Tropical Natural History, Supplement 7 (2023): 139–150
Date of publication: 6 May 2023

The First Record of a Ray-finned Fish (Actinopterygii, Palaeoniscidae) from the Lower to Middle Permian of Tak Fa Formation in Phetchabun, Central Thailand

SATAPAT KUMPITAK[1], SUTATCHA HONGSRESAWAT[2], PAIPHAN PAEJAROEN[3], AND KANTAPON SURAPRASIT[4]*

[1]*Department of Geology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND*
[2]*Division of Geoscience, Faculty of Science, Mahidol University, Kanchanaburi Campus, Kanchaburi 71150, THAILAND*
[3]*Conservation Biology Program, Faculty of Science, Mahidol University, Kanchanaburi Campus, Kanchaburi 71150, THAILAND*
[4]*Center of Excellence in Morphology of Earth Surface and Advanced Geohazards in Southeast Asia (MESA CE), Department of Geology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND*
*Corresponding author. Kantapon Suraprasit (kantapon.s@chula.ac.th)
Received: 21 August 2022; Accepted: 27 December 2022

ABSTRACT.– The actinopterygian fossil was found from the Permian carbonate succession of Tak Fa Formation, Saraburi Group, in Bueng Sam Phan District, Phetchabun Province, central northeast Thailand. The partially preserved body part with ganoid scales is identified as belonging to a ray-finned fish (subclass Actinopterygii). The squamation is composed of smooth-surfaced articulated scales with a hard-diamond shape. The posterior part of the specimen showed some translucent ganoine covering mineralized bone layers. The microstructure of squamation is characterized by the presence of 3–6 ridges running parallel to the antero-ventral margin of scales on the bone layer. This suggests that the Paleozoic actinopterygian specimens from Phetchabun likely belong to *Palaeoniscum* sp. The age of the fauna is assigned to the Early to Middle Permian based on the presence of microfossils and invertebrates recovered from nearby areas. The paleoenvironments of the area corresponded to lagoons or subtidal zones with a low-energy depositional condition according to lithological, stratigraphical, and petrographic examinations of limestones interbedded with shales. This study represents the first record of palaeoniscids from Southeast Asia during the Early to Middle Permian and supported the idea that the Indochina terrane was a part of epeiric seas at that time.

KEYWORDS: bony fish, paleobiogeography, paleoenvironment, Paleozoic, Southeast Asia, taxonomy

INTRODUCTION

Ray-finned fishes (subclass Actinopterygii) are one of the major vertebrate groups and the most successful fish radiations in a long evolutionary history (Nelson, 2006; Friedman and Smith, 2015). Actinopterygian scales first appeared during the Late Silurian according to fossil records in Gotland, Sweden (Märss, 2001). However, the diversity of osteichthyan fishes (known as a bony fish) decreased during the Early Permian. In freshwater environments, a group of fishes was dominated by lungfishes and palaeopterygians, while other contemporaneous fish groups such as subholosteans and marine palaeopterygians were the major bony fishes living in the ocean (Romano et al., 2016). After the end of the Guadalupian extinction event, environmental changes that occurred during that time have been dramatically affected the world largest fish populations such as chondrichthyan fishes (Pitrat, 1973; Koot, 2013). As a result, osteichthyan fishes became more dominant and abundant, while the diversity of chondrichthyan fishes dropped towards the end of the Permian (Pitrat, 1973; Koot, 2013).

In Thailand, the oldest-known vertebrate faunas (i.e., chondrichthyans, acanthodians, and Palaeoniscoidei indet.) were recorded from the Devonian limestones of Mae Sam Laep in Mae Hong Son Province (Long and Burrett, 1989). The fauna contained six taxa (*Thrinacodus* (*Harpagodens*) *ferox*, *Symmorium* sp?, *Cladodus* sp., cf. *Cladodus acutus*, *Phoebodus australiensis*, and *Siamodus janvieri* (Long and Burrett, 1989; Long, 1990). Later on, the fossils of indeterminate psammodontids were reported from the Carboniferous massive limestones of Ban Pak Chom and the remains of *Deltodus* sp. were recovered from the Lower Permian limestones strata of Ban Na Chareon in Loei Province by Janvier (1981). However, the majority of vertebrate fossils in Thailand have so far been found from the Mesozoic red bed sequences.

Abundant fossils of actinopterygians were reported from the Mesozoic continental red beds of the Khorat Group in Northeastern Thailand (Buffetaut and Suteethorn, 1998). A total of 6 species of actinopterygians have been named, including mostly ginglymodians such as *Isanichthys palustris* (Cavin & Suteethorn, 2006), *I. lertboosri* (Deesri et al., 2014), *Thaiichthys buddhabutrensis* (Cavin et al., 2013), *Khoratichthys gibbus* (Deesri et al., 2016), *Lanxangichthys alticepha-lus* (Cavin et al., 2019), and a single sinamid, *Siamamia naga* (Cavin et al., 2007). Another Palaeonisciformes, cf. *Ptycholepis*, was also found (Cavin et al., 2009). Other groups of actinopterygians including pycnodontids, sinamiids, vidalamiines and some ginglymodians were reported from this region but represented only by fragments of skins and teeth.

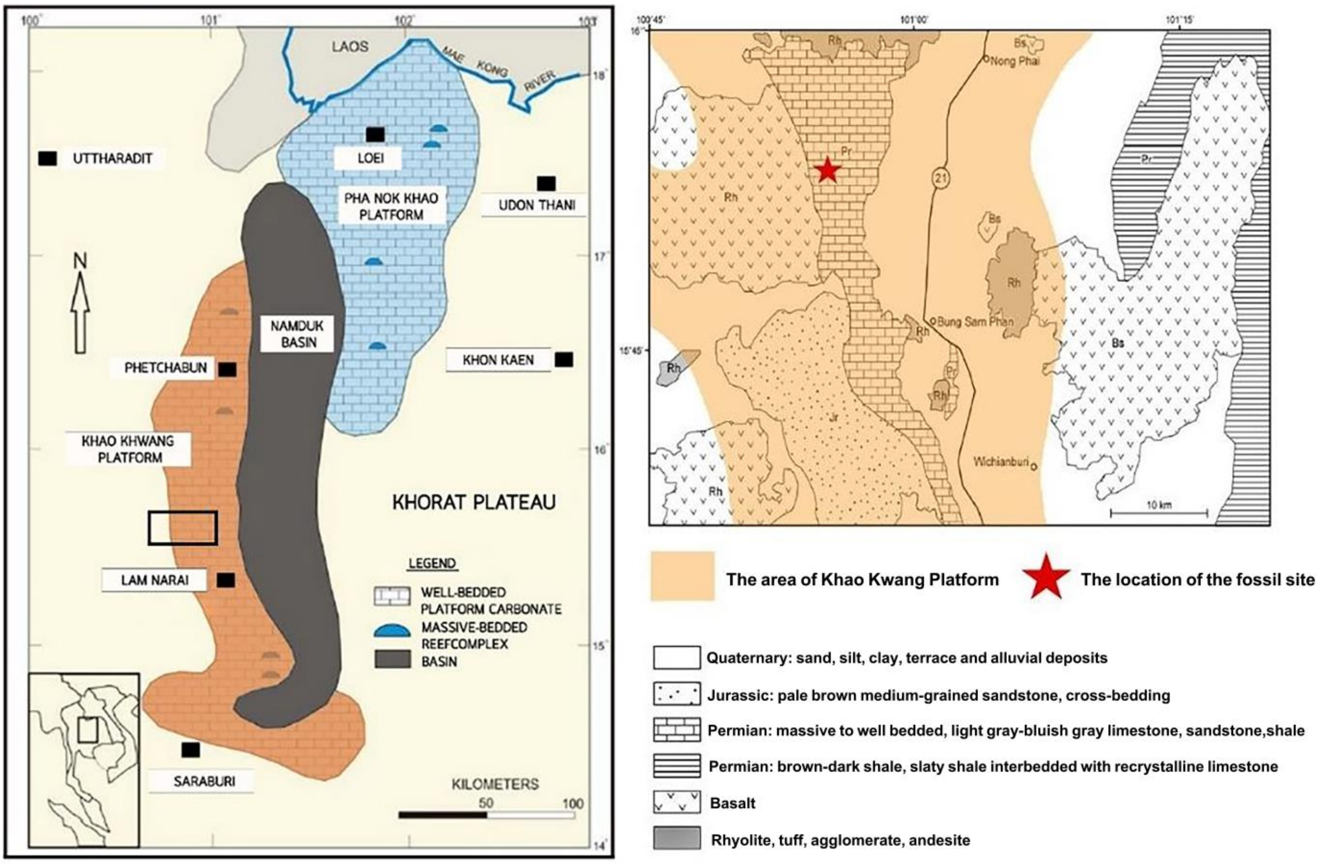

FIGURE 1. Permian carbonate platforms and siliciclastic basins along the western rim of Indochina Block. (modified from Chonglakmani and Fontaine, 1990) and the location of the fossil site (red star) on the area of Khao Kwang Platform (modified from Chitnarin et al., 2008).

