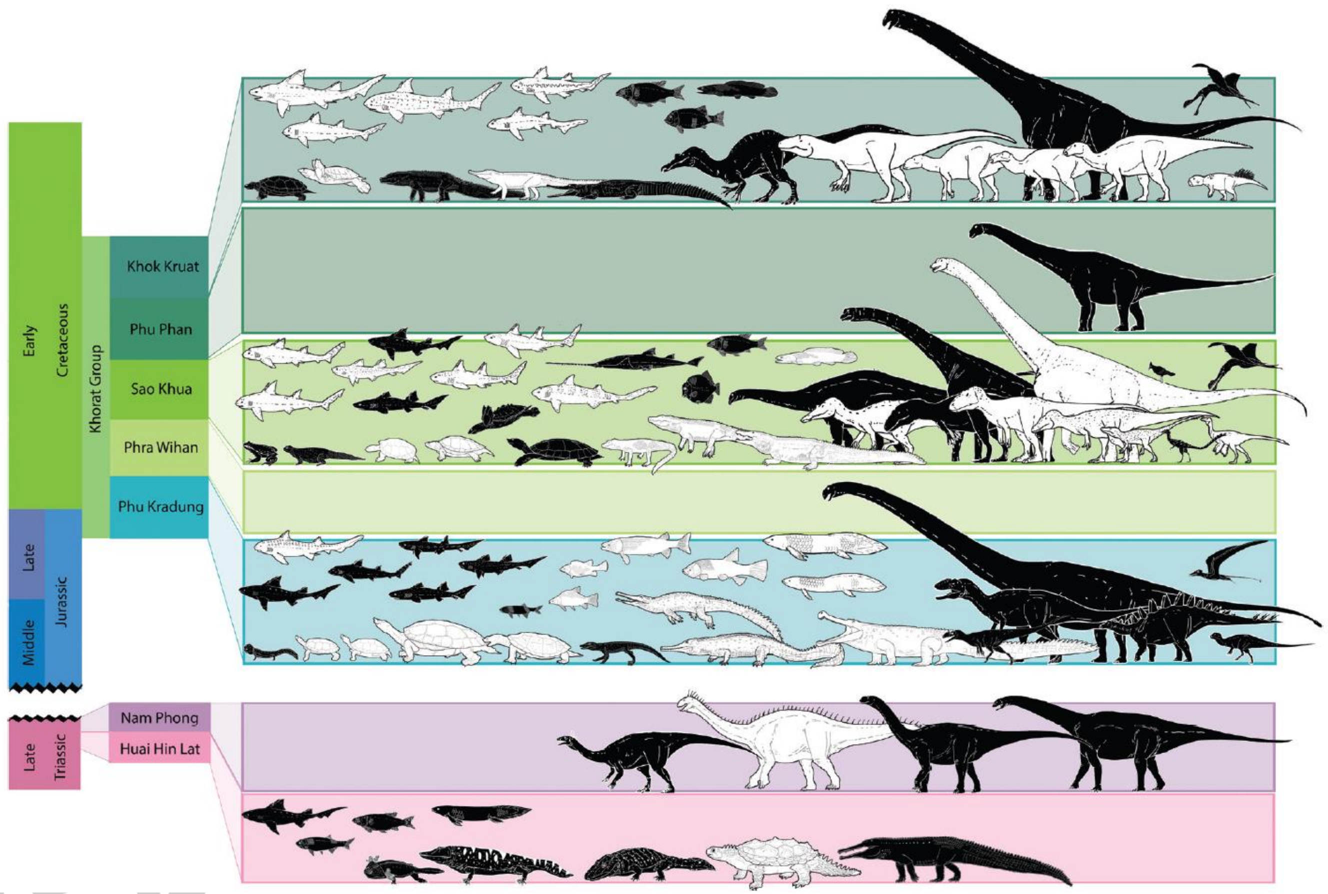

Figure 2 Mesozoic vertebrate fauna from the Indochina Terrane of NE Thailand, species-level identified taxa shown in white silhouettes, tentatively identified taxa in black silhouettes, and its explanation (Manitkoon et al., 2022).

Table 1 Mesozoic stratigraphic chart of the NE Thailand (Racey, 2009)

Formation	Description	Environments
Phu Tok	sandstone, siltstone, and claystone	meandering river systems
Maha Sarakham	brick-red siltstone and sandstone, thick beds of salt, gypsum, and anhydrite	salty lakes and ponds
Khok Kruat	sandstone, siltstone, mudstone, and conglomerate	meandering river system
Phu Phan	siltstone, shale, conglomerate with calcareous lens, and sandstone	braided streams and meandering rivers
Sao Khua	sandstone and siltstone, and claystone	meandering rivers and swamps on the riverbank
Phra Wihan	sandstone, siltstone, mudstone, and conglomerate	braided streams and meandering rivers
Phu Kradung	sandstone, siltstone, and mudstone	lacustrine-dominated alluvial floodplain
Nam Phong	sandstones, mudstones, and conglomerate	alluvial fan and flood plains
Huai Hin Lat	lacustrine bituminous limestone and shales	flat rolling at foot of mountains or a lacustrine environment

In the Shan-Thai block, the stratigraphy of the non-marine sediments in southern peninsular Thailand has been reviewed by Meesook et al., 2002; Teerarungsigul et al., 1999. These clastic red beds are known as the Trang Group, which is now subdivided into four formations based on lithology, texture, fossils, and lithification (Teerarungsigul, et al., 1999), which are as follows:

The Klong Min Formation is about 80 meters thick, which consists of fossiliferous limestone with interbedded shale, siltstone, and biomicrite (Department of Mineral Resources, 2014; Teerarungsigul et al., 1999). The vertebrate assemblages of this formation consist of hybodont sharks, actinopterygian fishes, lungfish, turtles, and crocodiles (Buffetaut et al., 1994b, c; Tong et al., 2002). The Klong Min Formation has considered Middle or Upper Jurassic in age based on charophytes and vertebrate remains (Buffetaut et al., 1994b; Girard et al., 2020; Tong et al., 2002). According to studies of sediments and vertebrate fossils indicated that deposited in a lacustrine depositional environment.

The Lam Thap Formation is 30 to 197 meters thick, unconformably overlies on the Khlong Min Formation. This formation consists of thick-bedded arkosic sandstone, siltstone interbedded with shale, and mudstone (Sha and Meesook, 2013). Based on studies of sediments indicate that the formation deposited in channel rivers, which dated as Aptian age (Sha and Meesook, 2013).

The Sam Chom Formation is about 140 meters thick, which conformably overlies on the Lam Thap Formation. This formation consists of conglomerate, medium-grained sandstone, and conglomeratic sandstone indicated that deposited in alluvial fan environment (Department of Mineral Resources, 2014; Sha and Meesook, 2013).

The Phun Phin Formation is 102-170 meters thick, which conformably overlies on the Sam Chom Formation. This formation consists of red, fine-grained, cross-bedded sandstone (Department of Mineral Resources, 2014). Based on sediment study indicated that deposited in braided streams and debris flows, which presumably Albian to Late Cretaceous in age (Sha and Meesook, 2013).

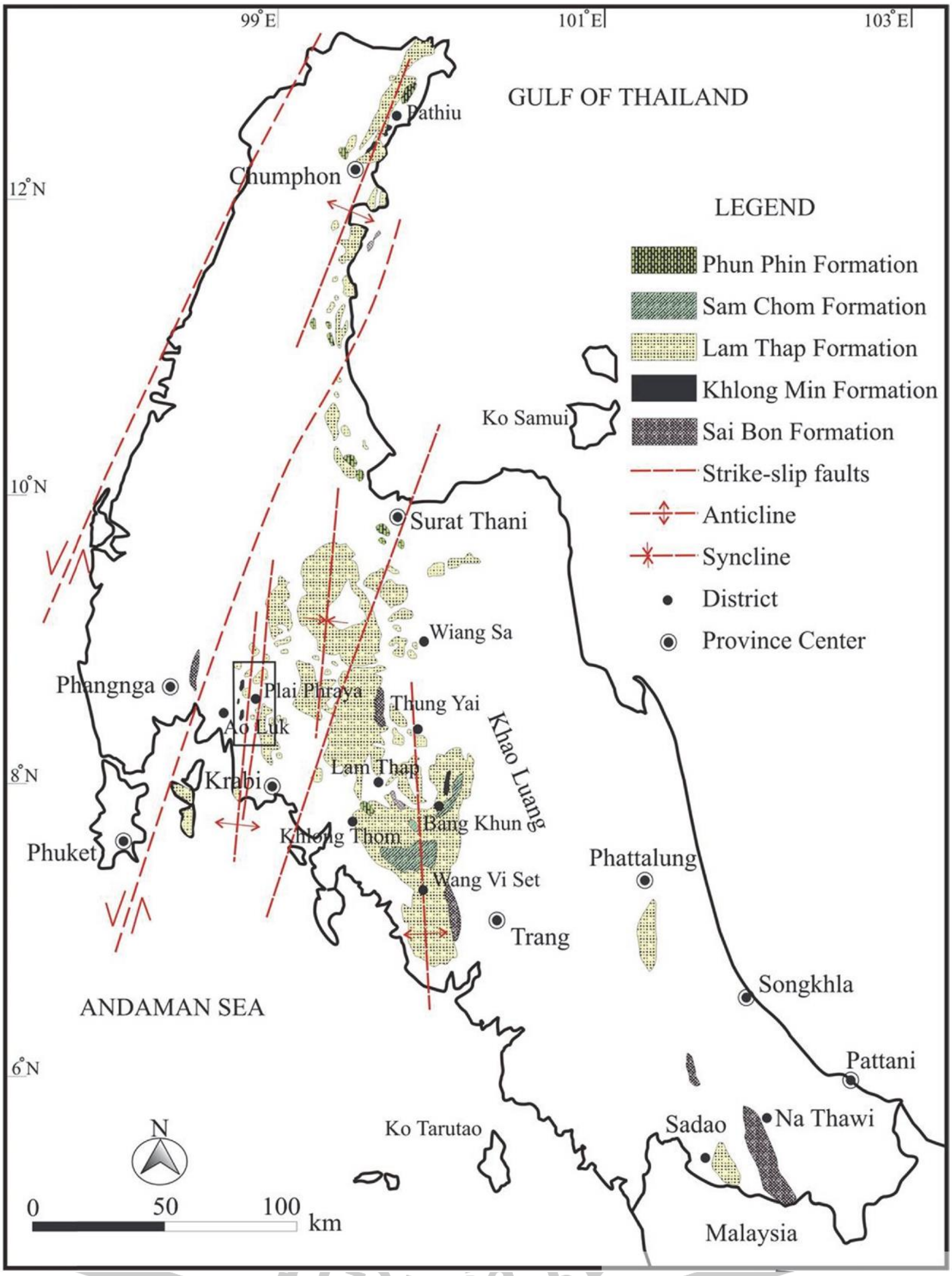

Figure 3 Mesozoic exposures in various areas of peninsular, Thailand
(Sha and Meesook, 2013)

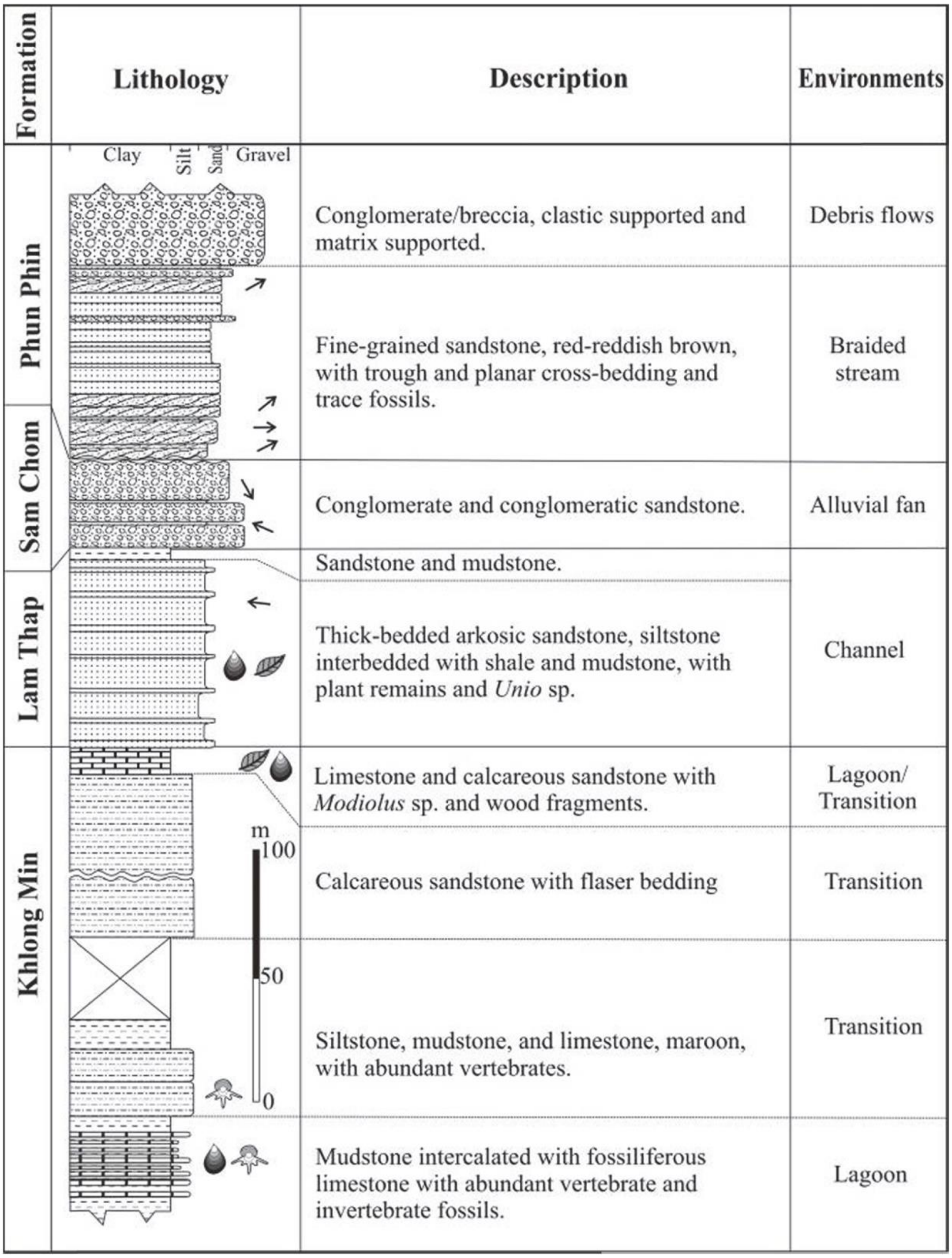

Figure 4 Generalized lithological column of the Mesozoic red bed in southern peninsular, Thailand (Sha and Meesook, 2013).

2.2 Geology of the Mesozoic amphibian localities from Thailand

The amphibian specimens were obtained from Indochina block and Sibumasu block), which are as follows.

Table 2 Mesozoic amphibian localities in Thailand

Terrane	Formation	Province	Locality
Indochina	Huai Hin Lat	Chaiyaphum	Chulabhorn Dam
			Huai Nam Aun
	Phu Kradung	Kalasin	Phu Noi
			Khao Wong
		Khon Kaen	Highway 12
	Sao Khua	Nong Bua Lamphu	Phu Phan Thong
	Sao Khua		Huai Lao Yang
Sibumasu	Klong Min	Nakhon Si Tamarat	Mab Ching

2.2.1 Mesozoic amphibian localities in Indochina block

2.2.1.1 The Chulabhorn Dam locality

The Chulabhorn Dam locality is near the entrance to a powerhouse of Chulabhorn Dam in Khon San District, Chaiyaphum Province (Fig. 5A). This area belongs to the Huai Hin Lat Formation, which consists mainly of calcareous brownish-grey shale, mudstone, sandstone, interbedded with grey to dark grey argillaceous limestone and turns into reddish-grey shale, siltstone, and mudstone in the upper part. The basal unit consists of a grey to red conglomerate (Fig 5B) (Ingavat and Janvier, 1981). The fossil assemblage layer consists of black shales and limestone. Vertebrate fossils in the Chulabhorn Dam locality included a shark denticle (Cuny et al., 2007), lungfish (Martin and Ingavat, 1982), temnospondyl (Ingavat and Janvier, 1981; Suteethorn et al., 1988), and phytosaur (Buffetaut and Ingavat, 1982). Based on sediments and vertebrate fauna indicated that this locality was deposited in a quiet lacustrine environment (Chonglakmani and Sattayarak, 1978).

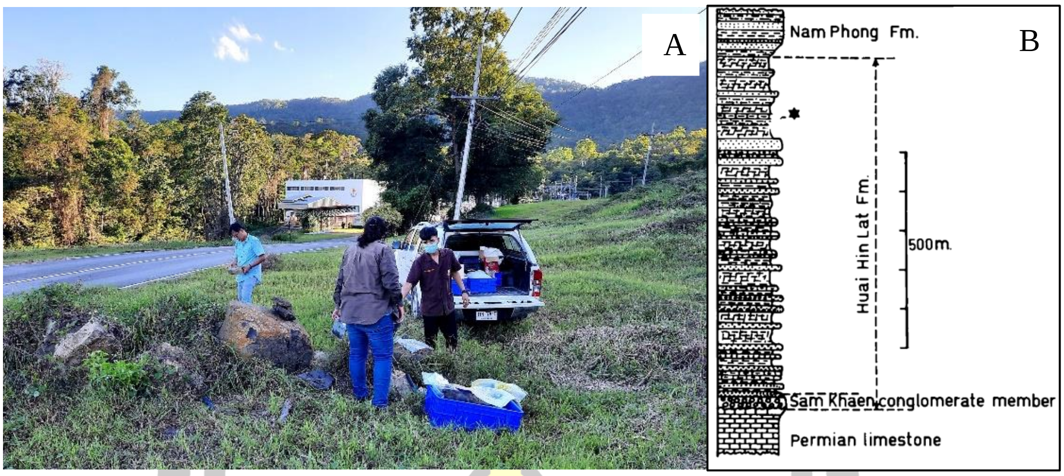

Figure 5 The Chulabhorn Dam locality near the entrance to a powerhouse of Chulabhorn Dam in Chaiyaphum Province (A). The section of the Huai Hin Lat Formation, with the vertebrate bearing layer indicated by a star (B), modified from Ingavat and Janvier, 1981).

2.2.1.2 The Huai Nam Aun locality

The Huai Nam Aun locality is situated near the Nongyakong village, Khonsan district, Chaiyaphum province, which belongs to the Huai Hin Lat Formation. Laojumpon et al. (2014) reported that this locality contains various beds of limestone and mudstone. The lower part consists of dark limestone with fossil algae. The upper part contains thinly laminated beds of calcareous mudstone (Fig. 6), which vertebrate fossil and coprolite in this bed. Based on sediments and fossils shows that Huai Nam Aun locality was deposited in brackish water near a calcium carbonate source with more or less anoxic conditions during the deposition of the basal layers (Laojumpon et al., 2014). The vertebrate fossils in this area consist of *Hybodus* teeth, bony fish scales, and temnospondyl fragments (Laojumpon et al., 2014, 2012; Nonsrirach et al., 2021).

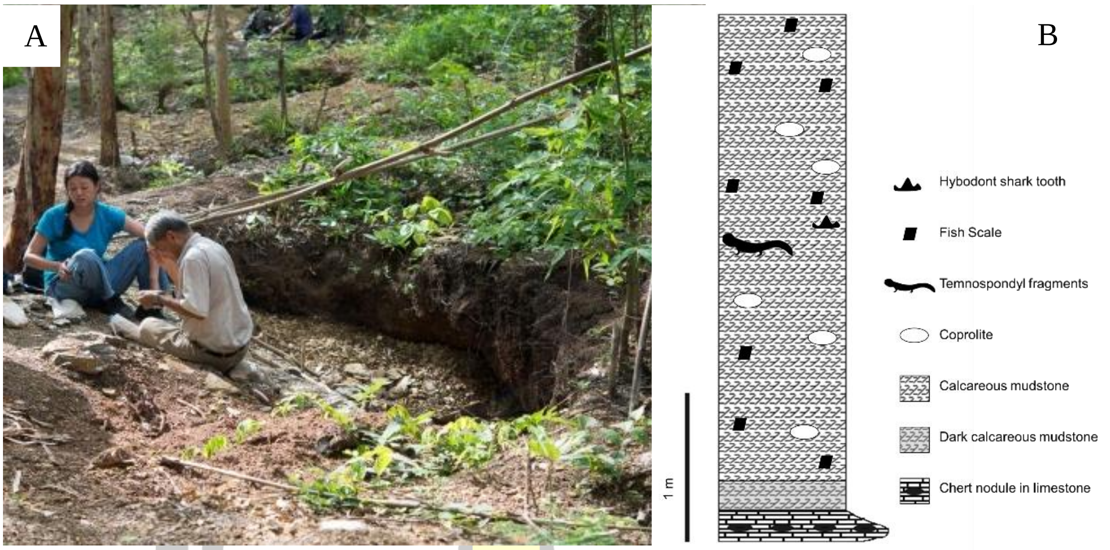

Figure 6 The Huai Nam Aun locality near the Nongyakong village, Khonsan district, Chaiyaphum province (A). The section of the Huai Nam Aun locality (B, modified from Laojumpon et al., 2012).

2.2.1.3 The Phu Noi locality

The Phu Noi locality is a small hill near Ban Dinchi village, Kham Muang District, Kalasin Province. Phu Noi locality belongs to the Phu Kradung Formation of the Khorat Group in Northeastern Thailand. The upper layer of this locality consists of maroon and reddish-brown sandstones with greenish-gray sandstones, very thin to thin-bedded. The layer below consists of siltstone interbedded with mudstones, reddish-brown to maroon and greenish-gray, very laminated and mica rich. The lowest layer consists of greenish-gray siltstone about 1 meter thick, interbedded with three layers of the plant remains, which present iron oxidation (limonite) (Fig.7) (Deesri, 2013). The vertebrate fossils consist of the hybodont shark *Acrodus kalasinensis*, the ginglymodian fish *Isanichthys lertboosi*, the lungfish *Ferganoceratodus annekempae*, the xinjiangchelyid turtles *Phunoichelys thirakupti* and *Kalasinemys prasarttongosothi*, the teleosaurid crocodilian *Indosinosuchus potamosiamensis*, dinosaurs, and pterosaurs (Buffetaut et al., 2014; Cavin et al., 2009; Cuny et al., 2014; Deesri et al., 2014; Martin et al., 2018; Tong et al., 2015, 2019).

Stratigraphically, the section locality is the lower part of the Phu Kradung Formation. The lithology and fossils indicated a depositional environment of channel and floodplain (Fig. 8) (Deesri, et al, 2017). Cuny et al., (2014) suggested that some vertebrate localities in the upper part of the Phu Kradung Formation may be Early Cretaceous in age, whereas in the lower part, are Jurassic.

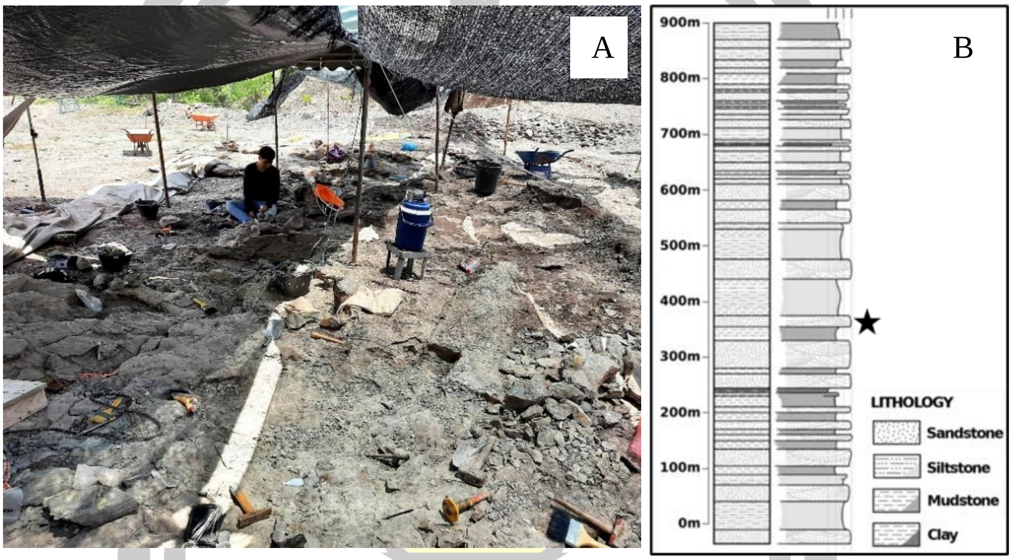

Figure 7 The section of Phu Noi locality, Kham Muang District, Kalasin Province (A). The section of the Upper Phu Kradung Formation (B, the vertebrate bearing layer of the Phu Noi locality indicated by a star, modified from Cuny et al., 2014).

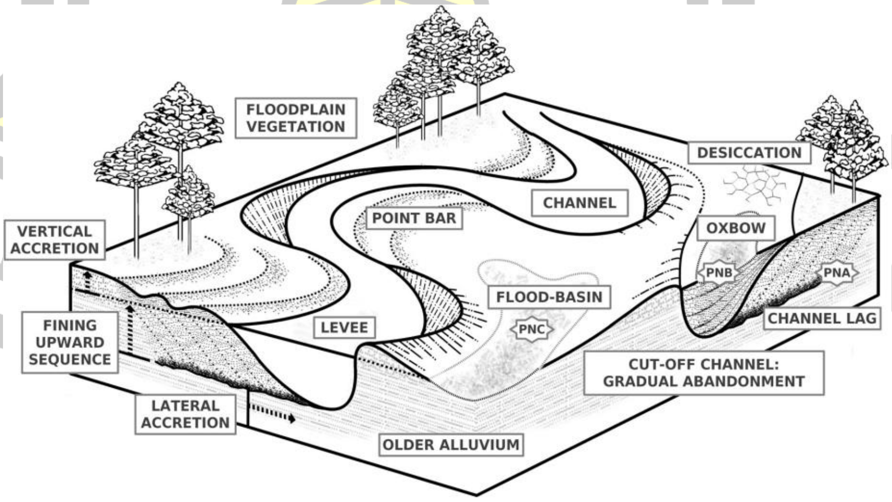

Figure 8 A depositional environment associated with the Phu Noi bone locality (Cuny et al., 2014).

2.1.1.5 The Khao Wong locality

The Khao Wong locality is in Khao Wong District, Kalasin province. This area consists of maroon and reddish-brown sandstones with greenish-gray sandstones, which belongs to the Phu Kradung Formation. The vertebrate fossils consist of temnospondyl and dinosaur bone fragments (Fig. 9).

Figure 9 The Khao Wong locality is in Khao Wong District, Kalasin province.

2.1.1.5 The highway 12 locality

The highway 12 locality is in a road cut area at kilometer 68, along Highway 12 from Chum Phae to Lom Sak, in Khon Kaen Province (Fig. 10), on the Khorat Plateau of northeastern Thailand. This area consists of reddish-grey silts and fine-grained reddish sandstone deposited in a meandering river channel (Buffetaut, et al., 1994a), which belongs to the Indochina block. The vertebrate fossils of this locality only founded temnospondyl bone fragments.

Figure 10 The highway 12 locality is in a road cut area at kilometer 68, along Highway 12 from Chum Phae to Lom Sak, in Khon Kaen Province.

2.1.1.6 The Phu Phan Thong locality

The Phu Phan Thong locality is in a road cut outcrop near Phu Phan Thong village, Muang District, Nong Bua Lamphu Province (Fig. 11). The amphibian bone were embedded in a pale olive fine-grained siltstone, belonging to the Sao Khu Formation (Srisuk, 2002). The vertebrate fossils of this locality only founded temnospondyl bone fragments.

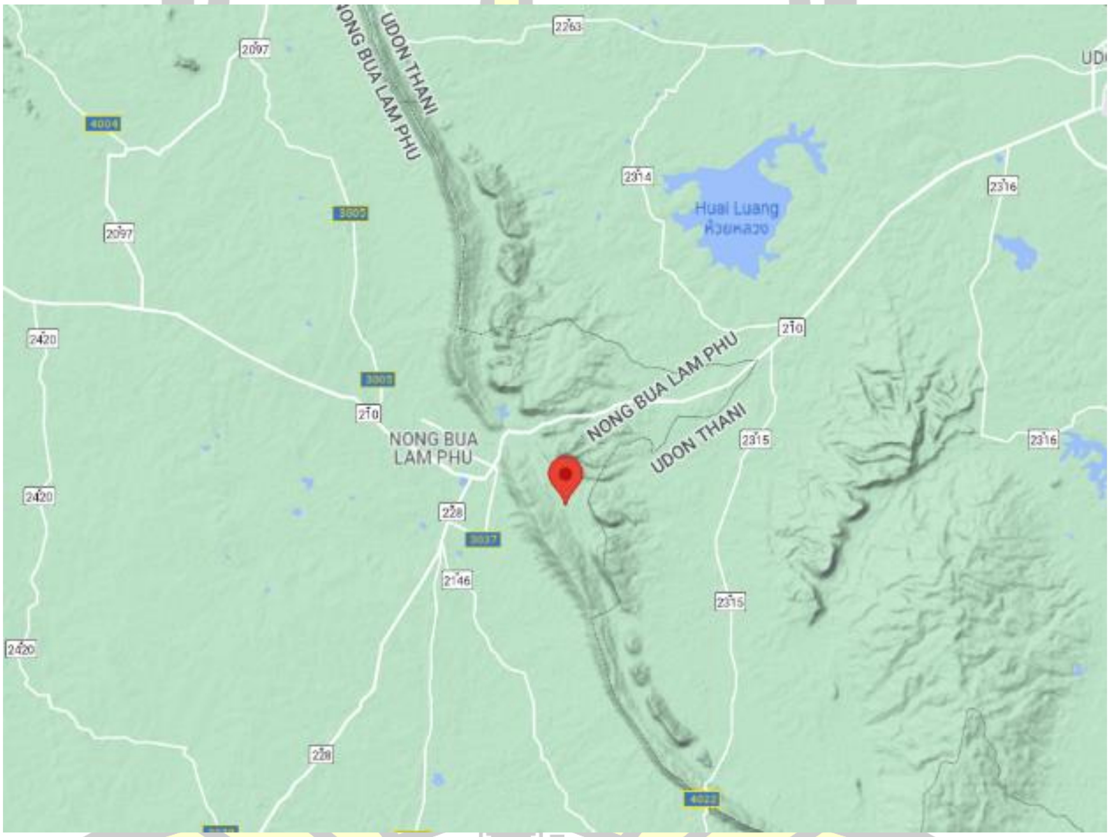

Figure 11 The Phu Phan Thong locality is in a road cut outcrop near Phu Phan Thong village, Muang District, Nong Bua Lamphu Province.

2.1.1.7 The Huai Lao Yang locality

The Huai Lao Yang locality is a road cut outcrop near the Huai Lao Yang reservoir road, Nong Bua Lamphu Province (Fig. 12). The outcrop is formed by reddish-brown micaceous siltstones and lime-nodule conglomerates, belonging to the Sao Khu Formation (Srisuk, 2005). The fossils remains consist of the bivalves, hybodont shark, actinopterygians, turtles, lizard, crocodilians, dinosaurs, and pterosaurs (Srisuk, 2005).

