



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on the Thai amphibian palaeo-diversity based on the literature, re-examination of published material, new findings, and unpublished material.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 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, 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 (Metcalf, 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).

- 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).
- 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), crocodylians (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.

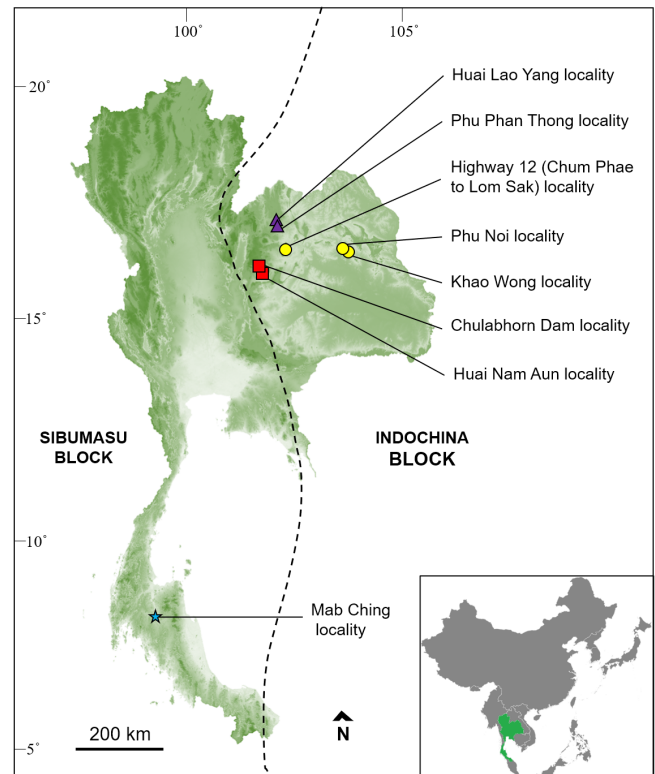


Figure 1. Mesozoic amphibian outcrops from Thailand (symbol); locality in ■ Huai Hin Lat Formation (Upper Triassic), ★ Klong Min Formation (Middle or Upper Jurassic), ● Phu Kradung Formation (Upper Jurassic), and ▲ Sao Khua Formation (Lower Cretaceous).

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).

Table 1. Mesozoic amphibian records from Thailand.

Formation	Systematic paleontology	Material	Reference
Huai Hin Lat Fm. (Carnian–Norian)	<i>Cyclotosaurus</i> cf. <i>posthumus</i>	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).

Plagiosauroida 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.