In 2009, an actinopterygian fossil was collected from the Permian limestones strata near Ban Wang Pla, Bueng Sam Phan District, Phetchabun Province in the upper central region of Thailand (Fig. 1). The outcrop of limestones interbedded with shales where the fossil was found has been correlated to the Tak Fa Formation within the Saraburi Group, suggesting the age ranging from the Early to late Middle Permian (Altermann, 1989).

In this study, we described and identified the fossil specimens of an actinopterygian in order to investigate the paleoenvironments of the area. The taxonomic study of this fish fossil will contribute not only to the understanding of an evolutionary history of bony fishes in Thailand, but also to the reconstruction of paleoenvironmental contrasts between the Shan-Thai terrane in the west and the Indochina terrane in the east. In addition, this study will provide the first empirical evidence of vertebrate remains from the Permian strata of central Thailand.

Geological Setting

The fossil site (coordinates: 15°53’02.9”N, 100°53’ 28.1”E) is located at Ban Wang Pla, Phaya Wang Sub-District, Bueng Sam Phan District, Phetchabun Province, 280 kilometers far from Bangkok, in the upper central part of Thailand. Most of the Permian carbonate sequences in this region are members of the Saraburi Group (Yanagida, 1967; Sakagami, 1975; Charoenprawat and Wongwanich, 1976; Nakornsri, 1977, 1981; Chonglakmani and Sattayalak, 1979; Hinthong, 1981, 1985; Wieldchowsky and Young, 1985), and can be correlated to the Khao Khad and the Pang Asok formations in the Saraburi Province based on the presence of marine invertebrate faunas.

According to Nakornsri (1977, 1981), the Tak Fa Formation is a part of the large carbonate facies in the Khao Kwang Platform (Fig. 1) containing limestones interbedded with shales and chert nodules. This formation covers the large area of central Thailand, expanding from the western to southern part of Phetchabun Province to the southeastern part of Nakhon Sawan Province and the Khao Luak in Lopburi Province. The age of the formation ranges from the Early Permian to late Middle Permian (Murgabian or Roadian-Wordian age) according to the presence of fusulinid and coral fossils (Altermann, 1989).

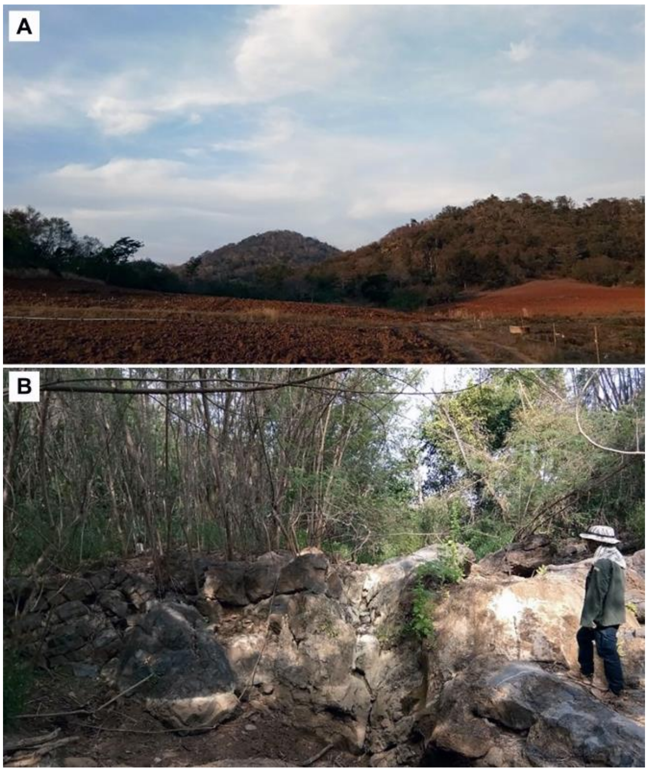

FIGURE 2. Views of the fossil locality (**A**) and the surrounding outcrop in the area (**B**) of Ban Wang Pla, Phaya Wang Sub-District, Bueng Sam Phan District, Phetchabun.

Yanagida (1967) and Sakagami (1975) described invertebrate fossils collected from the Nong Phai area and suggested a middle Middle Permian to late Middle Permian age. In Bueng Sam Phan, Phetchabun, Chonglakmani and Fontaine (1990) proposed that the age of carbonate strata distributed in the area was possibly attributed to the Middle to Late Permian based on the presence of fossil rugosa (*Ipciphyllum* and *Wentzelloides*) and tabulate (*Pseudohuangia* and *Sinopora*) corals, fusulinids (*Sumatrina longissimi* and *Verbeekina verbeeki*), and foraminifera (*Paleaeotextularia*, *Climacammina*, and *Pseudovermiporella nipponica*) along with other fauna elements such as brachiopods (Grant, 1976; Waterhouse, 1982), gastropods (Sone, 2010), fenestrate bryozoans, sponges, and bivalves, suggesting the continuous deposits within a shallow marine platform.

Later on, Ueno and Charoentitirat (2011) mentioned that the age of Tak Fa Formation ranges from the Latest Carboniferous to Middle or late Middle Permian based on biostratigraphic correlations (e.g., fusulinids, brachiopods, bryozoans, and conodonts). However, Ketwetsuriya et al. (2014, 2016a, b) proposed that the Tak Fa Formation is of a Yakhtashian or Artinskian age (late Early Permian) to a Midian or Capitanian age (late Middle Permian) based on the presence of fusulinoidean limestones from the eastern part of Nakhon Sawan (Napradit, 2005). Based on the study of fossil gastropods from Permian carbonate rocks at Tak Fa and Takhli Districts in Nakhon Sawan, Ketwetsuriya et al. (2016b) suggested a Wordian age for the fauna. However, Chitnarin et al. (2017) re-assigned the age of Tak Fa Formation to the Lower Permian (Artinskian age) due to the presence of the fusulinids *Pamirina* sp. and *Pseudofusulina* sp. In addition, the study of fossil conodonts and ostracods by Metcalfe and Sone (2008) and Chitnarin et al. (2012) revealed that the age of Tak Fa Formation might have been correlated to the late Early to early Middle Permian. The most recent study on the diversity patterns of Permian gastropod assemblages and ostracods in the Tak Fa Formation along with the presence of fusulinids *Verbeekina verbeeki* and *Parafusulina* sp. has indicated a late Middle Permian age (Wordian to Capitanian age) (Ketwetsuriya et al., 2021; Chitnarin et al., 2022b). In this study, based on the presence of foraminifera and invertebrate fossils from these aforementioned chronological data in Bueng Sam Phan (Chonglakmani and Fontaine, 1990), Nong Phai (Yanagida, 1967; Sakagami; 1975), and surrounding areas in Nakhon Sawan (Ketwetsuriya et al., 2014, 2016a, b), the age of the actinopterygian fish fossil possibly ranges from the Early to Middle Permian.

The outcrop is positioned on the small hill near an agricultural area (Fig. 2A) and consists of argillaceous limestones interbedded with shales, mudstones, and dolomitic limestones (Fig. 2B). In some parts of the formations, siliceous or chert nodules and invertebrate fossils such as bivalves, brachiopods, gastropods, tabulate corals, bryozoans, ostracods, and fusulinids were found, suggesting a shallow marine carbonate platform with lagoonal environments (Altermann, 1989; Chonglakmani and Fontaine, 1990; Chitnarin et al., 2008; Ueno and Charoentitirat, 2011; Ketwetsuriya et al., 2016a, b). The fish fossil was found from a loose block containing a thin layer of laminated limestones interbedded with calcareous shales. Based on the field observation and microscopic studies, the lithostratigraphic section is divided into four units (A–D) in ascending order (Fig. 3).