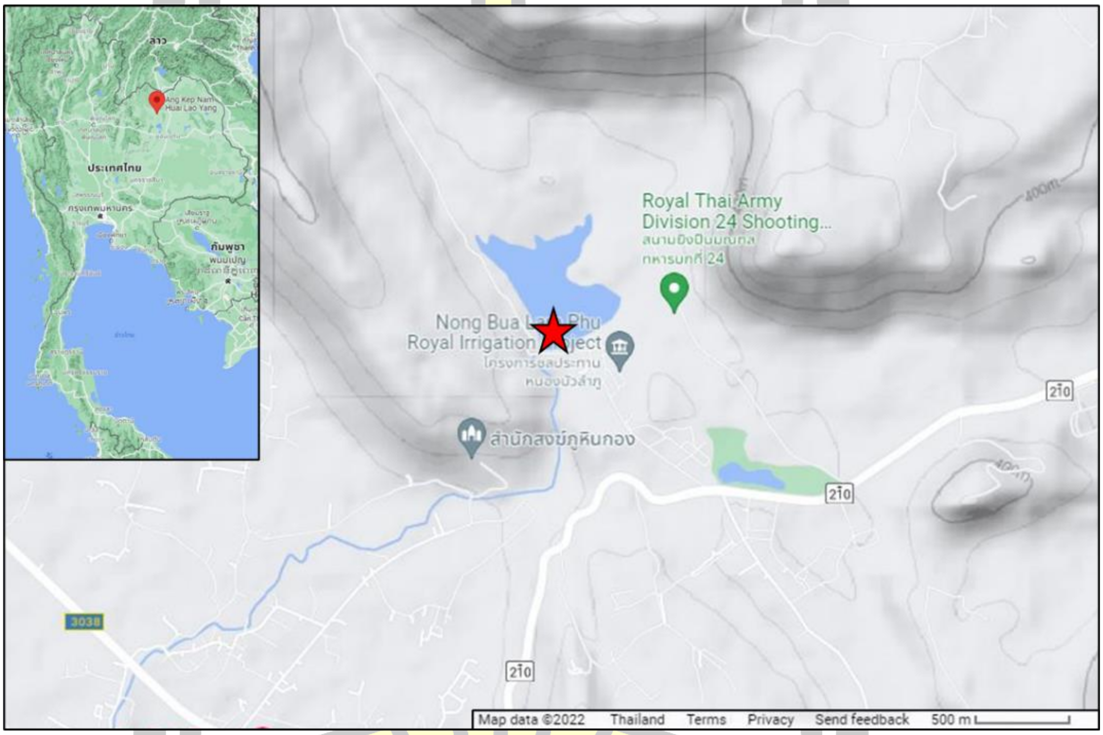

Figure 12 The Huai Lao Yang locality in the Huai Lao Yang reservoir road, Nong Bua Lamphu Province

2.2.2 Mesozoic amphibian localities in Sibumasu block

2.2.2.1 The Mab Ching locality

Mab Ching locality is situated in a road cutting near the Mab Ching village, west of the Thung Song town, Nakhon Si Tamarat Province, southern peninsular of Thailand. The sediments are greyish clays and siltstones, with some fresh-water limestone intercalations. The Mab Ching locality belongs to non-marine Middle or Upper Jurassic rocks based on charophyte algae, palynomorphs, and diatoms (Buffetaut et al., 1994a, b; Girard et al., 2020; Lei, 1993). In addition to the temnospondyl remains, vertebrate remains from Mab Ching include a spine of a large hybodont shark, scales of Lepidotes-like actinopterygian fish, lungfish tooth plates, turtle shell, and vertebrae, and teeth of mesosuchian crocodiles (Buffetaut et al., 1994b, c; Tong et al., 2002). The whole assemblage of this locality is suggested that deposited in a lacustrine environment.

Figure 13 Mab Ching locality along the road in Nakhon Si Tamarat Province, exposes alternating grey and brow clay interbedded limestones bed.

2.3 Introduction to the Early amphibians from the Late Paleozoic to Mesozoic

The word "amphibian" is derived from the Greek term amphíbios, which means "both kinds of life. The amphibians of the Paleozoic and the Mesozoic can be dived into three major clades: the Lepospondyli, the Seymouriamorpha, and the Temnospondyli (Fig. 14) (Vitt and Caldwell, 2014).

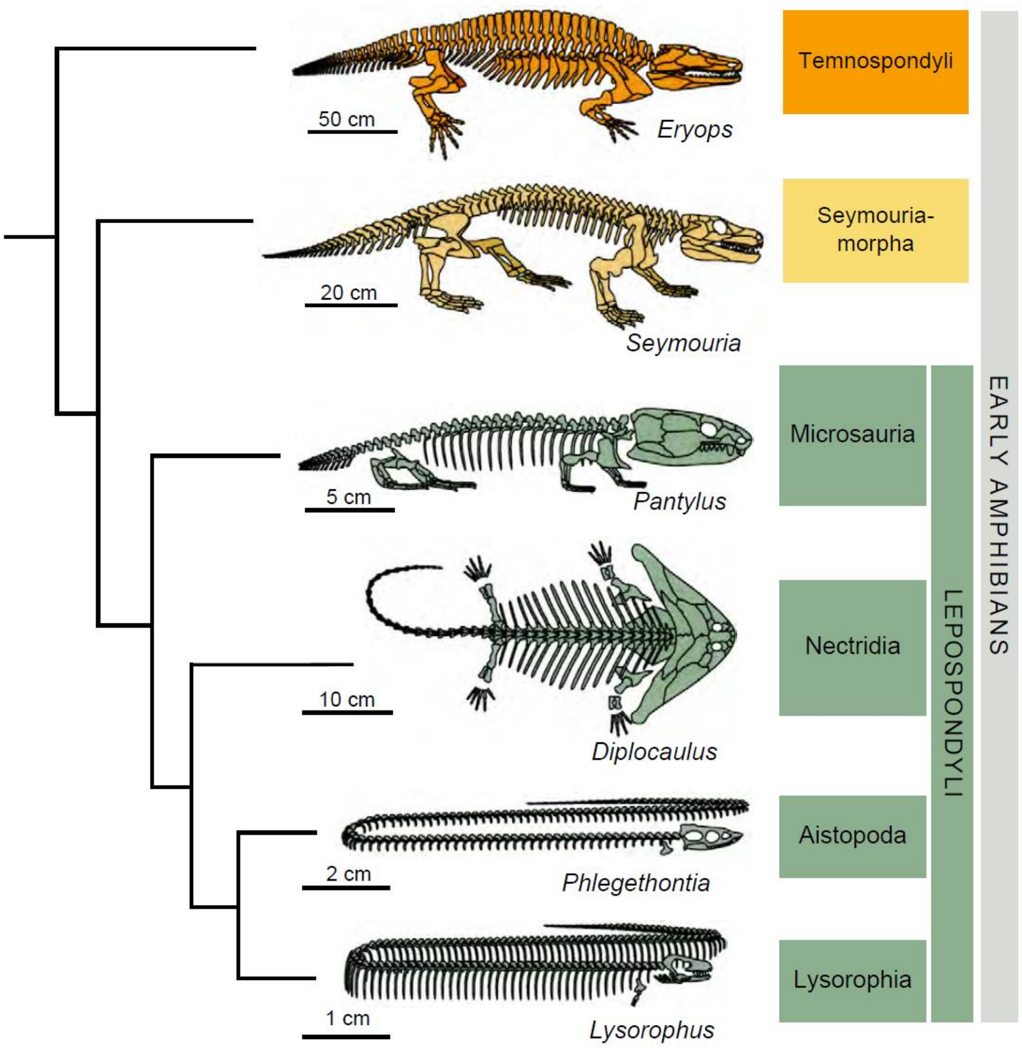

Figure 14 Paleozoic and early Mesozoic amphibians (Vitt and Caldwell, 2014).

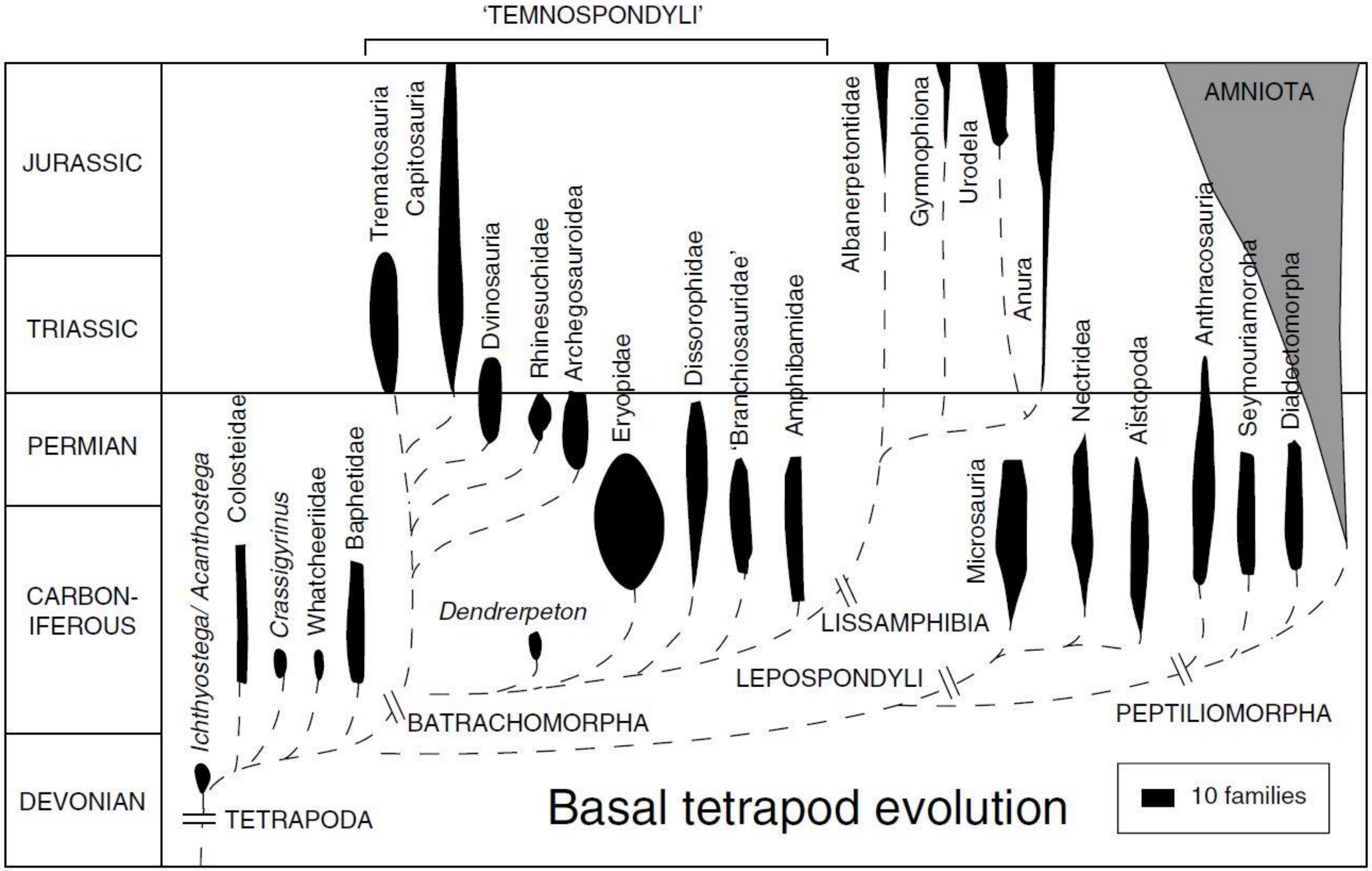

Figure 15 Diversity of basal tetrapod and their stratigraphic distribution (Benton, 2004).

2.3.1 Temnospondyli

Temnospondyli are primitive amphibians, which are a diverse subclass of tetrapods. They were medium to large (1–6 meter) salamander-like tetrapods. Basal members of temnospondyls were the most diverse and most successful group of amphibians in the Paleozoic, which lived during the Mesozoic Era (Damiani and Rubidge, 2003; Schoch, 2014). Temnospondyls are commonly retrieved in the tetrapod assemblages from Triassic continental deposits such as fluvial and lacustrine environments (Dias-Da-Silva and Dias, 2013). The character of Temnospondly is wide, plate-like vomers, a firm sutural contact between the exoccipitals and postparietals, the rounded, large interpterygoid vacuities, the wide squamosal embayments, the rodlike stapes with its two proximal heads and the articulation with the parasphenoid, and the relatively short ribs (Vitt and Caldwell, 2014).

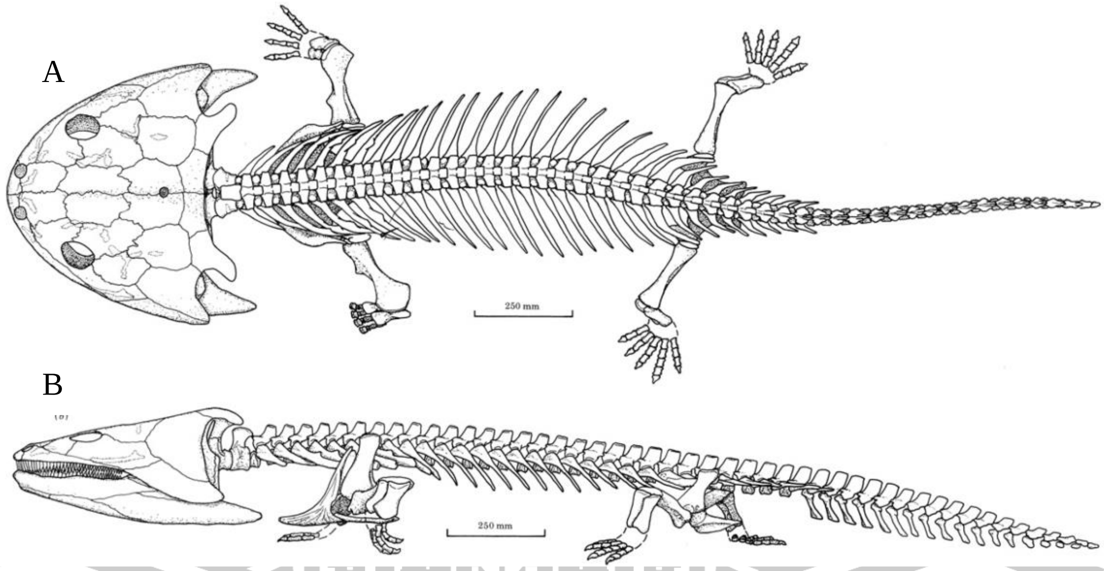

Figure 16 Temnospondyl skeletal reconstruction in dorsal (A) and lateral (B) view (Warren and Hutchinson, 1983).

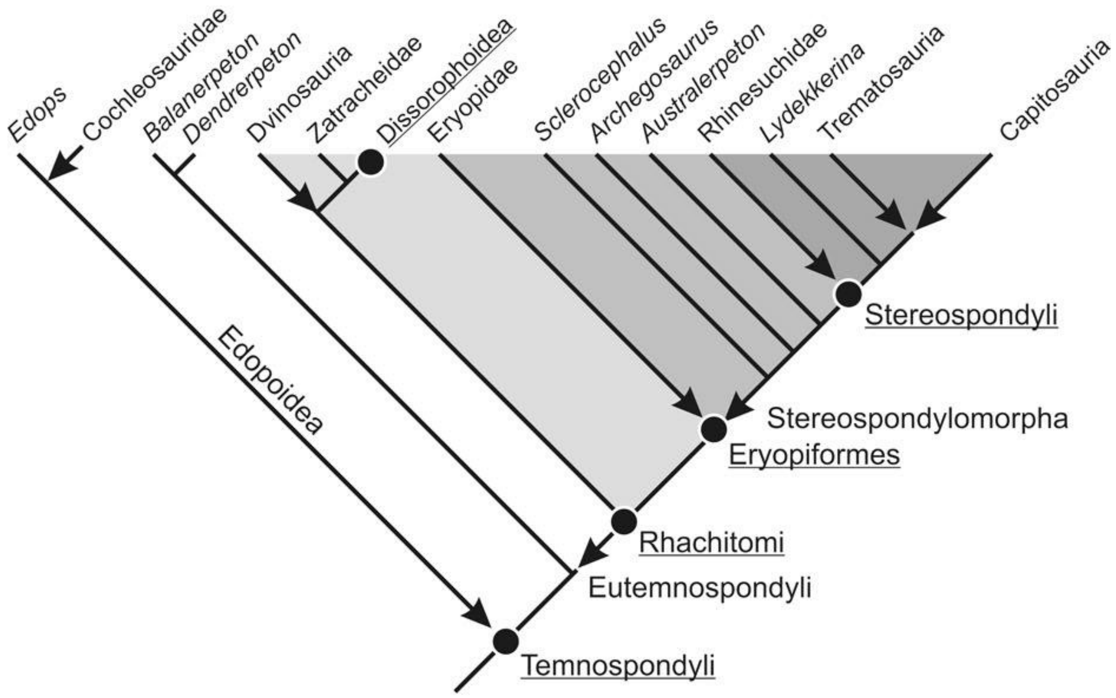

Figure 17 Phylogenetic definition of major clades within Temnospondyli. Underlined taxon names are node-based (black dots), the other ones are branch-based (arrows) (Schoch, 2013).

The main groups of Temnospondyli included:

2.3.1.1 Edopoids

Edopoids are large temnospondyls, which are 1-3 meters long. The body shape of them is similar to a modern giant salamander, but the skull sketchily look-alike alligators with the presence of an intertemporal bone that is absent in all other temnospondyls and the lack of a pineal foramen (Schoch, 2014). They are from the Late Carboniferous - Early Permian.

2.3.1.2 Eutemnospondyli (true Temnospondyli)

Eutemnospondyli includes a clade of Dendrerpeton and Balanerpeton that two taxa are currently known: *Balanerpeton* and *Dendrerpeton.* Both have a full complement of bones in the limbs and girdles, which 30-50 cm in length. It was nevertheless lightly built and occurred in terrestrial environments (Schoch, 2014). There were probably lung breathers but did not employ ribs in lung ventilation, no evidence of gills, and the retention of dermal bony scales suggests that skin respiration was also not extensive (Schoch, 2014). Dendrerpeton and Balanerpeton are known from the Early Carboniferous.

2.3.1.3 Rhachitomi

Dvinosauria is a group of primitive semi-aquatic to completely aquatic amphibians, presented in the Late Carboniferous to the Early Triassic. They are short snout, elongated body with more than 30 vertebrae, poorly developed limbs, and a long swimming tail (Schoch, 2014).

Dissorophoidea and Zatracheidae are a family of Late Carboniferous and Early Permian temnospondyl. In this group, two clades share a range of unique characters that fontanelle between the nares, a wide space between the eyes, and a large otic notch. (1) Dissorophoidea is a medium-sized, temnospondyl amphibians that appeared during the Moscovian in Euramerica and continued through to the Late Permian and even possibly the Early Triassic of Gondwana. This group included: *Trematopidae* and *Dissorophidae*, *Amphibamidae*, and *Branchiosauridae*. (Schoch, 2014). (2) Zatracheidae is a short-bodied taxon with a very large head, concluding that were sit-and-wait predators (Schoch, 2014). This group included three genera that *Acanthostomatops*, *Dasyceps*, and *Zatrachys* which occurred in the Early Permian of Europe and North America.

2.3.1.4 Eryopiformes

Eryopidae is a group of medium to large Temnospondyli, defined as all eryopoids with interpterygoid vacuities that are rounded at the front; and large external nares with robust limbs and long swimming tails (Schoch, 2014). They occurred in Pennsylvanian to Early Permian, in oxbow lakes and coastal lagoon depositional environment from North America and Europe.

2.3.1.5 Stereospondyli

Stereospondyli ranged from 1 to 6 meters, which simplified backbones, the vertebra was made of a single intercentrum. The vertebral structure of this temnospondyl was rather weak suggesting that most stereospondyls were aquatic and fish-eater predators (Schoch, 2014). They appear during the Late Permian, some appear to have survived into the Early Cretaceous.

2.3.2 Seymouriamorpha

The Seymouriamorpha, known from two different types of environment deposits, were represented by the aquatic Seymouriidae and the terrestrial Discosauriscidae.

2.3.2.1 Seymouriidae is 50-100 cm in length with a robust post-cranial skeleton, with massive girdles, limb elements with fully formed joints, and large hand and foot skeleton (Schoch, 2014). This amphibian occurred in stream and floodplain environments from the Early Permian of North America and Europe.

2.3.2.2 Discosauriscidae is 10-20 cm in length, salamander-like animals with external gill and long swimming tails (Schoch, 2014). It was aquatic tetrapods discovered in Europe, lakes, and ponds in the Early Permian.

2.3.3 Lepospondyli

Most Lepospondyli, are small (not exceeding 5 cm skull length) and varied in morphology some were flat with large, triangular-shaped heads, and some were even limbless (Schoch, 2014). The fossil remains were founded from the Carboniferous through the Permian. Lepospondyli character as vertebral central cylindrical, no squamosal embayment, No palatal tusks, teeth not labyrinthodont, odontoid peg, and basioccipital. They included four clades: Microsauria, Aistopods, Lysorophians, and Nectrideans.

2.3.3.1 Microsauria are salamander-like tetrapods with short legs and short tails. Some species had long and thin bodies, whereas others were rather short and stout, which lived on dry land and burrowed. Microsaurs have strong, conical teeth and some have bulbous dentition indicating crushing bite habits (Schoch, 2014; Vitt and Caldwell, 2014). It occurred from the late Carboniferous and early Permian.

2.3.3.2 Aistopods are eel-like body, limbless amphibians with 5 cm to 70 cm in length. Presumably, they were aquatic and semiaquatic because they had fragile skulls unlike those of burrowing animals (Schoch, 2014; Vitt and Caldwell, 2014). It is known from the Carboniferous and Early Permian of Europe and North America.

2.3.3.3 Lysorophians are similar to Aistopods. They are eel-like or snake-like that elongated bodies, tiny limbs which retained feeble hands, and foot skeletons. Lysorophians were aquatic amphibians and occurred during the Carboniferous and Permian (Schoch, 2014; Vitt and Caldwell, 2014).

2.3.3.4 Nectrideans are small to medium-sized (less than 0.5 meters in length), newt-like amphibians. The heads were arrow-shaped with large, laterally projecting horns. The shaped heads with strong dentition are used for snap-and-grasp feeding (Schoch, 2014; Vitt and Caldwell, 2014). It was a primarily aquatic group, existing from the Pennsylvanian to the Early Permian.

2.4 Overview of the Mesozoic amphibians in Thailand

In Asia, many Mesozoic amphibian fossils were found ranging from the Late Triassic to the Early Cretaceous in India, China, and Japan (Warren and Black, 1985; Mukherjee and Sengupta, 1998; Liu and Wang, 2005 Chowdhury, 1965; Sengupta 1988; Maisch and Matzke, 2005; Skutschas et al., 2009; Dong, et al., 2013).

In Thailand, Mesozoic Temnospondyl and Anura fossils were discovered in the continental rocks. The specimen was discovered by Ingavat and Janvier in 1981 at a locality from the Huai Hin Lat Formation (Upper Triassic) near the Chulabhorn Dam, Khon San District, Chaiyaphum Province. It was a partial skull of Mastodonsauroidea, with referred to *Cyclotosaurus* cf. *posthumus*. Seventeen years later, Suteethorn, et al. (1988) discovered a temnospondyl fragment from a locality near the Chulabhorn Dam. They described the specimen, with referred to a dermal bone fragment of plagiosauroid temnospondyl, based on shape and surface.

In 1994, Buffetaut et al. (1994a) reported a temnospondyl intercentrum from Phu Kradung Formation (Upper Jurassic). It was found in a road cut locality at kilometer 68, along Highway 12 from Chum Phae to Lom Sak, in Khon Kaen

Province. In the same year, Buffetaut et al., (1994b) described two temnospondyl intercentra that were collected from the outcrop of the Klong Min Formation (Middle or Upper Jurassic) a road cut locality near Mab Ching village, Thung Song District, Nakhon Si Thammarat Province. The intercentra from Phu Kradung Formation and Klong Min Formation is consistent with the intercentrum character of the Brachyopoidea which are similar to the intercentra discovered from the Jurassic Indochina block, e.g., *Gobiops desertus* from the Gobi Desert of Mongolia.

The left and right humeri of anura were collected by Srisuk (2002) from a road cut locality near Phu Phan Thong village, Muang District, Nong Bua Lamphu Province. This is the first occurrence of an Anura fossil in Thailand. Three years later, Srisuk (2005) described additional fossil in a road cut locality near the Huai Lao Yang reservoir road, Nong Bua Lamphu Province. It was a pelvic girdle consisting of parts of the ischium, pubis, and acetabulum. These features are reminiscent of an anuran amphibian.

CHAPTER 3
METHODOLOGY

3.1 Materials

The research is based on the study of a partly articulated amphibian bones in the collection room of Sirindhorn Museum (SDM) and the Palaeontological Research and Education Centre of Mahasarakham University (PRC). The materials are collected from the Huai Nam Aun locality, Chulabhorn Dam locality, Powerhouse near Chulabhorn Dam locality, Mab Ching locality, Highway 12 locality, Khao Wong locality, Phu Noi locality, Phu Phan Thong locality, and Huai Lao Yang locality (Table 3). All materials were collected and prepare by staff team of SDM and PRC.

3.2 Laboratory work

3.2.1 Preparation

The preparation of specimens includes the cleaning and repairing of fossil specimens. The specimens cleaned by pneumatic air pen, sand blasting machine, acetone, and acetic acid. Broken specimens will be repaired by using glue.

3.2.2 Measurement and description

The materials are measured in length and width. The materials will be description and classification based on morphology (size shape and surface). The skull, intercentra, dermal bones, and humerus will be described in term of comparative anatomy, geological age, and localities to another Mesozoic amphibian fossil in the world.

3.2.3 Phylogenetic analysis

The Brachyopoidea phylogenetic analysis of the posterior skull (KS34-1481) using TNT software version 1.5, following the parameters used by Damiani and Kitching (2003), which consist of on 61 cranial characters.

3.2.4 Micro-CT-scanning

The internal structure of the humerus (CY-HN 435) analysis using the Micro-CT-scanning machine to determine the exact sectioning plane. the specimen was scanned with a high-resolution micro-computed tomography scanner. The data was processed and bundled into image stacks with ImageJ/Fiji software.

3.2.5 Thin section

The coprolite (PRC 021) was hardened by embedding in epoxy resin, and then cut with a diamond saw in longitudinal and transversal sections using a standard thin section method (Chin, 2007; Dentzien-Dias et al., 2013). The material slices were glued to glass slides, and optimal thickness for transmission microscopy was obtained using a grinder with a graded series. All microscopic structures and fossil remain were photographed with a light microscope Nikon ECLIPSE E200, and multiple images taken with different focal distances were combined using a focus stacking technique.

Table 3 The material in this research

Formation	Locality	Material	Previous material	New material
Huai Hin Lat	Huai Nam Aun	intercentra,	CY-HN 378 (Laojumpon et al., 2014)	CY-HN 374, CY-HN 370, and CY-HN 378
		neural arch		CY-HN 376 and CY-HN 379
		humerus		CY-HN 435
		clavicle bone		CY-HN 364
		interclavicle or clavicle bones		CY-HN 365, CY-HN 368, CY-HN 403, CY-HN 349, CY-HN 454, and CY-HN 377
	Chulabhorn Dam	skull	D.M.R. no. Ch.D 001 (Ingavat and Janvier, 1981)	
	Powerhouse, Chulabhorn Dam	dermal bone	TF 1453 (Suteethorn, et al., 1988)	
Klong Min	Mab Ching	intercentra	TF 3328 and TF 3329 (Buffetaut et al., 1994b)	MC 233, and MC 234
Phu Kradung	Highway 12	intercentrum	TF 3144 (Buffetaut et al., 1994a)	
	Khao Wong	intercentrum		KS37-8
	Phu Noi	skull		KS34-1481
		intercentra		KS34-1471, KS34-1472, KS34-1473, KS34-1474, KS34-1476, KS34-1477, KS34-1478, KS34-1479, KS34-1482, KS34-1483, KS34-14784, KS34-1486, KS34-1489, KS34-2192, PN-710, PN 17-75, PN-723, KS34-3270, KS34-1480, KS34-1485, KS34-3270, KS34-2871, and PN-712
Sao Khua	Phu Phan Thong	humerus	SHM-PT 529 and SHM-PT 530 (Srisuk, 2002)	
	Huai Lao Yang	pelvic girdle	SHM-HY 231 (Srisuk, 2005)	

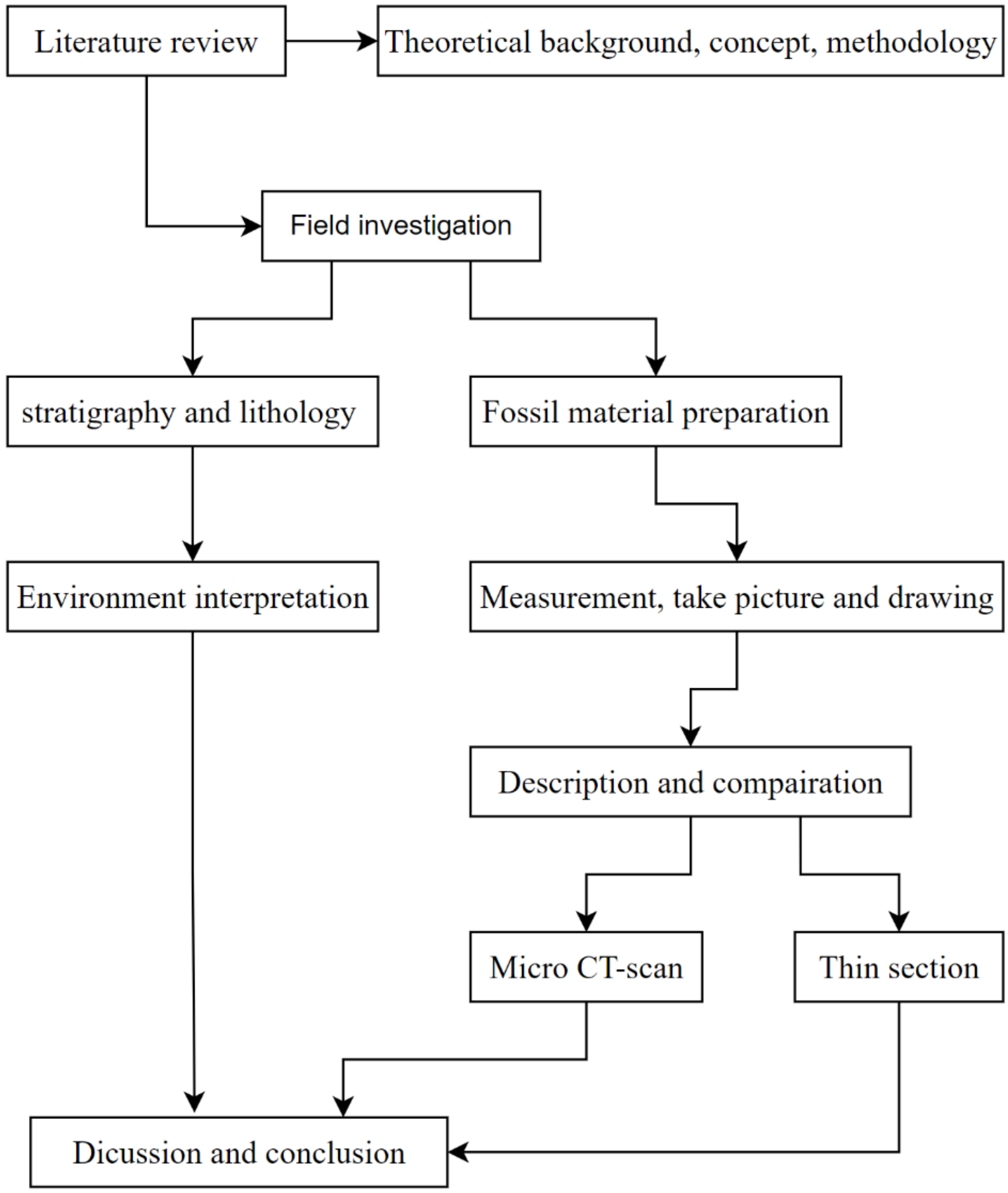

Figure 18 Methodology framework of this research

CHAPTER 4
RESULT AND DISCUSSION

4.1 Systematic description of the Mesozoic amphibian fossils in Thailand

The following descriptions concern the previously published and unpublished records of amphibians, which were founded in the Mesozoic locality in Thailand.