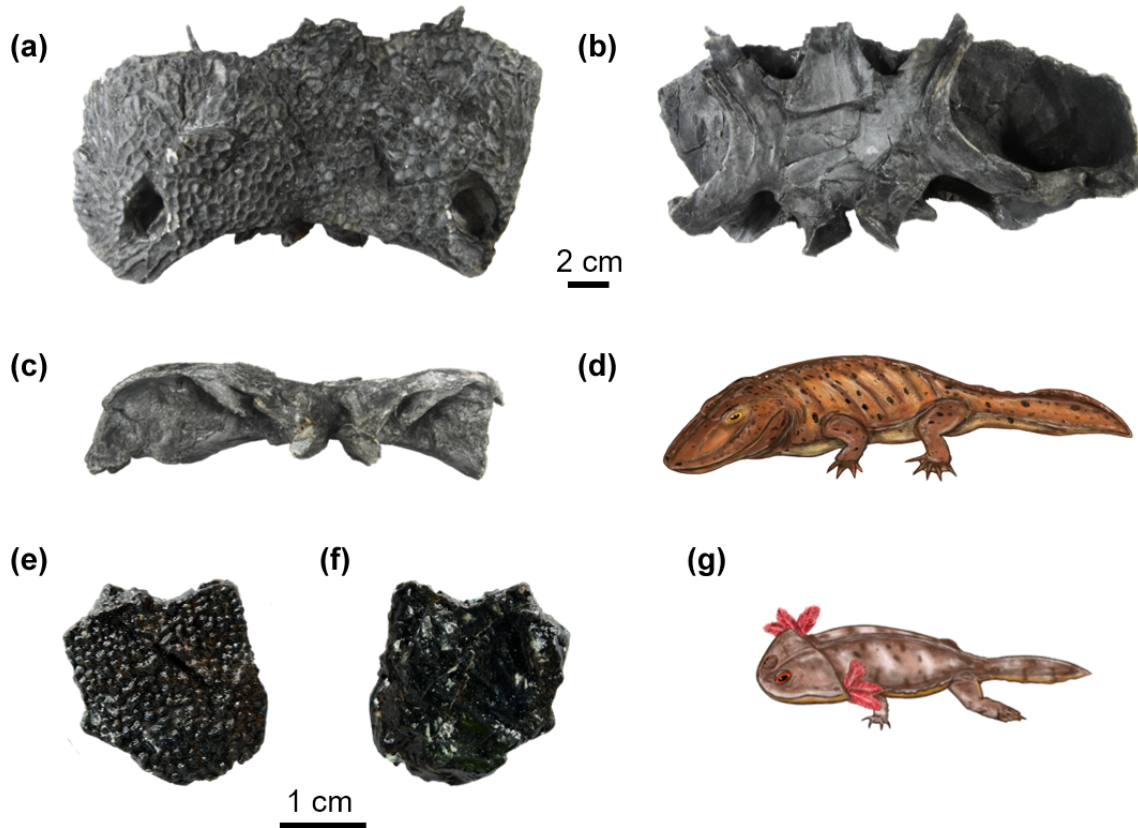


Figure 2. Triassic amphibian remains from Thailand. A replica skull of *Cyclotosaurus* cf. *posthumus* (D.M.R. Ch.D 001) in dorsal (a), palatal (b), and posterior views (c). A reconstruction of Thai *Cyclotosauridae* (d). A dermal bone of *Plagiosaurioidea* indet. (TF 1453) in ventral (e) and dorsal (f) views. A reconstruction of Thai *Plagiosaurioidea* (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.