- Unit A: argillaceous limestones with ostracod and bivalve fossils
- Unit B: laminated limestones interbedded with laminated shales
- Unit C: laminated calcareous shales interbedded with limestones lens and laminated/wavy limestones
- Unit D: laminated shales

Based on the petrographic analysis, the unit A contains fossiliferous biomicrites, whereas the unit B is

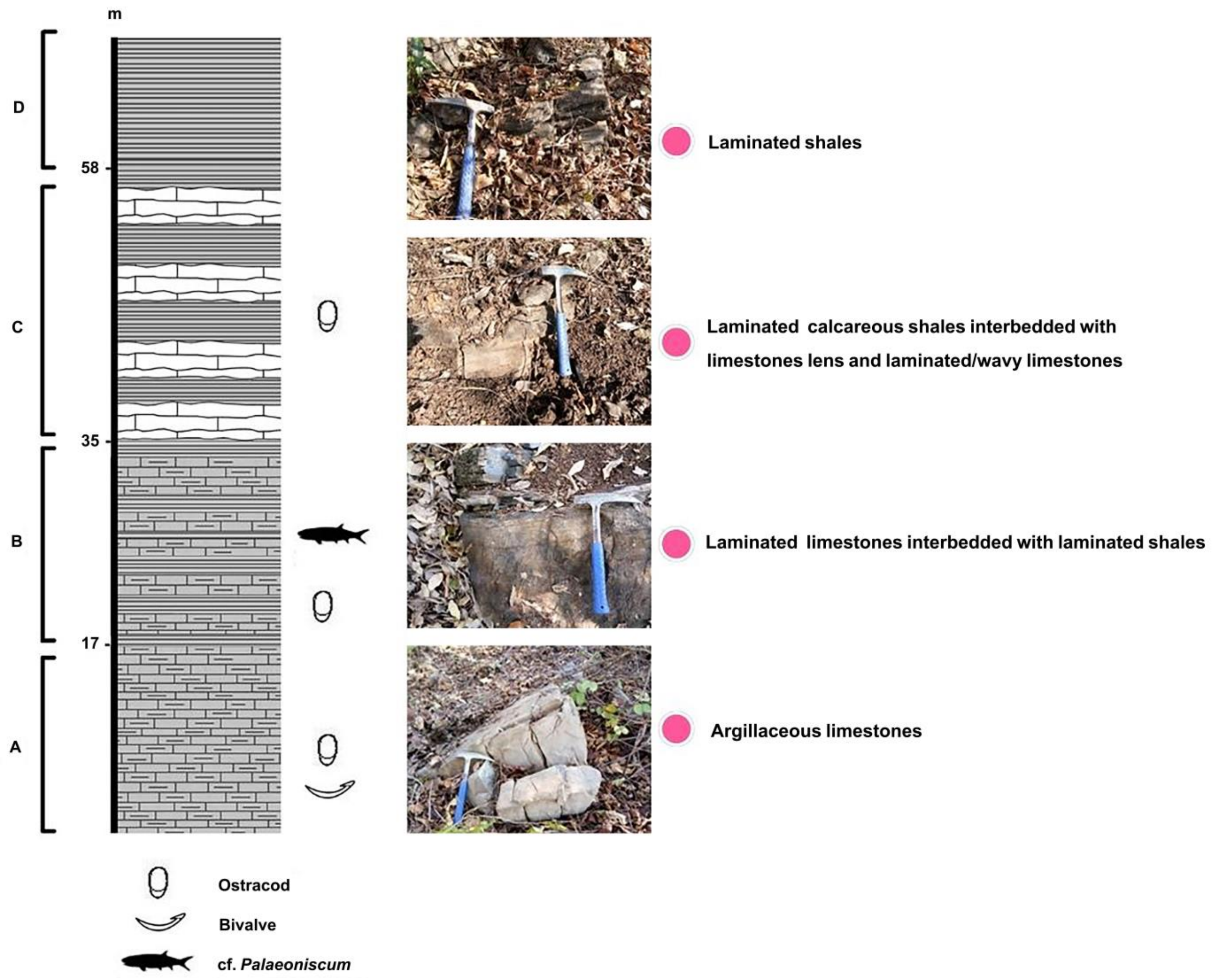

FIGURE 3. A lithologic column of fossil locality at Ban Wan Pla, Bueng Sam Phan District, Phetchabun. The section is divided into four units (**A–D**).

composed of micrites interbedded with calcareous mudstones with a sharp-gradational contact. Some ostracod fossils were observed on the surface of limestones. The actinopterygian fossil specimen was collected from the middle part of the unit B. The unit C comprises micrites interbedded with calcareous claystones and is characterized by limestones lens (probably ball and pillow structures) and lenticular-wavy laminations (irregular bedding). The unit D contains successive calcareous claystones with a sharp contact between each layer, up to the top of the hill (Fig. 2A).

Preliminary Taphonomic Assessment

Although the body part of a fish fossil has been well preserved, it lacks key features for identification such as cranial and caudal elements. However, the taphonomic process observed in the microstructure and the mode of preservation of fossils allow us to have access to the squamation (Figs 4, 5). The ganoin layer (enamel layer) and ridges on the bone layer are visible through the specimen.

In general, fossils of nektonic animals are extremely rare and are not often found in a well-preserved condition. The nektonic remains are usually buoyant by bacterial decay gases and are floated to the surface before sinking down to the sea floor (Elder and Smith, 1988). In the meantime, the remains have decayed and disintegrated before being deposited on the sediment layer by wave and physical energies (Elder and Smith, 1988). Despite the nektonic remains deposited on the sediment layer, they might have been disturbed by scavengers and oxygen reaction (Elderand and Smith, 1988). As evidenced by the preservation of the fossil specimen, lithostratigraphic information, and invertebrate faunas, fish remains sank down to the seafloor and were quickly buried in soft sediments under the low-energy environmental condition. This allowed the good preservation of remains without being disturbed by scavengers, turbulent flow, and/or oxygen reaction.

MATERIALS AND METHODS

The specimens CUF-BSP-F01 and CUF-BSP-F02 are stored at the Department of Geology, Faculty of Science, Chulalongkorn University. The specimen CUF-BSP-F02 is a broken and mirrored part of CUF-BSP-F01. These two specimens were cleaned, using a pneumatic pen, and were prepared at the fossil laboratory in the Sirindhorn Museum, Kalasin Province. The petrographic analysis of thin sections of rock samples was conducted at the Division of Geo-science, Mahidol University, Kanchanaburi Campus. We examined the detailed features and sculpture of scales under the stereomicroscope and compared these external morphologies with other previously described specimens achieved from the existing literature such as Agassiz (1833–1843), Aldinger (1937), Blainville (1818), Westoll (1934), Haubold and Schaumberg (1985), Štamberg (2010), Hoşgör and Štamberg (2014).

RESULTS

Systematic Paleontology

Class Actinopterygii Cope, 1871
Order Palaeonisciformes Hay, 1902
Family Palaeoniscidae Vogt, 1852

Genus *Palaeoniscum* Blainville, 1818

Emended diagnosis.– The generic diagnosis is modified from Hoşgör and Štamberg (2014). A fusiform actinopterygian. The parietals of square shape. The frontals large, posteriorly narrower than anteriorly. Distinct lateral process in the middle of the frontal length. Interfrontal suture curved. Small epitemporal between the dermosphenotic and infraorbital. The opercular large, twice as high as long. Antopercular missing. The subopercular markedly lower anteriorly than posteriorly. The branchiostegal rays number approximately ten or eleven. Only one series of small teeth on the maxillary. Dentary bears a large number of teeth of two sizes but without specially prominent laniaries. Lepidotrichia of the pectoral fin are segmented from their base. One or more large scales in front of the base of the dorsal fin. The diamond-shaped ganoid scales with small pores on the anterior of scales. Three to six ridges running parallel to the antero-ventral margin of flank scales on a bone layer. The number of maximum transverse scale rows between the head and the anterior part of a caudal fin varies from 38 to 81.

cf. *Palaeoniscum* sp.

Material.– Two specimens CUF-BSP-F01 and CUF-BSP-F02; CUF-BSP-F02 are broken and mirrored parts of CUF-BSP-F01.