4.1.1 Systematic description of Triassic amphibians

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Mastodonsauroidea Lydekker, 1885, (sensu Damiani, 2001)

Family: Cyclotosauridae Shishkin, 1964

Genus: *Cyclotosaurus* Fraas, 1889

Cyclotosaurus cf. *posthumus*

Occurrence: Chulabhorn Dam locality, Chaiyaphum province

Formation/age: Huai Hin Lat Formation (Carnian–Norian)

Reference material: Posterior skull; D.M.R. no. Ch.D 001 (Ingavat and Janvier, 1981)

Description: D.M.R. no. Ch.D 001 (Fig. 19 A-F) is a posterior part of a comparatively large skull (approximately 20 cm wide and 11 cm long), but the lateral part of the right side is missing. However, a pair of otic notches and pineal foramen are preserved. The skull table has slightly concaved downward, and the postero-lateral edges of the skull are estimated behind the occipital condyles.

Remark: The specimen described by Ingavat and Janvier, (1981) an assignment to *Cyclotosaurus* (Fraas, 1913) based on anatomical detail: 1) a distinct dorsolateral blade on the quadrate ramus of the pterygoid, bounding off ventrally the otic fenestra. 2) an oblique ridge limiting ventromedially the area of insertion for the depressor mandibulae muscle. 3) A participation of the quadratojugal to the articular condyle for the lower jaw. 4) A transverse crest of the pterygoid (the pterygosphenoid crest) joins medially the parateygoid crest. The ornamentation and sutures pattern almost point to point comparable to of *Cyclotosaurus posthumus* Fraas, 1913 from the Upper Middle Keuper, Bavaria (Germany).

Figure 19 A replica skull of *Cyclotosaurus* cf. *posthumus* (A, C, E) and reconstruct image (B, D, F) in dorsal (A, B), palatal (C, D), and posterior views (E, F) (After Ingavat and Janvier, 1981). A Reconstruction images of *Cyclotosaurus* cf. *posthumus* from Thailand (G). Reconstruction images are not to scale.

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Plagiosauroidea Abel, 1919

Family: Plagiosauridae Abel, 1919

Plagiosauridae *gen. et sp. indet.*

Occurrence: Powerhouse near Chulabhorn Dam locality, Chaiyaphum province

Formation/age: Huai Hin Lat Formation (Carnian–Norian)

Reference material: Dermal bone; TF 1453 (Suteethorn et al., 1988).

Description: The specimen (TF 1453, Fig 20 A-B), is approximately 22 mm wide, 25 mm long, and 4 mm thick. The specimen shows peculiar ornamentation consisting of tubercles or pustules on its ventral surface, which is characteristic of vertebrate dermal bone. Dorsally, the surface shows some faint radiating grooves and ridges.

Remark: According to its ornamentation, TF 1453 was interpreted as a dermal bone fragment of a temnospondyl and was assigned to Plagiosauridae. Comparable ornamentation is observed in Middle to Late Triassic Plagiosauridae, e.g., *Gerrothorax pulcherrimus* and *Plagioscutum ochevi* from Europe (Jenkins et al., 2008; Shishkin, 1986; Suteethorn et al., 1988; Warren and Snell, 1991).

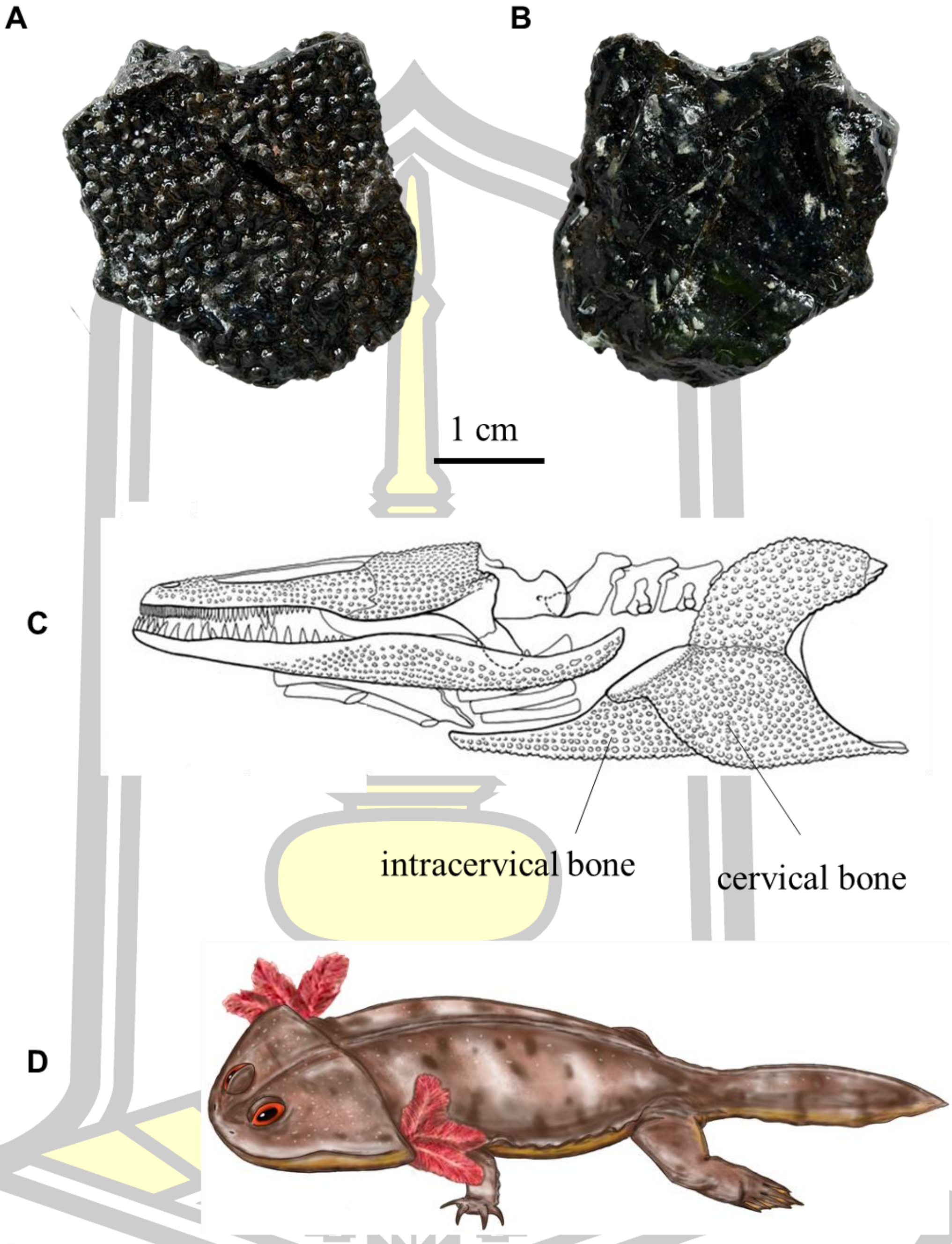

Figure 20 A dermal bone of Plagiosauridae *gen. et sp.* indet. in ventral view (A) and dorsal view (B). Skeleton reconstruction images of plagiosauridae (C, modified from Jenkins et al., 2008). Reconstruction images of plagiosauridae from Thailand (D). Reconstruction images are not to scale.

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Metoposauroidea

Metoposauroidea *fam. indet.*

Occurrence: Huai Nam Aun locality, Chaiyaphum province

Formation/age: Huai Hin Lat Formation (Carnian–Norian)

Reference material: Vertebrae; CY-HN 378 (Laojumpon et al., 2014), CY-HN 374, CY-HN 370, CY-HN 376, CY-HN 378 CY-HN 379.

Dermal bone: CY-HN 349, CY-HN 364, CY-HN 365, CY-HN 368, CY-HN 377, CY- HN 403, and CY-HN 454

Humerus: CY-HN 435

Description:

Vertebrate: an intercentrum, CY-HN 378 (Fig. 21 A-F) is preserved over a length of approximately 65 mm and is 33 mm thick. The CY-HN 378 is disk-shaped and subcircular in anterior and posterior views, with reduced or absent pleurocentra (Laojumpon et al., 2014). The anterior and posterior faces of CY-HN 378 are slightly concave. The parapophysis is located in less than half of the lateral surface.

The shape of the intercentrum or the size and the position of parapophysis can be used to classify the vertebral column. Based on the intercentrum shape and both of size and position of the parapophysis, the CY-HN 378 is obviously from the mid-dorsal to presacral intercentrum. Because the parapophysis of the anterodorsally intercentrum is large while post-sacral to dorsal intercentra is a very low position of parapophysis and almost flat or flat ventral surface of the intercentrum.

CY-HN 374 is a small intercentrum with crescent-shaped (Fig. 21 G-L). The anterior and posterior surfaces are slightly concave. It is preserved over a length of approximately 54 mm and is 27 mm thick. The notochordal canal is present on the dorsal edge of both anterior and posterior surfaces. The position of the parapophysis is unclear. In the ventral view, the surface is slightly concave. The CY-HN 374 is a characteristic feature of the post-sacral intercentrum, based on shape.

A partial intercentrum, CY-HN 370 (Fig. 21 M-P) is preserved over a length of approximately 63 mm and is 36 mm thick. The specimen was very fragment to described but preserved the anterior and posterior edge.

CY-HN 379 (Fig. 21 Q-T) and CY-HN 376 (Fig. 21 U-X) are presumably from the portion of the neural arch which is flat and concave on the dorsal surface. The CY-HN 378 is preserved over a length of approximately 48 mm and is 15 mm thick and the CY-HN 376 preserved over a length of approximately 46 mm and is 20 mm thick.

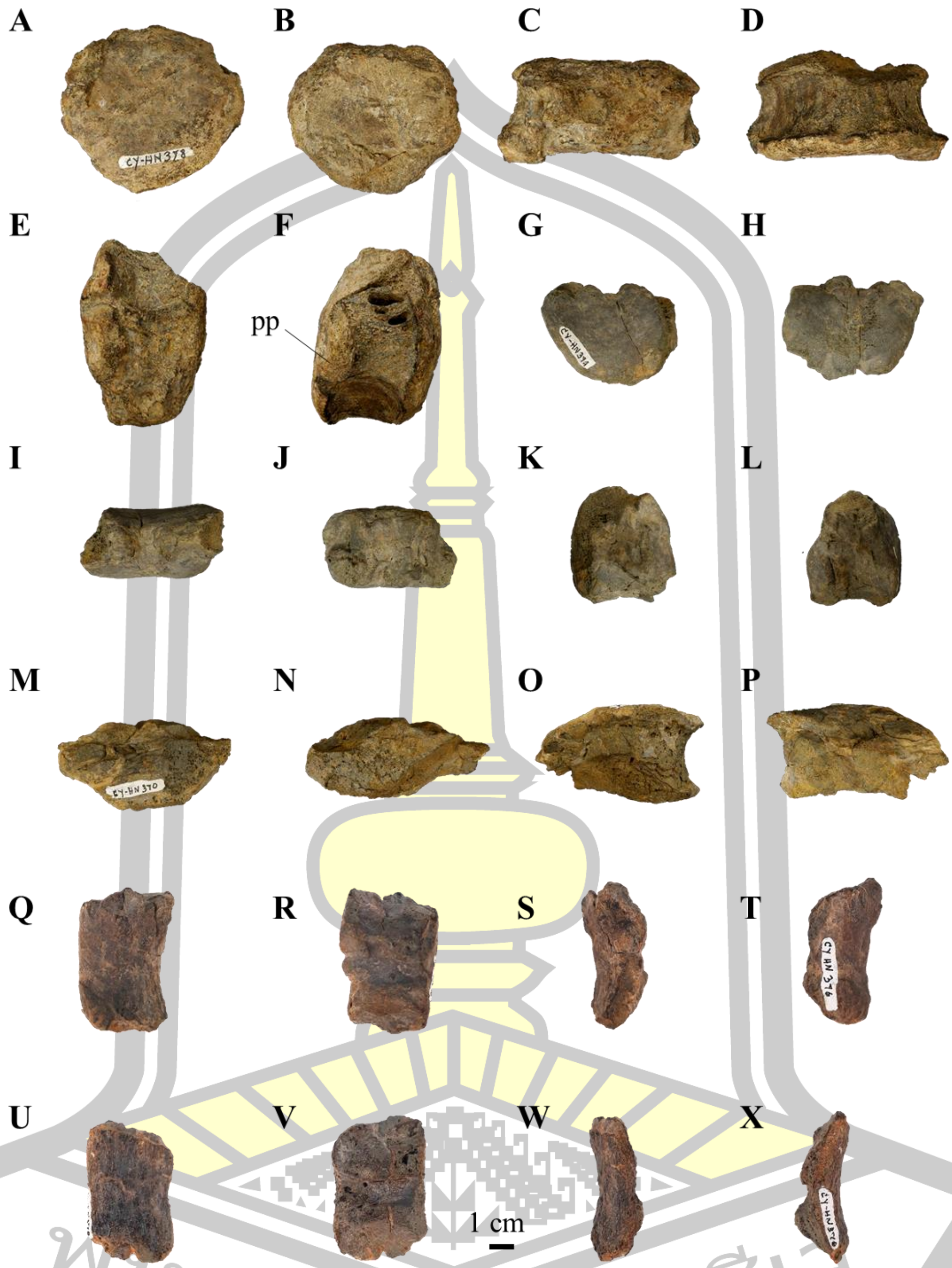

Figure 21 Metoposauroidea *fam*. *indet*. intercentra of the CY-HN 378 (A-F), and CY-HN 374 G-L), in anterior (A, G), posterior (B, H), dorsal (C, I), ventral (D, J), left (E, K), and right (F, L) views. The CY-HN 370 (M-P) in anterior or posterior (M-N), left, right (O-P) views. Neural arch of the CY-HN 376 (Q-T) and CY-HN 379 (U-X) in dorsal (Q, U), ventral (R, V), and lateral (S-T, W-X) views.

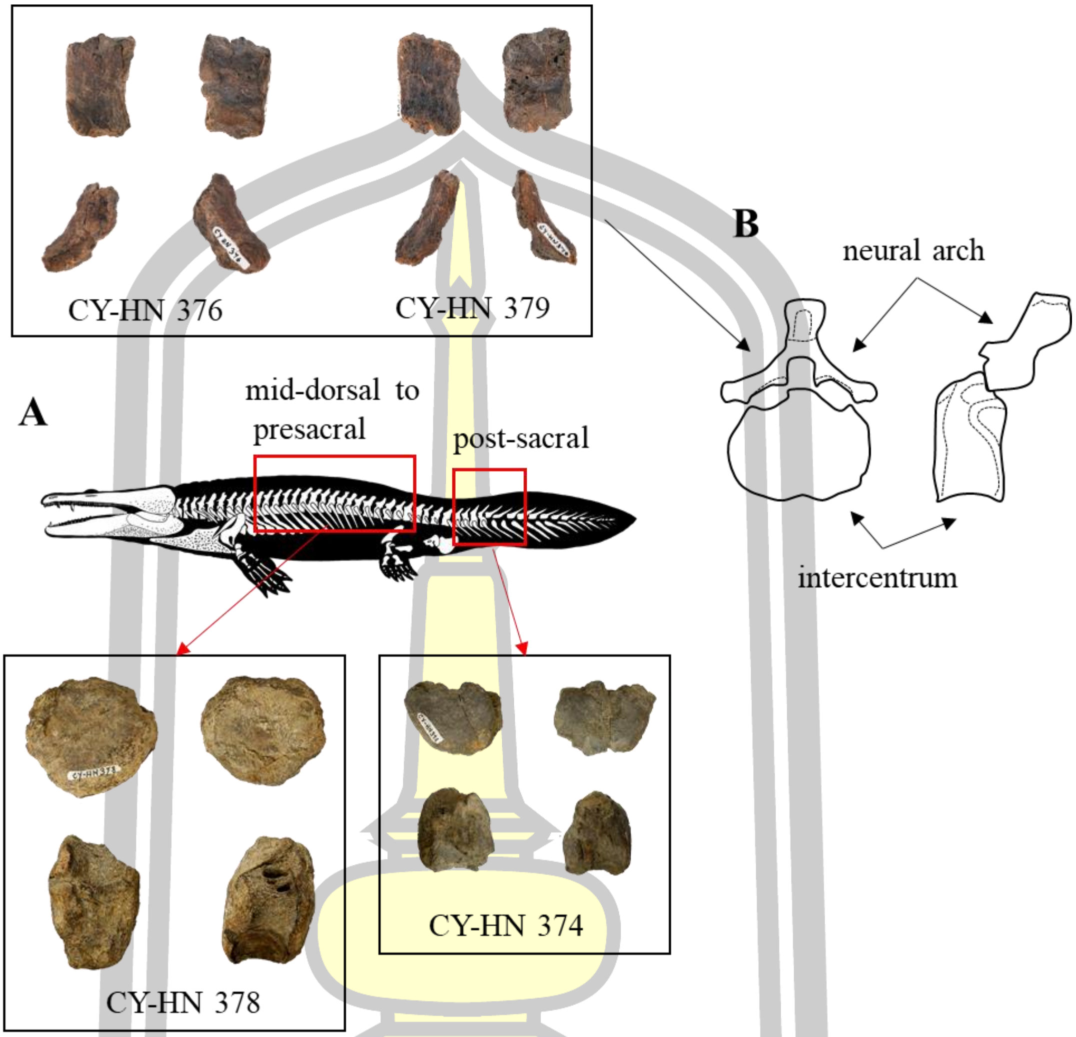

Figure 22 Skeleton reconstruction images (A) and vertebra out line (B, after Warren and Snell, 1991) of Metoposauroidea *fam. indet*. from Huai Nam Aun locality, which show the position of vertebra.

Dermal bone: a largest partial dermal bone, CY-HN 364 (Fig. 22 A-B) is preserved maximal width approximately 130 mm and 180 mm, and 33 mm thick. The specimen shows two distinct types of heavy ornamentation in ventral surface, i.e., radial and polygonal sculptures. The radial sculpture consists of parallel or radial ridges without transverse ridges, while the polygonal sculpture, located close to the lateral edge of the bone, consists of short ridges connected and forming polygons in a honeycomb or hexagonal shape. The dorsal surface is smooth with a part of the ascending process located along the lateral edge. The polygonal ornamentation located close to the lateral edge and the presence of an ascending process indicate that CY-HN 364 is a left clavicle bone.

CY-HN 365 (Fig. 22 C-D) and CY-HN 368 (Fig. 23 G-H) are dermal bones with shows radial and polygonal sculptures on the ventral surface. The dorsal surfaces are very smooth. CY-HN 365 is preserved maximal width approximately 70 mm and 130 mm and 23 mm thick, while CY-HN 368 is preserved maximal width approximately 53 mm and 92 mm and 21 mm thick. These specimens are presumably a part of interclavicle or clavicle bones in the center area.

CY-HN 454 (Fig. 23 I-J) is dermal bones with only show radial sculptures on the ventral surface. The dorsal surfaces are very smooth. CY-HN 454 is preserved maximal width approximately 57 mm and 121 mm and 22 mm thick. This specimen could be assigned as either interclavicle or clavicle bones.

CY-HN 349 (Fig. 23 E-F) and CY-HN 377 (Fig. 22 K-L) are cylindrical elongate dermal bones. The ventral surface only shows radial sculptures whereas the dorsal surfaces are smooth. CY-HN 377 is preserved maximal width approximately 44 mm and 102 mm and 22 mm thick. CY-HN 349 is preserved maximal width approximately 26 mm and 72 mm and 16 mm thick. These fragments are presumably a process of clavicle bones.

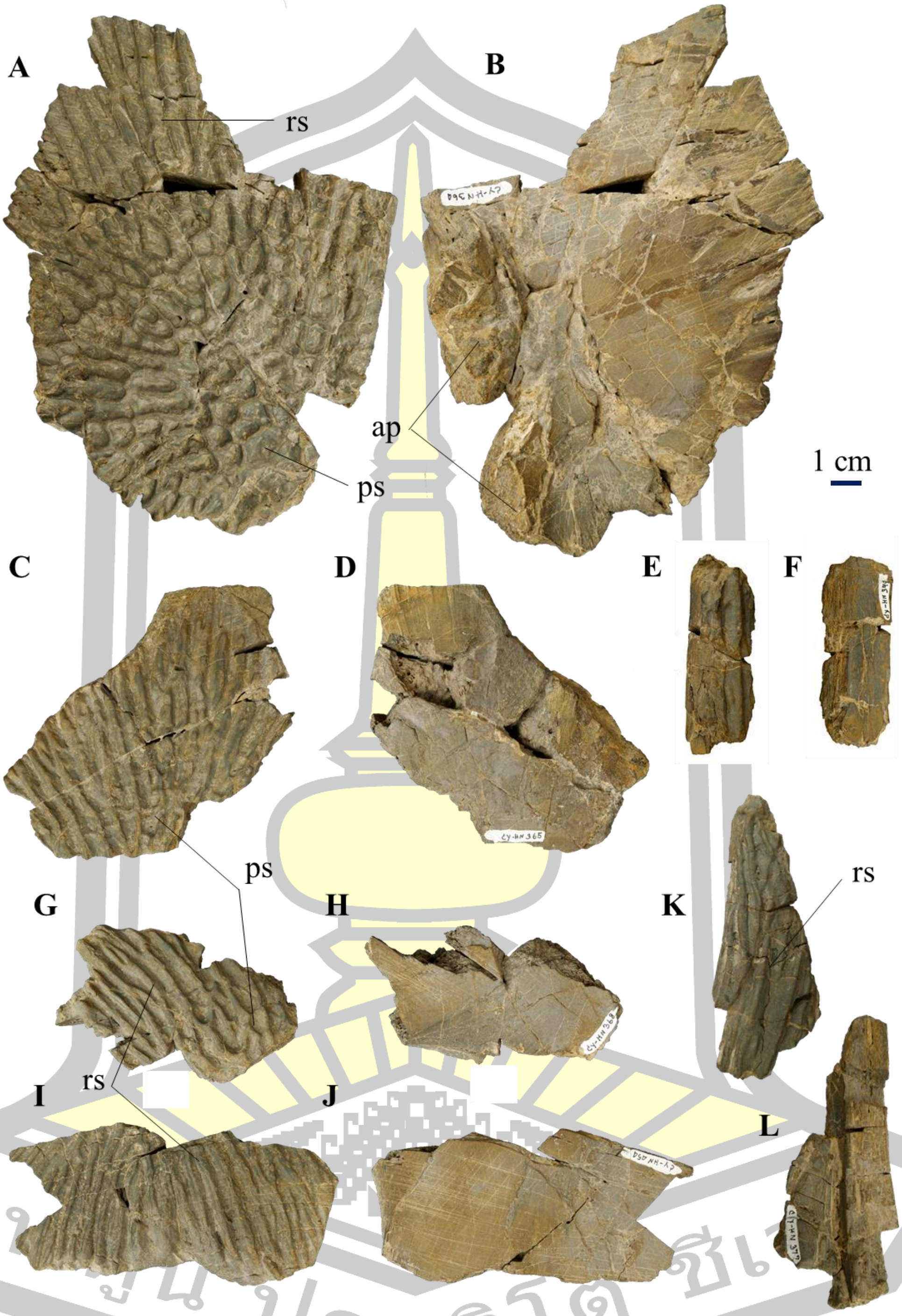

Figure 23 dermal bone fragments of Metoposauroidea *fam. indet*. of CY-HN 364 (A-B), CY-HN 365 (C-D), CY-HN 349 (E-F), CY-HN 368 (G-H), CY-HN 454 (I-J), and CY-HN 377 (K-L) in ventral view (A, C, E, G, I, K) and dorsal view (B, D, F, H, J, L).

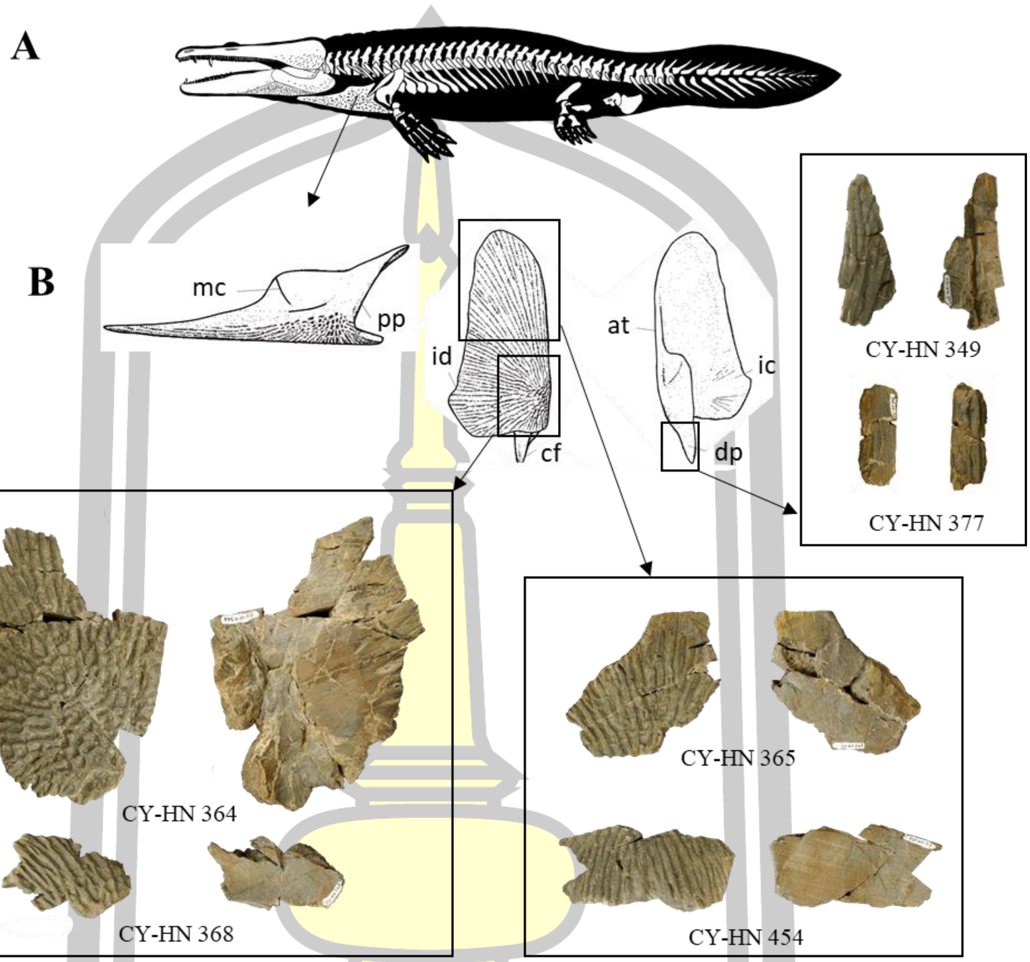

Figure 24 Skeleton reconstruction images (A) and clavicle bone out line (B, after Sulej, 2007) of Metoposauroidea *fam. indet.* from Huai Nam Aun locality.

Humerus: CY-HN 435 is a flat humerus and wide head, 141 mm long. At its narrowest point, in the middle of the shaft, it is 40 mm wide, whereas it has a maximum width of 64 mm at the distal end. In lateral view, the radial crest (rc) is centered along the shaft and expands from its proximal posterior edge to the distal anterior edge in a slight curve. The proximal end is blunt, with a maximum width of 44 mm. The anterior margin is concave and shows clear torsion. The deltopectoral crest (dc) forms the anterior edge and extends almost to the midshaft.

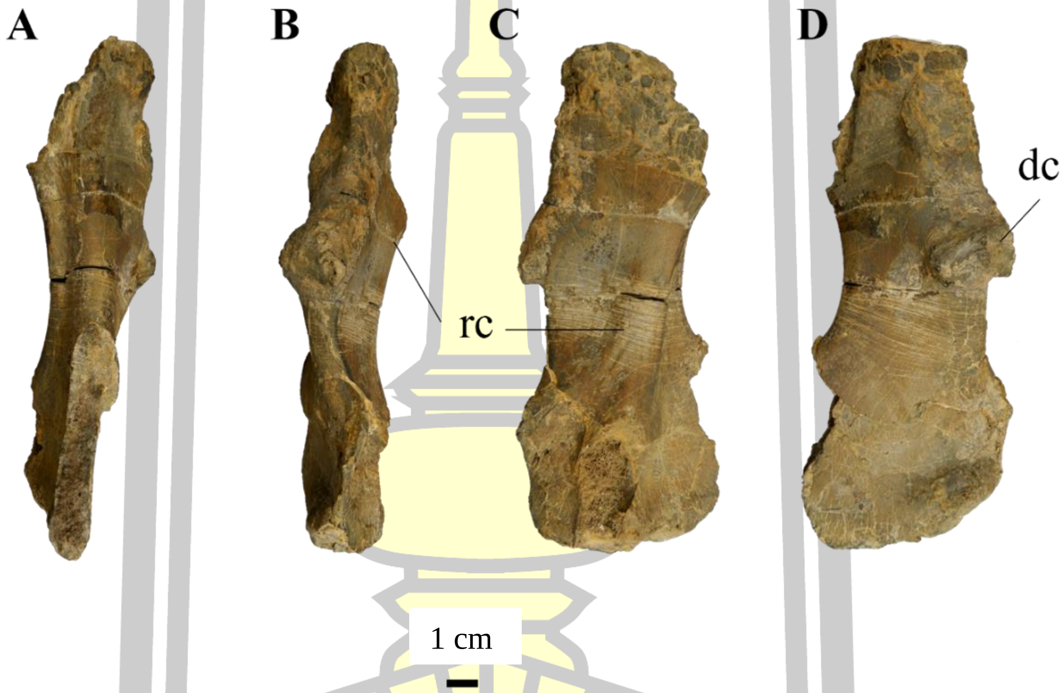

Figure 25 humerus fragments of Metoposauroidea *fam. indet*. (CY-HN 435) in anterior (A), posterior (B), and lateral (C-D) views.

Remark: The specimens were all fragmentary and unarticulated, but they were all collected in the same area. These are predicated on the assumption that all the specimens came from the same individual. All intercentra features share characters with Stereospondyli (Laojumpon et al., 2014; Milner et al., 1994; Witzmann and Gassner, 2008). The shape of CY-HN 378 is comparable to those of the Metoposauroidea or Mastodonsauroidea intercentrum (Dizik and Sulej, 2007; Fortuny et al., 2019; Marzola et al., 2017; Moser and Schoch, 2007). The Plagiosauroidea possesses cylindrical intercentra (Konietzko-Meier et al., 2014; Warren and Snell, 1991). The Brachyopoidea commonly show a wedge-shaped intercentrum in lateral view (Averianov et al., 2008; Shishkin, 1991; Warren et al., 1997; Warren and Damiani, 1999; Warren et al., 2011; Warren and Snell, 1991).

At first glance, the disk shape and circular periphery of CY-HN 378 resemble Metoposauroidea more than Mastodonsauroidea (Warren and Snell, 1991). However, recent studies indicated that the intercentra of both taxa are very similar in shape (Fortuny et al., 2019; Marzola et al., 2017; Moser and Schoch, 2007; Sulej, 2007). Therefore, it is difficult to assign the Thai intercentrum to a specific level. Based on dermal sculptures of clavicles (CY-HN 364, CY-HN 365, CY-HN 368, CY-HN 403, CY-HN 349. CY-HN 454, and CY-HN 377), consisting of polygonal and radial patterns are similar to the ornamentation observed in Metoposauroidea, e.g., *Metoposaurus algarvensis*, *Metoposaurus maleriensis*, and *Metoposaurus krasiejowensis* (Antczak and Bodzioch, 2018; Brusatte et al., 2015; Chowdhury, 1965) than a Mastodonsauroidea, e.g., *Cyclotosaurus intermedius* (Sulej and Majer, 2005) (Fig. 26). The stereospondyli material from Huai Nam Aun locality could potentially be Metoposauroidea.

