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# The Richest Diversity and Highest Abundance of Freshwater Bivalve Fossils from the New Fossil Locality of the Early Cretaceous Sao Khua Formation at Roi Et Province, Northeastern Thailand

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**ABSTRACT. –** A new fossil freshwater bivalves locality in the Sao Khua Formation was discovered at the top of a small hill named Phu Kum Khao in the Pho Chai District, Roi Et Province, northeastern Thailand. The fossils bed is a mud-nodule conglomeratic sandstone of the Sao Khua Formation and has proved to be both of high abundance and species diversity (6,637 specimens of nine species). The most abundant species is *Pseudohyria (Matsumotoina) somanai* Tumpeesuwan, Sato, and Nakhapadungrat, 2010, which is not only the dominant species of the Sao Khua Formation but also the index fossil representative of the Late Barremian age for the formation. The bivalves from this locality are preserved as both articulated and disarticulated shells. Associated vertebrate fossils are preserved as bone fragments and micro remains. According to the fossil assemblage and its taphonomy and orientation, lithology, and geometry, we interpret this fossil bed as having been deposited by a crevasse splay of a meandering river system.

**KEYWORDS: *Pseudohyria (Matsumotoina) somani*, freshwater bivalve fossil assemblage, vertebrate fossil, crevasse splay, meandering river system**

## INTRODUCTION

The Sao Khua Formation has been studied extensively by both palaeontologists and geologists, having the richest diversity and highest abundance of Mesozoic vertebrate fossils in Thailand (Buffetaut and Suteethorn 1998; Buffetaut et al. 2003, 2005, 2006, Manitkoon et al. 2022). The first ever sauropod dinosaur bone reported from Thailand was from this formation at Huai Phu Pratu Tee Ma in Phu Wiang Mountain (Ingavat and Taquet 1978). Other new fossils were continuously discovered from this formation at many locations on Phu Wiang Mountain (PW) (Buffetaut and Suteethorn 1989, 1993; Martin et al. 1993). The top of Phu Pratu Tee Ma (PW1), this locality yielded the crocodile *"Goniopholis" phuwiangensis* Buffetaut and Ingavat, 1983; the spinosaurid dinosaur, *Siamosaurus suteethorni* Buffetaut and Ingavat, 1986a; and the sauropod dinosaur *Phuwiangosaurus sirindhornae* Martin et al., 1994. The theropod dinosaur *Siamotyrannus isanensis* Buffetaut, Suteethorn and Tong, 1996 was discovered and described from site PW9, and the ostrich dinosaur *Kinnareemimus khonkaenensis* Buffetuat, Suteethorn and Tong, 2009 was found at site PW5. An additional locality, Wat Sak Kawan (K4: Phu Kum Khao) in Kalasin is a very rich locality that has yielded more than 700 bones belonging to at least seven individuals of three sauropod taxa (Suteethorn et al. 1995a, b; Suteethorn et al. 2009; Suteethorn and Le Loeuff 2012). Recently, two new basal coelurosaurian theropod dinosaurs were described by Samathi, Chanthasit and Sander (2019) comprise *Phuwiang-venator yaemniyomi* from site PW9b, and *Vayuraptor nongbualamphuensis* from Phu Wat site A1 in Nong Bua Lamphu. Other vertebrate fossils were also discovered near the top of Phu Pratu Teema, comprising fragmented bones of a compsognathid dinosaur, isolated teeth of a freshwater hybodont shark, scales and button-shaped teeth of ginglymodian fish, and many shells of two taxa of trionychoid turtle (Buffetaut and Ingavat 1983; Buffetaut 1984; Buffetaut and Ingavat 1984, 1985, 1986b, 1987; Cavin et al. 2009; Tong et al. 2003).

Palynological study of the samples that were collected and analysed from Phu Phan Thong (Sao Khua Formation) in Nong Bua Lamphu province has yielded an assemblage dominated by *Dicheiropollis etruscus* suggesting a Berriasian-early Berremain age for the formation. (Racey and Goodall, 2009). However, recent radiometric dating of detrital zircons suggests the middle and upper parts of the Sao Khua Formation were deposited not older than Valanginian (Tucker et al. 2022).

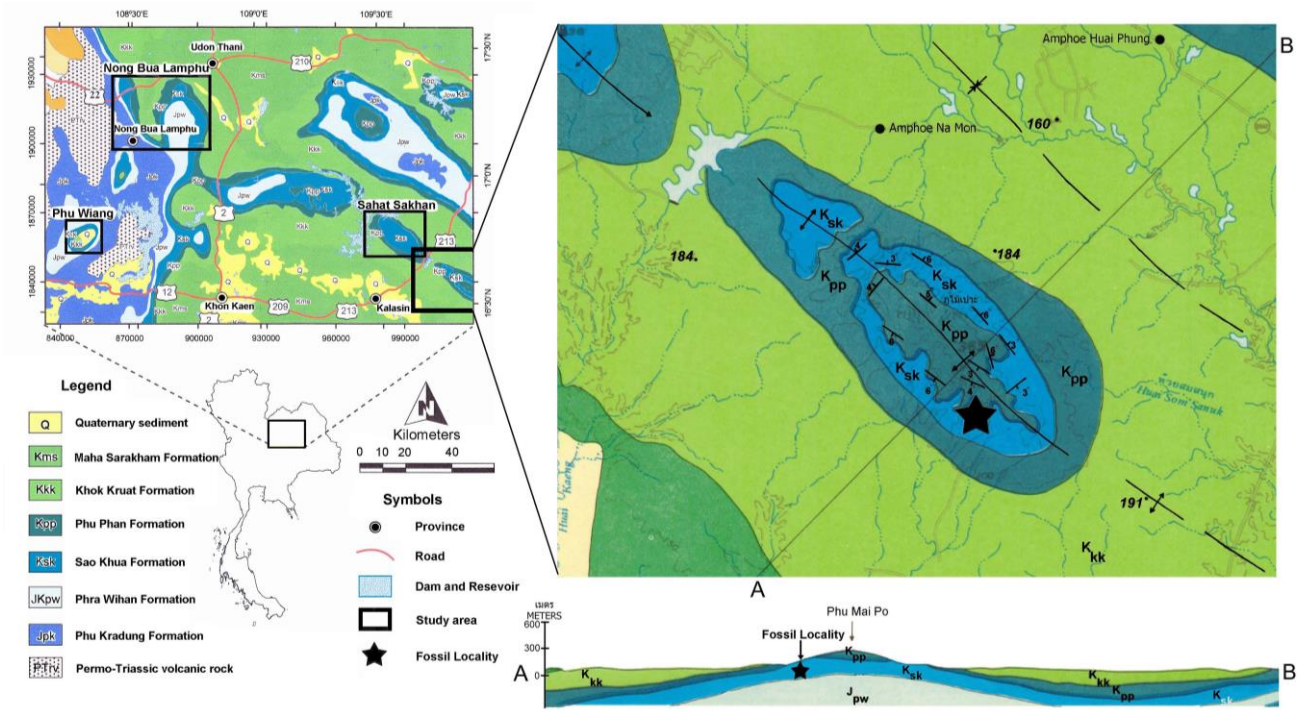


**FIGURE 1.** A geological map showing the three important sites of freshwater bivalve fossils of the Sao Khua Formation (in black square) and the new fossil locality (star) (Adapted after Suteethorn & Jarnyaharn (1985) and Tumpeesuwan (2010)).