Horizon and locality.– Tak Fa Formation (Lower to Middle Permian), Ban Wang Pla, Phaya Wang Sub-District, Bueng Sam Phan District, Phetchabun.

Description

The specimen preserves only a body part with scales (lacking the head, fins, and tail) and is deformed and compressed (Fig. 4A, B). The body part has a fusiform or torpedo-like shape with a maximum length of around 30–35 cm and is covered with tiny diamond-shaped ganoid scales without a peg or socket (Fig. 4C–H). Ganoid scales are approximately 4–5 mm long (Fig. 4C). The scales have pores at the anterior margin on a ganoine layer (Fig. 4F, G). Thirty-eight to forty-two scale rows are visible from anterior to posterior parts (with the estimation of 65–81 scale rows for the maximum number) (Fig. 4A, B). The center of flank scales in the bone layer shows characteristics of three to six ridges, all of which run parallel to the antero-ventral margin of the flank scale (Fig. 4C, D, G, H). The center of scales is surrounded by a concentric growth line. Based on the degree of preservation and squamation structures observed in CUF-BSP-F01, we divided the body part of the specimen into three parts: I, II, and III (Fig. 4B).

Part I: In this part, the ganoid layer is absent. Three to six ridges on the bone layer run parallel to the antero-ventral margin of flank scales with a concentric growth line.

Part II: The ornaments and ganoid layer are eroded, allowing the exposure of underlying bone layers. The bone layer is broken away and shows obviously a white color with a concentric growth line.

Part III: The surface of the scales is covered by ganoin layers (enamel layers) at the anterior part of scales with microscopic pores.

The CUF-BSP-F02 preserves only around 15% of the posterior mirrored part of a body, as observed from the area II to III with the presence of the sculpture of ridges (Fig. 5A, B). This specimen is characterized by the absence of ornamentation on the scale surface and the underlying bone layer, the presence of a ganoin layer (enamel layer), concentric growth lines, and ridges on the flank scale (Fig. 5C).

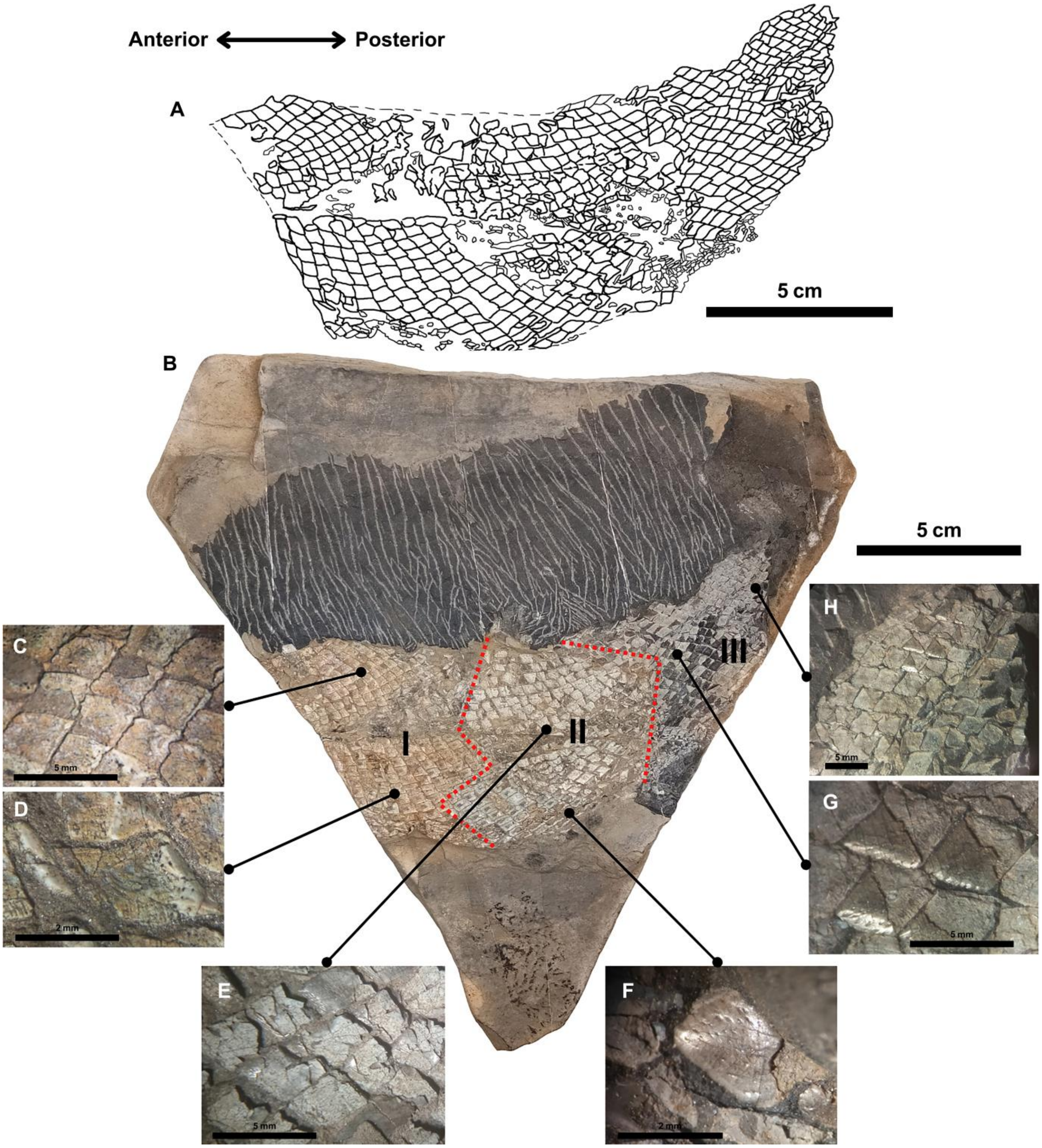

FIGURE 4. Squamation structures of the specimen CUF-BSP-F01. (**A**) Drawing of the specimen CUF-BSP-F01; (**B**) The specimen CUF-BSP-F01; (**C, D**) Scales in part I with ridges; (**E, F**) Eroded scales in part II; (**G, H**) Scales in part III with a ganoid layer and microscopic pores.

Morphological comparisons

During the 19th century, the family Palaeoniscidae has been recognized to be an early group of a ray-finned fish. This family was typically found in Europe including in Germany, northern England, eastern Greenland, and Russia (Diedrich, 2009; King, 1850; Blainville, 1818; Agassiz, 1833–1843; Westoll, 1934; Nurgaliev et al., 2015) (Fig. 6). Within the family, the genus *Palaeoniscum* was first established by Blainville (1818) but was later misspelled as *Palaeoniscus* by

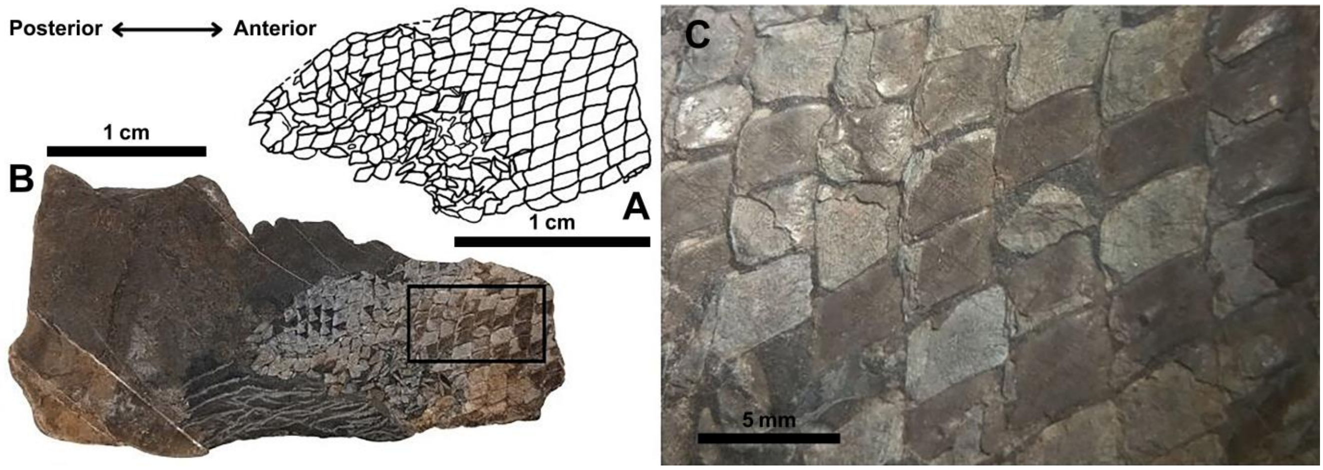

FIGURE 5. Squamation structures of the specimen CUF-BSP-F02. (**A**) Drawing of specimen CUF-BSP-F02; (**B**) The specimen CUF-BSP-F02; (**C**) The squamation in part III, the posterior mirrored of the body between the part II and III.