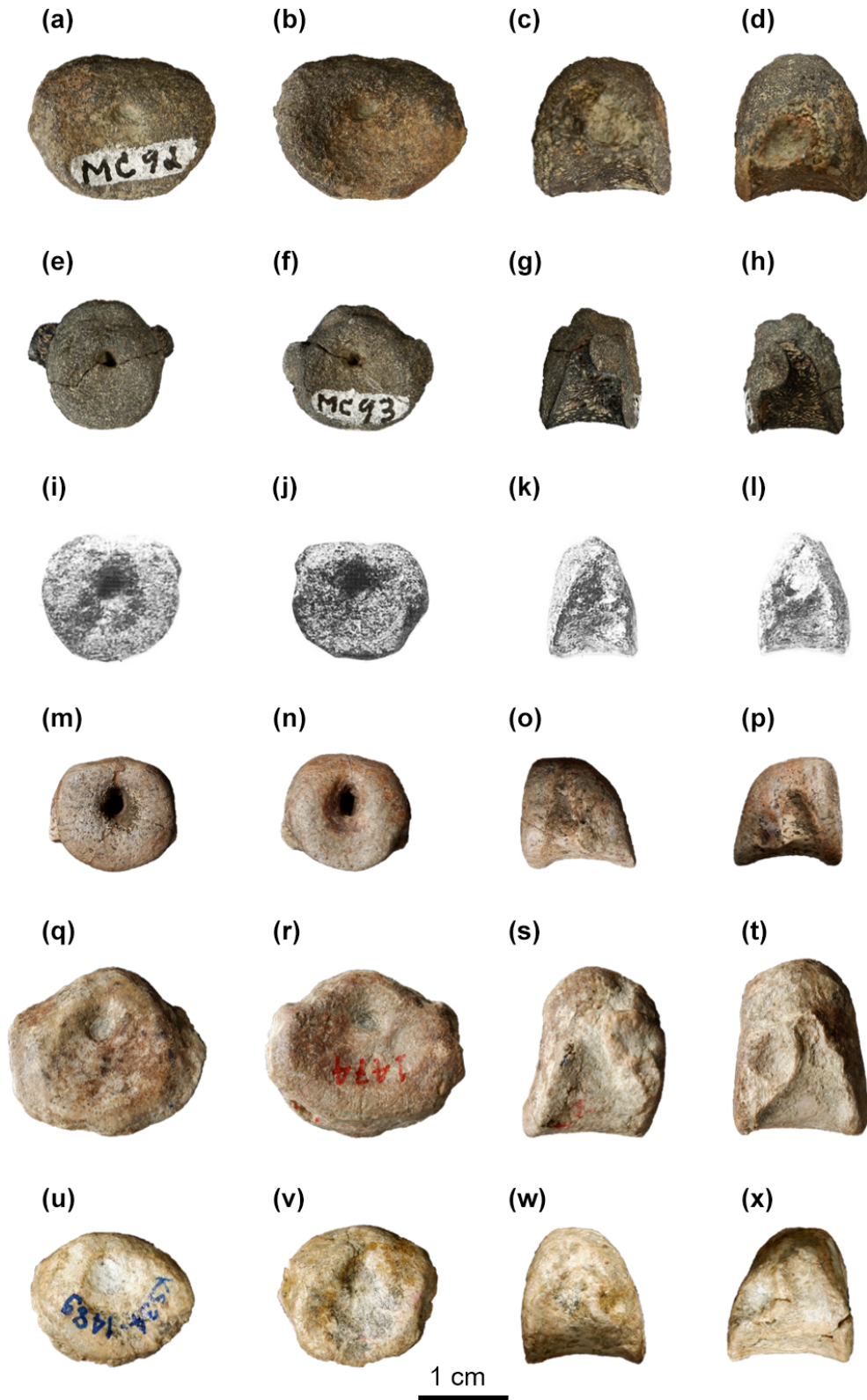


Figure 3. Thai Brachyopoidea indet. intercentra, TF 3228 (a–d), TF 31229 (e–h), TF 3144 (i–l, after Buffetaut et al., 1994b; fig. 1), and KS37-8 (m–p). Thai Brachyopidae indet. intercentra, KS34-1474 (q–t) and KS34-1489 (u–x). Anterior views (a, e, i, m, q, u), posterior views (b, f, j, n, r, v), left 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 Metoposauroida or Mastodonsauroida intercentrum (Moser and Schoch, 2007; Sulej, 2007; Fortuny et al., 2019; Marzola et al., 2017). The Plagiosauroida 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