According to the studies on freshwater molluscan fossils by Kobayashi (1963, 1968), Kobayashi et al. (1963), Hayami, (1968), Hahn (1982), and Tumpeesuwan (2010), twelve nominal taxa had been reported from the Sao Khua Formation including *"Cardinioides" magnus* Kobayashi and Hayami, 1963; "*Mytilus (Pachymytilus)" rectangularis* Kobayashi and Hayami, 1963; *"Goniomya" koratensis* Kobayashi and Hayami, 1963 (all three nominal species described in Kobayashi et al., 1963). Tumpeesuwan (2010) discovered 3 species of bivalve's fossil from Phu Noi in Phu Wiang Mountain, comprise *Nippononaia* sp. cf. *N. mekongensis*; *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus* Hoffet, 1937; *Pseudohyria (Matsumotorna) somanai* Tumpeesuwan et al., 2010. This bivalves assemblage is normally found in conglomeratic sandstone bed of the upper part of the Sau Khua Formation at Phu Pratu Tee Ma in Phu Wiang area; Phu Kum Khao, Phu Po and Phu Sing in Sahat Sakhan area; Phu Lon, Phu Chan, Ban Huai Dua in Nong Bua Lamphu area (Fig. 1); Tumpeesuwan (2010) also reported the second bivalves assemblage from the red brown mudstone-siltstone bed at the lowermost part of the Sao Khua Formation at Huai Lao Yang in Nong Bua Lamphu area (Fig. 1). This assemblage comprises *Nakamuranaia* sp.; *Yannanoconcha* sp.; *Sinonaia* sp.; *Koreanaia (Eokorreania)* sp. *Yunnanoconcha* sp. cf. *Y. khoratensis* Kobayashi, 1963 was also reported from red brown mudstone-siltstone bed at the upper part of the Sao Khua Formation at Hin Lat Yao in Phu Wiang area by Tumpeesuwan (2010).

Recently, a new fossil bivalve locality in Roi Et Province was discovered and studied. This shell bed contains abundant bivalves, some bone fragments and isolated teeth of hybodont shark, and dinosuars. The shell bed is a mud-nodule conglomeratic sandstone similar to that at Phu Noi in the Phu Wiang area (see Figs. 2A and 2B in Tumpeesuwan et al. 2010), this new shell bed might contain fossil assemblages similar to Phu Noi and other localities in the Phu Wiang, Sahat Sakhan, and Nong Bua Lamphu areas.

## Institutional abbreviations

**KP** Kham Pa-ung Local Site Museum Collection, Roi Et, Thailand.

**PRC** Palaeontological Research and Education Centre, Mahasarakham University, Thailand.

## Geological settings

The new freshwater bivalve fossil locality is located on the small hill "Phu Kum Khao" in Kham Pa-ung Subdistrict, Pho Chai District, Roi Et Province, northeastern Thailand (UTM WGS 84 Zone 48Q 377164 E 1816419 N; Fig.1). Geologically, the locality is located in the northern part of the Khorat Basin, and it is the eastern part of Sahat Sakhan anticline. The bivalve fossils have been found in deposits

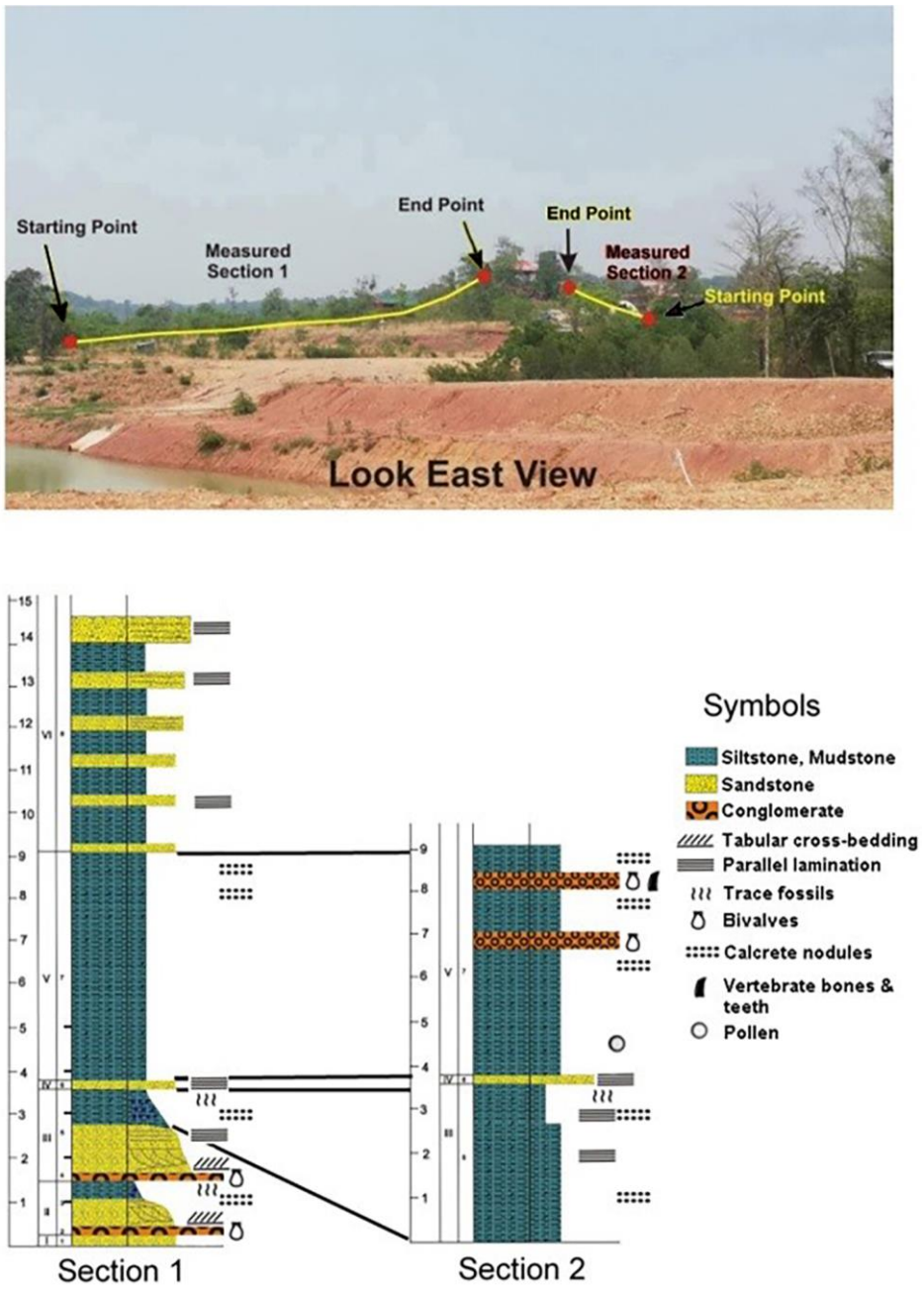


**FIGURE 2.** Western side of Phu Kum Khao, showing the locations of stratigraphic columnar sections 1 & 2 (Adapted after Nulay, 2023).