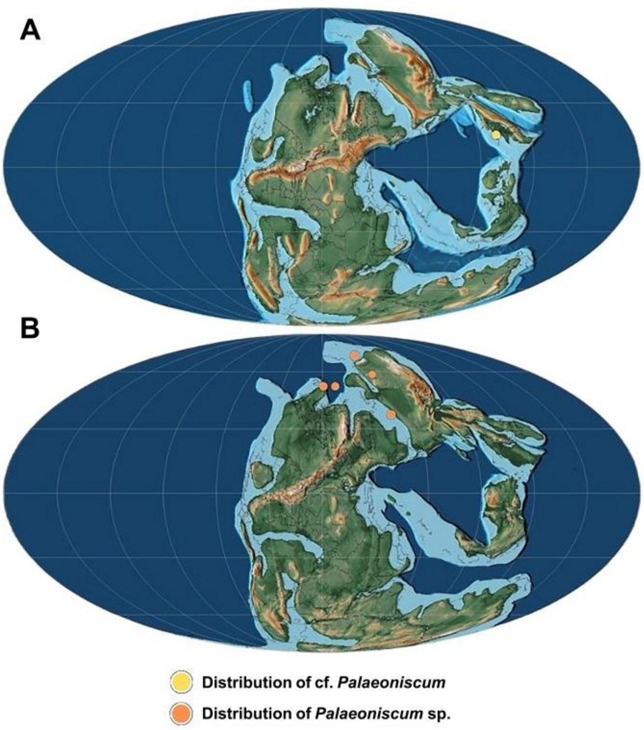

FIGURE 6. Fossil records of (**A**) cf. *Palaeoniscum* sp. between 275 and 265 Ma and (**B**) *Palaeoniscum* sp. between 265 and 255 Ma. The map is generated by the GPlates software version 2.3 (Chin, 2021).

Agassiz (1833–1843). Other synonyms of the species within the genus have been considered to be invalid (e.g., *Palaeoniscum voltzii*, *Palaeoniscum angustum* (Rzehak, 1881), *Palaeoniscum landrioti* (Sauvage, 1890) and *Palaeoniscum macropterum* (Bronn, 1829)). However, some of them have been transferred to other different genera (e.g., *Acentrophorus* sp., *Aeduella* sp., *Amblypterus* sp., *Rhabdolepis macropterus*, *Rhabdolepis saarbrueckensis*) (Woodward, 1891; Sauvage, 1890; Bronn, 1829; Gardiner, 1963; Štamberg, 2010; Schindler, 2018). Additionally, *Pygopterus* sp. (Aldinger, 1937) was initially considered to belong to *Palaeoniscum* sp. (Traquair, 1877b), but the taxonomic identification remains ambiguous due to the lack of a cranial osteology.

The specimens CUF-BSP-F01 and CUF-BSP-F02 from the Tak Fa Formation in Phetchabun show typical features of palaeoniscids such as the ganoid scale and fusiform shape (Moy-Thomas and Miles, 1971; Schultze, 1977; Janvier, 1996). The Thai specimen is larger than *Aeduella blainvillei* (Agassiz, 1833–1843) and *Rhabdolepis macropterus* (Bronn, 1829; Schindler, 2018) (Table 1) but comparable in size to *Palaeoniscum freieslebeni* (Blainville, 1818; Traquair, 1877a; Aldinger, 1937: fig. 26; Hoşgör and Štamberg, 2014) and *Pygopterus nielseni* (Aldinger, 1937).

The scale rows of the Thai specimens are similar to those of *P. freieslebeni* from Greenland, the material described by Aldinger (1937) and Traquair (1877a), and *R. saarbrueckensis* from Turkey (Gardiner, 1963; Hoşgör and Štamberg, 2014). The Thai fossils also differ from *A. blainvillei* and *R. macropterus* in having the higher number of scale rows.

The scale of the Thai specimens is diamond-shaped, differing from that of *A. blainvillei*, but similar to that of *P. freieslebeni*, *R. saarbrueckensis*, *R. macropterus* and *P. nielseni*. For the Thai specimens, the sculpture on their scale is similar to that of *P. freieslebeni*. It clearly differs from *R. saarbrueckensis and R. macropterus* in having a less-developed sculpture in which three to six ridges run parallel to the antero-ventral margin of the scale.

Based on the comparisons with other Permian palaeoniscids, the morphological characters (i.e., squamation and scale sculpture) and the size of the Thai specimens are comparable to *Palaeoniscum*. However,

TABLE 1. Morphological and dimensional comparisons between the Thai specimens and other palaeoniscids.

Taxon	Specimen No.	Body size (cm)	Squamation (scale rows)	Shape and scale sculpture	References
cf. *Palaeoniscum* sp.	CUF-BSP-F01 CUF-BSP-F02	30–35	38–42 (with the maximum estimation of 65–81)	diamond shape, 3–6 ridges running parallel to the antero-ventral margin of scales	This study
Palaeoniscum freieslebeni	Text figs 3–5	30	-	-	Blainville (1818)
Palaeoniscum freieslebeni	Text pl. 1, fig. 1	15–45 cm (with an average of 30 cm)	68–70	-	Traquair (1877a)
Palaeoniscum freieslebeni	Text fig. 26	28	68–70	-	Aldinger (1937)
Palaeoniscum freieslebeni	MTA-TTM 2014–744	30	53	small scales with peg and socket articulation. The surface of scales is ornamented with one or more ridges (2–4 ridges) passing anteroposteriorly across the scale.	Hoşgör and Štamberg (2014)
Aeduella blainvillei	UNISTA.2013.0.133 UNISTA.2013.0.136 UNISTA.2013.0.135	5–20	37–40	long and more rhombic-shaped scales	Agassiz (1833–1843)
Rhabdolepis macropterus	BMNH P3453 BMNH P6196	25	up to 40	field of ridges running parallel to the dorsal border of scales	Bronn (1829), Schindler (2018)
Rhabdolepis saarbrueckensis	BMNH 32576 NMP SC 95	34	64	small and numerous scales. The outer surface of scales bears striae, which run from the anterior-superior corner to the posterior-inferior corner.	Gardiner (1963), Štamberg (2010)
Pygopterus nielseni	Text-figs 37	30	135	small diamond-shaped scales	Aldinger (1937)

the specimen lacks some important parts for genus- and/or species-level identification (e.g., cranial and caudal elements). We therefore assign the Thai specimens to cf. *Palaeoniscum* sp.

DISCUSSION

Paleobiogeographical records

Based on the petrographic analyses (Fig. 7) under the microscope, the strata contain mostly clay particles such as micrites and wackestones (Folk, 1959, 1962; Dunham, 1962). The unit A to unit D is composed of fossiliferous biomicrites (Fig. 7A1, A2), micrites interbedded with shales (Fig. 7B1, B2), shales interbedded with micrites (Fig. 7C1, C2), and lamination shales (Fig. 7D1, D2), respectively. The sedimentary characteristics and structures (lamination, irregular bedding and lens to wavy lamination) observed in the unit C indicate low-energy environments (Tucker, 1991, 2013; Flügel, 2010). The depositional environments of the strata matched the schematic representation of reef facies and associated sediments (Nicholas, 2009), corresponding to lagoons or subtidal zones in a continental margin.

As shown in the sediment structure of micrites interbedded with shales, the characteristics of seawater inlet and clastic sediment input from freshwater were found from some parts of strata. The limestones lens to wavy lamination of limestones have indicated the flood tide periods of sea water or weak storms in the offshore environments (Reineck and Singh, 1980; Dalrymple, 2010). The structure of an intertidal zone (flooded by daily tides) and a supratidal zone (flooded by wind and spring tides) is characterized by a thin bed of fine grain sediments and sharp contacts (Tucker and Wright, 1990).