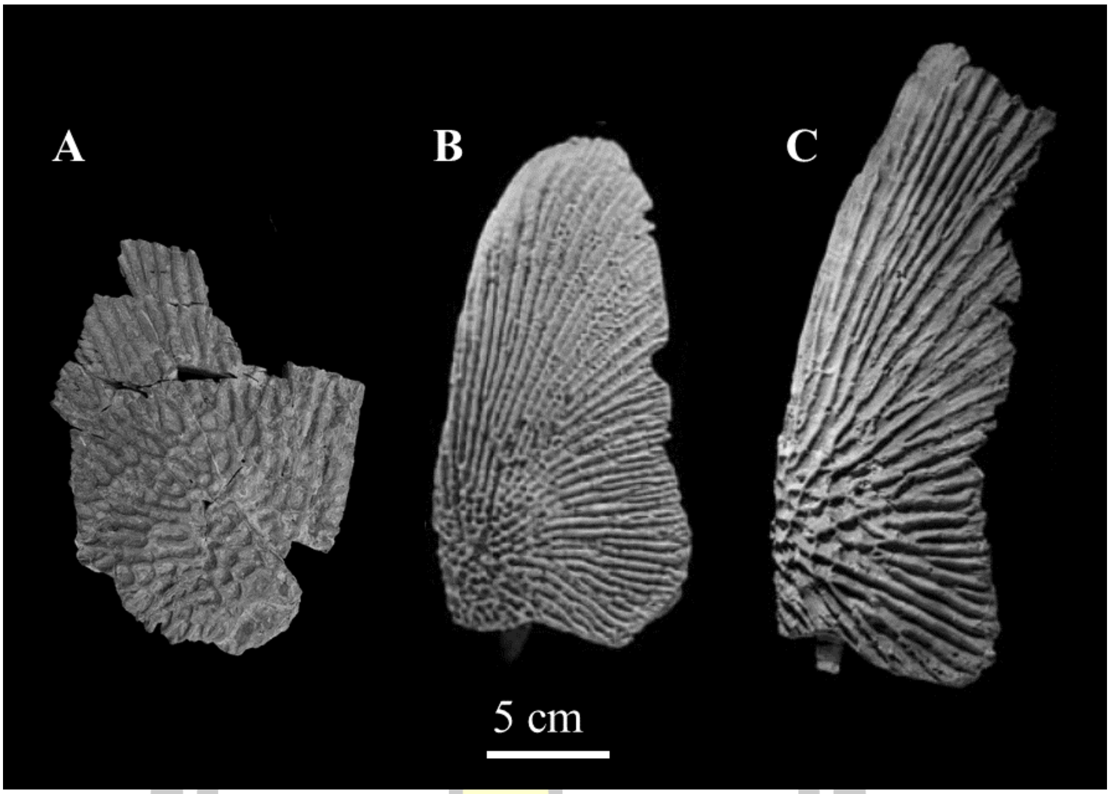

Figure 26 Temnospondyl clavicle in ventral view of Metoposauroidea *fam. indet.* from Huai Nam Aun locality (A), Metoposauroidea; *Metoposaurus* (B, modified from Sulej, 2007), Mastodonsauroidea; *Cyclotosaurus* (C, after Sulej and Majer, 2005)

The internal structure of the humerus (CY-HN 435) analysis using the Micro-CT-scanning method to determine the exact sectioning plane. the specimen was scanned with a high-resolution micro-computed tomography scanner. The humerus was scan of the mid-shaft region at a higher resolution in the horizontal plane at a slice thickness of 30.9 μm and contains 2,225 images. The micro-CT scan images allows interpretation of the different colors. The largest vascular canal area, with low density is black. Whereas the mineralized bone area, with high density is light grey.

The compact bone of humerus visible as light grey at outer zone. The black or low-density area is indicated spongy bone. In the material studied here, six annual growth cycles can be observed as a pattern of variable grey-scale layers in the cross-section of the humerus (Fig. 27).

An annual growth mark is typically composed of a zone, an annulus, and a Line of Arrested Growth (LAG). The presence of annual growth cycles implies that the present individual died in the sixth year of life.

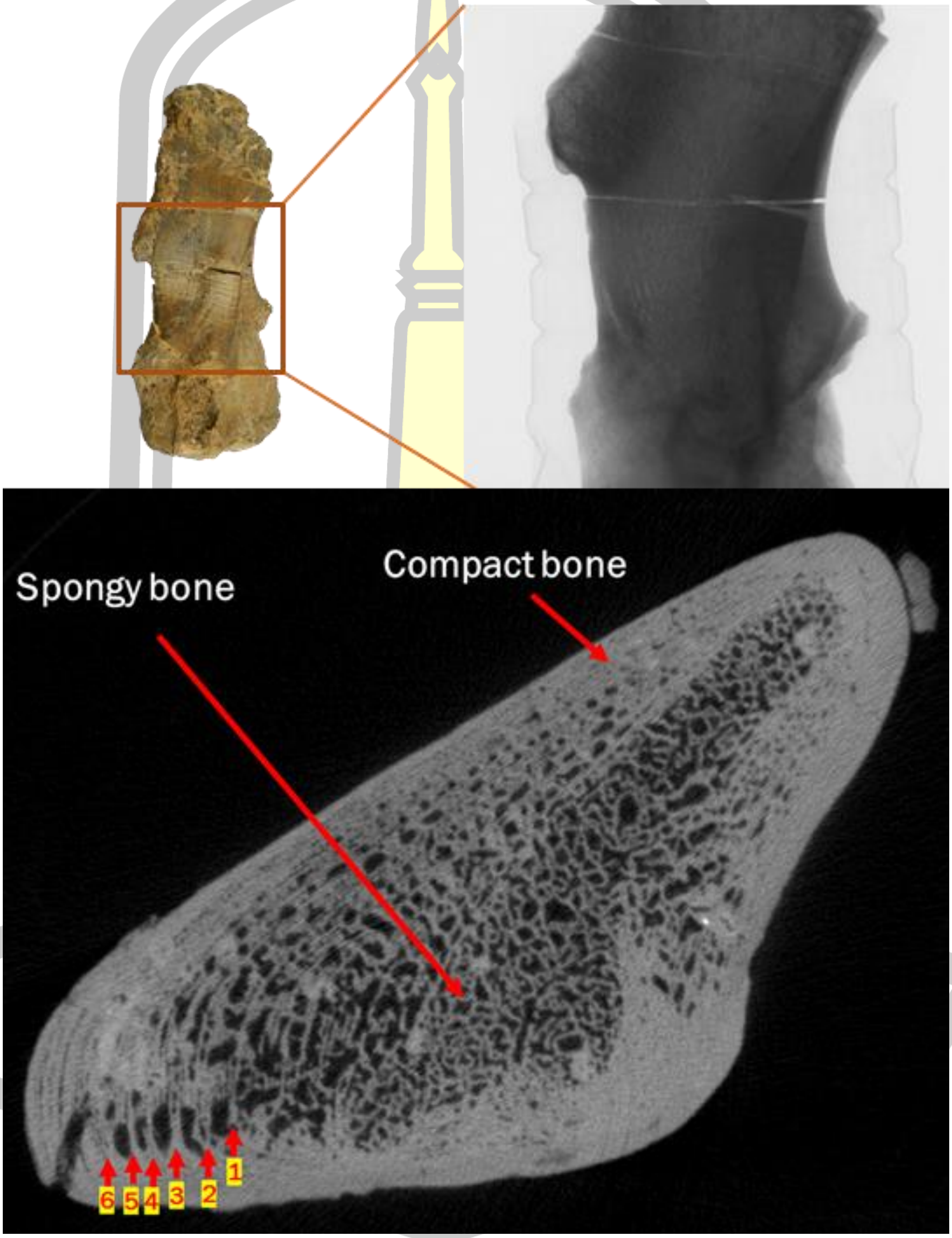

Figure 27 Micro-CT scan images of the Metoposauroidea indet. humerus from Huai Nam Aun locality in the horizontal plane at a mid-shaft region.

4.1.2 Systematic description of Triassic amphibians

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Brachyopoidea Lydekker, 1885

Brachyopoidea *gen. et sp. indet.* (Family: Brachyopidae or Chigutisauridae)

Occurrence: Mab Ching locality, Nakhon Sri Thamarat province.

Formation/age: Klong Min Formation (Middle or Upper Jurassic)

Reference material: Intercentra; TF 3328, TF 3329 (Buffetaut et al., 1994b), MC 233, and MC 234

Description: TF 3328, TF 3329, MC 233, and MC 234 (Fig. 28) are wedge-shaped intercentrum, both anterior and posterior surfaces show a marked circular notochordal canal. The posterior surfaces concave more than anterior surfaces. The ventral surface is concave. In the lateral view, the parapophysis marks are large and located in the posterodorsal.

TF 3329 is a wedge-shaped intercentrum, smaller than TF 3328 (14 mm width, 16 mm high, and 11 mm thick). The anterior and posterior surfaces are concave. Both of anterior and posterior surfaces show very clear a marked circular notochordal canal, which is visible as a circular pit. The ventral surface is concave. In the lateral view, parapophysis marks are very well preserved and located in posterodorsal.

Remark: The pleurocentra are reduced or absent, which is a typical feature of stereospondyls (Milner et al., 1994; Witzmann and Gassner, 2008). The wedge-shaped morphology and the notochordal pit of the intercentra (TF 3328, TF 3329, MC 233, and MC 234) are consistent with the intercentrum morphology of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997, 2011; Warren and Damiani, 1999), which are similar to the intercentra discovered from the Jurassic Indochina block, e.g., *Gobiops desertus* from the Gobi Desert of Mongolia (Shishkin, 1991).

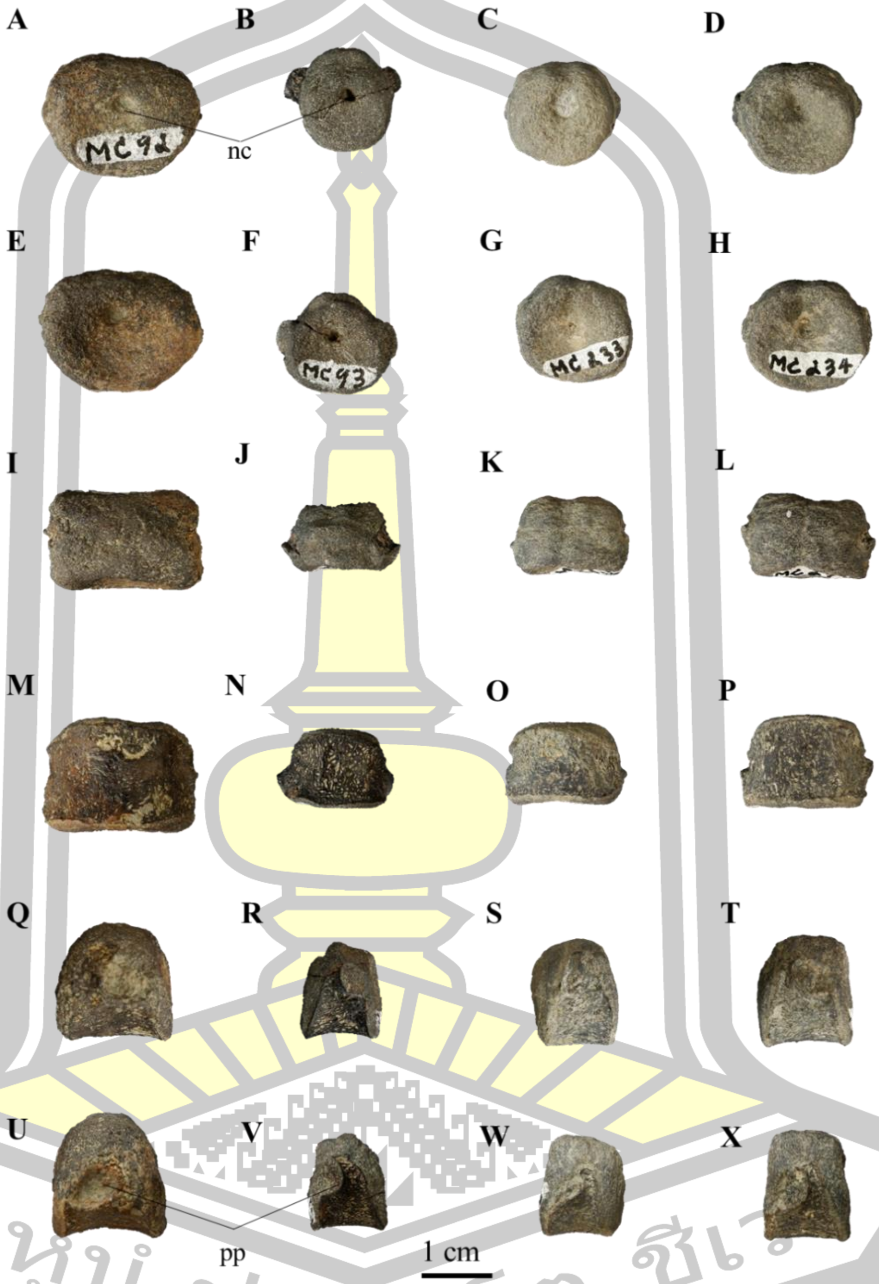

Figure 28 Thai Brachyopoidea *gen. et sp. indet*. intercentra from Mab Ching locality, 3328 (A, E, I, M, O, U), TF 3329 (B, F, J, N, R, V), MC 233 (C, G, K, O, S, W), MC 234 (D, H, L, P, T, X) in anterior (A-D), posterior (E-H), dorsal (I-L), ventral (M-P), left (Q-T), and right views (U-X).

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Brachyopoidea Lydekker, 1885

Brachyopoidea *gen. et sp. indet*. (Family: Brachyopidae or Chigutisauridae)

Occurrence: The road cut locality in Highway 12 from Chum Phae to Lom Sak, Khon Kean province and the Khao Wong locality, Kalasin province.

Formation/age: Phu Kradung Formation (Upper Jurassic)

Reference material: TF 3144 (Buffetaut et al., 1994a), KS37-8 (Nonsrirach et al., 2021)

Description: The intercentra from Highway 12 locality: TF 3144 (Fig. 29) is wedge-shaped intercentra. The anterior surface is very slightly convex, the posterior is concave. the anterior and posterior surfaces show a notochordal canal, visible as a deep circular pit. In the lateral view, parapophysis is visible in the posterodorsal position.

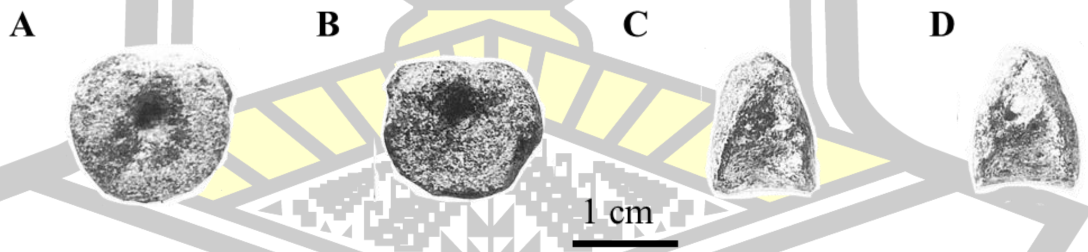

Figure 29 An intercentrum of Brachyopoidea *gen. et sp. indet*. (TF 3144) in anterior (A), posterior (B), left (C), and right (D) after Buffetaut et al., 1994a; fig. 1).

Remark: This vertebrate shares a common character with stereospondyls (Milner et al., 1994; Witzmann and Gassner, 2008). The wedge-shaped morphology and the notochordal pit of TF 3144 are consistent with the intercentrum morphology of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997, 2011; Warren and Damiani, 1999), which very closely resemble the truck intercentra of the brachyopid *Gobiops desertus* described by Shishkin, (1991) from the Upper Jurassic of the Gobi Desert.

The intercentra from Khao Wong locality: KS37-8 (Fig. 30) is a wedge-shaped intercentrum with a dorsal edge much shorter than the ventral edge. It preserved about 13 mm width, 12 mm high and 11 mm thick. The parapophysis is close to the posterodorsal margin on the lateral surface. Both anterior and posterior surfaces are concave and show a marked circular notochordal canal, which is visible as a circular pit. The surface dorsal shows a suture along from anterior to anterior.

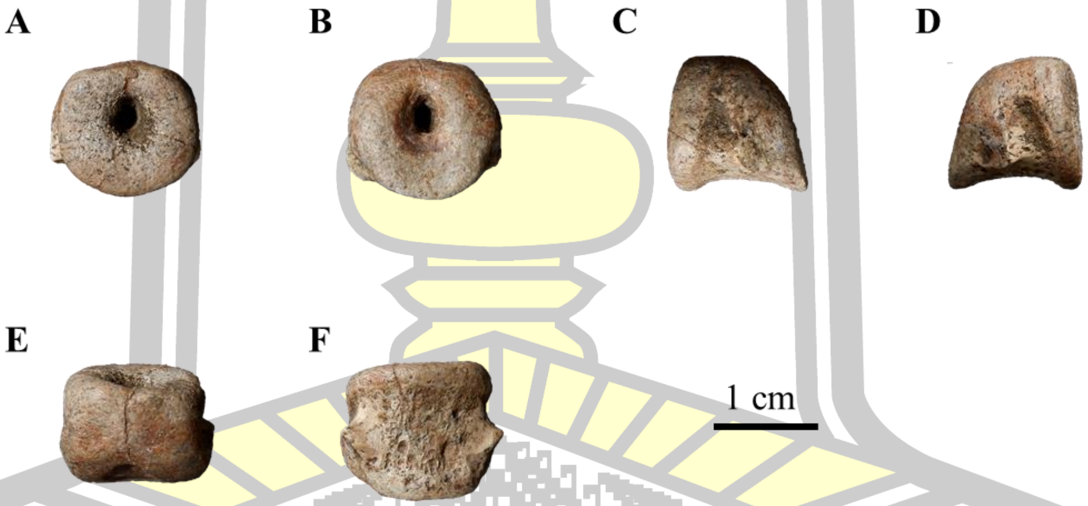

Figure 30 An intercentrum of Brachyopoidea *gen. et sp. indet.* (KS37-8) in anterior (A), posterior (B), left (C), right (D), dorsal (E), and ventral views (F).

Remark: This intercentrum KS37-8 probably belongs to Brachyopoidea since it is the only Stereospondyli superfamily retrieved beyond the Triassic (Buffetaut et al., 1994b). Furthermore, the wedge-shaped morphology of KS37-8 resembles the intercentra of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997, 2011; Warren and Damiani, 1999), which are similar to the intercentra discovered from the Indochina block (TF 3144) and Sibumasu blocks (TF 3328 and TF 3329) of Thailand (Buffetaut et al., 1994a, c). However, the intercentrum is not sufficiently diagnostic for identification at the family level.

Order: Temnospondyli Zittel, 1888

Suborder: Stereospondyli Zittel, 1888

Superfamily: Brachyopoidea Lydekker, 1885

Family: Brachyopidae

Brachyopidae *gen. et sp. indet.*

Occurrence: Phu Noi locality, Kalasin province

Formation/age: Phu Kradung Formation (Upper Jurassic)

Reference material: Posterior part of a skull; KS34-1481

Intercentrum; KS34-1471, KS34-1472, KS34-1473, KS34-1474, KS34-1476, KS34-1477, KS34-1478, KS34-1479, KS34-1480, KS34-1482, KS34-1483, KS34-14784, KS34-1485, KS34-1486, KS34-1489, KS34-2192, KS34-2871, KS34-3270, PN-710, PN-712, PN-723, PN 17-75

Description: Intercentra: all the investigated intercentra differ in size and shape, with can be divided into three morphotypes (Fig. 31).

Table 4 Three different morphotypes of intercentra from Phu Noi locality

Morphotype	Morphology	Position	intercentra
I	Amphicoelous with wedge shape in lateral view	dorsal	18
II	Amphicoelous with extremely elongate	anterior caudal	2
III	Amphicoelous with strongly convex ventral surface	posterior caudal	2

Intercentra morphotype I

Reference material: KS34-1471, KS34-1472, KS34-1473, KS34-1474, KS34-1476, KS34-1477, KS34-1478, KS34-1479, KS34-1482, KS34-1483, KS34-14784, KS34-1486, KS34-1489, KS34-2192, PN-710, PN 17-75, PN-723, KS34-3270 (Fig. 32-36)

The intercentra are amphicoelous and wedge-shaped with have a rim around the parapophysis on the lateral surface. The parapophysis is situated close to the posterodorsal margin and slightly higher than halfway up the lateral surface of the intercentra. The notochordal pits are found on both anterior and posterior surfaces, situated slightly above the center of the bone. The ventral surface is smooth and concave.

Intercentra morphotype II

Reference material: KS34-1480, KS34-1485 (Fig. 37)

The intercentra are also wedged shape outlines but are extremely elongate in lateral view. Both anterior and posterior surfaces are concave and present a notochordal pit. The dorsal surface is convex, and the ventral surface is almost flattened. The parapophysis marks are situated slightly lower than halfway up the lateral surface of the bone.

Intercentra morphotype III

Reference material: KS34-2871, PN-712 (Fig. 38)

This morphotype is a very small intercentra. Both anterior and posterior surfaces are concave and present notochordal pit. There are strongly convex ventral surfaces and lack of parapophysis marks on the lateral surface.

All the observed specimens are typically stereospondylous intercentra. Stereospondylous intercentra are commonly present in the Metoposauridae, Mastodonsauridae, Plagiosauridae, and Brachyopoidea. The intercentra from Phu Noi locality are very similar to those the brachyopid in their general shape, especially in that the wedge-shape outline and notochordal canal (Wang et al., 2006; Warren et al., 1997, 2011) e.g. *Gobiops desertus* Shishkin, 1991. The exact position of intercentra from the Phu Noi locality is difficult to determine because there are not aculeated. However, the vertebra has a different form in each position. Based on the wedge shape and parapophysis position of the intercentra morphotype I are indicating that there are probably from the middle dorsal region. Morphotype II are probably anterior caudal because of their ventral flattened and the presence of parapophysis marks which are lost in more posterior caudal. Morphotype III could represent posterior caudal intercentra because of their ventral convex.

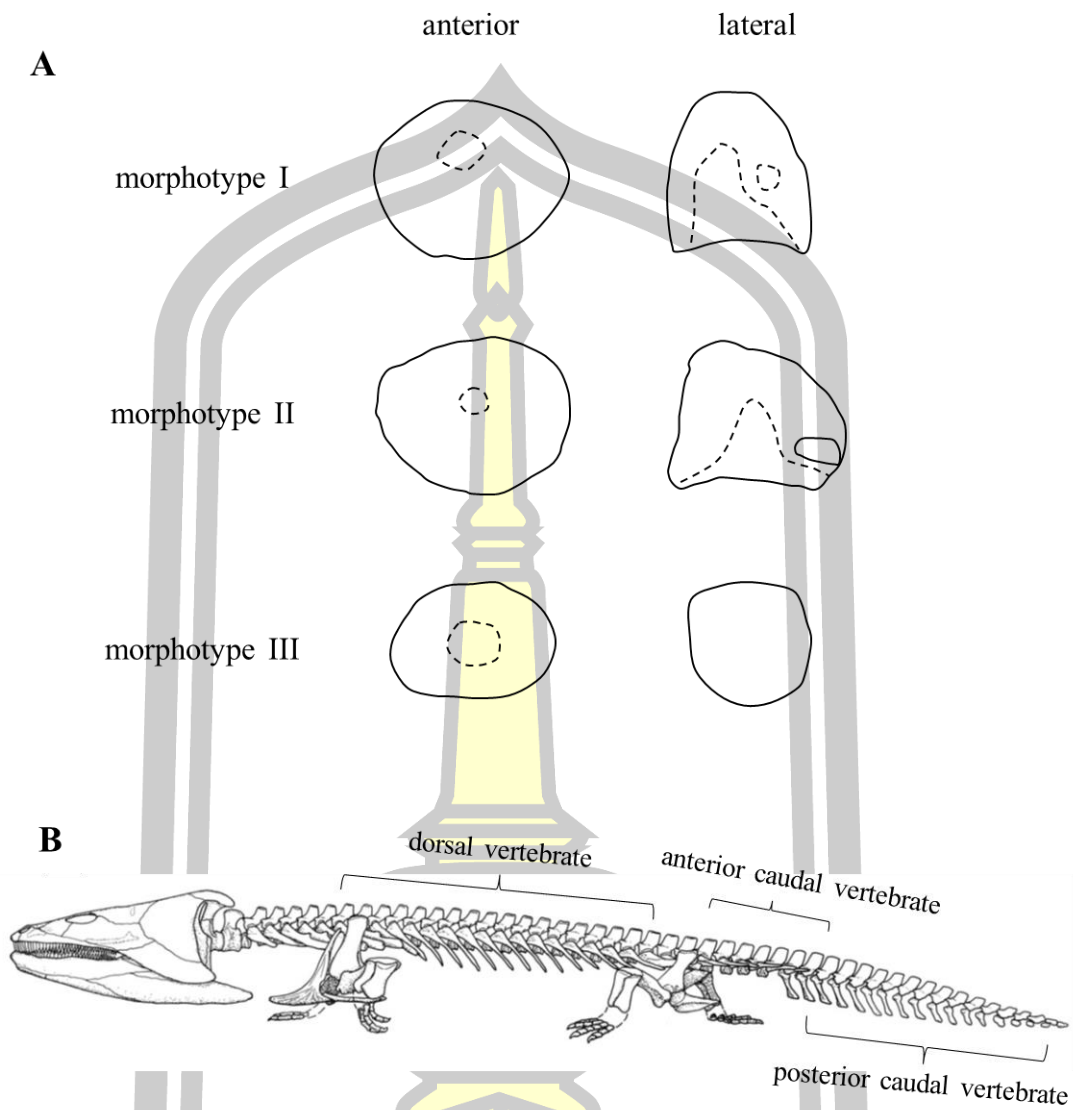

Figure 31 Three different morphotypes of intercentra from Phu Noi locality (A). Brachyopoidea skeletal reconstruction in lateral (B) view (after Warren and Hutchinson 1983).

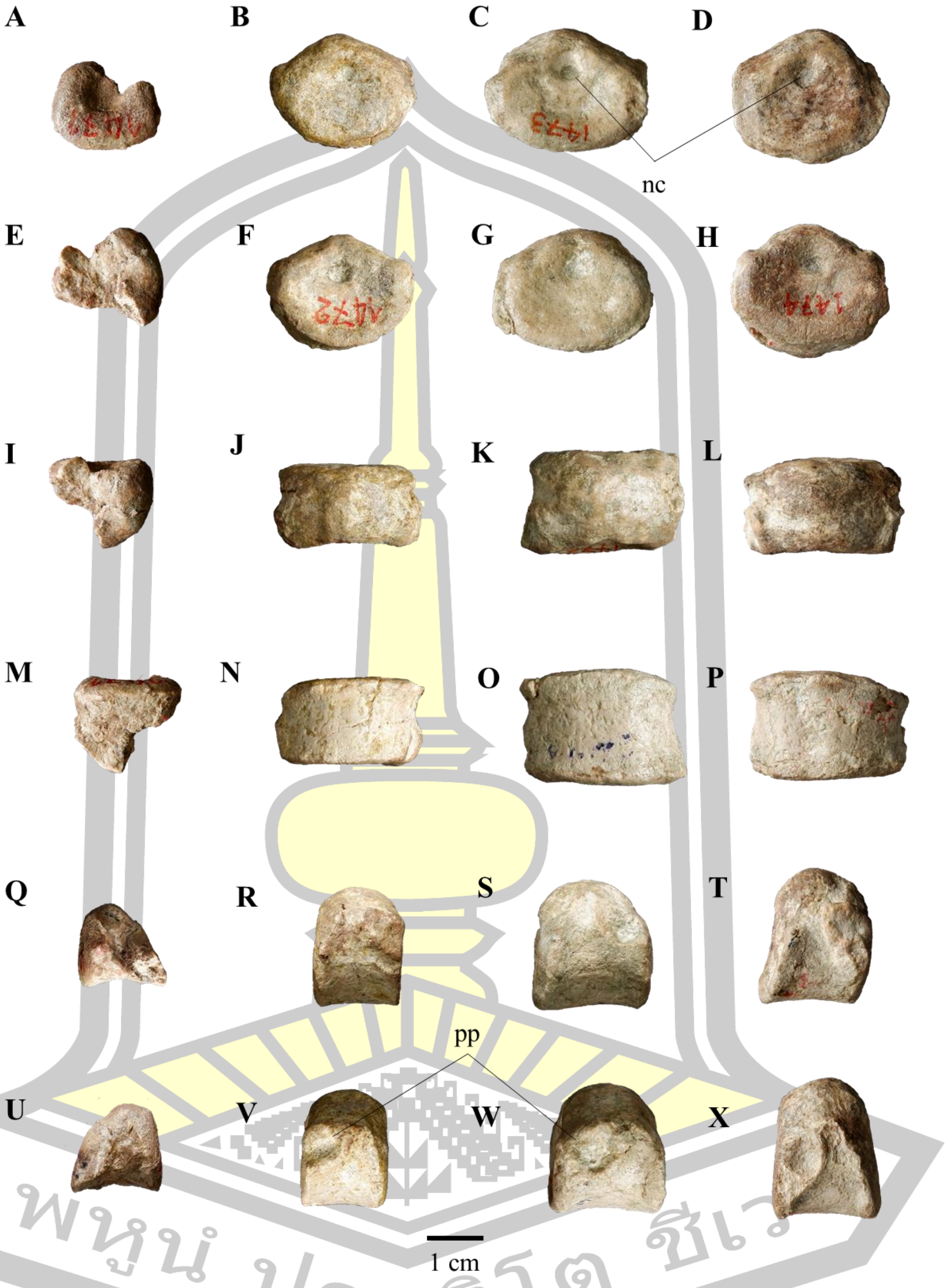

Figure 32 Brachyopoidea *gen. et sp. indet*. intercentra morphotype I, KS34-1471 (A, E, I, M, O, U), KS34-1472 (B, F, J, N, R, V), KS34-1473 (C, G, K, O, S, W), KS34-1474 (D, H, L, P, T, X) in anterior (A-D), posterior (E-H), dorsal (I-L), ventral (M-P), left (Q-T), and right views (U-X).