corresponding to the Sao Khua Formation (Fig. 1). The Sao Khua Formation is the third formation of the Khorat Group (Racey and Goodall, 2009), which overlying on the Phra Wihan Formation and underlying the Phu Phan Formation. The Sao Khua Formation was determined to be deposited in the meandering river system under semi-arid condition (Racey et al., 1996; Meesook, 2000). Stratigraphical and sedimentological study of the locality was reported by Nulay (2023), the lower part of columnar section 1 of the fossil locality, reveals the two cycles of fining upward sequence, the cycle starts with lime- or mud-nodule conglomeratic sandstone that contain bivalve shell fragments overlying by tabular cross-bedding reddish brown, fine- to very fine-grained lithic arkose sandstone. The top of the cycle is overlying with fining and thining of siltstone, mudstone with abundant of bioturbation and calcrete nodule. There are thin bedded (0.1-0.5 m thick), reddish-brown, fine- to medium-grained lithic arkose sandstone, sharp planar contract overlying on siltstone-mudstone bed. The very thick bedded reddish-brown siltstone, mudstone with abundant of calcrete nodule overlying on the thin-bedded lithic arkose sandstone. The mud- or lime-nodule conglomeratic sandstone beds with abundant bivalve fossil interbedded in the very thick bedded siltstone- mudstone (section 2 of

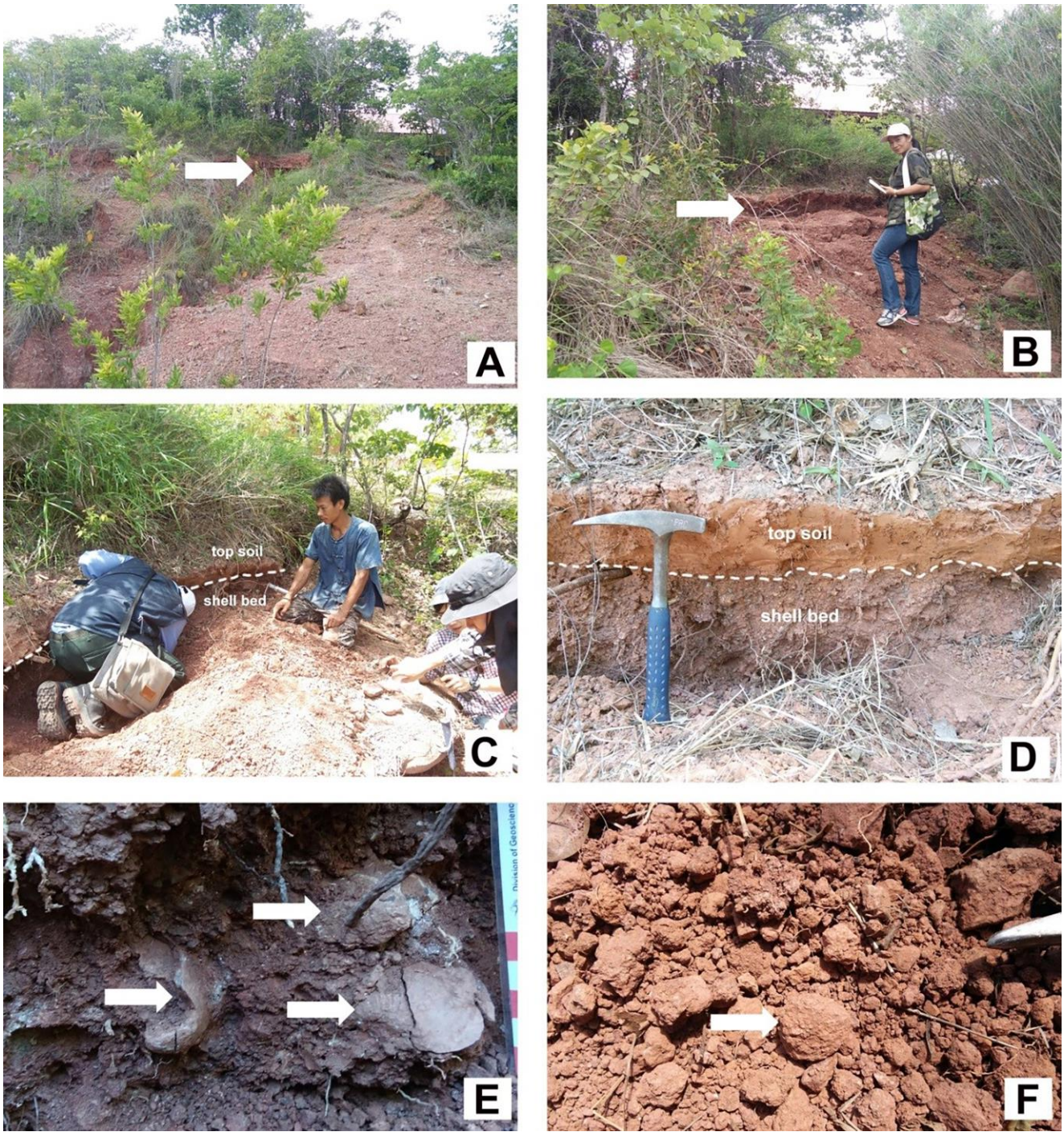


**FIGURE 3.** Phu Kum Khao bivalve fossil locality in 2019; A. outcrop of shell bed (arrow) near the top of the small sandstone hill; B. position of shell bed (arrow) on stratigraphic section; C and D. view of shell bed underlying the topsoil from anthropogenic activity; E. disarticulated valves of *Pseudohyria (Matsumotoina) somanai* (arrows); F. articulated valves of *P. (M.) somanai* (arrow) on the surface of weathered mud nodule conglomeratic sandstone bed.

Fig. 2). There are four shell beds in lime and mud nodule conglomeratic sandstone were recorded in the Sao Khua Formation (Fig. 2). More than six thousand articulated and disarticulated bivalve fossils were found on the eroded and weathered surface of the lime and mud nodule conglomeratic sandstone bed (upper shell bed of section 2; Figs. 2, 3) at the top of the southwestern side of this small hill, whereas other shell beds contained only a few shell fragments. Fragments of dinosaur bone and other vertebrate remains were also discovered in this shell bed.