Other invertebrate faunas associated with the Tak Fa formation may provide some additional information about the paleoenvironmental context of a palaeoniscid fauna. For instance, gigantic bivalve alatoconchids preferred to dwell in soft substrate (Udchachon et al., 2007). Furthermore, ostracod fossils were found from thin sections of limestones stratigraphically above and below the fish fossil layer. They are similar in shape with ostacod fossils from the Nam Phong Formation (Chitnarin et al., 2022a). Ostracods are members of zooplanktons (most typically) and benthos dwelling on or inside the top layer of the sediments in aquatic environments (Wilkinson, 1996). They are common in a freshwater lake, although they may have been found in marine or brackish water (Balian et al., 2008). Ostracods generally avoid high energy water by moving into sediments or subtrate, although they may be abundant in some habitats under the high energy environments (Creuzé des Chatelliers and Marmonier, 1993). As a

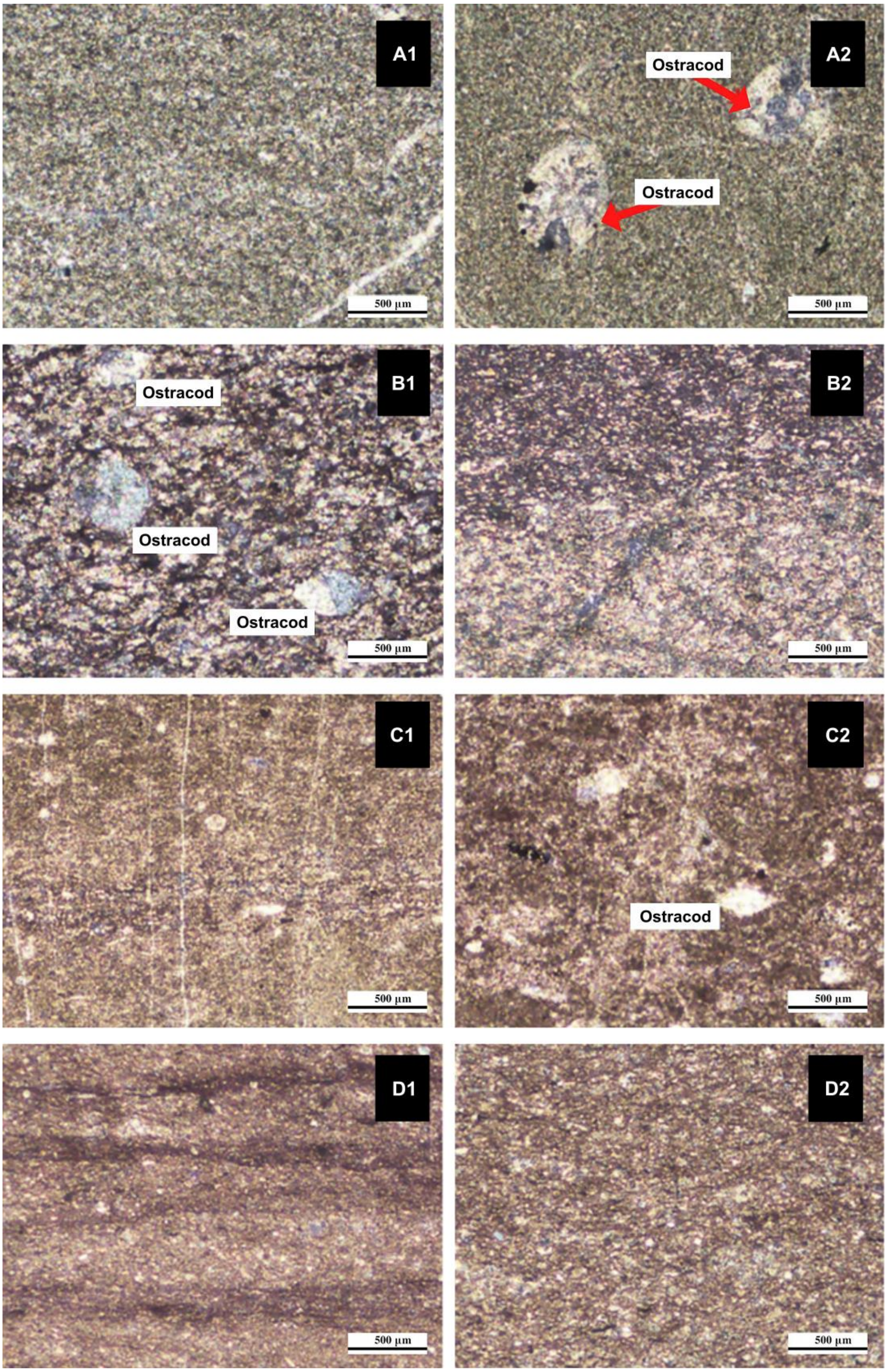

FIGURE 7. Petrographic analysis of rock samples from units **A–D**. **A1.** Fossiliferous biomicrites, **A2.** Fossiliferous biomicrites with ostracods, **B1.** Ostracods in fossiliferous biomicrites, **B2.** Micrites interbedded with calcareous mudstones showing a gradational contact, **C1.** interbedded with calcareous claystones, **C2.** Ostracods in claystone matrix, **D1.** Lamination of calcareous claystones, **D2.** Matrix of calcareous claystones.

result, the paleoenvironments of the Tak Fa formation where the paleoniscid fossil was found likely corresponded to a lagoon and/or subtidal zone with a low-energy depositional condition, as supported by petrographical, stratigraphical, and faunal information.

CONCLUSIONS

In this study, the first actinopterygian fossil from the Tak Fa Formation, Ban Wang Pla, Phaya Wang Sub-District, Bueng Sam Phan District, Phetchabun has been described. The Thai palaeoniscid specimen is morphologically close to *Palaeoniscum freieslebeni*. The age of invertebrate faunas associated with the paleoniscid fossil strata suggested an Early to Middle Permian age, contemporaneous with most of previously described palaeoniscid specimens from Europe and Russia. The paleoenvironments of the area corresponded to lagoons or subtidal zones in epeiric seas with a low-energy depositional condition according to lithological, stratigraphical, and petrographic examinations of limestones interbedded with shales. This study highlights the importance of exploring additional marine vertebrate fossils in the Permian strata of Thailand in the future.

ACKNOWLEDGMENTS

We especially thank Phornphen Chanthasit and other members of the fossil laboratory team from the Department of Mineral Resources at the Sirindhorn Museum for their information and fossil preparation. We would like to extend our grateful thanks to Sirot Salyapongse for his helpful comments on the petrographic analysis and to Ekkapob Poonsawat for his assistance during the fieldwork. We are grateful to Suphat Prasopsin who facilitated us the laboratory equipment at Mahidol University, Kanchanaburi Campus, and to Fa-is Jindewha for his technical advice on the paleogeographic reconstruction. Finally, we would like to thank Uthumporn Deesri, and two anonymous reviewers for their insightful and helpful comments that have improved the quality of the manuscript.

LITERATURE CITED

Agassiz, L. 1833–1843. Recherches sur les poissons fossiles II, 2. 336 pp. Petitpierre, Neuchatel, 336 pp.

Aldinger, H. 1937. Permische ganoidfische aus Ostgrönland. Meddelelser om Grønland, 102(3): 1–392.

Altermann, W. 1989. Facies Development in the Permian Petchabun Basin, Central Thailand. Verlag Für Wissenschaft und Bildung, Berlin, 155 pp.

Balian, E., Segers, H., Lévèque, C. and Martens, K. 2008. An Introduction to the freshwater animal diversity assessment (FADA) project. Hydrobiologia, 595(1): 3–8. doi:10.1007/s10750-007-9235-6.

Buffetaut, E. and Suteethorn, V. 1998. The biogeographical significance of the Mesozoic vertebrates from Thailand. In: Hall, R. and Holloway, J.D. (Eds), Biogeography and Geological Evolution of SE Asia, Backhuys, Leiden, 83–90.

Blainville, H.-M.D. 1818. Sur les Ichthyolites, les Poisons Fossiles; Article extrait du Nouveau Dictionnaire d'Histoire Naturelle, Vol 28, Abel Lange, 16.