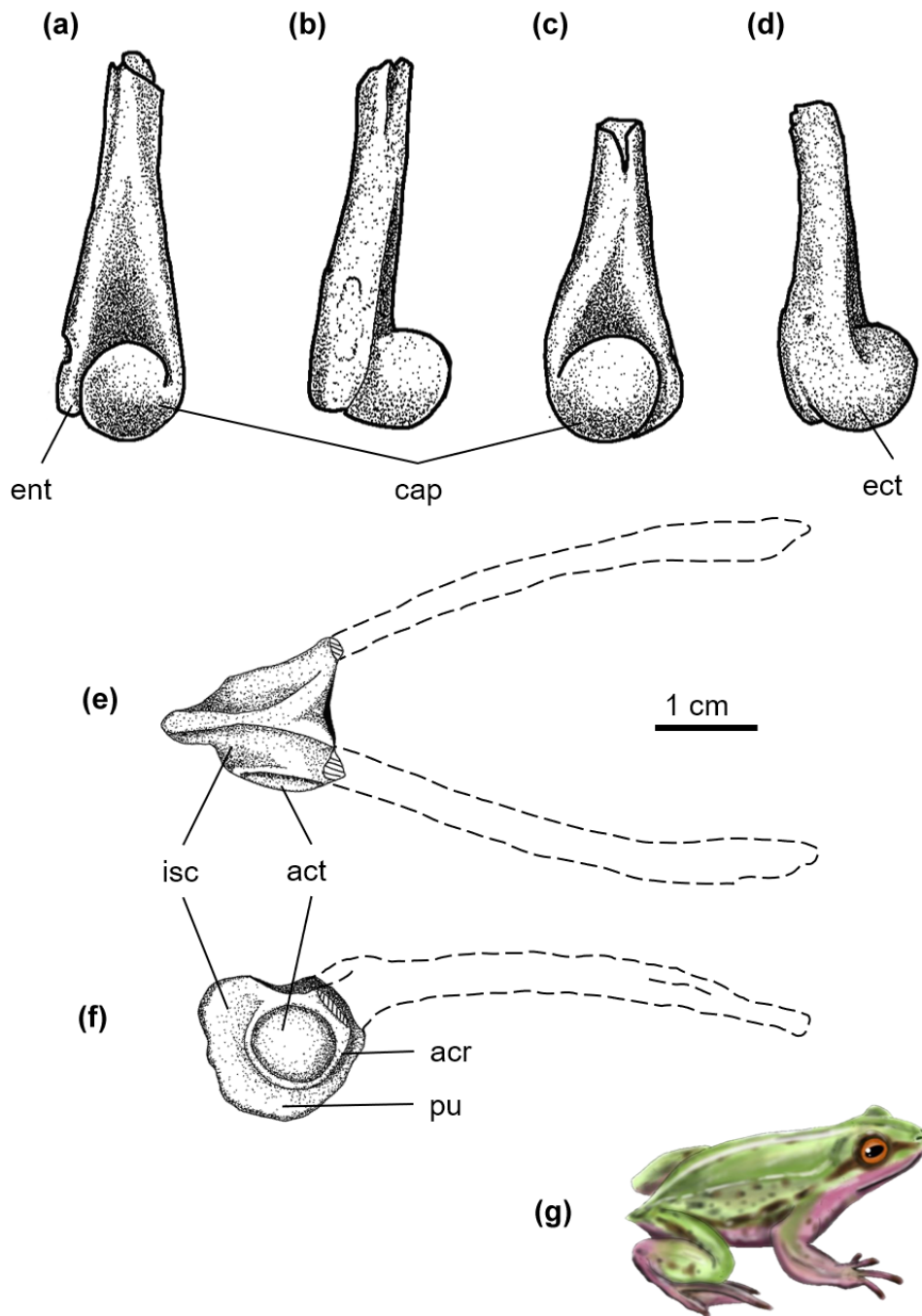


Figure 4. Cretaceous anuran remains from Thailand: left humerus, SHM-PT 529 in ventral (a) and medial view (b); right humerus, SHM-PT 530 in ventral (c) and medial view (d). Partial pelvic girdle, SHM-HY 231 in dorsal (e) and lateral view (f) (after Srisuk, 2002, 2005). Reconstruction of Thai anuran (g) is not to scale (drawn by Sita Manitkoon). Abbreviations: act, acetabulum; acr, acetabulum rim; cap, capitulum; ect, ectepicondyle; ent, entepicondyle; isc, ischium; pu, pubis.

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. The other small dermal fragments, i.e., CY-HN 365 (Fig. 5g–h), CY-HN-368 (Fig. 5i–j), and CY-HN-377 (Fig. 5k–l), are covered by radial and polygonal ornamentation in ventral view. These specimens, however, could be as-