**FIGURE 4.** Microremains study in 2020. A. digging on weathered lime-nodule conglomeratic sandstone shell bed to collect sediment for sieving; B. pouring sediment in water; C. washing and sieving sediment; D. sediment from sieving process was aired and dried for at least 2 days before examining this dry sediment under stereo microscope.

## MATERIALS AND METHODS

The specimens were collected by local people and monks from Wat Pa Phu Kum Khao at Ban Phu Khao Thong, Kham Pa-ung Subdistrict, Pho Chai District, Roi Et Province, (Figs. 1–2). All specimens discovered were cleaned, registered, identified and classified according to preservation (articulated/disarticulated shell fragments). Almost all the specimens are housed in the local site museum collection (KP). The voucher specimens used in further taxonomic and palaeontological research were deposited in the collections of the Palaeontological Research and Education Centre, Mahasarakham University (PRC).

Two hundred kilograms of weathered sediment from the lime nodule conglomeratic sandstone shell bed were screen-washed using 0.5 and 1.7-mm mesh-sized sieves (Fig. 4). Then they were examined for microremains under a stereomicroscope, and light microscope at the PRC and the Department of Biology, Faculty of Science, Mahasarakham University.

Palynomorphs were collected from red purple mudstone beds, from an underlying of the fossil bivalve's bed. Three sediment samples (500 g/each) were collected at 25 cm intervals from the bottom to the top of the bed (Fig.2; section 2). Palynological extraction techniques used hydrofluoric and hydrochloric acids, and observation under a LM (light microscope).

## RESULTS

According to Tumpeesuwan (2010) and Tumpeesuwan et al. (2010), there are 15 bivalve fossil localities reported from the Sao Khua Formation, but only the Huai Lao Yang site in Nong Bua Lamphu Province (671 individuals, six taxa) and Phu Noi site in Phu Wiang Area, Khon Kaen Province (222 individuals, three taxa) contain large numbers of well-preserved bivalves with high species diversity (Table 1). The freshwater bivalve fossils discovered from a new site at Phu Kum Khao in Roi Et comprised at least 6,643 individual shells belonging to nine taxa (Table 2), this represents the highest abundant and highest species diversity discovered within one shell bed of the Sao Khua Formation.

**TABLE 1.** List of bivalve taxa from the localities that contain a great number of well-preserved bivalve fossils.

| Taxa | Huai Lao Yang, Nong Bua Lamphu (Tumpeesuwan, 2010) | Phu Noi in Phu Wiang Area, Khon Kaen (Tumpeesuwan, 2010) | Phu Kum Khao, Roi Et (This study) |
|---|---|---|---|
| 1. *Nakamuranaia* sp. | 17 | - | - |
| 2. *Yunnanoconcha* sp. | 227 | - | - |
| 3. *Yunnanoconcha* sp. cf. *Y. khoratensis* | - | - | 127 |
| 4. *Sinonaia* sp. | 2 | - | - |
| 5. *Nippononaia* sp. cf. *N. mekongensis* | - | 1 | 28 |
| 6. *Koreanaia (Eokoreanaia)* sp. | 422 | - | - |
| 7. *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus* | - | 6 | 57 |
| 8. *Pseudohyria (Mastumotoina) somanai* | - | 215 | 6,339 |
| 9. *Cardinioides magnus* | 2 | - | - |
| 10. Unionoida *superfam. indet.* 1 | - | - | 8 |
| 11. Unionoida *superfam. indet.* 2 | - | - | 12 |
| 12. Unionoida *superfam. indet.* 3 | - | - | 64 |
| 13. Unionoida *superfam. indet.* 4 | - | - | 1 |
| 14. Unionoida *superfam. indet.* 5 | - | - | 1 |
| Total species | 5 | 3 | 9 |
| Total specimens | 670 | 222 | 6,637 |

**TABLE 2.** Occurrence of bivalve fossils assemblage from Phu Kum Khao bivalve fossil locality, Kham Pa-ung Subdistrict, Pho Chai District, Roi Et Province.

| Species | Number | Articulation | | Fragments |
|---|---|---|---|---|
| | | Articulate | Disarticulate | |
| *Yunnanoconcha* sp. cf. *Y. khoratensis* | 127 | 51 | 20 | 56 |
| *Nippononai* sp. cf. *N. mekongensis* | 28 | 26 | 2 | - |
| *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.)* | 57 | 38 | 12 | 7 |
| *Pseudohyria (Matsumotoina) somanai* | 6,339 | 1,730 | 4,081 | 528 |
| Unionoida *superfam. indet.* 1 | 8 | 1 | 2 | 5 |
| Unionoida *superfam. indet.* 2 | 12 | 10 | 2 | - |
| Unionoida *superfam. indet.* 3 | 64 | 12 | 51 | 1 |
| Unionoida *superfam. indet.* 4 | 1 | 1 | - | - |
| Unionoida *superfam. indet.* 5 | 1 | - | 1 | - |

## The bivalve assemblage

The higher taxonomy of the early Cretaceous bivalve fossils is based mainly on Cox et al. (1969), Sha and Fursich (1993), Sha (2007), and Fang et al. (2009) as follows.

**Phylum Mollusca Cuvier, 1797**
**Class Bivalvia Linné, 1758**
**Subclass Palaeoheterodonta Newell, 1965**
**Order Unionoida Stolizka, 1870**
**Superfamily Trigonioidoidea Cox, 1952**

**Diagnosis.—** anterior pedal retractor scar present, distinctly separate from anterior adductor scar.

**Family Nakamuranaiidae Guo, 1981**

**Diagnosis.—** Nakamuranaiidae without outer shell ornamentation

**Genus *Yunnanoconcha* Gu & Ma, 1976 in Ma et al. 1976**

***Yunnanoconcha* sp. cf. *Y. khoratensis* (Kobayashi, 1963) (Fig. 5A).**

**Diagnosis.—**oblong shell, shell length (27.53–114.44 mm) longer than shell height (17.74–58.63 mm). Outer shell surface smooth, without ornamentation.