Bronn, H. 1829. Ueber die Fisch-Abdrücke in Eisenstein-Nieren des Mittel-Rheinischen Steinkohlen-Gebirges, und über *Palaeoniscum macropterum* n. sp. insbesondere. Zeitschrift für Mineralogie, 2: 483–493.

Cavin, L. and Suteethorn, V. 2006. A new Semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic–Lower Cretaceous deposits of north-east Thailand, with comments on the relationships of Semionotiforms. Palaeontology, 49: 339–353. doi:10.1111/j.1475-4983.2006.00539.x.

Cavin, L., Suteethorn, V., Buffetaut, E., Claude, J., Cuny, G., Le Loeuff, J. and Tong, H. 2007. The first sinamiid fish (Holostei: Halecomorpha) from Southeast Asia (Early Cretaceous of Thailand). Journal of Vertebrate Paleontology, 27(4): 827–837. doi:10.1671/0272-4634(2007)27[827: tfsfhh]2.0.co;2.

Cavin, L., Deesri, U., and Suteethorn, V. 2009. The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand. Geological Society, London, Special Publications, 315(1): 125–139. doi:10.1144/sp315.10.

Cavin, L., Deesri, U. and Suteethorn, V. 2013. Osteology and relationships of *Thaiichthys* nov. gen.: a Ginglymodi from the Late Jurassic - Early Cretaceous of Thailand. Palaeontology, 56(1): 183–208. doi:10.1111/j.1475-4983.2012.01184.x.

Cavin, L., Deesri, U., Veran, M., Khentavong, B., Jintasakul, P., Chanthasit, P. and Allain, R. 2019. A new Lepisosteiformes (Actinopterygii: Ginglymodi) from the Early Cretaceous of Laos and Thailand, SE Asia. Journal of Systematic Palaeontology, 17(5): 393–407. doi:10.1080/14772019.2018.1426060.

Charoenprawat, A. and Wongwanich, T. 1976. Preliminary Report on the Geological Map of Changwat Loei Quadrangle (ND44–12), 1: 250,000. Department of Mineral Resources, Bangkok, Thailand.

Chin, M. 2021. GPlates 2.3 [computer software]. EarthByte Group, School of Geosciences, University of Sydney NSW, Australia. Available from: https://www.earthbyte.org/download-gplates-2-3/.

Chitnarin, A., Crasquin, S., Chonglakmani, C., Broutin, J., Grote, J. and Thanee N. 2008. Middle Permian Ostracods from Tak Fa Limestone, Phetchabun Province, Central Thailand. Geobios, 41(3): 341–353.

Chitnarin, A., Crasquin, S., Charoentitirat, T., Tepnarong, P. and Thanee, N. 2012. Ostracods (Crustacea) of the Early-Middle Permian from Central Thailand (Indochina block). Part I. Order Palaeocopida. Geodiversitas, 34(4): 801–835.

Chitnarin, A., Crasquin, S., Forel, M.B. and Tepnarong, P. 2017. Ostracods (Crustacea) of the Early-Middle Permian (Cisarulian-Guadalupian) from Central Thailand (Indochina Block): Part II, Orders Podocopida, Platycopida and Myodocopida. Geodiversitas, 39(4): 651–690.

Chitnarin, A., Hanta, R., Ketmuangmoon, P. and Forel, M.B. 2022a. Ostracoda (Crustacea) from the Lower Jurassic of northeastern Thailand: stratigraphic and paleoenvironmental implications. Revue de Micropaléontologie, 75: 100611. doi:10.1016/j.revmic. 2022.100611.

Chitnarin, A., Forel, M.B. and Tepnarong, P. 2022b. Permian ostracods from limestones associated with a coal deposit, Tak

Fa Formation (Guadalupian), central Thailand. 19th International Symposium on Ostracoda, Lyon, France, Claude Bernard University Lyon 1.

Chonglakmani, C. and Fontaine, H. 1990. The Lam Narai-Phetchabun Region: A platform of early carboniferous to late permian age. Proceedings of the Technical Conferences on Development Geology for Thailand into the Year 2000. Chulalongkorn University, Thailand, 39–98.

Chonglakmani, C. and Sattayalak, N. 1979. Geological Map of Thailand on 1: 250000 Scale: Sheet Changwat Phetchabun (NE47–16). Department of Mineral Resources, Bangkok.

Cope, E.D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society (New Series). 14(3): 445–483.

Creuzé des Châtelliers, M. and Marmonier, P. 1993. Ecology of Benthic and Interstitial Ostracods of the Rhône River, France. Journal of Crustacean Biology, 13(2): 268–279. doi:10.2307/1548974.

Dalrymple, R.W. 2010. Tidal depositional systems. In: James, N.P., Dalrymple, R.W., (Eds). Facies Models 4. Geological Association of Canada, St. John's, Newfoundland, 201–232.

Deesri, U., Lauprasert, K., Suteethorn, V., Wongko, K. and Cavin, L. 2014. A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, northeastern Thailand. Acta Palaeontologica Polonica. 59(2): 313–331. doi:10.4202/app.2012.0013

Deesri, U., Jintasakul, P. and Cavin, L. 2016. A new Ginglymodi (Actinopterygii, Holostei) from the Late Jurassic–Early Cretaceous of Thailand, with comments on the early diversification of Lepisosteiformes in Southeast Asia. Journal of Vertebrate Paleontology, 36(6): e1225747. doi:10.1080/02724634.2016.1225747.

Diedrich, C.G. 2009. A coelacanthid-rich site at Hasbergen (NW Germany): taphonomy and palaeoenvironment of a first systematic excavation in the Kupferschiefer (Upper Permian, Lopingian). Palaeobiodiversity and Palaeoenvironments, 89(3): 67–97.

Dunham, R.J. 1962. Classification of Carbonate Rocks according to Depositional Texture. In: Ham, W. E (Ed.), Classification of Carbonate Rock. American Association of Petroleum Geologists Memoir, 1: 108–121.

Elder, R.L. and Smith, G.R. 1988. Fish taphonomy and environmental inference in paleolimnology. Palaeogeography, Palaeoclimatology, Palaeoecology, 62(1–4): 577–592. doi:10.1016/0031-0182(88)90072-7.

Flügel, E. 2010. Microfacies of Carbonate Rocks Analysis, Interpretation and Application. Springer-Verlag, Berlin, 976 pp.

Folk, R.L. 1959. Practical Petrographic Classification of Limestones. The American Association of Petroleum Geologists Bulletin, 43: 1–38.

Folk, R.L. 1962. Spectral subdivision of limestone types. In: Ham, W.E. (Ed.), Classification of Carbonate Rocks: A Symposium. American Association of Petroleum Geologists Memoir 1, Tulsa, Okla, 62–84.

Friedman, M. and Smith, A. 2015. The early evolution of ray-finned fishes. Palaeontology, 58(2): 213–228. doi:10.1111/pala.12150.

Gardiner, B.G. 1963. Certain Plaeoniscoid fishes and the evolution of the snout in Actinopterygians. Bulletin of the British Museum (Natural History), Geology, 8(6): 257–325.

Grant, R. 1976. Permian Brachiopods from Southern Thailand. Journal of Paleontology, 50(S9): 1–261. doi:10.1017/S0022336000061795.

Haubold, H. and Schaumberg, G. 1985. Die Fossilien des Kupferschiefers, Die Neue Brehm-Bu cherei 333, Ziemsen Verlag, Lutherstadt, Wittenberg, 223.

Hay, O.P. 1902. Bibliography and Catalogue of the Fossil Vertebrata of North America. Bulletin of the United States Geological Survey, 179: 1–868.

Hinthong, C. 1981. Geology and mineral resources of the Changwat Phranakorn Sri Ayutthaya (Map ND 47–8). Department of Mineral Resources, Bangkok, Thailand.

Hinthong, C. 1985. Upper Paleozoic system: the central plain and lower Phetchabun ranges. Geological Survey Division, Bangkok, 42.

Hoşgör, I. and Štamberg, S. 2014. A first record of late Middle Permian actinopterygian fish from Anatolia, Turkey. Acta Geologica Polonica, 64(2): 147–159.

Janvier, P. 1981. On some fish remains from the Permian of North-Eastern Thailand. Journal of the Geological Society of Thailand, 4: 24–28.

Janvier, P. 1996. Early Vertebrates. Oxford Monographs on Geology and Geophysics 33. Oxford, Clarendon Press, XIII, 393 pp.