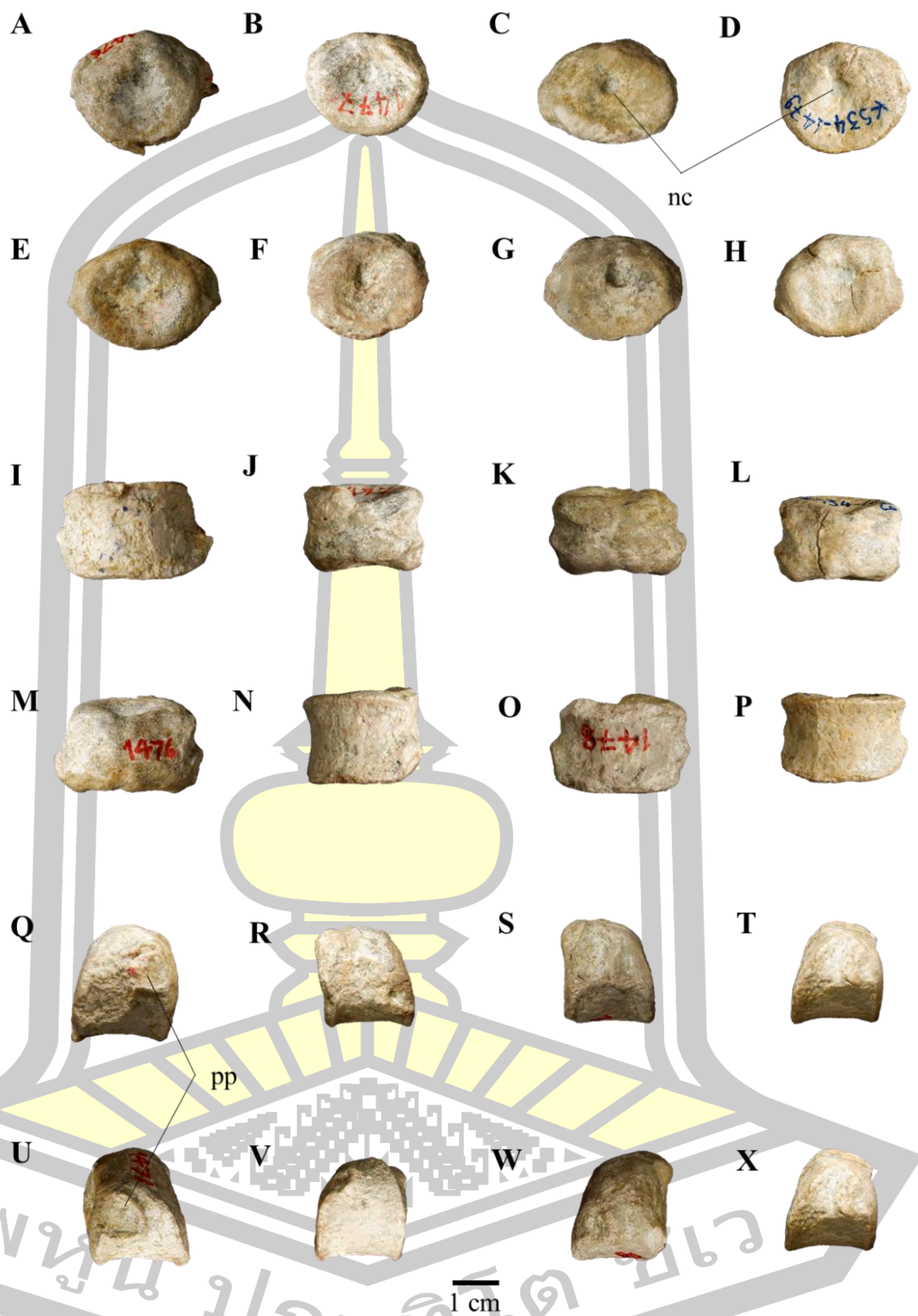

Figure 33 Thai Brachyopoidea *gen. et sp. indet*. intercentra morphotype I, KS34-1476 (A, E, I, M, O, U), KS34-1477 (B, F, J, N, R, V), KS34-1478 (C, G, K, O, S, W), KS34-1479 (D, H, L, P, T, X) in anterior (A-D), posterior (E-H), dorsal (I-L), ventral (M-P), left (Q-T), and right views (U-X).

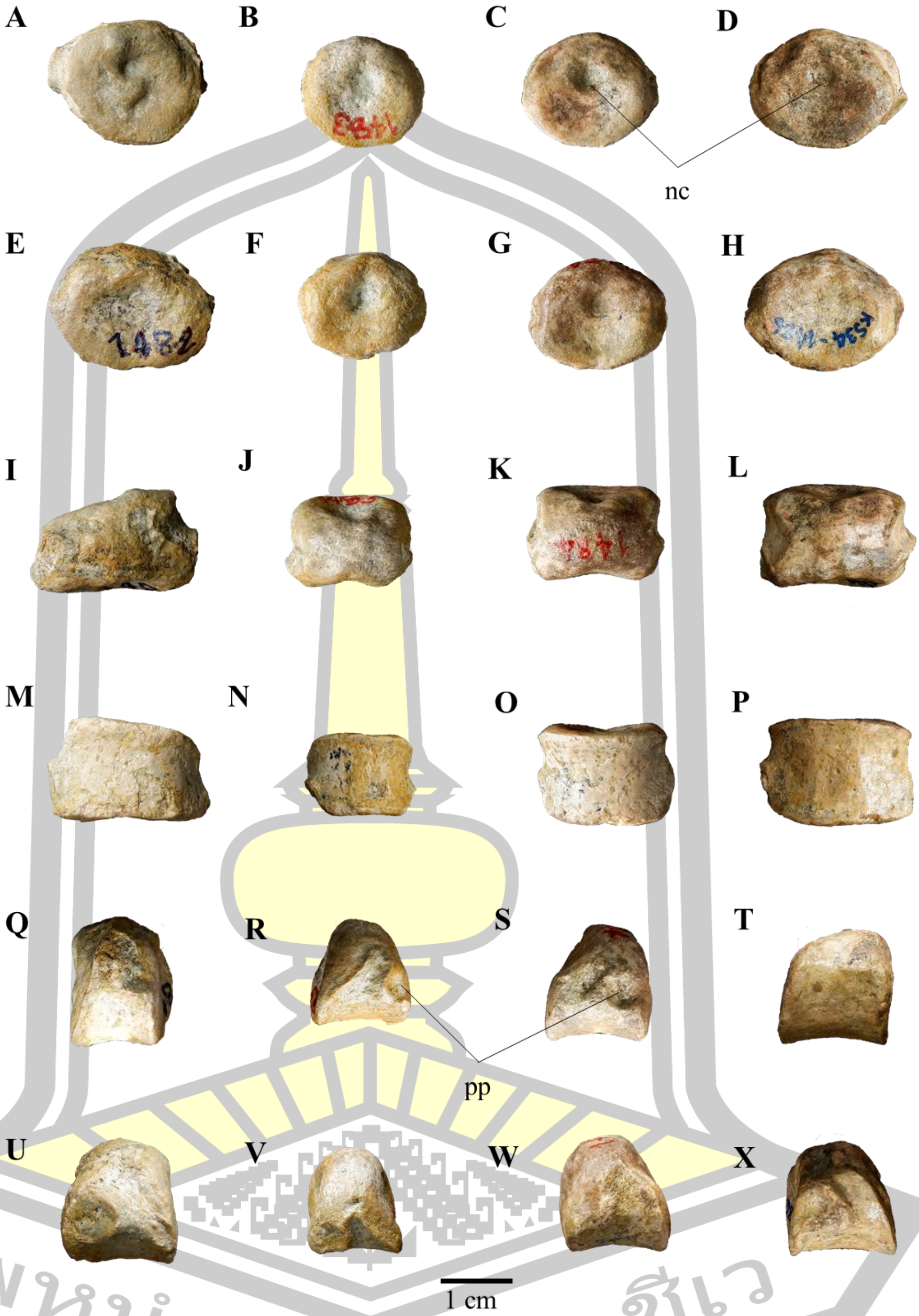

Figure 34 Thai Brachyopoidea gen. et sp. indet. intercentra morphotype I, KS34-1482 (A, E, I, M, O, U), KS34-1483 (B, F, J, N, R, V), KS34-14784 (C, G, K, O, S, W), KS34-1486 (D, H, L, P, T, X) in anterior (A-D), posterior (E-H), dorsal (I-L), ventral(M-P), left (Q-T), and right views (U-X).

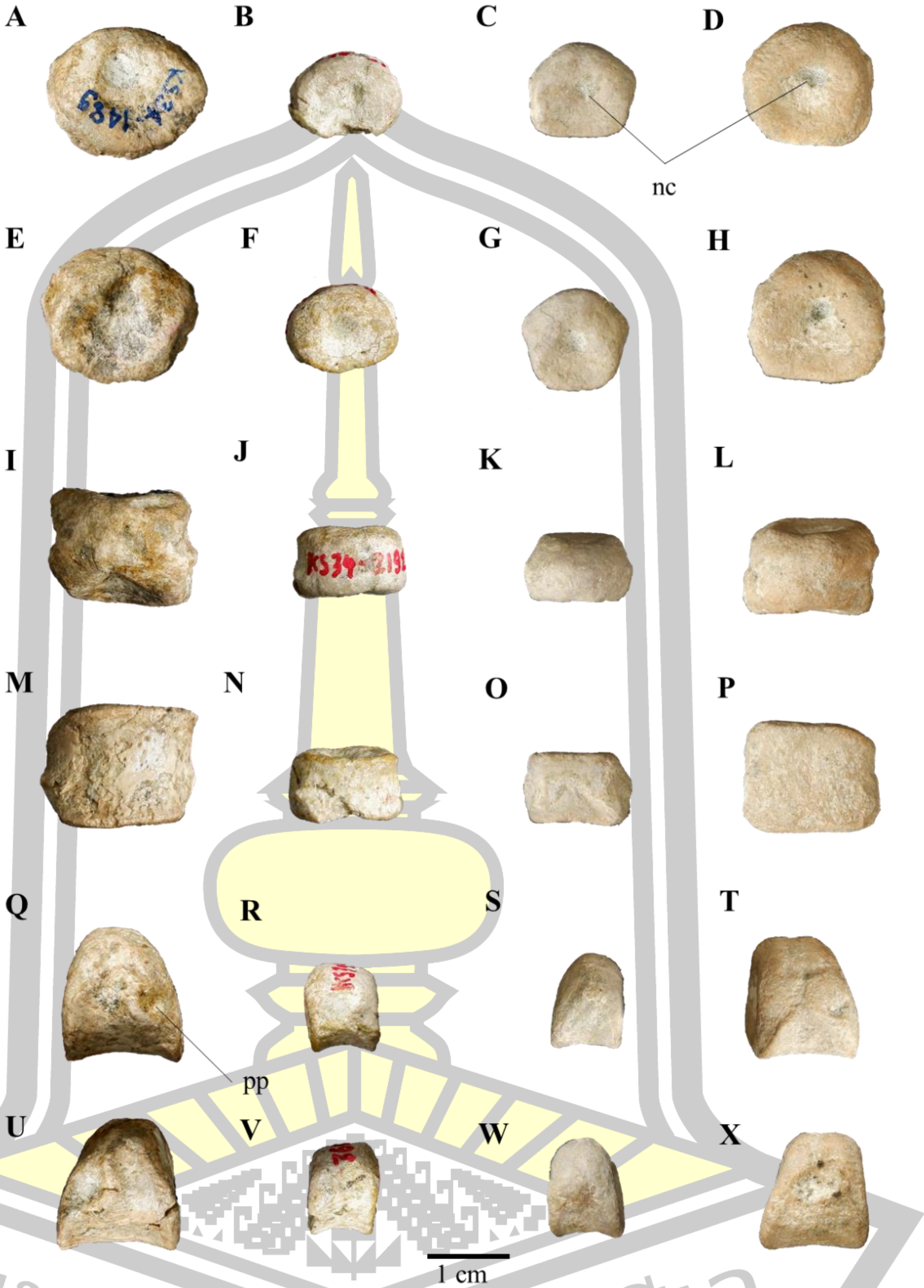

Figure 35 Thai Brachyopoidea *gen. et sp. indet*. intercentra morphotype I, KS34-1489 (A, E, I, M, O, U), KS34-2192 (B, F, J, N, R, V), PN-710 (C, G, K, O, S, W), PN 17-75 (D, H, L, P, T, X) in anterior (A-D), posterior (E-H), dorsal (I-L), ventral (M-P), left (Q-T), and right views (U-X).

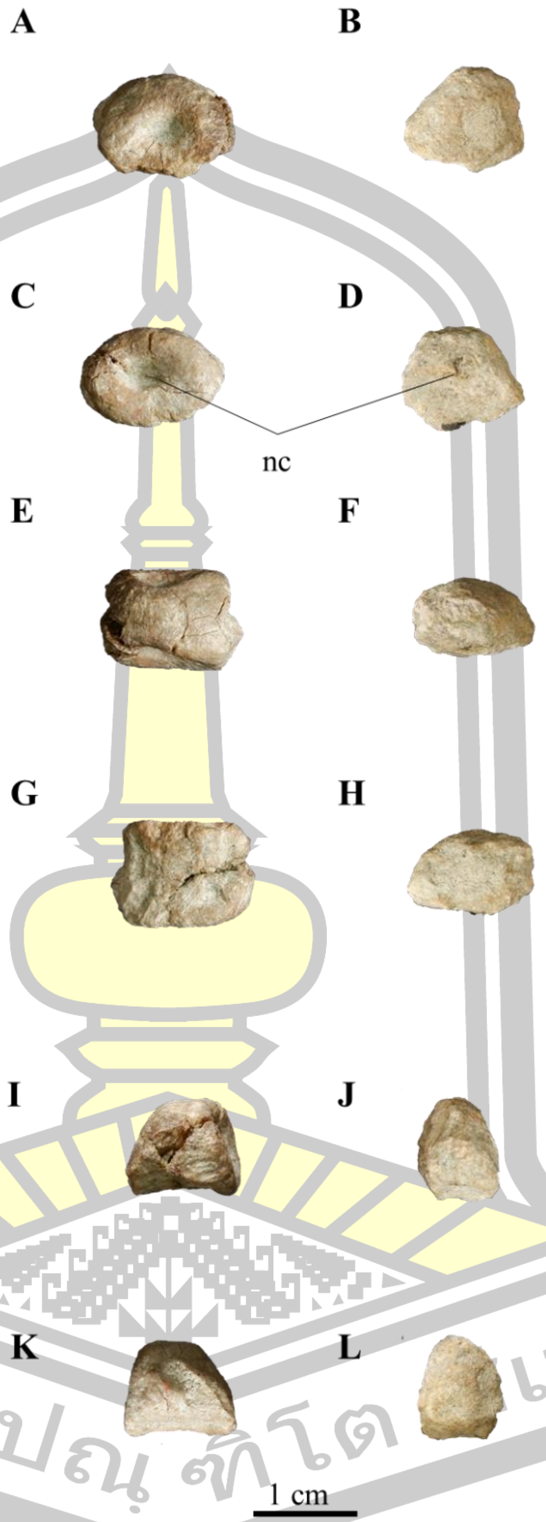

Figure 36 Thai Brachyopoidea *gen. et sp. indet*. intercentra morphotype I, KS34-3270 (A, C, E, G, I, K), PN-712 (B, D, F, H, J, L) in anterior (A-B), posterior (C-D), dorsal (E-F), ventral (G-H), left (I-J), and right views (K-L).

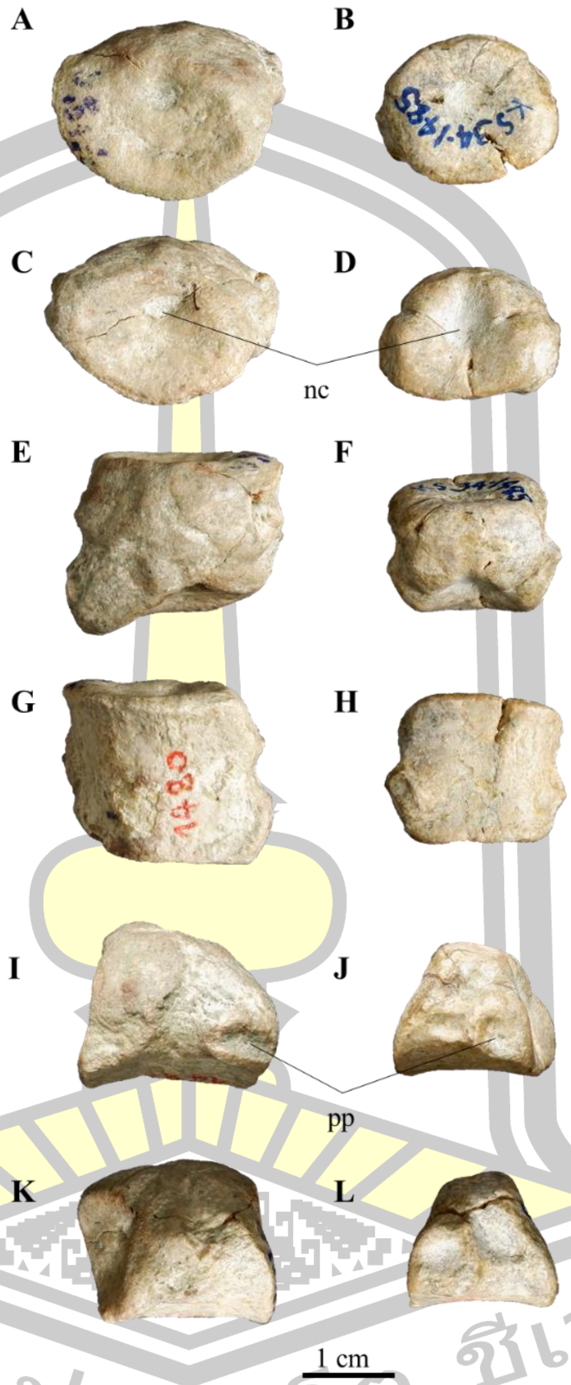

Figure 37 Thai Brachyopoidea *gen. et sp. indet*. intercentra morphotype II, KS34-1480 (A, C, E, G, I, K), KS34-1485 (B, D, F, H, J, L) in anterior (A-B), posterior (C-D), dorsal (E-F), ventral (G-H), left (I-J), and right views (K-L).

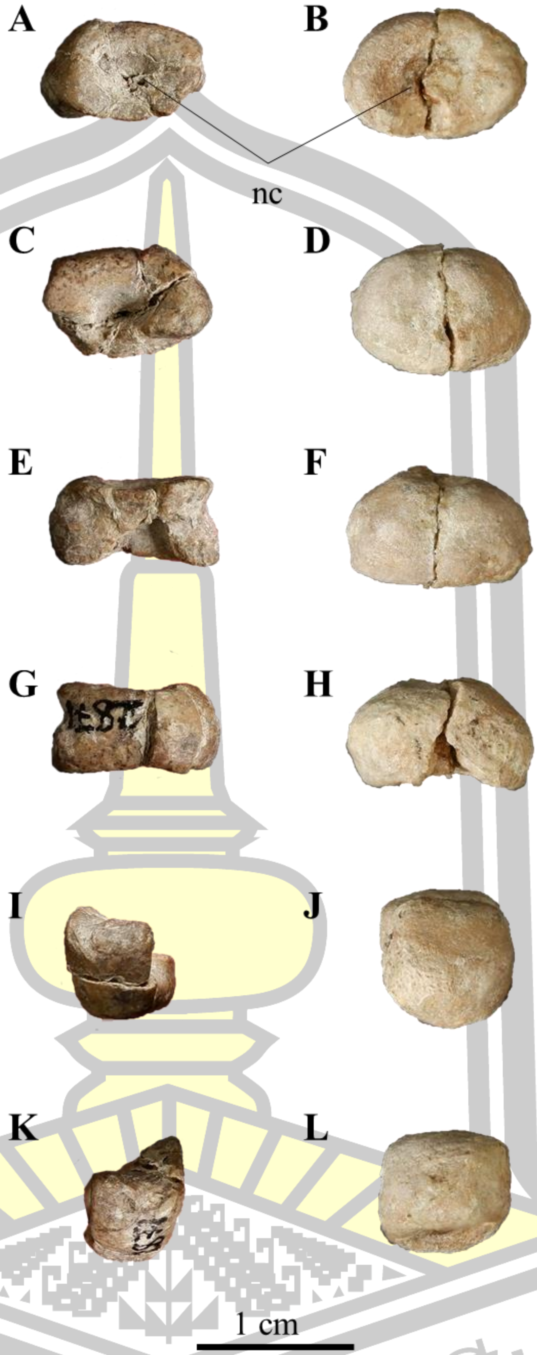

Figure 38 Thai Brachyopoidea *gen. et sp. indet*. intercentra morphotype III, KS34-1471 (A, C, E, G, I, K), KS34-2871 (B, D, F, H, J, L) in anterior (A-B), posterior (C-D), dorsal (E-F), ventral (G-H), left (I-J), and right views (K-L).

The skull (KS34-1481, Fig. 39) is incomplete poster dorsal especially on the right side, while its anterior part is also missing. The anterior skull is broken on a line from midway along with the left orbit position to the right squamosal. The specimen is short (approximately 14 cm width and 12 cm length), with large orbits. The dorsal surface of the skull has a pattern of radiating reticulate ornamentation typical of the labyrinthodont amphibians. The suture line and sensory canal are not clearly observable because of this obscurity by the cranial ornamentation. The skull roof lacks post squamosal process, post quadratojugal process, and post postparietal process. The posterolateral margin of the skull sloping forward.

In ventral view, the right and subtemporal fossa pterygoid is not preserved but could be reconstructed based on the left side. Body of the pterygoid and quadrate ramus of the pterygoid form a sharp edge on the occiput. The lateral border of the pterygoid beside the subtemporal vacuity concave so that the subtemporal vacuity is wide. The pterygoid quadrate ramus sharply downturned (inverted U-shaped palate). The subtemporal vacuity extends anteriorly further than the midpoint of the interpterygoid vacuity. The posterior process on the margin of the medial part of the quadrate ramus of the pterygoid is present. The pterygoid-exoccipital suture are present. The cultriform process of parasphenoid narrow and flat. The corpus of the parasphenoid antero-posteriorly nearly as long as wide. The quadrate condyle double with the two parts subequal in size. The paraquadrate foramen present on occipital portion of quadratojugal.

In the posterior view, the skull is slightly flat because it is compressed. Both a tabular horn and otic notch are absent in the supratemporal region. The exoccipital condyles rounded and held on a short stalk. The exoccipitals contact on the palate suture in the midline, which projected well behind the posterior edge of the skull.

The short skull, which lacks an otic notch and tabular horn, and the position of occipital condyles are typical characters of Brachyopidae (Warren and Marsicano, 1988, 2000), similar to those of the Jurassic brachyopid temnospondyl skull from China such as *Sinobrachyops placenticephalus* (Dong, 1985).

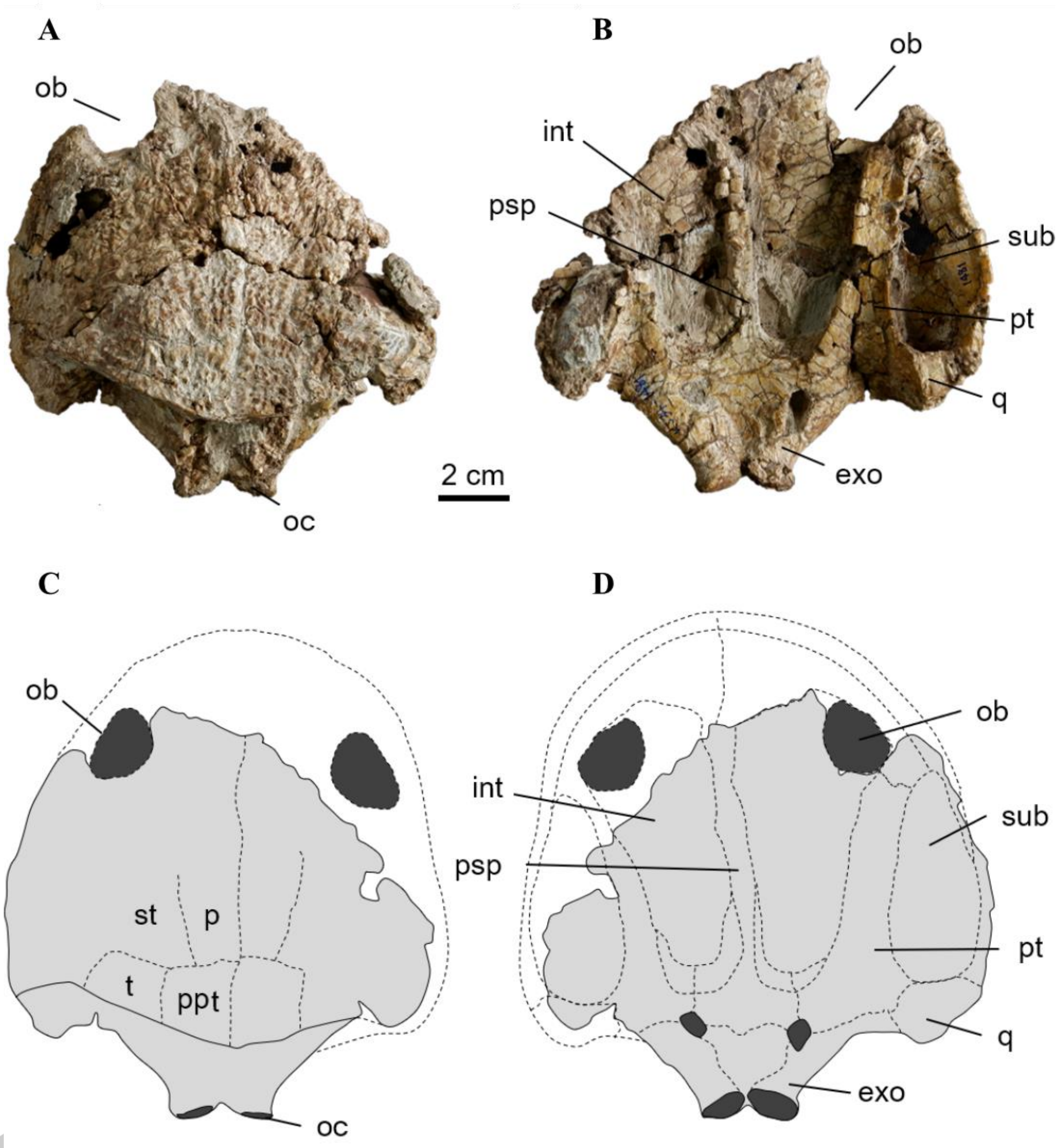

Figure 39 Brachyopidae *gen. et sp. indet.* skull (KS34-1481) from Phu Noi locality, in dorsal (A) and palatal views (B). Reconstruction outline of KS34-1481 (estimate reconstruction outline of the anterior part based on *Sinobrachyops placenticephalus* Dong, 1985) in dorsal (C) and palatal views (D).

Preliminary phylogenetic analysis of Brachyopidae skull from Phu Noi locality

The Brachyopoidea phylogenetic analysis was using TNT 1.5, following the parameters used by Damiani and Kitching (2003) based on 61 cranial characters for 27 amphibian taxa. This phylogenetic analysis uses the same complement of terminal taxa and outgroups, the latter including a hypothetical ‘outgroup,’ the Dvinosauridae, the Tupilakosauridae, the rhinesuchid Rhineceps, and the mastodonsaurid *Watsonisuchus.* These were chosen based on previous phylogenetic analyses (Damiani and Kitching, 2003; Warren and Marsicano, 2000), presumably as characteristic of basal (but supposedly convergent) non-stereospondyls (Dvinosauridae and Tupilakosauridae) and basal stereospondyls (Dvinosauridae and Tupilakosauridae) (*Rhineceps* and *Watsonisuchus*).

The phylogenetic analysis of 27 amphibian taxa (include: Dvinosauridae, Tupilakosauridae, *Rhineceps*, *Watsonisuchus*, Rhytidosteidae, *Brachyops*, *Bothriceps*, *Platycepsion*, B. *browni*, B. *watsoni*, *Xenobrachyops*, B. *concordi*, B. *henwoodi*, *Banksiops*, *Vigilius*, *Notobrachyops*, *Batrachosuchoides*, *Sinobrachyops*, K. *australis*, *Keratobrachyops*, *Pelorocephalus* spp., Kuttycephalus, Compsocerops, Siderops, Koolasuchus, Vanastega, and Phu Noi specimen), with 61 characters. The Phu Noi specimen has 29 of the 61 characters.

The Phu Noi skull appears in the brachyopidae node in the strict consensus cladogram of 67 trees (Fig. 40), united by 5 characters: 11) The otic notch absent, 12) The tabular horn absent, and 56) The prearticular process (hamate process) in the mandible absent. Moreover, The Brachyopoidea phylogenetic placed Phu Noi skull appears as the sister taxon to the *Sinobrachyops placenticephalus* with characters 23) The posterior process on the margin of the medial part of the quadrate ramus of the pterygoid present.

This result confirmed that the Phu Noi skull was a relative of the brachyopidae family and it closely resembles the middle Jurassic brachyopid *Sinobrachyops placenticephalus* from China. However, the Phu Noi skull cannot be considered as the *Sinobrachyops placenticephalus* because the Phu Noi specimen lacks anterior cranial character and both Thai and Chinese specimens were collected from different ages.

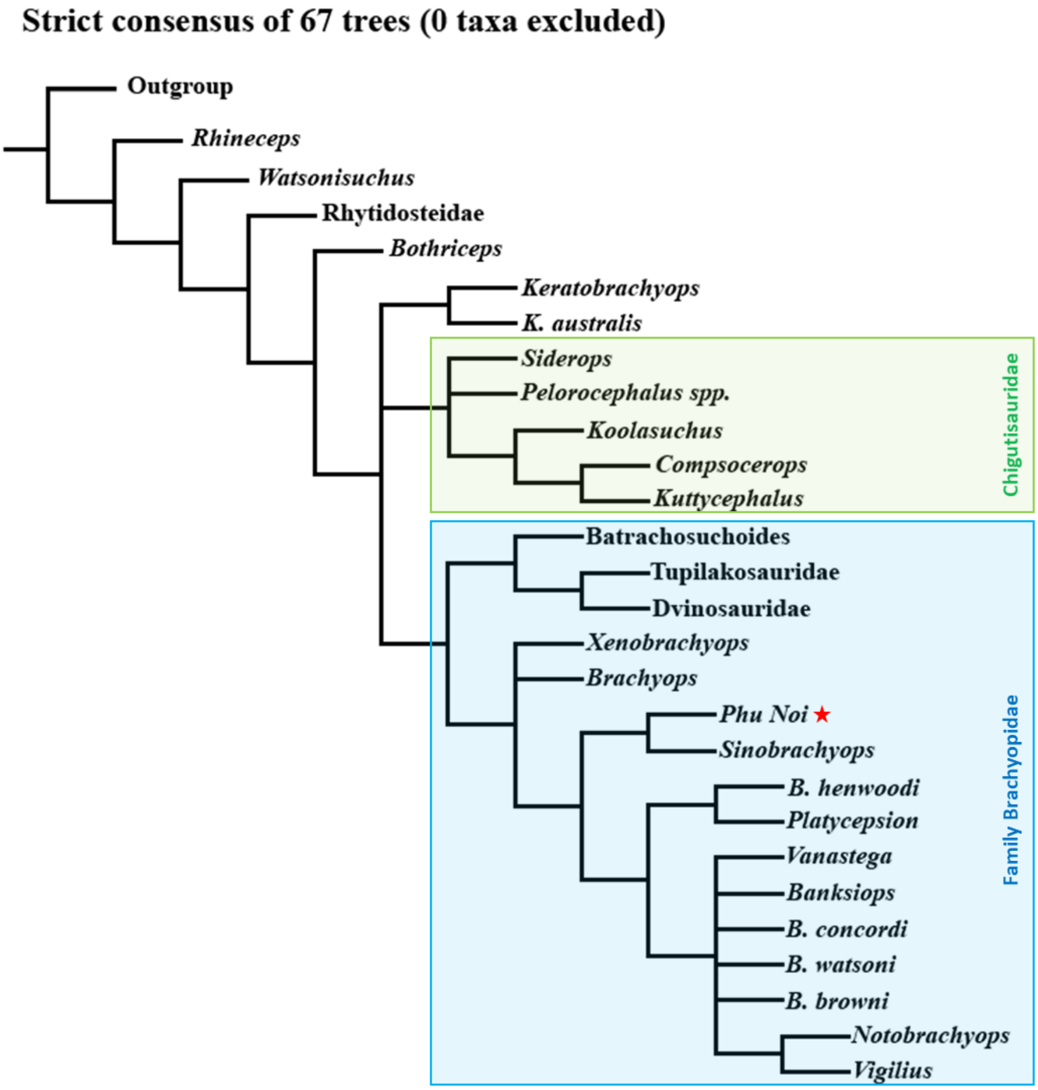

Figure 40 Cladogram showing phylogenetic position of Thai brachyopid generated by TNT 1.5.