**Material.—** 127 registered specimens, including 51 articulated valves (KP-8–12, KP-14, KP-16–17, KP-20, KP-555, KP-999–1004, KP-1007, KP-1009, KP-1011–1012, KP-1098–1101, KP-1604–1607, KP-2477–2483, KP-2492, KP-2498–2500, KP-2507, KP-2509, KP-3011, KP-3014, KP-3016–3017, KP-3023, KP-3304, KP-3339, KP-5181, KP-5761, KP-6023, KP-6218), and 20 disarticulated valves (eight right valves (KP-15, KP-17, KP-19, KP-1008, KP-2501–2502, KP-2508, KP-6028) and twelve left valves (KP-13, KP-1608–1609, KP-2505–2506, KP-3250–3253, KP-3341, KP-4952–3253, KP-6201)) and 56 pieces of shell fragments (KP-1005–1006, KP-1610–1614, KP-2475–2476, KP-2484–2491, KP-2493–2497, KP-2503–2504, KP-3010, KP-3012–3013, KP-3015, KP-3018–3019, KP-3024–3027, KP-3049, KP-3303, KP-3340, KP-

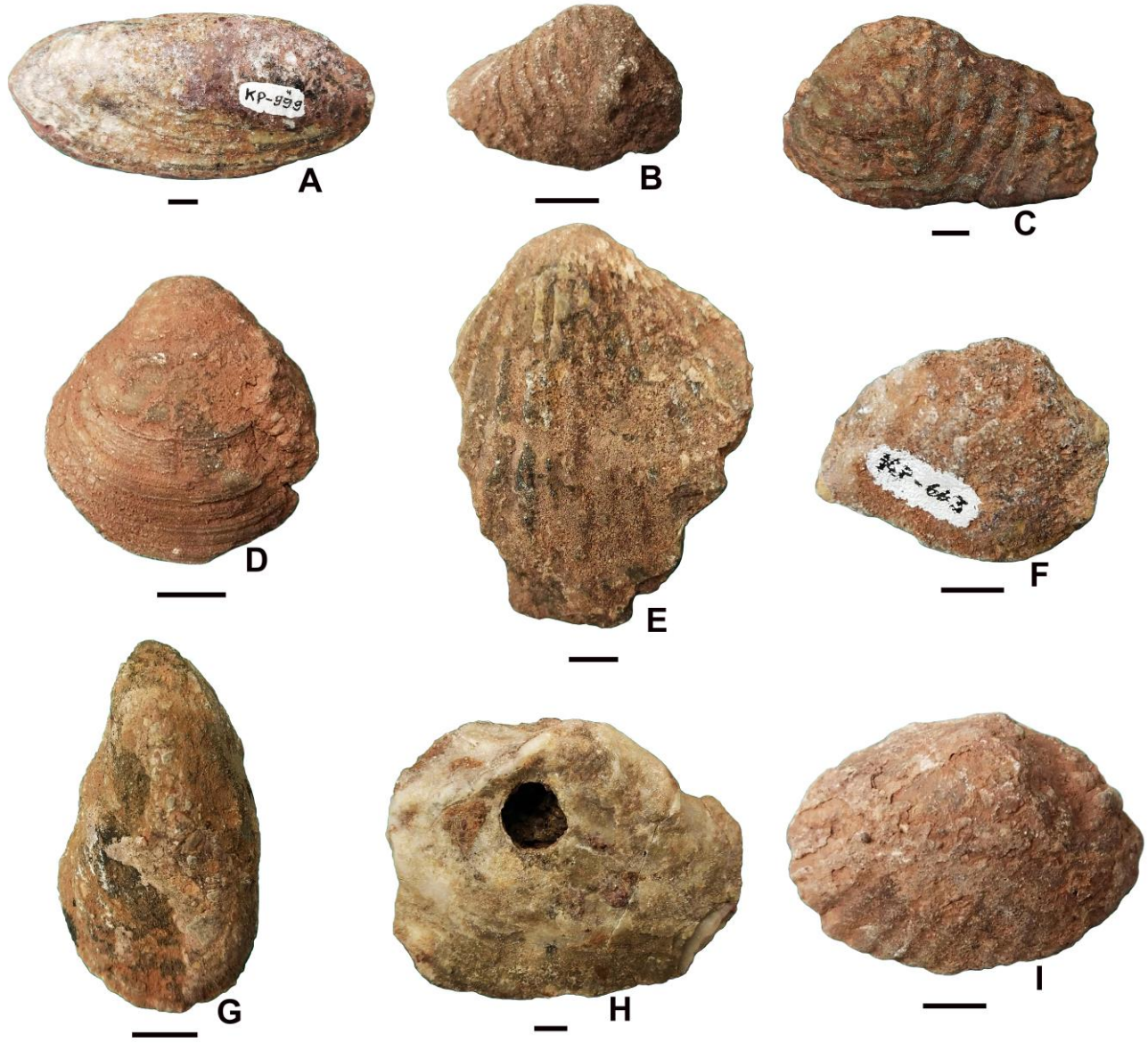


**FIGURE 5.** A. Articulated valves of *Yunnanoconcha* sp. cf. *Y. khoratensis*; B. Articulated valves of *Nippononaia* sp. cf. *N. mekongensis*; C. *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus*; D. *Pseudohyria (Matsumotoina) somanai*; E. Unionoida *superfam. indet.* 1; F. Unionoida *superfam. indet.* 2; G. Unionoida *superfam. indet.* 3; H. Unionoida *superfam. indet.* 4; I. Unionoida *superfam. indet.* 5. (Scale bars = 1 cm)

3342, KP-4444, KP-4488, KP-5649, KP-5799, KP-6200, KP-6202–6210) (Tables 2, 3).

**Family Trigonioididae Cox, 1952**
**Subfamily Trigonioidinae Cox, 1952**
**Diagnosis.—** Flanks with V-shaped ridges below the umbo with reverse V-shaped ridges on the anterior and posterior flanks.
**Genus *Nippononaia* Suzuki, 1941**
***Nippononaia* sp. cf. *N. mekongensis* Kobayashi, 1963 (Fig. 5B)**

**Diagnosis.—** *Nippononaia* has a pyriform shell, of slightly small size. Shell length 26.78–67.63 mm and shell height 15.36–44.46 mm. The outer shell surface possesses a V-shape ridge under the umbo, which the main sub-median rib (ridge) sets have a VA of 40°–64°. The anterior and posterior parts of the shell possesss a reverse V-shape ridge. Hinge teeth with crenulation. Submedian teeth absent.
**Material.—** 28 registered specimens, comprise 26 articulated valves (KP-2, KP-21, KP-561, KP-888–902, KP-1106, KP-1500–1503, KP-3316, KP-6212–6213)

**TABLE 3.** Occurrence of disarticulated valves of bivalves fossil assemblage from Phu Kum Khao bivalves fossil locality.

| Species | Disarticulated valves | | |
|---|---|---|---|
| | Right valves | Left valves | Un-identify |
| *Yunnanoconcha* sp. cf. *Y. khoratensis* | 8 | 12 | - |
| *Nippononai* sp. cf. *N. mekongensis* | - | 2 | - |
| *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus* | 7 | 5 | - |
| *Pseudohyria (Matsumotoina) somanai* | 1,878 | 2,203 | - |
| Unionoida *superfam. indet.*1 | 1 | 1 | - |
| Unionoida *superfam. indet.*2 | 1 | - | 1 |
| Unionoida *superfam. indet.*3 | 5 | 8 | 38 |
| Unionoida *superfam. indet.*4 | - | - | - |
| Unionoida *superfam. indet.*5 | - | 1 | - |

and two disarticulated valves (two left valves (KP–1, KP-2370) (Tables 2, 3).