Ketwetsuriya, C., Nützel, A., Kanjanapayont, P. 2014. A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand—a report of preliminary results. Zitteliana A, 54: 137–146.

Ketwetsuriya, C., Nützel, A. and Kanjanapayont, P. 2016a. Depositional Environment of Permian Tak Fa Formation, Nakhonsawan, Northern Thailand. Geophysical Research Abstracts, 18.

Ketwetsuriya, C., Nützel, A. and Kanjanapayont, P. 2016b. Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. Bulletin of Geosciences, 91(3): 481–513. doi:10.3140/bull.geosci.1617.

Ketwetsuriya, C., Hausmann, I.M. and Nützel, A. 2021. Diversity patterns of Middle Permian gastropod assemblages from the Tak Fa Formation, Central Thailand. Palaeobiodiversity and Palaeoenvironments, 101: 907–925. doi:10.1007/s12549-021-00482-3.

King, W. 1850. Monograph of the Permian fossils of England. *Palaeontographical Society Monograph. London*, 30: 1–258.

Koot, M.B. 2013. Effects of the Late Permian mass extinction on chondrichthyan palaeobiodiversity and distribution patterns. PhD Thesis, Faculty of Science and Technology, Plymouth University.

Long, J.A. and Burrett, C. 1989. Fish from the Upper Devonian of the Shan-Thai terrane indicate proximity to east Gondwana and south China terranes. Geology, 17(9): 811–813.

Long, J.A. 1990. Late Devonian Chondrichthyans and other microvertebrate remains from Northern Thailand. Journal of Vertebrate Paleontology, 10(1): 59–71. doi:10.1080/02724634.1990.10011790.

Märss, T. 2001. *Andreolepis* (Actinopterygii) in the Upper Silurian of northern Eurasia. Proceedings of the Estonian Academy of Sciences, Geology, 50(3): 174–189. doi:10.3176/geol.2001.3.03.

Metcalfe, I. and Sone, M. 2008. Biostratigraphy and palaeobiogeography of Lower Permian (lower Kungurian) conodonts from the Tak Fa Formation (Saraburi Limestone), Thailand. Palaeogeography, Palaeoclimatology, Palaeoecology, 257(1–2): 139–151.

Moy-Thomas, J.A. and Miles, R.S. 1971. Palaeozoic Fishes, 2nd ed; extensively revised by R.S. Miles. Chapman and Hall, London, 259 pp.

Nakornsri, N. 1977. Geological Map of Thailand on 1:250,000 scale: Sheet Amphoe Ban Mi (ND 47–4). Department of Mineral Resources, Bangkok, Thailand.

Nakornsri, N. 1981. Geology and Mineral Resources of Amphoe Ban Mi (ND 47–4), Geological Survey Report Number 3. Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand.

Napradit, T. 2005. Permian Fusulinoidean Limestones from East of Changwat Nakhon Sawan. Master Thesis, Department of Geology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand.

Nelson, J.S. 2006. Fishes of the World, 4th Edition. John Wiley and Sons, Hoboken, New Jersey, 90–91.

Nicholas, G. 2009. Sedimentology and Stratigraphy, Wiley and Sons, New York, 225–246.

Nurgaliev, D.K., Silantiev, V.V. and Nikolaeva, S.V. 2015. Type and reference sections of the Middle and Upper Permian of the Volga and Kama River Regions: A Field Guidebook of XVIII International Congress on Carboniferous and Permian. Kazan University Press, 208 pp.

Pitrat, C.W. 1973. Vertebrates and the Permo-Triassic extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 14: 249–264.

Reineck, H. E., Singh, I. B. 1980. Depositional Sedimentary Environments, 2nd edition. Springer-Verlag, Berlin, 549 pp.

Romano, C., Koot, B.M., Kogan, I., Brayard, A., Minikh, V.A., Brinkmann, W., Bucher, H. and Kriwet, J. 2016. Permian-Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution: Diversity and size of Permian-Triassic bony fishes. Biological Reviews, 91(1): 106–147. doi:10.1111/brv.12161.

Rzehak, A. 1881. Die Fauna des mährischen Rotliegenden. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt, Wien, 5: 78–79.

Sakagami, S. 1975. Permian Bryozoa from Khao Hin Kling, near Phetchabun, North-Central Thailand. Geology and Palaeontology of Southeast Asia, 16: 33–43.

Sauvage, H.-E. 1890. Bassin houiller et Permien d'Autun et d'Epinac, fascicule III, poisons fossiles. Études des gîtes minéraux de la France, Carnets de Géologie. Imprimerie Nationale, Paris, 31 pp.

Schindler, T. 2018. Revision of *Rhabdolepis macropterus* (Bronn, 1829) (Osteichthyes, lower Actinopterygii; Lower Permian, SW Germany). Paläontologische Zeitschrift, 92: 651–660.

Schultze, H.-P. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). Palaeontologische Zeitschrift, 51: 152–168.

Sone, M. 2010. A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). Alcheringa, 34: 1–6.

Štamberg, S. 2010. Taxonomic remarks on *Rhabdolepis saarbrueckensis* Gardiner, 1963 (Osteichthyes: Actinopterygii) and its relationships to some actinopterygians from the Late Carboniferous of the Bohemian Massif, Czech Republic. Journal of the National Museum (Prague), Natural History Series, 179(15): 153–170.

Traquair, R.H. 1877a. The ganoid fish of the British Carboniferous formations, Part I: Palaeoniscidae. Palaeontographical Society, 31(140): 1–60. doi:10.1080/02693445.1877.12027943.

Traquair, R.H. 1877b. On the Agassizian genera *Amblypterus*, *Palaeoniscus*, *Gyrolepis*, and *Pygopterus*. Quarterly Journal of the Geological Society, 33: 548–578.

Tucker, M.E. and Wright, V.P. 1990. Carbonate Sedimentology. Wiley, Blackwell Science, Oxford, 482 pp.

Tucker, M.E. 1991. Sedimentary Petrology: An Introduction to the Origin of Sedimentary Rocks, 2nd Edition. Wiley, Blackwell Science, Oxford, 260 pp.

Tucker, M. 2013. Sedimentary Petrology Sedimentary Petrology: An Introduction to the Origin of Sedimentary Rocks, 3rd Edition, Wiley, Blackwell Science, Oxford, 272 pp.

Udchachon, M., Chonglakmani, C., Campbell, H. and Thanee, N. 2007. Late Middle Permian alatoconchid-bearing limestone from the south of the Khao Khwang platform, central Thailand. In: Tantiwanit, W. (Ed.), Proceedings of the International Conference on Geology of Thailand: Towards Sustainable Development and Sufficiency Economy. Bangkok, 169–176.

Ueno, K. and Charoentitirat, T. 2011, Carboniferous and Permian. In: Ridd, M.F., Barber, A.J., Crow, M.J. (Eds), The Geology of Thailand. The Geological Society, London, 71–136.

Vogt, C. 1852. Ueber die Siphonophoren. Zeitschrift für Wissenschaftliche Zoologie, 3(4): 522–525.

Waterhouse, J.B. 1982. An Early Permian cool-water fauna from pebbly mudstones in south Thailand. Geological Magazine, 119(4): 337–354.

Westoll, T.S. 1934. The Permian palaeoniscid fishes of Northumberland and Durham. University of Durham, 14–15.

Wieldchowsky, C.C. and Young, J.D. 1985. Regional Facies Variation in Permian Rocks of the Phetchabun Fold and Thrust Belt, Thailand. In: Thanvarachorn, P., Hokjaroen, S., and Youngme, W. (Eds), Proceeding on Geology and Mineral Resources Development of the Northeastern Thailand. Khon Kaen University, Khon Kaen, Thailand, 41–56.

Wilkinson, I.P. 1996. British Geological Survey, Ostracods. Nottingham, UK, 1. Available from: https://www.bgs.ac.uk/discovering-geology/fossils-and-geological-time/ostracods/,(11 June 2022)

Woodward, A.S. 1891. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part II. Catalogue of the Fossil Fishes in the British Museum (Natural History), London.

Yanagida, J. 1967. Early Permian brachiopods from north-central Thailand: contribution of the geology and paleontology of Southeast Asia. Journal of Geology and Paleontology of Southeast Asia, 3: 46–97.