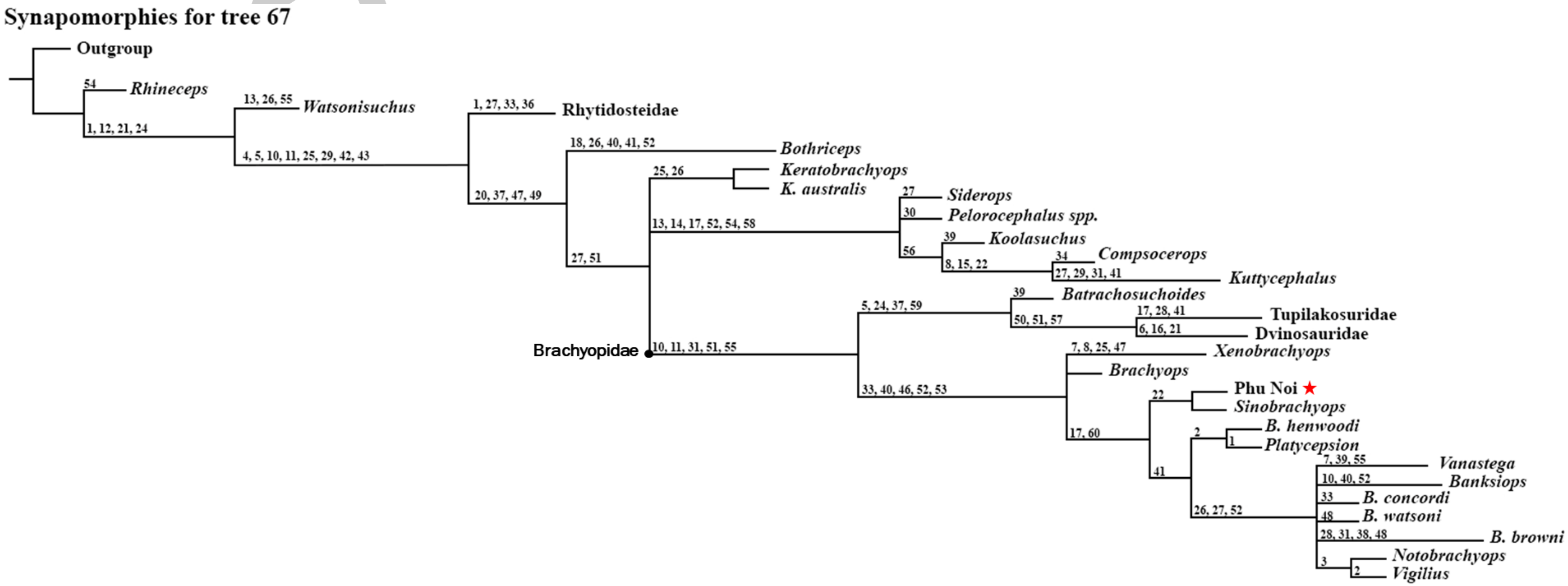

Figure 41 Cladogram shows a close relationship between the Phu Noi skull (star) and *Sinobrachyops placenticephalus* skull.

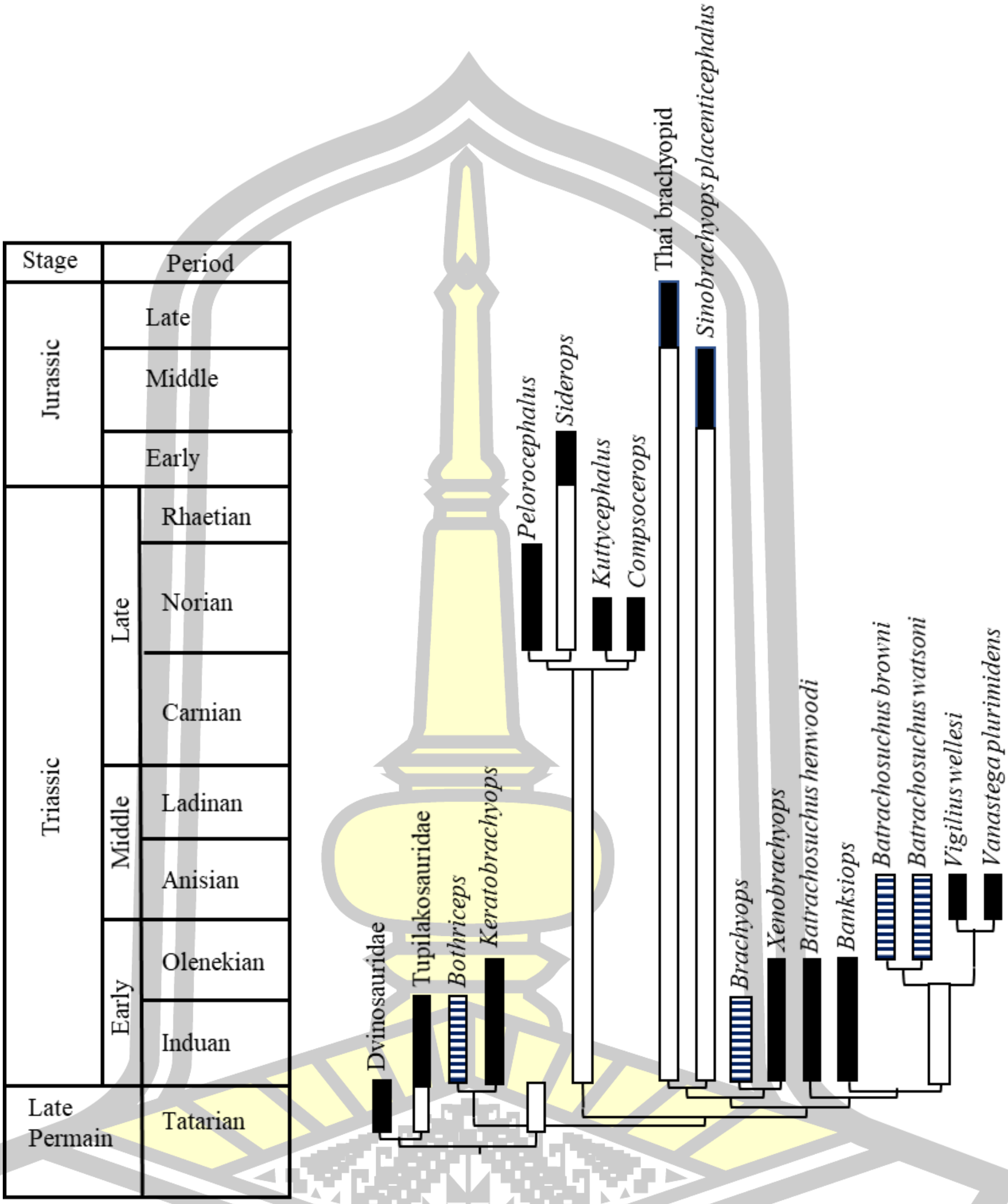

Figure 42 Stratocladogram of brachyopoid interrelationships, based on Brachyopoid phylogeny (after Damiani and Kitching, 2003). Solid bars indicate stratigraphic ranges for terminal taxa; open bars indicate ghost lineages.

Remark: The short skull, which lacks otic notch and tabular horn, and the position of occipital condyles are typical characters of Brachyopidae (Warren and Marsicano, 1998, 2000), similar to those of the Jurassic brachyopid temnospondyl skull from China such as *Sinobrachyops placenticephalus* (Dong, 1985).

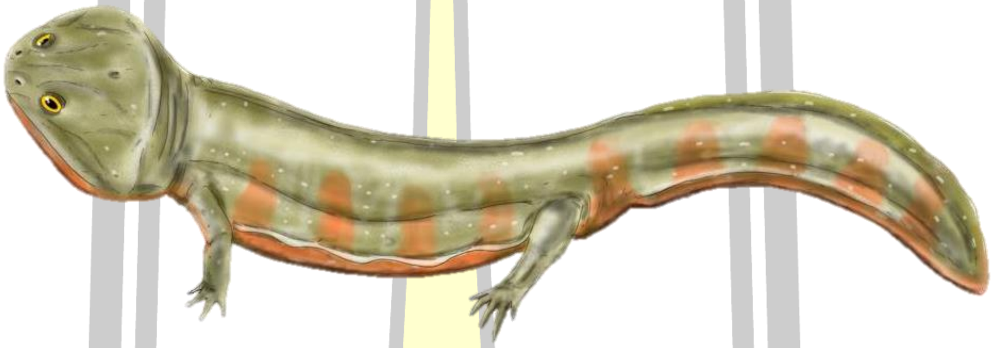

Figure 43 Reconstruction of Brachyopidae *gen. et sp. indet*. from Phu Noi locality in Thailand

4.1.3 Systematic description of Cretaceous amphibians

Order: Anura Fischer von Waldheim, 1813

Anura *fam. indet.*

Occurrence: Phu Phan Thong locality and Huai Lao Yang locality, Nong Bua Lamphu Province

Formation/age: Sao Khua Formation (Lower Cretaceous)

Reference material: The humeri; SHM-PT 529 and SHM-PT 530 (Srisuk, 2002), Pelvic girdle; SHM-HY 231 (Srisuk, 2005)

Description:

The humeri: SHM-PT 529 (Fig. 44 A-B) belong to the distal part of a left humerus, with the proximal part is broken. The SHM-PT 529 is an elongated and slender bone. The distal end is about twice the diameter of the shaft. The shaft broadens from the narrowest point to the distal end. The shaft is slightly curved. The deltoid crest extends to the narrowest point of the shaft. The capitulum is rounded.

SHM-PT 530 (Fig. 44 C-D) belongs to the distal part of the right humerus, with the proximal part is broken. The bone is a slender shaft, slightly curved in lateral view, with a rounded capitulum. It is very similar to the left humerus (SHM-PT 529).

The pelvic girdle: The specimen (SHM-HY 231, Fig. 44 E-F**)** consists of parts of the ischium, pubis, and acetabulum, while the ilium shaft is not preserved. The acetabular fossa is nearly circular with a posteriorly widened acetabular rim. The base of the ilium shaft has a triangular cross-section.

Remark: Based on morphology of the material (SHM-PT 529 and SHM-PT 530, and SHM-HY 231) are reminiscent of an anuran amphibian, but it is difficult to identify isolated incomplete humerus with great taxonomic accuracy.

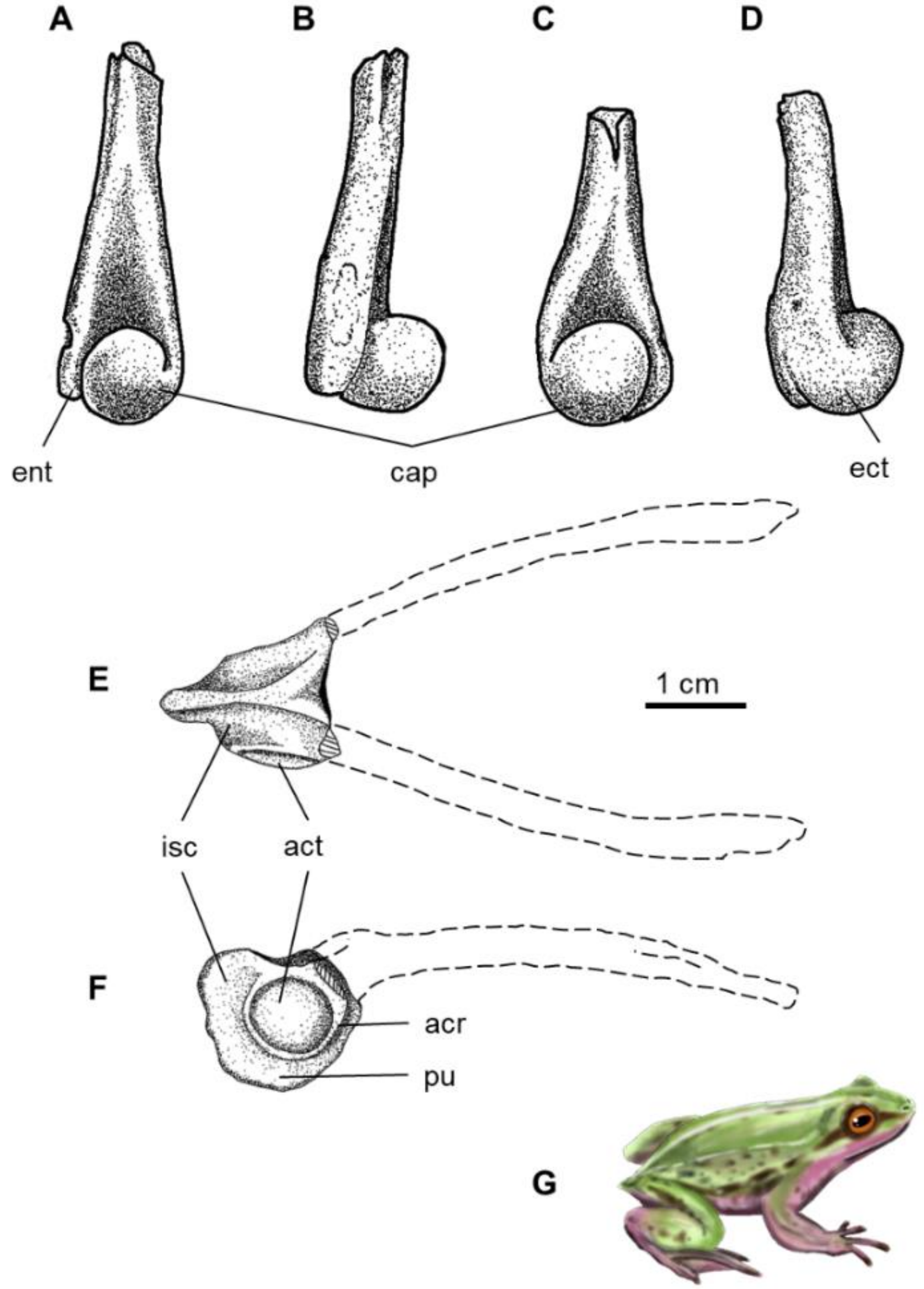

Figure 44 Cretaceous anuran remains from Thailand: left humerus, SHM-PT 529 in ventral (A) and medial view (B); right humerus, SHM-PT 530 in ventral (C) and medial view (D). Partial pelvic girdle, SHM-HY 231 in dorsal (E) and lateral view (F) (after Srisuk, 2002, 2005). Reconstruction of Thai anuran (G) is not to scale.

4.2 Additional Late Triassic fossil from the Huai Hin Lat Formation

4.2.1 Vertebrate coprolite

Occurrence: Huai Nam Aun locality, Chaiyaphum province

Reference: material: PRC 021

Description: The coprolite has an elongated cylindrical shape with a rounded end; it is curved in lateral view (Fig. 45). The specimen is approximately 74 mm. in length and 21 mm. in diameter. The surface is smooth, hard, and grey in color. In cross-section, the specimen is composed of dark clay-like material with high density.

Remark: The cylindrical with curve shape of coprolite in this study are characteristics of crocodylomorphs excrement, especially in crocodile-like animals (Cardia et al., 2019; Dentzien-Dias et al., 2018; Lucas et al., 2012; Milàn, 2012). Moreover, the excrement of modern crocodilians noted that the crocodylomorphs had very strong acid in the digestive system to decompose prey remains (Dentzien-Dias et al., 2018; Lucas et al., 2012; Milàn, 2012). This coprolite was therefore probably likely produced by archosauromorphs. Abundant vertebrate assemblages were founded in the Huai Hin Lat Formation such as actinopterygian fishes (Martin, 1984), lungfish (Martin and Ingavat, 1982), temnospondyls (Ingavat and Janvier, 1981; Nonsrirach et al., 2021; Suteethorn et al., 1988), archosaur (Laojumpon et al., 2014), and phytosaurs (Buffetaut and Ingavat, 1982). However, this coprolite was probably produced by a crocodile-like reptile or possibly phytosaur, which tooth and bone remains were found in this Formation (Buffetaut and Ingavat, 1982; Laojumpon et al., 2014).

Figure 45 The vertebrate coprolite with parasite eggs found in the Huai Nam Aun locality, Chaiyaphum province (Upper Triassic).

4.2.2 Parasite eggs in vertebrate coprolite

Phylum: Nematoda Diesing, 1861

Class: Chromadorea

Family: Ascaridoidea Baird, 1853

Description: Microscopic observations of all slides showed a dark, high-density clay-like material and absence of soft tissue, e.g., folded or spiral traces. Three different morphotypes of parasite eggs were visible in the coprolite slices (table 5).

Table 5 Three different parasite egg morphotypes in the vertebrate coprolite from the Huai Nam Aun locality (Upper Triassic).

Morphotype	Morphology	Length (µm)	Width (µm)	Shell thickness (µm)	Eggs
I	Oval shape, very thick shell, the embryo inside the egg	60	43	10	1
II	Rounded shape, thick shell, development apparently at one-cell stage inside the egg	87-147	79-118	3-5	4
III	Rounded or oval shape, the shell is unclear or unidentifiable	59-132	44-105	-	6

Morphotype I (Fig. 46) is an oval shape with a vary thick shell. The eggs measure 60 µm long and 43 µm wide. In this morphotype, the undeveloped unicellular embryo is preserved inside the egg with multiple layers (inner and outer layer) e.g., vitelline layer, and thick chitin shell. The size and morphological traits are characteristic of Ascaridoidea eggs.

Morphotype II (Fig. 47) has a rounded shape with thick shell (thinner than morphotype I). This morphotype is approximal 87-147 µm in length and 79-118 µm in width. The surface is eclipsed and apparently at the one-cell stage inside the egg. These traits suggest that the eggs of morphotype II also belong to the Ascaridoidea. The morphotype II similar in size to the *Ascarites rufferi* egg (Da Silva et al., 2014).

Morphotype III (Fig. 48) is rounded or oval shape with the eclipsed surface. The outer shell is unclear or unidentifiable. They are approximal 59-132 µm in length and 44-105 µm in width. They could potentially be parasite eggs, but the outer shell is unclear and unidentifiable. There is thus insufficient morphological information for a systematic assignment.

Remark: The rounded to broadly oval and thick wall of the eggs of morphotype I and II found in the coprolite are diagnostic of nematode egg of the Ascaridoidea superfamily. The parasite of this superfamily is commonly found in terrestrial vertebrates such as fishes, amphibians, reptiles, birds, mammal-like reptiles, and mammals (Bouchet et al., 2003; Cardia et al., 2018; Da Silva et al., 2014; Hugot et al., 2014; Sprent, 1985).

The trace fossils were found in Early Triassic of marine coprolites from nothosaurids is the oldest recorded nematode body (Brachaniec et al., 2015). The oldest recorded of Ascarididae eggs are *Ascarites rufferi* (Da Silva et al., 2014) from terrestrial Triassic coprolite identified as cynodont origin from Brazil. Other, *Ascarites gerus* and *Ascarites priscus* (Poinar and Boucot, 2006) from Early Cretaceous archosaur coprolite (Iguanodontian dinosaur) from Belgium and Ascarididea eggs discovered in Crocodyliformes coprolite from the Early Cretaceous of Brazil (Cardia et al., 2018). The current study constitutes the first report of Ascaridoidea eggs in terrestrial vertebrate hosts of the Late Triassic in Asia.

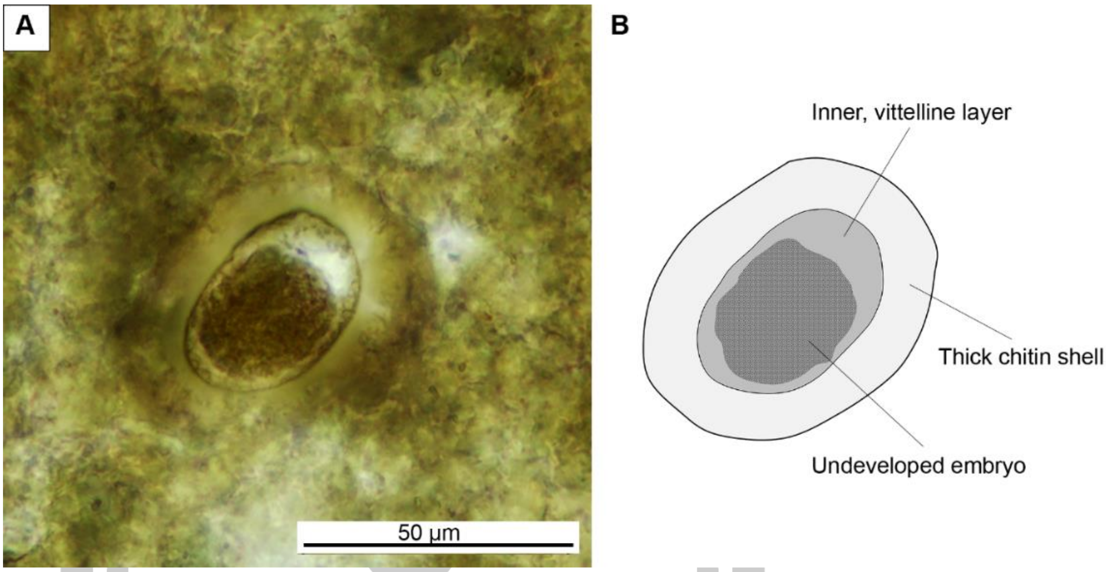

Figure 46 parasite egg morphotype I found in the vertebrate coprolite. The egg with an undeveloped embryo (A) and reconstruction image of the egg (B).

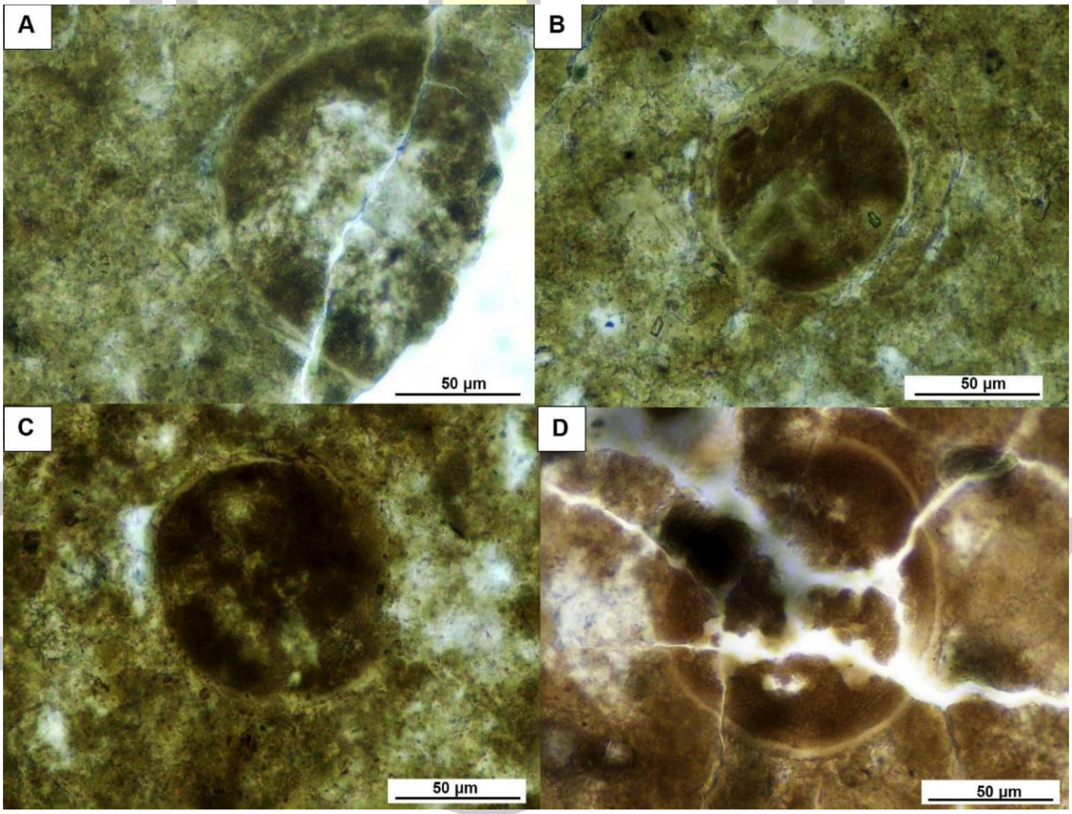

Figure 47 parasite egg of morphotype II found in the vertebrate coprolite.

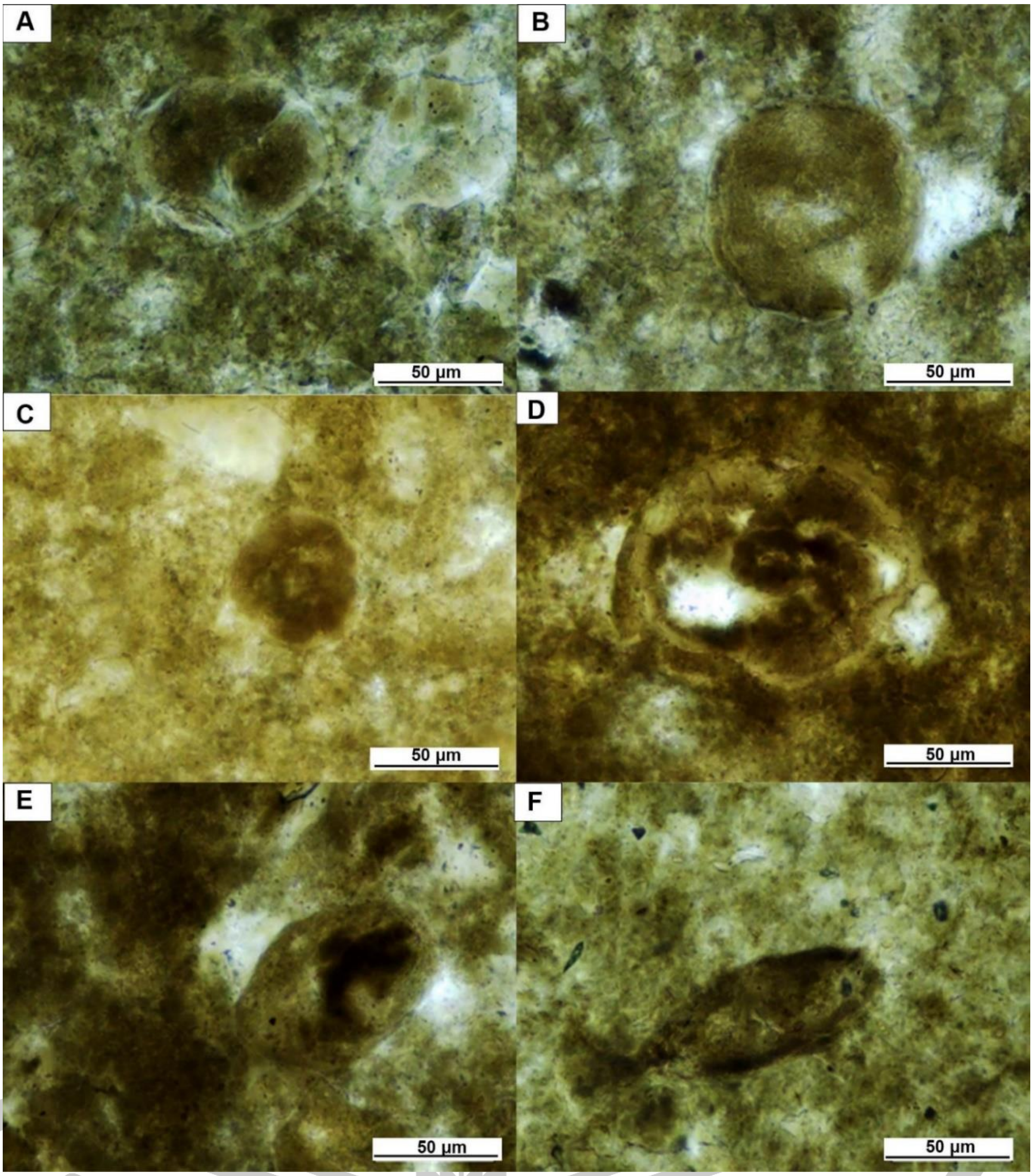

Figure 48 structures that are potentially parasite eggs Morphotype III found in the vertebrate coprolite.

CHAPTER 5
CONCLUSION

5.1 Species diversity of Mesozoic amphibians in Thailand

The non-marine Mesozoic sedimentary rocks from Thailand were formed in the Indochina and Sibumasu blocks. These blocks have yielded at least four taxa of amphibians, including three taxa of temnospondyls (*Cyclotosaurus* cf. *posthumus*, Plagiosauridae *gen. et sp. indet*., and Brachyopidae *gen. et sp. indet*.) and one taxon of anuran from four formations (Huai Hin Lat, Khlong Min, Phu Kradung, and Sao Khua) with ranges from the Late Triassic to Early Cretaceous. The Thai amphibian fossils show the most diverse Mesozoic amphibian record in Southeast Asia.

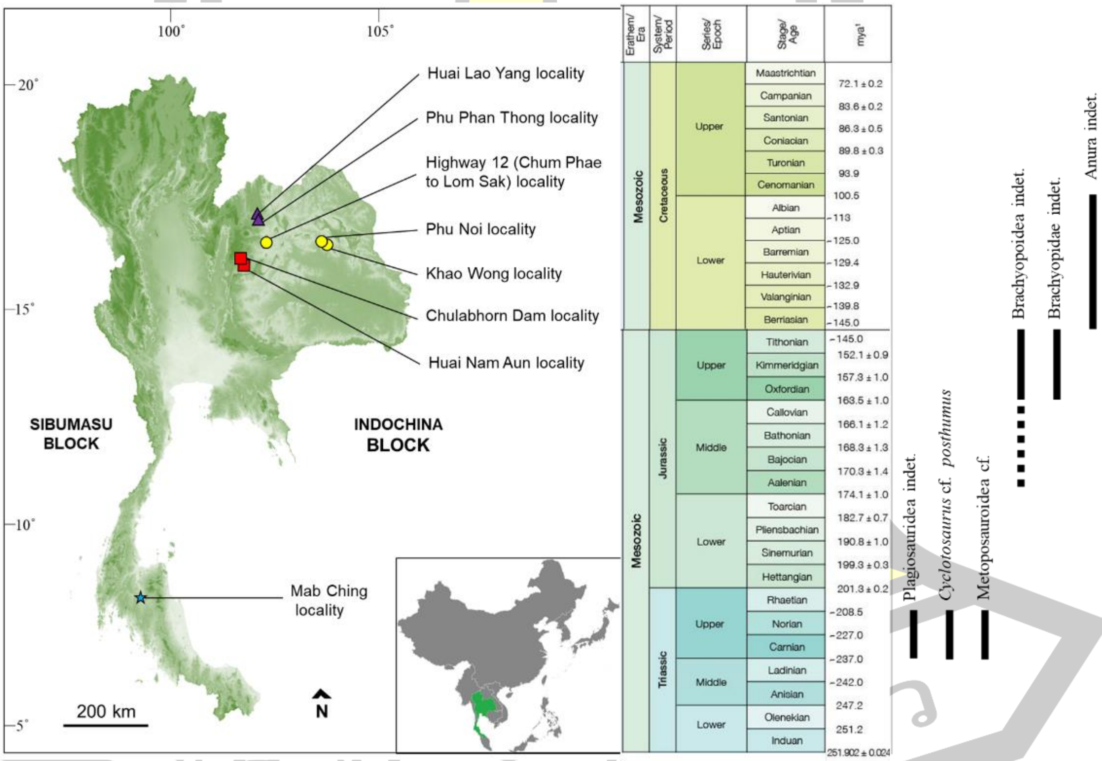

Figure 49 Mesozoic amphibian localities from Thailand (symbol; locality in ■ Huai Hin Lat Formation (Upper Triassic), ★ Khlong Min Formation (Middle or Upper Jurassic), ○ Phu Kradung Formation (Upper Jurassic), ▲ Sao Khua Formation (Lower Cretaceous) and stratigraphic range of Mesozoic amphibians in Thailand (the geology time scale modified from www.britannica.com).