**Genus *Trigonioides* Kobayashi and Suzuki, 1936**

**Diagnosis.—** *Trigonioides* possesses V-shaped ridges on center of external shell surface, which the main sub-median rib (ridge) sets have a VA of 5°–52°, and reversed V-shaped ridges on anterior and posterior portions of shell. Hinge teeth have less to more crenulation, submedian tooth present.

**Subgenus *Diversitrigonioides* Gu, 1976 in Gu et al. 1976**

***Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus* (Hoffet, 1937) (Fig. 5C)**

**Diagnosis.—** *Diversitrigonioides* possesses asymmetrically submedian V-shaped ridges, which the main sub-median rib (ridge) sets have a VA of 45°- 52°. The posterior branches being broader than the anterior one. Shell length 20.33–83.71 mm and shell height 14.60–62.73 mm.

**Material.—** 57 registered specimens comprise 38 articulated valves (KP-3–4 KP-6–7, KP-556, KP-558–559, KP-903–911, KP-1010, KP-1102–1105, KP-1108, KP-1111, KP-1122, KP-1301, KP-1603, KP-1615, KP-1945, KP-3300, KP-3305–3308, KP-3312, KP-3315, KP-3333–3335) and 12 disarticulated valves (seven left valves and five right valves) (KP-5, KP-557, KP-1602, KP-3301, KP-3309–3310, KP-3313–3314, KP-3320, KP-5272, KP-5796, KP-6214) and 7 pieces of shell fragments (KP-230, KP-560, KP-1122, KP-1862, KP-1957, KP-2110, KP-5796) (Tables 2, 3).

**Family Pseudohyriidae Kobayashi, 1968**

**Genus *Pseudohyria* MacNeil, 1936**

**Diagnosis.—** *Pseudohyria* has a triangular shell shape, the outer shell surface possesses chevron shaped ridges on the postero-dorsal part.

**Subgenus *Matsumotoina* Guo, 1982**

**Diagnosis.—** *Matsumotoina* possesses submedian pseudocardinal teeth, all hinge teeth without crenulation.

***Pseudohyria (Matsumotoina) somanai* Tumpeesuwan, Sato, and Nakhapadungrat, 2010 (Fig. 5D)**

**Diagnosis.—** Shell thick, fairly large in size, trigonally suboval or subelliptical in outline, Shell length 14.70–93.24 mm and shell height 12.35–92.55 mm., fairly inflated; anterior margin well rounded, postero-dorsal one rather arcuated, postero-ventral corner sharp angulate, ventral margin fairly arcuated. Surface ornamented with concentric growth lines. The posterior ridge is fairly prominent with short 5 to 8 chevron ribs on the posterior ridge.

**Material.—** 6,339 registered specimens comprising 1,730 articulated valves and 4,081 disarticulated valves (1,878 right valves, and 2,203 left valves ), and 528 pieces of shell fragments (KP-22–66, KP-70–71, KP-73–79, KP-81–103, KP-104–111, KP-113–129, KP-131–152, KP-153–162, KP-165–166, KP-169–185, KP-186–196, KP-197, KP-198–202, KP-205–209, KP-210–226, KP-229–298, KP-300–322, KP-324–335, KP-336–491, KP-492–519, KP-520–527, KP-532–533, KP-537, KP-538–570, KP-571–574, KP-575–579, KP-580, KP-581–621, KP-626–639, KP-643–659, KP-664–685, KP-687–699, KP-701–887, KP-912–985, KP-988–998, KP-1014–1097, KP-1109–1121, KP-1123–1151, KP-1152–1300, KP-1302–1419, KP-1421–1458, KP-1464–1494, KP-1495–1499, KP-1506–1537, KP-1539–1601, KP-1616–1872, KP-1874–1944, KP-1946–2109, KP-2111–2474, KP-2511–2999, KP-3001–3008, KP-3075–3248, KP-3257, KP-3261–3264, KP-3266–3299, KP-3317–3319, KP-3321–3332, KP-3343–3350, KP-3352–3527, KP-3529–3814, KP-3816–4159, KP-4161–4443, KP-4445–4487, KP-4489–4837, KP-4839–4951, KP-4953–4999, KP-5001–5648, KP-5650–5760, KP-5762–5798, KP-5800–6027, KP-6029–6199, KP-6215–6217, KP-6219–6635) (Tables 2, 3)

**Unionoida *superfam. indet.***

**Diagnosis.—** No specimens at hand of these taxa reveal the position of anterior pedal retractor scar and anterior adductor scar, therefore, we cannot exactly judge them into the precise Superfamily.

**Unionoida *superfam. indet.* 1 (Fig. 5E)**

**Diagnosis.—** With no complete shell at hand, the assessment of possible complete shell shape might be a triangular shape, shell length 23.32–78.40 mm and shell height 27.47–84.06 mm. The unique character of this taxon is the prominent radial ridges and grooves that cause the shell to look like a scallop.
**Material.—** 8 registered specimens comprising one articulated valves (KP-700) and two disarticulated valves (KP-1107, KP-4838) (one right valve and one left valve) and five pieces of shell fragments (KP-500, KP-3333–3334, KP-3336, KP-6211) (Tables 2, 3).

**Unionoida *superfam. indet.* 2 (Fig. 5F)**
**Diagnosis.—** Shell of triangular shape with concave postero-ventral margin, shell length 23.19–50.68 mm and shell height 20.94–51.52 mm.,.
**Material.—** 12 registered specimens comprising ten articulated valves (KP-660–663, KP-686, KP-1301, KP-1459–1462) and two disarticulated valves (one right valves (KP-1463) and one un-identified valves (KP-3000)) (Tables 2, 3).

**Unionoida *superfam. indet.* 3 (Fig. 5G)**
**Diagnosis.—** Shell of obovate shape, look like *Mytilus* without any sculpture, shell length 21.58–49.77 mm and shell height 27.64–56.98 mm.,.
**Material.—** 64 registered specimens comprising 12 articulated valves (KP-299, KP-3028, KP-3041, KP-3058, KP-3068, KP-3071, KP-3256, KP-3258–3259, KP-3528, KP-3703, KP-4160) and 51 disarticulated valves (KP-1420, KP-1505, KP-3351, KP-3030–3040, KP-3042–3057, KP-3059–3067, KP-3069–3070, KP-3072–3074, KP-3254–3255, KP-3060, KP-3065, KP-3337–3338, KP-3815) and one pieces of shell fragments (KP-3029) (Tables 2, 3).

**Unionoida *superfam. indet.* 4 (Fig. 5H)**
**Diagnosis.—** Shell of very large size with trapezoid shape, shell length 96.18 mm and shell height 81.05 mm., Surface smooth.
**Material.—** Only one articulated valve was found (KP-5555) (Tables 2, 3).