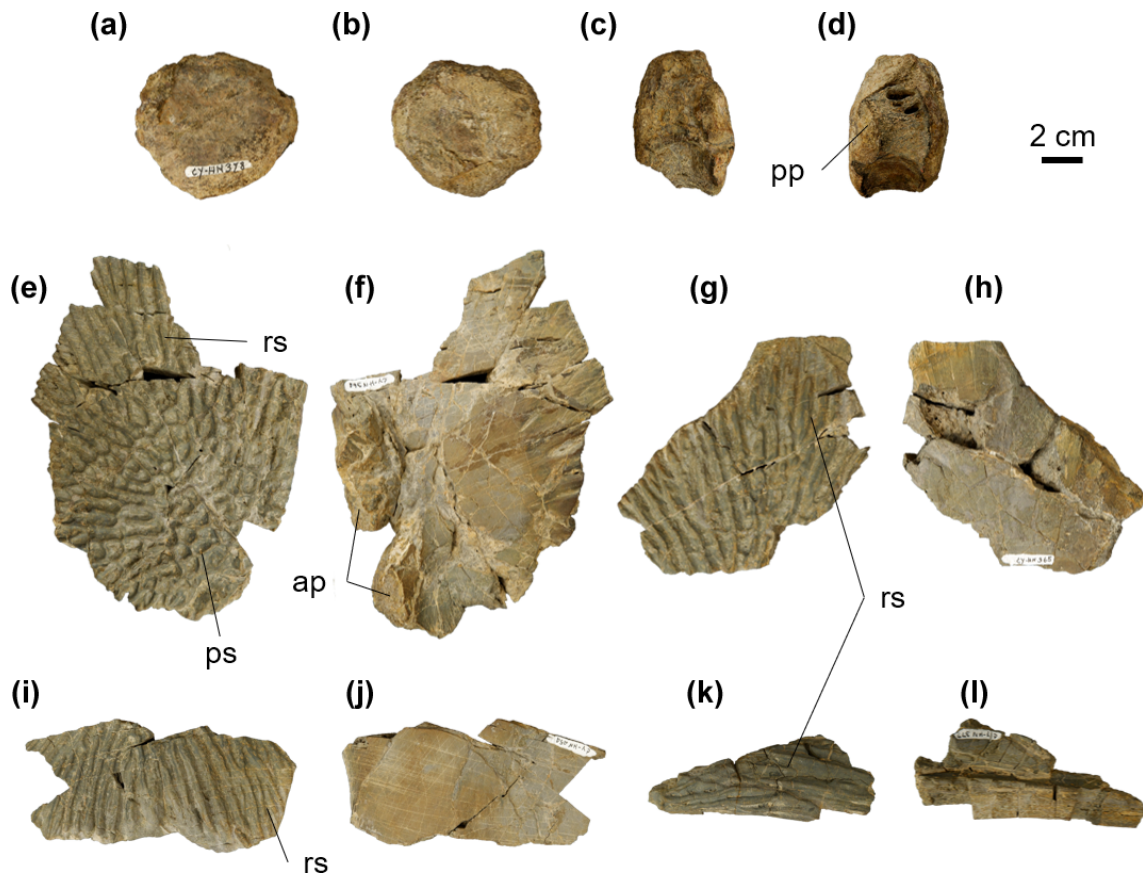


Figure 5. New Triassic amphibian remains from Thailand. An intercentrum of *Stereospondyli* indet. (CY-HN 378) in anterior (a), posterior (b), left (c), and right (d) views. Dermal bone fragments of *Stereospondyli* indet. of CY-HN 364 (e–f), CY-HN 365 (g–h), CY-HN-368 (i–j), and CY-HN-377 (k–l) in ventral 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 annekepaie*, the xinjiangchelyid turtles *Phunoichelys thirakupti* and *Kalasinemys prasarttongosothi*, the teleosaurid crocodylian *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. malleriensis*, 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; Peacock 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