Table 6 Distribution of the different taxa of Mesozoic amphibians in Thailand.

Formation	Material	Previous study	This study
Huai Hin Lat	skull (D.M.R. no. Ch.D 001)	*Cyclotosaurus* cf. *posthumus* (Ingavat and Janvier, 1981)	
	dermal bone (TF 1453)	Plagiosauridae (Suteethorn, et al., 1988)	Plagiosauridae
	intercentrum (CY-HN 378)	Capitosauridae (Laojumpon et al., 2014)	Metoposauroidea
	5 vertebrae (CY-HN 374, CY-HN 370, CY-HN 376, CY-HN 378 CY-HN 379), humerus (CY-HN 435), and dermal bone (CY-HN 349, CY-HN 364, CY-HN 365, CY-HN 368, CY-HN 377, CY-HN 403, and CY-HN 454)		Metoposauroidea
Khlong Min	2 intercentra (TF 3328, TF 3329)	Labyrinthodont (Buffetaut et al., 1994b)	Brachyopoidea
	2 intercentra (MC 233, and MC 234)		Brachyopoidea
Phu Kradung	intercentrum (TF 3144)	Labyrinthodont (Buffetaut et al., 1994a)	Brachyopoidea
	intercentrum (KS37-8)		Brachyopoidea
	Skull (KS34-1481) and 22 intercentra (KS34-1471 to KS34-1474, KS34-1476, KS34-1477 to KS34-1480, KS34-1482 to KS34-1486, KS34-1489, KS34-2192, KS34-2871, KS34-3270, PN-710, PN-712, and PN-723PN 17-75)		Brachyopidae
Sao Khua	2 humeri (SHM-PT 529 and SHM-PT 530)	Anura (Srisuk, 2002)	
	pelvic girdle (SHM-HY 231)	Anura (Srisuk, 2005)	

5.2 Paleobiogeographic significance of the Mesozoic amphibian fossils

Hitherto, the Upper Triassic Indochina block of Thailand revealed at least two taxa of temnospondyls consisting of *Cyclotosaurus* (Ingavat and Janvier, 1981) and the plagiosaurids (Suteethorn et al., 1988). Moreover, the newly discovered specimens from the Huai Hin Lat Formation, i.e., dermal bones, humerus, and intercentra are possibly related to Metoposauroidea or Mastodonsauroidea.

Metoposauroidea is known from the Late Triassic of Africa (Dutuit, 1978; Fortuny et al., 2019), Europe (Brusatte et al., 2015; Meyer, 1842; Schoch and Milner, 2004; Sulej, 2002, 2007), North America (Branson and Mehl, 1929; Case, 1922; Lucas et al., 2010; Zeigler et al., 2002), and India (Chakravorti and Sengupta, 2019; Chowdhury, 1965; Sengupta, 2002), but they have not been reported in Southeast Asia.

Mastodonsauroidea have been reported in Europe (Maryańska and Shishkin, 1996; Schoch, 1999; Sulej and Niedźwiedzki, 2013), Australia (Damiani, 1999; Warren, 1972), North and South America (Eltink et al., 2017; Marzola et al., 2017; Schoch, 2000), Africa (Dahoumane et al., 2016; Damiani, 2001; Peecook et al., 2017; Shishkin et al., 2004), Russia (Novikov and Ilyina, 1995), India (Damiani, 2001; Mukherjee and Sengupta, 1998), Japan (Nakajima and Schoch, 2011), China (Liu, 2016; Liu and Wang, 2005), and Thailand (Ingavat and Janvier, 1981). Dizik and Sulej (2007) noted that Metoposauroidea and Mastodonsauroidea have sometimes been discovered in the same locality, i.e., the Krasiejów clay pit in Poland, suggesting that the discovery of fossils of Metoposauroidea in the Late Triassic rocks of Thailand is possible as well.

From the biological point of view, Buffetaut and Suteethorn (1998) noted that the freshwater vertebrate remains from the Late Triassic Huai Hin Lat Formation are reminiscent of the Norian Stubensandstein Formation from Germany. Both formations have yielded remains of actinopterygian fishes (semionotids), turtles, amphibians (cyclotosaurids), and phytosaurs (Buffetaut and Ingavat, 1982; Havlik et al., 2013; Ingavat and Janvier, 1981; Laojumpon et al., 2014; López-Arbarello, 2008; Schoch and Milner, 2004; Tong et al., 2003), suggesting a biogeographical link between the Indochina block, and Laurasia. This conclusion agrees with the hypothesis of a large physical connection between the North China block, South China block, Indochina block, and Laurasia during the Mesozoic era (Permo–Triassic boundary) (Arbez et al., 2019; Bercovici et al., 2012; Ingavat and Janvier, 1981; Olivier et al., 2019).

In the Jurassic sequence of Thailand, the previous records of Mesozoic amphibians were limited to intercentra remains (TF 3328, TF 3329, and TF 3144), which share common characteristics with Brachyopoidea intercentra (Shishkin, 1991). Remains of Brachyopoidea have been discovered in Australia (Cosgriff, 1973; Damiani and Warren, 1996; Warren and Hutchinson, 1983; Warren et al., 2011), Africa (Chernin, 1977; Damiani and Kitching, 2003; Damiani and Rubidge, 2003; Warren and Damiani, 1999), South America (Dias-da-Silva et al., 2012; Marsicano, 1993, 1999; Ruta and Bolt, 2008), Russia (Shishkin, 1967), Antarctica (Cosgriff and Hammer, 1984), India (Sengupta, 1995), Mongolia (Shishkin, 1991), and China (Dong, 1985). The new Brachyopidae skull (KS34-1481) from the Phu Noi locality, briefly described in this study, resembles that of *Sinobrachyops placenticephalus* Dong, 1985 from China, suggesting that these forms are related. This would indicate a biogeographical link between the Sibumasu block and the Chinese sediments. Moreover, the wide distribution of temnospondyls in Asian continental blocks during the Jurassic supports the view that the Sibumasu block and Indochina block were already in contact (Buffetaut and Suteethorn, 1998; Buffetaut et al., 1994c).

Amphibian fossils from the Early Cretaceous of northeastern Thailand are described and related to anurans, although these specimens are too fragmentary to be more precisely identified. In the Cretaceous, Asian anurans have been discovered in Kazakhstan (Skutschas and Kolchanov, 2017), Mongolia (Gao and Chen, 2017), India (Prasad and Rage, 2004), Japan (Evans and Manabe, 1998), China (Dong et al., 2013b; Wang et al., 2000; wang, 2004), and Myanmar (Xing et al., 2018). Thus, the discovery of this taxon suggests that during the Early Cretaceous, anurans were already present in Thailand.

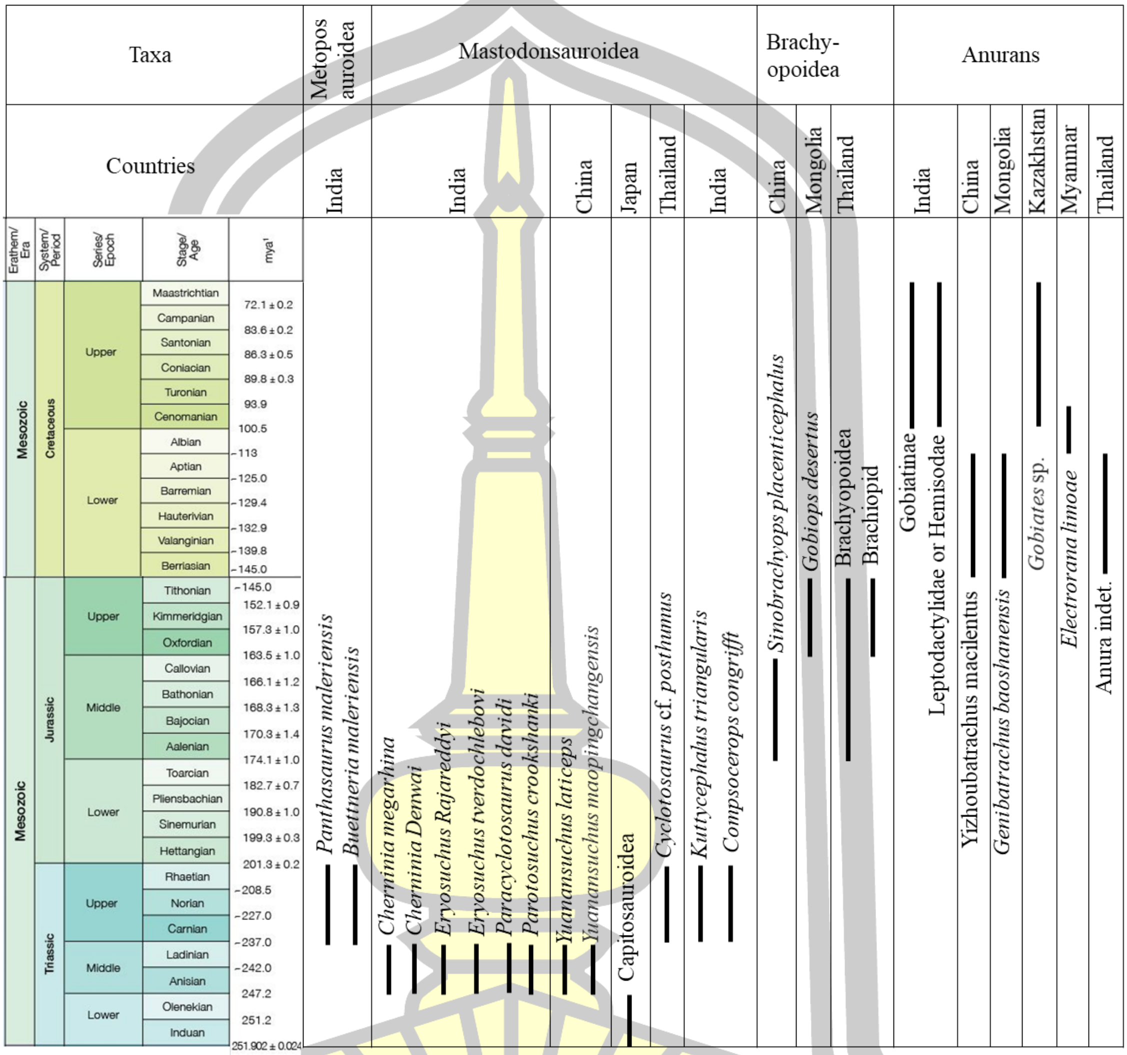

Figure 50 stratigraphic range of Mesozoic amphibians in Asia (the geology time scale modified from www.britannica.com)

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APPENDIX 1

Characters used in the Brachyopid phylogenetic analysis follow by Damiani and Kitching 2003

1. Skull elongate (0); skull shortened, as wide as long or wider than long (1). In Rhytidosteidae some skulls are straight-sided as are the skulls of Lydekkerinidae, but some are parabolic. Hence the term parabolic as it is usually applied to brachyopoids is inappropriate in this data matrix. All of these taxa share the shortened skull although they are not necessarily closely related. This character applies in adult individuals only.

2. Orbits located posterior to the skull midlength (0); orbits located about half way along skull midline (1); orbits located anterior to the skull midlength (2).

3. Orbits not enlarged in the adult (maximum width of skull more than 7 times maximum width of orbit) (0); orbits enlarged (maximum width of skull less than 6.5 times maximum width of orbit) (1).

4. sensory sulci absent (0); poorly developed (1); well developed (2).

5. Jugal extends well anterior to orbit (0); anterior end of jugal about level with or posterior to anterior orbital margin (1).

6. Lacrimal bone present on skull roof (0); absent (1).

7. Maxilla and nasal not in contact (0); maxilla and nasal forming a suture (1).

8. Nares not close to skull midline (distance between nares twice width of one naris, or greater) (0); nares close to skull midline (distance between nares approximates width of one naris) (1).

9. Maxilla enters narial border (0); maxilla excluded from narial border by premaxilla-nasal suture (1).

10. Lateral exposure of the palatine (LEP) absent (0); reduced and unornamented, barely exposed on skull roof (1); well exposed on skull roof and ornamented (2). A small slip of the palatine bone is present on the inner wall of the lateral margin of the orbit in Xenobrachyops and Sinobrachyops. It is difficult to detect and the character cannot be checked in most material because of poor or incomplete preservation. On the other hand, the LEP of Batrachosuchoides is easily detected as it is in Dvinosauria.

11. Otic notch present (0); reduced to otic embayment (1); otic notch absent (2).

12. Tabular horns present, robust, supported from below by an extension of the paroccipital process (0); reduced and unsupported distally (1); tabular horn absent (2).

13. Tabular horn with posteroventral extension (0); posteroventral extension absent (1). A marked extension of the dorsal part of the paroccipital process is present immediately below and posterior to the tabular horn of the skull roof in Archegosauridae and Rhinesuchidae.
14. Post squamosal process of the skull roof, absent (0); present (1).
15. Post quadratojugal process of the skull roof, absent (0); present (1).
16. Post postparietal process of the skull roof, absent (0); present (1).
17. Dorsomedial process of the body of the pterygoid abuts the parasphenoid (0); the pterygoid forms a longitudinal contact or suture with the lateral margins of the parasphenoid plate in the adult (1).
18. Pterygoid separated from exoccipital by the parasphenoid (0); pterygoid-exoccipital suture present (1).
19. Palatine ramus of the pterygoid bears a posterolateral flange which projects into the subtemporal vacuity (0); flange absent (1).
20. Lateral border of the pterygoid beside the subtemporal vacuity concave so that the subtemporal vacuity is wide (0); lateral border of the pterygoid parallel to skull midline resulting in a narrow subtemporal vacuity (1).
21. Quadrate ramus of the pterygoid level with palate (0); sharply downturned (inverted U-shaped palate) (1).
22. Palatine ramus of the pterygoid reaches the vomer (0); palatine ramus of the pterygoid retracted posteriorly so that the palatine is exposed in the interpterygoid vacuity (1).
23. Posterior process on the margin of the medial part of the quadrate ramus of the pterygoid, absent (0); present (1).
24. Quadrate condyle double and markedly screw-shaped with the medial condyle extended anteriorly (0); quadrate condyle double and triangular, the apex of the triangle lateral (1); quadrate condyle double with the two parts subequal in size (2).
25. Basioccipital ossified so that it contributes to occipital condyle (0); not ossified (1).
26. Pterygoid meets palatine on the lateral margin of interpterygoid vacuity (0); pterygoid retracted so ectopterygoid is exposed in the interpterygoid vacuity and contriqbutes to strut between interpterygoid and subtemporal vacuities (1); pterygoid

markedly retracted so ectopterygoid makes a large contribution to strut between interpterygoid and subtemporal vacuities (2).

27. Ornament absent from ventral surface of the corpus of the parasphenoid and pterygoids (0); present in both parasphenoid and pterygoids, or at least in one of them (1).

28. Cultriform process of parasphenoid narrow and rounded (0); narrow and flat (1); broad and flat (2); broad, flat and expanded anteriorly between the vomers (3).

29. Vomerine depression or foramen just anterior to cultriform process of the parasphenoid, absent (0); present (1); present as a vacuity (2). The presence of a vacuity in this position is scored for Thabanchuia as the region is not preserved in any specimen of Tupilakosaurus.

30. Corpus of the parasphenoid antero-posteriorly elongated (0); nearly as long as wide (1).

31. Median keel on cultriform process absent (0); median keel present throughout the length of the cultriform process (1); median keel developed on part of the cultriform process only (2).

32. Tooth row present on palatine and ectopterygoid (0); tooth row reduced (1); tooth row absent (2).

33. Ectopterygoid tusks present (**0**); absent (**1**).

34. Maximum width of interpterygoid vacuity pair less than 90% of their maximum length (0); width of pair greater than 90% of their length (1).

35. Subtemporal vacuity extends anteriorly less than half way up the interpterygoid vacuity or as far as the mid point of the vacuity (0); subtemporal vacuity extends anteriorly further than the mid point of the interpterygoid vacuity (1).

36. Occipital border of the quadrate ramus of the pterygoid sutures with quadrate (0); pterygoid does not suture with quadrate forming a lower palatoquadrate fissure (1).

37. Occipital portion of the ascending ramus of the pterygoid sutures with descending occipital flange of squamosal (0); reduced in height leaving an upper palatoquadrate fissure (1).

38. Exoccipital condyles elliptical, facing posteromedially (0); more rounded, facing posteriorly, held on short stalk (1).

39. Exoccipitals separated in the midline of the palate by the parasphenoid (0); exoccipitals contact or suture in the midline (1).

40. More than one distinct small foramen on lateral wall of exoccipital (0); an enlarged foramen on lateral wall of exoccipital (1).

41. Posttemporal fenestra markedly wider than deep (0); about as wide as deep or deeper than wide (1).

42. Paraquadrate foramen present on occipital portion of quadratojugal (0); present on posteroventrolateral ornamented portion of quadratojugal (1); absent (2).

43. Occipital wall of squamosal and quadratojugal vertical or convex (0); vertically concave (squamosal-quadratojugal trough) (1).

44. Body of the pterygoid and quadrate ramus of the pterygoid curve smoothly onto occiput forming an oblique ridge (0); body of the pterygoid and quadrate ramus of the pterygoid form a sharp edge on occiput
(1).

45. No substapedial ridge on posterodorsal surface of the pterygoid (0); substapedial ridge present (1). This ridge is characteristic of chigutisaurids in which the area is preserved. It varies in shape in the different taxa.

46. Ascending ramus of the pterygoid forms a continuous curve with posterior edge of quadrate ramus (0); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a shallow, curved lamina (1); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a shallow, uncurved lamina (2); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a gently concave lamina which is also recurved posteriorly in vertical section (3); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a gently concave lamina (4).

47. Ascending ramus of the pterygoid thickened by an ascending column positioned towards its medial edge (0); column absent (1).

48. Exoccipital condyles not projected beyond the posterior margin of the skull table (0); exoccipital condyles projected well beyond the posterior margin of the skull table (1).

49. Vertical margin of the occipital portion of the squamosal, beside palatoquadrate fissure, smooth (0); flanged (1). This flange is well developed in *Batrachosuchus*

browni and a broken edge of the squamosal in the same position indicates that it was present in *B. watsoni*.

50. Chordatympanic foramen of the mandible present on prearticulararticular suture (0); chordatympanic foramen contained within prearticular (1); absent (2).

51. Mandibular sulcus of sensory canal absent from ornamented area of mandible (0); well-developed (1); slightly developed (2).

52. PGA (post glenoid area) of mandible undeveloped (0); PGA of mandible short (1); PGA of mandible slender, elongate (2); PGA of mandible slender, very elongate (3).

53. Articular forms lingual border of PGA (post glenoid area) of mandible (0); prearticular extends posteriorly on PGA of mandible so that the articular is exposed on the lingual wall posteriorly only (1); articular almost excluded from lingual wall by a posterior growth of the prearticular, thus restricted to a longitudinal tongue on the PGA (2); prearticular- surangular suture on the PGA so articular is completely excluded from the PGA (3).

54. Articular level with dentary tooth row (0); below level of dentary tooth row (1).

55. Posterior meckelian foramen bordered by the prearticular, postsplenial and angular (0); posterior meckelian foramen bordered by the prearticular and postsplenial alone (1); prearticular and angular alone (2).

56. Prearticular process (hamate process) in the mandible absent (0); slightly developed (1); well developed (2).

57. Teeth or denticles present on all coronoids (0); present on posterior and/or middle coronoids only (1); absent from all coronoids (2).

58. Transverse trough on the postglenoid area (PGA) just behind the glenoid area, present (0); absent (1). The presence of a transverse trough is a synapomorphy of Dvinosauridae and Tupilakosauridae and absent from stereospondyls with an elongate PGA (Brachyopoidea).

59. Dorsal process of clavicle (prescapular process) short and with an anterior flange (0); without anterior flange and tall, with the tip of the process terminating above or just posterior to the posterior margin of the clavicular blade (1); without anterior flange and tall, with the tip of the process terminating well behind the posterior margin of the clavicular blade (2). In brachyopoids the dorsal process of the clavicle arises from a narrow base at the postero-lateral point of the clavicular blade. In

chigutisaurs it is initially perpendicular to the blade but may slope posteriorly toward the distal end. In brachyopids it slopes posteriorly from the base.

60. Ceratobranchials present in adult (0); lost in adult (1).

61. Posterolateral margin of the skull straight (0); sloping forward (1).

APPENDIX 2

Publication

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Fossil Record
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First occurrence of brachyopid temnospondyls in Southeast Asia and review of the Mesozoic amphibians from Thailand

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Abstract. The non-marine Mesozoic sedimentary rocks of Thailand, which consist of the Indochina block and the Sibumasu block, have yielded several terrestrial and aquatic vertebrate fossils, but only few amphibian remains have been reported. Here, we present an overview on the Thai amphibian palaeo-diversity based on the literature, re-examination of published material, new findings, and unpublished material. Thai amphibian fossil remains are assigned to Stereospondyli (Cyclotosauridae, Plagiosauridae, and Brachyopoidea) and Anura and were discovered from four formations, ranging from the Upper Triassic to Lower Cretaceous of Thailand. The occurrence of Brachyopidae in Thailand, which are related to Chinese forms, supports the previous hypothesis of physical connections between the Indochina blocks and the Sibumasu block during the Mesozoic era.

1 Introduction

The amphibians of the Paleozoic and the Mesozoic can be dived into three major clades: the Seymouriamorpha, the Lepospondyli, and the Temnospondyli (Vitt and Caldwell, 2014). Basal members of temnospondyls were the most diverse and most successful group of amphibians in the Paleozoic, which lived during the Mesozoic Era (Damiani and Rubidge, 2003; Schoch, 2014). Temnospondyls are commonly retrieved in the tetrapod assemblages from Triassic continental deposits such as fluvial and lacustrine environments (Schoch and Milner, 2000; Dias-da-Silva and Dias, 2013).

We present here an update of the amphibian continental fossil record during the Mesozoic in Thailand. The Mesozoic rocks of Thailand consist of two sub-continent blocks. The western part, called "Shan-Thai block" or "Sibumasu block", includes the eastern part of Myanmar and northern, western, and southern parts of Thailand as well as the western peninsula of Malaysia (Fig. 1). The eastern part is the Indochina block, which includes northeastern and eastern parts of Thailand, southern parts of Laos and Cambodia, and the western part of Vietnam (Metcalfe, 1996; Buffetaut and Suteethorn, 1998; Racey, 2009). The Mesozoic rocks in the northeastern part of Thailand, which belong to Indochina, consist of a non-marine red bed sequence deposited in a continental environment (Racey et al., 1996; Racey, 2009). This block consists of seven formations considered Upper Triassic to Cretaceous in age based on invertebrate and vertebrate remains as well as palynomorphs (Meesook et al., 1995; Racey et al., 1996). However, fossils of Thai amphibians (i.e., *Cyclotosaurus* cf. *posthumus*, Plagiosauridae, Temnospondyli indet., and Anura) were discovered only from three formations of the Indochina block (Ingavat and Janvier, 1981; Suteethorn et al., 1988; Buffetaut et al., 1994a; Srisuk, 2002, 2005) which are as follows.

1. The Huai Hin Lat Formation is mainly formed by lacustrine bituminous limestone and shales (Buffetaut and Suteethorn, 1998). It is considered Upper Triassic based on palynomorphs, plant macro-remains, conchostracans, and vertebrate remains (Kobayashi, 1975; Racey et al., 1996; Buffetaut and Suteethorn, 1998; Department of Mineral Resources, 2014). The vertebrate assemblages from the Huai Hin Lat Formation consist of actinopterygian fishes (Martin, 1984), lungfish (Martin and Ingavat, 1982), temnospondyls (Ingavat and Janvier, 1981; Suteethorn et al., 1988), and phytosaurs (Buffetaut and Ingavat, 1982).

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2. The Phu Kradung Formation consists of sequences of sandstone, siltstone, and mudstone deposited on a lacustrine-dominated alluvial floodplain environment (Meesook, 2000; Racey, 2009). This formation is assigned to Upper Jurassic based on palynomorphs, bivalves (Racey et al., 1994, 1996; Meesook, 2000), and vertebrate remains which consist of hybodont sharks (Cuny et al., 2005), actinopterygians (Cavin et al., 2003; Cavin and Suteethorn, 2006), temnospondyls (Buffetaut, et al., 1994a), turtles (Tong et al., 2009), crocodiles (Buffetaut and Ingavat, 1980), and dinosaurs (Buffetaut, et al., 2014).

3. The Sao Khua Formation consists of sequences of red clays, sandstones, and conglomerates deposited on a floodplain with a meandering river environment (Buffetaut and Suteethorn, 1998). This formation is assigned to Lower Cretaceous based on palynomorphs, bivalves (Racey et al., 1994, 1996; Meesook, 2000), and vertebrate remains, i.e., hybodont sharks (Cuny et al., 2007), actinopterygian fishes (Cavin et al., 2009), anurans (Srisuk, 2002, 2005), turtles (Tong et al., 2009), crocodilians (Buffetaut and Ingavat, 1980), and dinosaurs (Buffetaut and Suteethorn, 1999).

In the Sibumasu block of the southern peninsula of Thailand, temnospondyls were discovered in the Klong Min Formation (Buffetaut et al., 1994b, c), which is formed by limestone and grey to brown clays, indicating a lacustrine depositional environment (Tong et al., 2002). The Klong Min Formation is considered Middle or Upper Jurassic in age, based on charophytes and vertebrate remains (Buffetaut et al., 1994b; Tong et al., 2002; Girard et al., 2020). The vertebrate assemblages of this formation consist of hybodont sharks, actinopterygian fishes, lungfish, turtles, and crocodiles (Buffetaut et al., 1994b, c; Tong et al., 2002).

Although thousands of vertebrate remains have been found, few amphibian remains have been reported. More recently, new specimens of amphibians (intercentra and a posterior part of a skull) were collected from new Mesozoic localities in Thailand, i.e., Huai Nam Aun locality, Phu Noi locality, and Khao Wong locality (Laojumpon et al., 2014; Chanthasit et al., 2019). In order to understand the diversity and biogeography of Thai Mesozoic amphibians, we describe and re-check the taxonomic status of all amphibian remains housed in the collections of the Sirindhorn Museum (SDM, Kalasin Province) and the Palaeontological Research and Education Centre of Mahasarakham University (PRC, Mahasarakham Province). The relationships between these amphibians and their Asian relatives are used in a palaeobiogeographical framework for a better reconstruction of the physical connections in Southeast Asia.

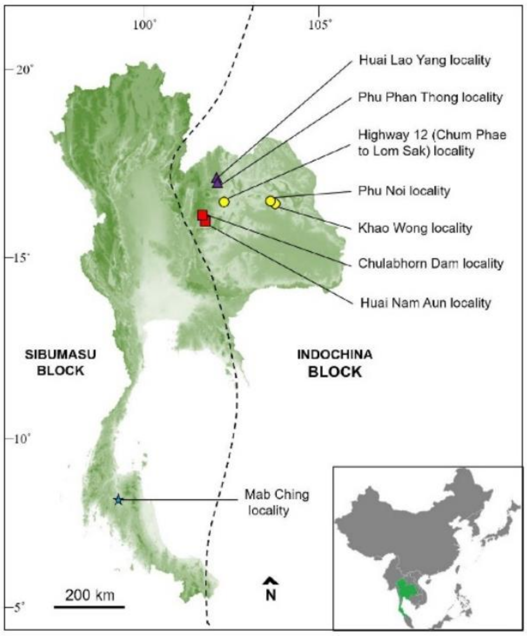

Figure 1. Mesozoic amphibian outcrops from Thailand (symbol); locality in ■ Huai Hin Lat Formation (Upper Triassic), ★ Khlong Min Formation (Middle or Upper Jurassic), ○ Phu Kradung Formation (Upper Jurassic), and ▲ Sao Khua Formation (Lower Cretaceous).

2 Abbreviations

D.M.R.: Department of Mineral Resources; Ch.D.: Chulabhorn Dam; TF: Thai Fossil; KS: Kalasin; CY-HN: Chaiyaphum – Huai Nam Aun; SHM-PT: Srisuk's House Museum – Phu Phan Thong; SHM-HY: Srisuk's House Museum – Huai Lao Yang.

3 Materials

The material consists of isolated intercentra, parts of dermal bones, and a posterior part of a skull. It is housed in (1) the Department of Mineral Resources, *Cyclotosaurus* cf. *posthumus* (D.M.R. no. Ch.D 001); (2) the Sirindhorn Museum, Plagiosauridae (TF 1453) and Brachyopoidea (KS34-1481, KS34-1474, KS34-1489, and KS37-8); and (3) the Palaeontological Research and Education Centre, Mahasarakham University, Brachyopoidea (TF 3228 and TF 3229), Stereospondyli indet. (CY-HN 364, CY-HN 365, CY-HN 368, CY-HN 377, and CY-HN 378) and anuran (SHM-PT 529-530 and SHM-HY 231).

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Table 1. Mesozoic amphibian records from Thailand.

Formation	Systematic paleontology	Material	Reference
Huai Hin Lat Fm. (Carnian–Norian)	*Cyclotosaurus* cf. *posthumus*	Posterior part of skull (D.M.R. no. Ch.D 001)	Ingavat and Janvier (1981)
	Plagiosauridea indet.	Clavicle (TF 1453)	Suteethorn et al. (1988)
	Stereospondyli indet.	Intercentrum (CY-HN 378)	Laojumpon et al. (2014)
	Stereospondyli indet.	Dermal bone (CY-HN 364, CY-HN 365, CY-HN 368, CY-HN 377)	This paper
Khlong Min Fm. (Middle–Upper Jurassic)	Brachyopoidea indet.	Intercentra (TF 3328, TF 3329)	Buffetaut et al. (1994c)
Phu Kradung Fm. (Upper Jurassic)	Brachyopoidea indet	Intercentrum (TF 3144)	Buffetaut et al. (1994a)
	Brachyopoidea indet	Intercentrum (KS37-8)	This paper
	Brachyopidae indet.	Posterior part of skull (KS34-1481) and intercentra (KS34-1474, KS34-1489)	This paper
Sao Khua Fm. (Lower Cretaceous)	Anura indet.	Humeri (SHM-PT 529, SHM-PT 530) and Pelvic girdle (SHM-HY 231)	Srisuk (2002, 2005)

4 Systematic paleontology

4.1 Previous published records

Temnospondyli Zittel, 1888

Stereospondyli Zittel, 1888

Mastodonsauroidea Lydekker, 1885
(sensu Damiani, 2001)

Cyclotosauridae Shishkin, 1964

Cyclotosaurus Fraas, 1889

Cyclotosaurus cf. *posthumus*

Reference material

D.M.R. no. Ch.D 001 (Fig. 2a–c); a posterior part of a skull (Ingavat and Janvier, 1981).

Formation/age

Huai Hin Lat Formation (Carnian–Norian).

Locality and sediment

The specimen was discovered in 1981 at an outcrop near the Chulabhorn Dam, Khon San District, Chaiyaphum Province. The fossil assemblage layer consists of a grey to red conglomerate.

Description

D.M.R. no. Ch.D 001 is a posterior part of a comparatively large skull (approximately 20 cm wide and 11 cm long), but the lateral part of the right side is missing. However, a pair of otic notches and a pineal foramen are preserved. The pattern of the ornamentation and the shallow interotic embayment of this skull allow an assignment to *Cyclotosaurus* (Fraas, 1913; Ingavat and Janvier, 1981; Damiani, 2001) and are similar to those of the holotype of *Cyclotosaurus posthumus* Fraas, 1913 from the Upper Middle Keuper, Bavaria (Germany).