**Unionoida *superfam. indet.* 5 (Fig. 5I)**
**Diagnosis.—** Shell of elliptical shape with radial ridge on ventral margin, shell length 51.91 mm and shell height 39.19 mm.,
**Material.—** Only one disarticulated valve (left valve) was discovered (KP-5000) (Tables 2, 3).

**Vertebrates**
**Phylum Chordata Haeckel, 1874**
**Subphylum Vertebrata J-B. Lamarck, 1801**
**Class Chondrichthyes Huxley, 1880**
**Subclass Elasmobranchii Bonaparte, 1838**
**Order Hybodontiformes Patterson, 1966**
**Family *incertae cedis***
**Genus *Heteroptychodus* Yabe and Obata, 1930**
***Heteroptychodus steinmanni* Yabe and Obata, 1930 (Fig. 6A)**
**Diagnosis.—** The complete teeth are parallelogram-shaped in outline, and almost flat. Occlusal face ornamentation consists of 30-35 parallel ridges running mesio-distally. From each of the parallel ridges originate many, short, non-branching ridges perpendicular to the parallel ridges.
**Material.**— Only two tiny tooth fragment was found (PRC-PC 11 and PRC-PC 14)

**Class Osteichthyes Huxley, 1880**
**Subclass Actinopterygii Klein, 1885**
**Actinopterygii *order indet.* (Fig. 6B)**
**Diagnosis.—** Based on the apical view of this unprepared specimen; the bone is polygonal shape, rather thick, with the apical surface covered with radiating ridges from center to margin. One side of this bone possesses a prominent spike, which might be preliminarily identified as part of an Osteichthyes skull connected to the suborbital bone.
**Material**.— Only one part of skull bone was found (PRC-PC-O-1(KP-1873))

**Subclass Diapsida Osborn, 1903**
**Infraclass Archosauromorpha Von Huene, 1946**
**Archosauromorpha *indet.* (Fig. 6C)**
**Diagnosis.—** Teeth looklike elongate conical and curved. Surface covered with longitudinal ridges and grooves along the length of the tooth, there are two major ridges on both sides of the teeth. The cross section of teeth is circular. However, all specimens at hand are really very poor. These tiny fragments may belong to a crocodile or a spinosaurid dinosaur.
**Material.—** Many tooth fragments were found, almost all with crown and root broken PRC-PC-D-1)

**Superorder Dinosauria Owen, 1842**
Order Saurischia **Seeley, 1887**
Suborder Theropoda **Marsh, 1881**
**Theropoda *fam. et gen. indet.* (Figs. 6D–E)**
**Diagnosis.—** Teeth compressed, surface smooth and glossy. Cross section of teeth is elliptical. Prominent serrations present on teeth ridges.
**Remarks.—** The tooth fragment of conical shape (Fig. 6D), is 1.7 cm in length. Apical part and root broken. Cross section of tooth is elliptical (Fig. 6E), diameter 1 cm, and length 1.3 cm; almost all enamel and serrations eroded, (for this reason this specimen cannot be exactly identified). **Material.—** Theropod teeth and

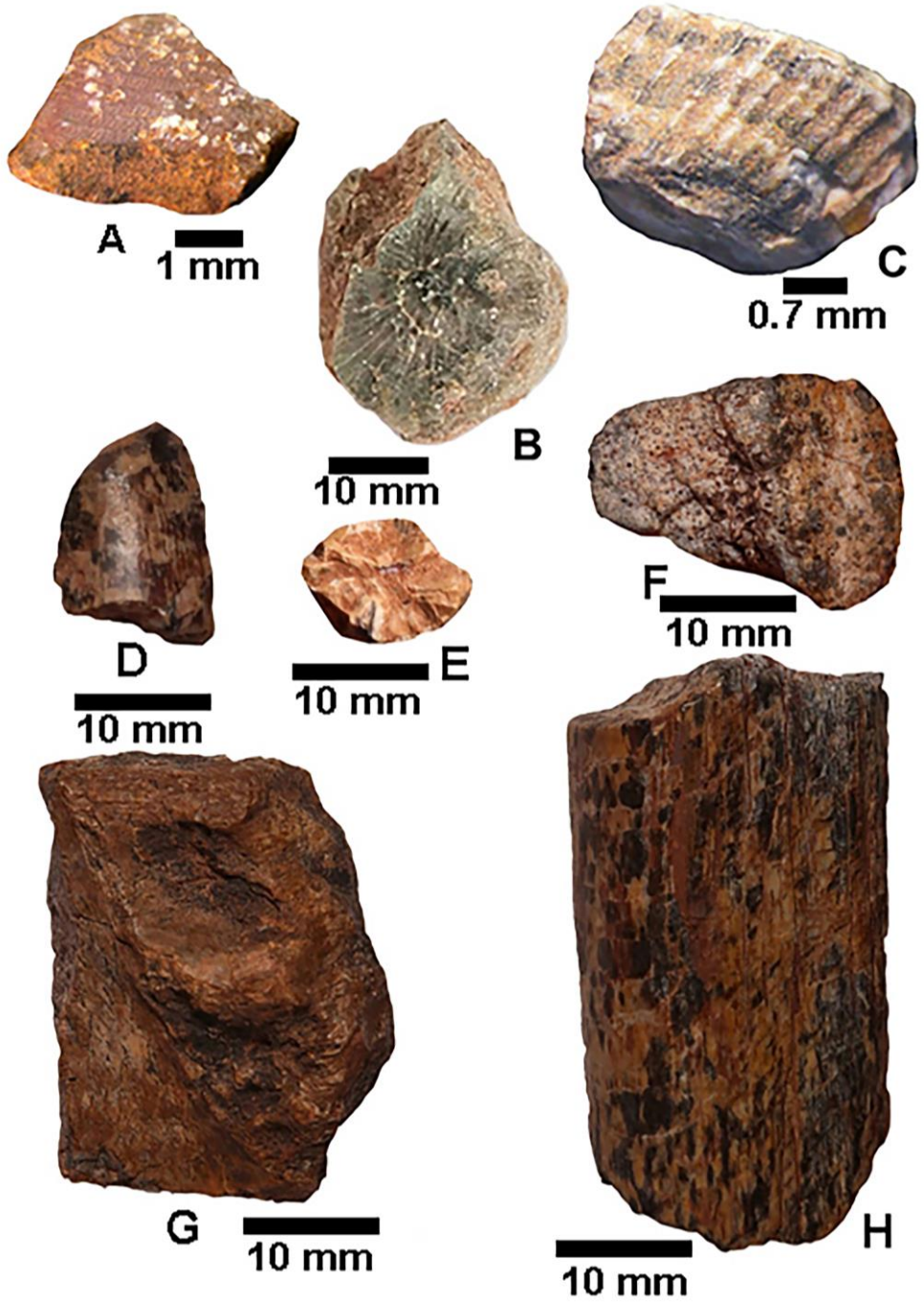


**FIGURE 6.** A. Hybodont shark teeth *Heteroptychodus steinmanni*; B. unknown Osteichthyes fish skull bone; C. fragmented tooth of archosaur; D-E. Theropod dinosaur tooth: D. side view; E. cross section view; F-H. Dinosaur bones: F. top view; G. cross-section; H. side view.

bones found in this shell bed comprised both complete and incomplete teeth. No root present (PRC-PC-D-2).