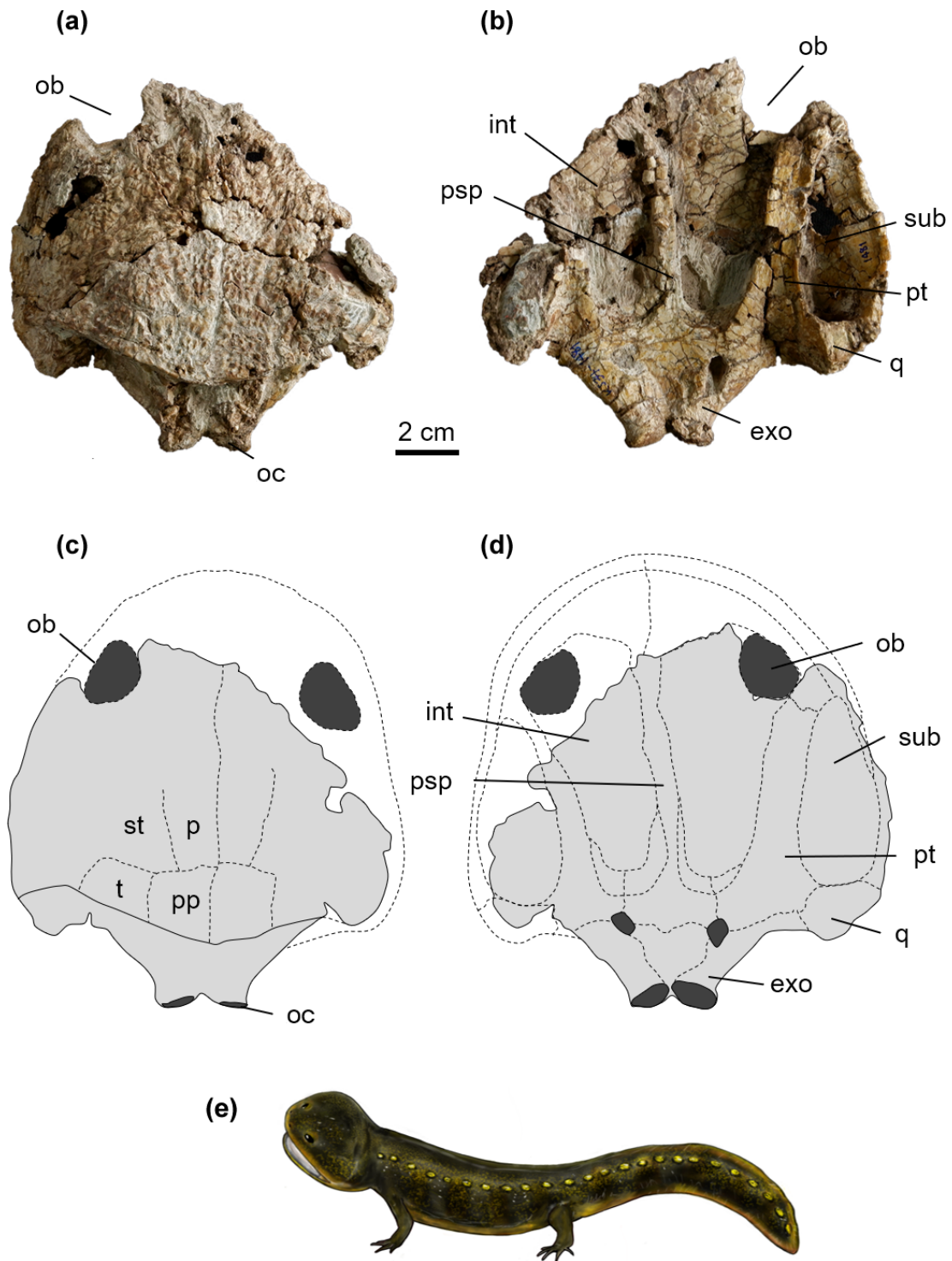


Figure 6. Posterior part skull of Brachyopidae indet. (KS34-1481) from Phu Noi locality, in dorsal (a) and palatal views (b). Reconstruction outline of KS34-1481 (estimate reconstruction outline of the anterior part based on *Sinobrachyops placenticephalus* Dong, 1985) in dorsal (c) and palatal views (d). Reconstruction of Thai Brachyopidae (e) is not to scale (drawn by Sita Manitkoon). Abbreviations: oc, occipital condyles; exo, exoccipital; int, interpalatal vacuities; ob, orbit; p, parietal; pp, postparietal; pt, pterygoid; psp, parasphenoid; st, supratemporal; sub, subtemporal fossa; t, tabular; q, quadrate.

connection between the North China block, South China block, Indochina block and Laurussia during the Mesozoic era (Permo–Triassic boundary) (Ingavat and Janvier 1981; Bercovici et al., 2012; Arbez et al., 2018; 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, 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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