Plagiosauroidea Abel, 1919

Plagiosauridae Abel, 1919

Plagiosauridae indet.

Reference material

TF 1453 (Fig. 2e–f), a dermal bone (Suteethorn et al., 1988).

Formation/age

Huai Hin Lat Formation (Carnian–Norian).

Locality and sediment

Outcrop near the Chulabhorn Dam, Kon San District, Chaiyaphum Province. The outcrop is located in the upper part of the Huai Hin Lat Formation (Suteethorn et al., 1988). The specimen was embedded in a block of carbonaceous black shale rock.

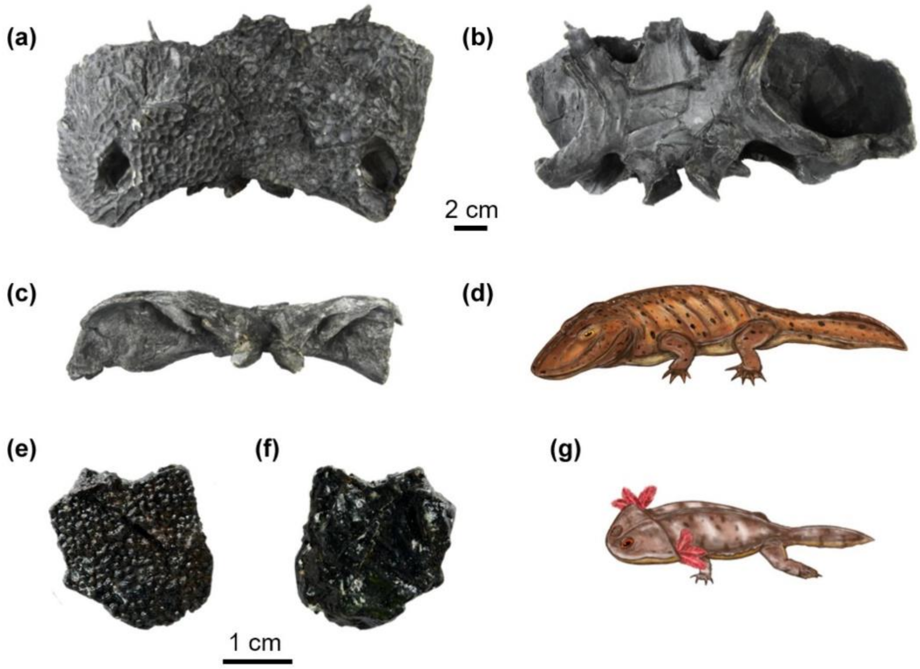

Figure 2. Triassic amphibian remains from Thailand. A replica skull of *Cyclotosaurus* cf. *posthumus* (D.M.R. Ch.D 001) in dorsal **(a)**, palatal **(b)**, and posterior views **(c)**. A reconstruction of Thai Cyclotosauridae **(d)**. A dermal bone of Plagiosauroidea indet. (TF 1453) in ventral **(e)** and dorsal **(f)** views. A reconstruction of Thai Plagiosauroidea **(g)**. Reconstruction images **(d, g)** are not to scale (drawn by Sita Manitkoon).

Description

The specimen TF 1453, approximately 22 mm wide and 25 mm long, shows a peculiar ornamentation consisting of tubercles or pustules on its ventral surface. Dorsally, the surface shows some faint radiating grooves and ridges. Based on its ornamentation, TF 1453 was interpreted as a dermal bone fragment of a temnospondyl and was assigned to Plagiosauridae. A comparable ornamentation is observed in Middle to Late Triassic Plagiosauridae, e.g., *Gerrothorax pulcherrimus* and *Plagioscutum ochevi* from Europe (Shishkin, 1986; Warren and Snell, 1991; Suteethorn et al., 1988; Jenkins et al., 2008).

Brachyopoidea Lydekker, 1885

Brachyopoidea indet.

Reference material

TF 3328 (Fig. 3a–d), TF 3329 (Fig. 3e–h), and TF 3144 (Fig. 3i–l), intercentra (Buffetaut et al., 1994a, c).

Formation/age

Klong Min Formation (Middle or Upper Jurassic) and Phu Kradung Formation (Upper Jurassic).

Locality and sediment

TF 3328 and TF 3329 were found in a road cut outcrop near Mab Ching village, Thung Song District, Nakhon Si Thammarat Province, in the southern peninsula of Thailand, which belongs to the Sibumasu block. This outcrop is formed by greyish clays and siltstones, with some freshwater limestone intercalations. It belongs to non-marine Middle or Upper Jurassic rocks based on charophyte algae, palynomorphs, and diatoms (Lei, 1993; Buffetaut et al., 1994c; Girard et al., 2020).

TF 3144 was found in a road cut outcrop at kilometer 68, along Highway 12 from Chum Phae to Lom Sak, in Khon Kaen Province. This area consists of reddish-grey silts and fine-grained reddish sandstone deposited in a meandering river channel (Buffetaut et al., 1994a), which belongs to the Indochina block.

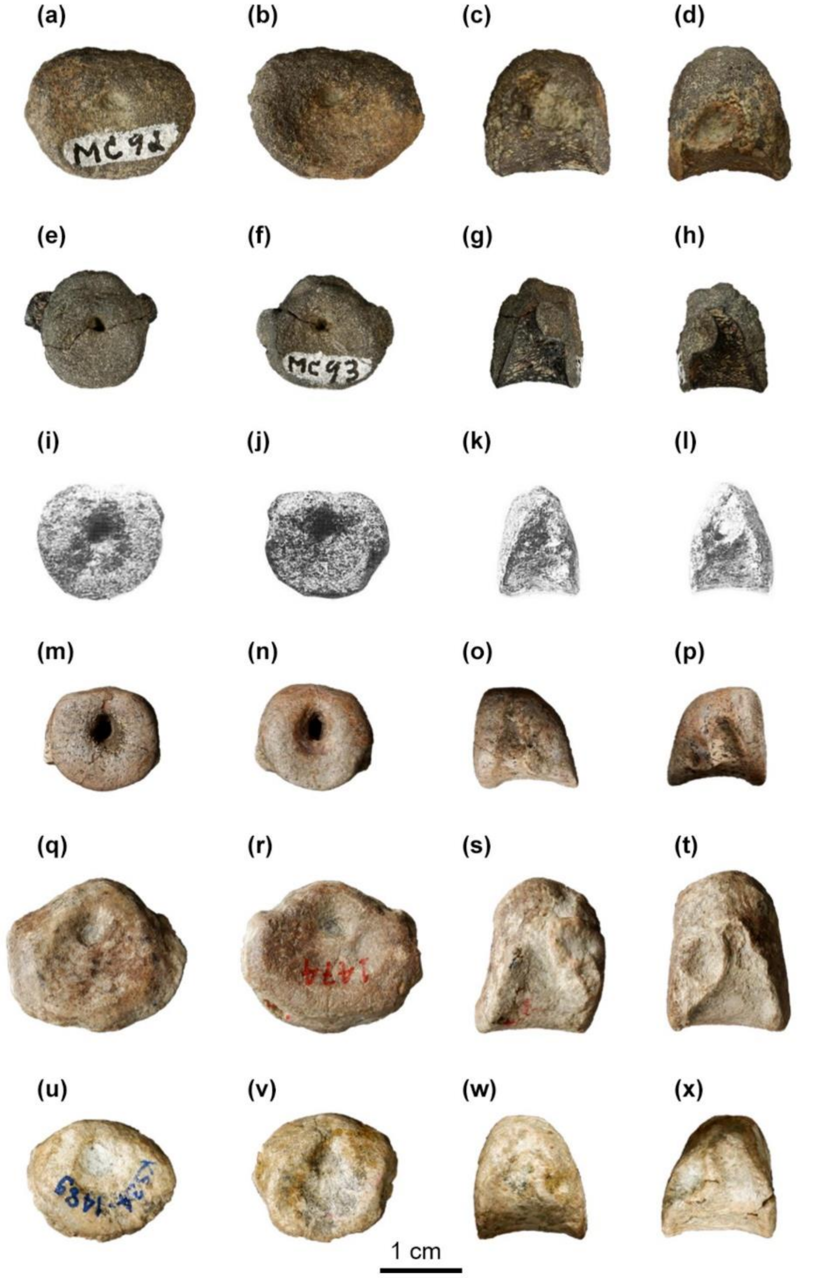

Figure 3. Thai Brachyopoidea indet. intercentra, TF 3228 **(a–d)**, TF 31229 **(e–h)**, TF 3144 (**i–l**, after Buffetaut et al., 1994b; fig. 1), and KS37-8 **(m–p)**. Thai Brachyopidae indet. intercentra, KS34-1474 **(q–t)** and KS34-1489 **(u–x)**. Anterior views **(a, e, i, m, q, u)**, posterior views **(b, f, j, n, r, v)**, left views **(c, g, k, o, s, w)**, and right views **(d, h, l, p, t, x)**.

Description

All specimens are wedge-shaped intercentra. Both anterior and posterior surfaces are concave and show a marked circular notochordal canal, which is visible as a circular pit. The pleurocentra are reduced or absent, which is a typical feature of stereospondyls (Milner et al., 1994; Witzmann and Gassner 2008). The wedge-shaped morphology and the notochordal pit of TF 3328, TF 3329, and TF 3144 is consistent with the intercentrum morphology of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997, 2011; Warren and Dammiani, 1999), which are similar to the intercentra discovered from the Jurassic Indochina block, e.g., *Gobiops desertus* from the Gobi Desert of Mongolia (Shishkin, 1991).

Anura Fischer von Waldheim, 1813

Anura indet.

Reference material

SHM-PT 529 (Fig. 4a–b) and SHM-PT 530 (Fig. 4c–d), humeri; SHM-HY 231 (Fig. 4e–f), pelvic girdle (Srisuk, 2002, 2005).

Formation/age

Sao Khua Formation (Lower Cretaceous).

Locality and sediment

The humeri (SHM-PT 529 and SHM-PT 530) were collected in a road cut outcrop near Phu Phan Thong village, Muang District, Nong Bua Lamphu Province. These fossils were embedded in a pale olive fine-grained siltstone (Srisuk, 2002).

The pelvic girdle (SHM-HY 231) was discovered in a road cut outcrop near the Huai Lao Yang reservoir road, Nong Bua Lamphu Province. The outcrop is formed by reddish-brown micaceous siltstones and lime-nodule conglomerates (Srisuk, 2005).

Description

The left (SHM-PT 529) and right humeri (SHM-PT 530) are represented by their distal parts. They are elongated with a slender shaft, slightly curved in lateral view, with rounded capitulum.

The partial pelvic girdle (SHM-HY 231) consists of parts of the ischium, pubis, and acetabulum, while the ilium shaft is not preserved. The acetabular fossa is nearly circular with a posteriorly widened acetabular rim. The base of the ilium shaft has a triangular cross section. These features are reminiscent of an anuran amphibian, but the taxonomic identification of these incomplete specimens is difficult.

4.2 Unpublished material

Temnospondyli Zittel, 1888

Stereospondyli Zittel, 1888

Stereospondyli indet.

Reference material

CY-HN 378 (Fig. 5a–d), intercentrum (Laojumpon et al., 2014); CY-HN 364 (Fig. 5e–f), left clavicle bone; and CY-HN 365 (Fig. 5g–h), CY-HN 368 (Fig. 5i–j), and CY-HN 377 (Fig. 5k–l), dermal bones.

Formation/age

Huai Hin Lat Formation (Carnian–Norian).

Locality and sediment

These specimens were collected by a Thai–French paleontological team during an excursion in 2010 at Huai Nam Aun, an outcrop situated near the Nong Yakong village, Khon San District, Chaiyaphum Province. This locality contains various beds of limestone and mudstone, deposited in brackish water near a calcium carbonate source (Laojumpon et al., 2014). Other fossils such as *Hybodus* teeth, bony fish scales, and coprolites have also been found from this locality (Laojumpon et al., 2012, 2014).

Description

The material consists of an intercentrum and several fragments of dermal bones. A large intercentrum (CY-HN 378, Fig. 5a–d) is preserved over a length of approximately 65 mm and is 33 mm thick. CY-HN 378 is a disk-shaped intercentrum with reduced or absent pleurocentra (Laojumpon et al., 2014). The anterior and posterior faces of CY-HN 378 are concave. Laterally, the parapophyses are located in less than half of the total length. These features share characters with Stereospondyli (Milner et al., 1994; Witzmann and Gassner, 2008; Laojumpon et al., 2014). The shape of CY-HN 378 is comparable to those of the Metoposauroidea or Mastodonsauroidea intercentrum (Moser and Schoch, 2007; Sulej, 2007; Fortuny et al., 2019; Marzola et al., 2017). The Plagiosauroidea possess cylindrical intercentra (Warren and Snell, 1991; Konietzko-Meier et al., 2014). The Brachyopoidea commonly show a wedge-shaped intercentrum in lateral view (Shishkin, 1991; Warren and Snell, 1991; Warren et al., 1997, 2011; Warren and Dammiani, 1999; Averianov et al., 2008).

The other undescribed specimens are dermal bone fragments. The largest fragment (CY-HN 364, Fig. 5e–f) shows two distinct types of heavy ornamentation in ventral view, i.e., radial and polygonal sculptures. The radial sculpture

Description

All specimens are wedge-shaped intercentra. Both anterior and posterior surfaces are concave and show a marked circular notochordal canal, which is visible as a circular pit. The pleurocentra are reduced or absent, which is a typical feature of stereospondyls (Milner et al., 1994; Witzmann and Gassner 2008). The wedge-shaped morphology and the notochordal pit of TF 3328, TF 3329, and TF 3144 is consistent with the intercentrum morphology of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997, 2011; Warren and Dammiani, 1999), which are similar to the intercentra discovered from the Jurassic Indochina block, e.g., *Gobiops desertus* from the Gobi Desert of Mongolia (Shishkin, 1991).

Anura Fischer von Waldheim, 1813

Anura indet.

Reference material

SHM-PT 529 (Fig. 4a–b) and SHM-PT 530 (Fig. 4c–d), humeri; SHM-HY 231 (Fig. 4e–f), pelvic girdle (Srisuk, 2002, 2005).

Formation/age

Sao Khua Formation (Lower Cretaceous).

Locality and sediment

The humeri (SHM-PT 529 and SHM-PT 530) were collected in a road cut outcrop near Phu Phan Thong village, Muang District, Nong Bua Lamphu Province. These fossils were embedded in a pale olive fine-grained siltstone (Srisuk, 2002).

The pelvic girdle (SHM-HY 231) was discovered in a road cut outcrop near the Huai Lao Yang reservoir road, Nong Bua Lamphu Province. The outcrop is formed by reddish-brown micaceous siltstones and lime-nodule conglomerates (Srisuk, 2005).

Description

The left (SHM-PT 529) and right humeri (SHM-PT 530) are represented by their distal parts. They are elongated with a slender shaft, slightly curved in lateral view, with rounded capitulum.

The partial pelvic girdle (SHM-HY 231) consists of parts of the ischium, pubis, and acetabulum, while the ilium shaft is not preserved. The acetabular fossa is nearly circular with a posteriorly widened acetabular rim. The base of the ilium shaft has a triangular cross section. These features are reminiscent of an anuran amphibian, but the taxonomic identification of these incomplete specimens is difficult.

4.2 Unpublished material

Temnospondyli Zittel, 1888

Stereospondyli Zittel, 1888

Stereospondyli indet.

Reference material

CY-HN 378 (Fig. 5a–d), intercentrum (Laojumpon et al., 2014); CY-HN 364 (Fig. 5e–f), left clavicle bone; and CY-HN 365 (Fig. 5g–h), CY-HN 368 (Fig. 5i–j), and CY-HN 377 (Fig. 5k–l), dermal bones.

Formation/age

Huai Hin Lat Formation (Carnian–Norian).

Locality and sediment

These specimens were collected by a Thai–French paleontological team during an excursion in 2010 at Huai Nam Aun, an outcrop situated near the Nong Yakong village, Khon San District, Chaiyaphum Province. This locality contains various beds of limestone and mudstone, deposited in brackish water near a calcium carbonate source (Laojumpon et al., 2014). Other fossils such as *Hybodus* teeth, bony fish scales, and coprolites have also been found from this locality (Laojumpon et al., 2012, 2014).

Description

The material consists of an intercentrum and several fragments of dermal bones. A large intercentrum (CY-HN 378, Fig. 5a–d) is preserved over a length of approximately 65 mm and is 33 mm thick. CY-HN 378 is a disk-shaped intercentrum with reduced or absent pleurocentra (Laojumpon et al., 2014). The anterior and posterior faces of CY-HN 378 are concave. Laterally, the parapophyses are located in less than half of the total length. These features share characters with Stereospondyli (Milner et al., 1994; Witzmann and Gassner, 2008; Laojumpon et al., 2014). The shape of CY-HN 378 is comparable to those of the Metoposauroidea or Mastodonsauroidea intercentrum (Moser and Schoch, 2007; Sulej, 2007; Fortuny et al., 2019; Marzola et al., 2017). The Plagiosauroidea possess cylindrical intercentra (Warren and Snell, 1991; Konietzko-Meier et al., 2014). The Brachyopoidea commonly show a wedge-shaped intercentrum in lateral view (Shishkin, 1991; Warren and Snell, 1991; Warren et al., 1997, 2011; Warren and Dammiani, 1999; Averianov et al., 2008).

The other undescribed specimens are dermal bone fragments. The largest fragment (CY-HN 364, Fig. 5e–f) shows two distinct types of heavy ornamentation in ventral view, i.e., radial and polygonal sculptures. The radial sculpture

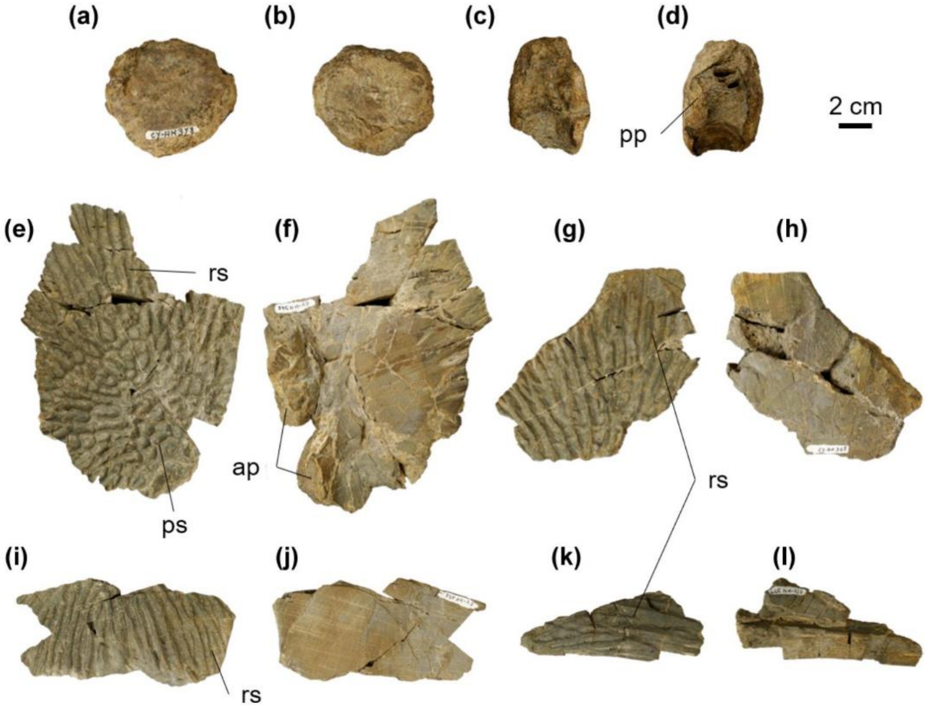

Figure 5. New Triassic amphibian remains from Thailand. An intercentrum of Stereospondyli indet. (CY-HN 378) in anterior **(a)**, posterior **(b)**, left **(c)**, and right **(d)** views. Dermal bone fragments of Stereospondyli indet. of CY-HN 364 **(e–f)**, CY-HN 365 **(g–h)**, CY-HN-368 **(i–j)**, and CY-HN-377 **(k–l)** in ventral view and dorsal view. Abbreviations: ap, ascending process; pp, parapophyses; ps, polygonal sculpture; rs, radial sculpture.

signed as either interclavicle or clavicle bones. Based on the shape of the intercentrum and ornamentation pattern, these specimens could refer to either the late Triassic Mastodonsauroidea (e.g. *Cyclotosaurus*) or Metoposauroidea (Chowdhury, 1965; Warren and Snell, 1991; Sulej and Majer, 2005; Sulej, 2007; Brusatte et al., 2015; Antczak and Bodzioch, 2018). Therefore, more evidence is required for a family-level identification.

Brachyopoidea Lydekker, 1885

Brachyopoidea indet.

Reference material

KS37-8 (Fig. 3m–p), intercentrum.

Formation/age

Phu Kradung Formation (Upper Jurassic).

Locality and sediment

KS37-8 was collected at the Khao Wong locality in Khao Wong District, Kalasin Province. Sediments in this locality are grey to green siltstones.

Description

KS37-8 is a wedge-shaped intercentrum with the dorsal edge much shorter than the ventral edge. The parapophyses are close to the posterodorsal margin on the lateral surface. Both anterior and posterior surfaces are concave and show a marked circular notochordal canal, which is visible as a circular pit. The pleurocentra are reduced or absent. This intercentrum KS37-8 probably belongs to Brachyopoidea since it is the only Stereospondyli superfamily retrieved beyond the Triassic (Buffetaut et al., 1994b). Furthermore, the wedge-shaped morphology of KS37-8 resembles the intercentra of the Brachyopoidea (Shishkin, 1991; Warren et al., 1997; Warren and Dammiani, 1999; Warren et al., 2011), which are similar to the intercentra discovered from the Indochina block (TF 3144) and Sibumasu blocks (TF 3328 and TF

3329) of Thailand (Buffetaut et al., 1994a, c). However, the intercentrum is not sufficiently diagnostic for identification at the family level.

Brachyopidae indet.

Reference material

KS34-1481, posterior part of a skull (Fig. 6a–b); KS34-1474 (Fig. 3q–t) and KS34-1489 (Fig. 3u–x), intercentrum.

Formation/age

Phu Kradung Formation (Upper Jurassic).

Locality and sediment

The specimens were found in an outcrop at the Phu Noi locality, near Ban Dinchi village, Kham Muang District, Kalasin Province. Sediments at this site are grey to green siltstones. Other vertebrate fossils consist of the hybodont shark *Acrodus kalasinensis*, the ginglymodian fish *Isanichthys lertboosi*, the lungfish *Ferganoceratodus annekempae*, the xinjiangchelyid turtles *Phunoichelys thirakupti* and *Kalasinemys prasarttongosothi*, the teleosaurid crocodilian *Indosinosuchus potamosiamensis*, dinosaurs, and pterosaurs (Buffetaut et al., 2014; Cuny et al., 2014; Deesri et al., 2014; Tong et al., 2015, 2019; Martin et al., 2018; Cavin et al., 2020).

Description

The material consists of three temnospondyl specimens not found in association: the posterior part of the skull (KS34-1481, Fig. 6a–b) and two intercentra (KS34-1474, Fig. 3q–t and KS34-1489, Fig. 3u–x). The skull (KS34-1481) is short (approximately 14 cm width and 12 cm length), lacking otic notch and tabular horn in the supratemporal region. Ventrally, the interpterygoid vacuities are large, and the cultriform process of the parasphenoid is gracile and long. Posteriorly, the occipital condyles are rounded and projected well behind the posterior edge of the skull. This specimen is under study for a more detailed anatomical description. The intercentra (KS34-1474 and KS34-1489) are wedge-shaped with concave posterior surface and slightly convex anterior surface. The anterior surface shows a well-marked deep circular pit. The short skull, which lacks otic notch and tabular horn, and the position of occipital condyles are typical characters of Brachyopidae (Warren and Marsicano, 1998, 2000), similar to those of the Jurassic brachyopid temnospondyl skull from China such as *Sinobrachyops placenticephalus* (Dong, 1985).

5 Discussion

Hitherto, the Upper Triassic Indochina block of Thailand revealed at least two taxa of temnospondyls consisting of *Cyclotosaurus* (Ingavat and Janvier, 1981) and the plagiosaurids (Suteethorn et al., 1988). Moreover, the newly discovered specimens from the Huai Hin Lat Formation, i.e., dermal bones (CY-HN 364, 365, 368, and 377) and an intercentrum (CY-HN 378), are of uncertain affinities. At first glance, the disk shape and circular periphery of CY-HN 378 resemble Metoposauroidea more than Mastodonsauroidea (Warren and Snell, 1991). However, recent studies indicated that the intercentra of both taxa are very similar in shape (Moser and Schoch, 2007; Sulej, 2007; Marzola et al., 2017; Fortuny et al., 2019). Therefore, it is difficult to assign the Thai intercentrum to a specific taxon. In addition, the dermal sculptures of clavicles (CY-HN 364, CY-HN 365, CY-HN 368, and CY-HN 377), consisting of polygonal and radial patterns, are comparable to the ornamentation observed in Metoposauroidea, e.g., *Metoposaurus algarvensis*, *M. maleriensis*, and *M. krasiejowensis* (Chowdhury, 1965; Brusatte et al., 2015; Antczak and Bodzioch, 2018), and Mastodonsauroidea, e.g., *Cyclotosaurus intermedius* (Sulej and Majer, 2005).

For the aforementioned reasons, the Thai postcranial specimens are possibly related to Metoposauroidea or Mastodonsauroidea. Metoposauroidea are known from the Late Triassic of Africa (Dutuit, 1978; Fortuny et al., 2019), Europe (von Meyer, 1842; Sulej, 2002, 2007; Milner and Schoch, 2004; Brusatte et al., 2015), North America (Case, 1922; Branson and Mehl, 1929; Zeigler et al., 2002; Lucas et al., 2010), and India (Chowdhury, 1965; Sengupta, 2002; Chakravorti and Sengupta, 2019), but they have not been reported in Southeast Asia. Mastodonsauroidea have been reported in Europe (Maryanska and Shishkin, 1996; Schoch, 1999; Fortuny et al., 2011; Sulej and Niedźwiedzki, 2013), Australia (Warren, 1972; Damiani, 1999), North and South America (Schoch, 2000; Eltink et al., 2017; Marzola et al., 2017), Africa (Damiani, 2001; Shishkin et al., 2004; Dahoumane et al., 2016; Peecook et al., 2017), Russia (Novikov and Ilyina, 1995), India (Mukherjee and Sengupta, 1998; Damiani, 2001), Japan (Nakajima and Schoch, 2011), China (Liu and Wang, 2005; Liu, 2016), and Thailand (Ingavat and Janvier, 1981). Dzik and Sulej (2007) noted that Metoposauroidea and Mastodonsauroidea have sometimes been discovered in the same locality, i.e., the Krasiejów clay pit in Poland, suggesting that the discovery of fossils of Metoposauroidea in the Late Triassic rocks of Thailand is possible as well.

From the biological point of view, Buffetaut and Suteethorn (1998) noted that the freshwater vertebrate remains from the Late Triassic Huai Hin Lat Formation are reminiscent of the Norian Stubensandstein Formation from Germany. Both formations have yielded remains of actinopterygian fishes (semionotids), turtles, amphibians (cyclotosaurids), and phytosaurs (Ingavat and Janvier 1981; Buffetaut and Ingavat, 1982; Tong et al., 2003; Milner and Schoch, 2004; Lopez-Arbarello, 2008; Havlik et al., 2013; Laojumpon et al., 2014), suggesting a biogeographical link between the Indochina block, and Laurussia. This conclusion agrees with the hypothesis of a large physical

3329) of Thailand (Buffetaut et al., 1994a, c). However, the intercentrum is not sufficiently diagnostic for identification at the family level.

Brachyopidae indet.

Reference material

KS34-1481, posterior part of a skull (Fig. 6a–b); KS34-1474 (Fig. 3q–t) and KS34-1489 (Fig. 3u–x), intercentrum.

Formation/age

Phu Kradung Formation (Upper Jurassic).

Locality and sediment

The specimens were found in an outcrop at the Phu Noi locality, near Ban Dinchi village, Kham Muang District, Kalasin Province. Sediments at this site are grey to green siltstones. Other vertebrate fossils consist of the hybodont shark *Acrodus kalasinensis*, the ginglymodian fish *Isanichthys lertboosi*, the lungfish *Ferganoceratodus annekempae*, the xinjiangchelyid turtles *Phunoichelys thirakupti* and *Kalasinemys prasarttongosothi*, the teleosaurid crocodilian *Indosinosuchus potamosiamensis*, dinosaurs, and pterosaurs (Buffetaut et al., 2014; Cuny et al., 2014; Deesri et al., 2014; Tong et al., 2015, 2019; Martin et al., 2018; Cavin et al., 2020).

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In the Jurassic sequence of Thailand, the previous records of Mesozoic amphibians were limited to intercentra remains (TF 3328, TF 3329, TF 3144), which share common characters with Brachyopoidea intercentra (Shishkin, 1991). Remains of Brachyopoidea have been discovered in Australia (Damiani and Warren, 1996; Cosgriff, 1973; Warren and Hutchinson, 1983; Warren et al., 2011), Africa (Chernin, 1977; Warren and Dammiani, 1999; Damiani and Rubidge, 2003; Damiani and Kitching, 2003), South America (Marsicano, 1993, 1999, 2005; Ruta and Bolt, 2008; Dias-da-Silva et al., 2012), Russia (Shishkin, 1967), Antarctica (Cosgriff and Hammer, 1984), India (Sengupta, 1995), Mongolia (Shishkin, 1991), and China (Dong, 1985). The new Brachyopidae skull (KS34-1481) from the Phu Noi locality, briefly described in this study, resembles that of *Sinobrachyops placenticephalus* Dong, 1985 from China, suggesting that these forms are related. This would indicate a biogeographical link between the Sibumasu block and the Chinese sediments. Moreover, the wide distribution of temnospondyls in Asian continental blocks during the Jurassic supports the view that the Sibumasu block and Indochina block were already in contact (Buffetaut et al., 1994a; Buffetaut and Suteethorn, 1998).

Amphibian fossils from the Early Cretaceous of northeastern Thailand are described and related to anurans, although these specimens are too fragmentary to be more precisely identified. In the Cretaceous, Asian anurans have been discovered in Kazakhstan (Skutschas and Kolchanov, 2017), Mongolia (Gao and Chen, 2017), India (Prasad and Rage, 2004), Japan (Evans and Manabe, 1998), China (Wang et al., 2000; Yuan, 2004; Dong et al., 2013), and Myanmar (Xing et al., 2018). Thus, the discovery of this taxon suggests that during the Early Cretaceous, anurans were already present in Thailand.

6 Conclusions

The non-marine Mesozoic sedimentary rocks from Thailand were formed in the Indochina and Sibumasu blocks. These blocks have yielded at least four taxa of amphibians, including three taxa of temnospondyls (*Cyclotosaurus* cf. *posthumus*, Plagiosauridae, and Brachyopidae) and one taxon of anuran from four formations (Huai Hin Lat Formation, Khlong Min Formation, Phu Kradung Formation, and Sao Khua Formation) with ranges from the Late Triassic to Early Cretaceous. The Thai amphibian fossils show the most diverse Mesozoic amphibian record in Southeast Asia, and this agrees with the hypothesis of a large physical connection between the Indochina block and Laurussia during the Mesozoic era.

Data availability. All material included in this paper is deposited in the Palaeontological Research and Education Centre, Mahasarakham University and in the collection of the Department of Mineral Resources (Thailand).

Author contributions. TN and SM produced the images. TN and KL drafted the manuscript. All authors prepared the paper and contributed to the editing.

Competing interests. The authors declare that they have no conflict of interest.

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