**Suborder Sauropodomorpha Huene, 1932**
**Sauropodomorpha *fam. et gen. indet.* (Fig. 7)**
**Diagnosis.—** Specimens embedded in sandstone block (Fig. 7), length 20 cm, this bone is a partial cervical vertebra. A flat parapophysis process was fused with the left cervical rib. The broken centrum shows large camerate structures, the air chambers. This is a character of Neosauropoda. However, there are three sauropod taxa present in the Sao Khua Formation, thus more material is needed to identify this dinosaur.
**Material.—** Partial cervical vertebra of Sauropod was found in this shell bed (PRC-PC-D-3) Dinosauria *indet.*

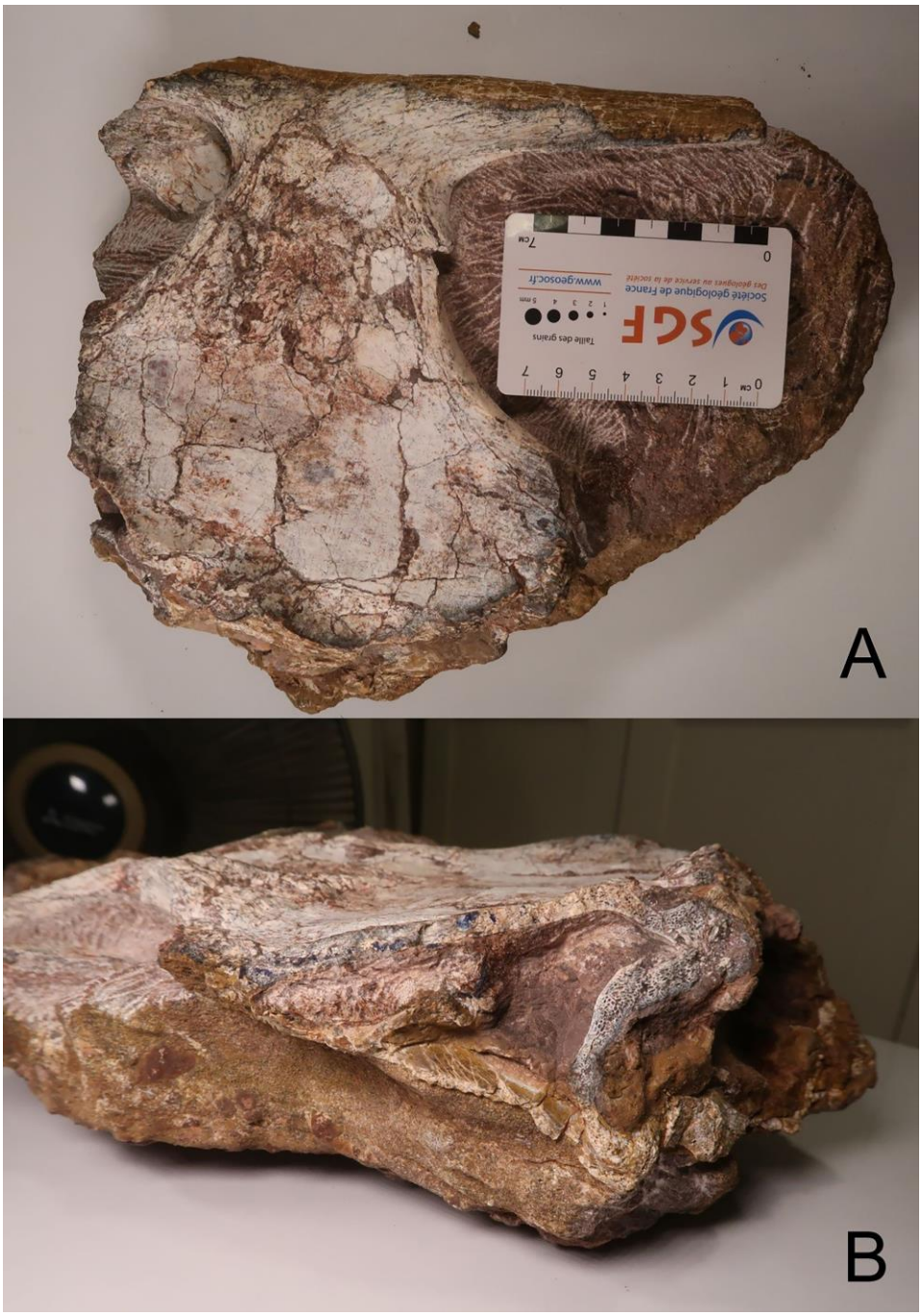


**FIGURE 7.** Sauropod cervical vertebra. A. ventral view; B. anterior view showing the internal structure of the centrum with large air chamber (camerae).

**Diagnosis.—** Based on two bone fragments that were found in the shell bed, the first one is a pentagonal thin plate, 1 cm thick, one side smooth, other side rough; this bone is probably part of vertebral bone (Fig. 6F). Second one is short cylindrical shape (Fig. 6H), not hollow, and cross section is slightly triangular (Fig. 6G), this bone is small, incomplete, and no diagnostic characters, it could identify beyond "Dinosauria indet.".
**Material.—** Bone fragments of Dinosaur were found in this shell bed (PRC-PC-D-4–5)

Plant
**Pollen assemblage**
**Angiospermae**
**Poales**
**Poaceae (Fig. 8A)**
**Diagnosis.—** Monad, subspheroid, heteropolar, medium sized, P × E = 26 × 28 µm. Exine 1.5 µm thick, scabrate sculpture. 1-polate aperture, 8 µm long with dome shaped operculum, 8X5 µm in size.
**Material.**— PRC-PKK-2


**FIGURE 8.** Palynomorph from mudstone beds underlying bivalve bearing bed at Phu Kum Khao, Roi Et. A. Poaceae pollen; B. un-identified pollen; C. Poales pollen.

**Un-identified pollen (Fig. 8B)**

**Diagnosis.—** Monad, oblique-ovoid, heteropolar, medium sized, 35 × 23 µm. Exine 2 µm thick, recticulate sculpture. Inaperturate palynomorph.

**Material.**— PRC-PKK-2

**Angiospermae**

**Poales (Fig. 8C)**

**Diagnosis.—** Monad, spheroid, Isopolar, medium sized, 26 × 24 µm. Exine 1 µm thick, scabrate sculpture. Inaperturate palynomorph.

**Material.**— PRC-PKK-2

**Remarks.—** The pollen of flowering plants (Poales) and un-identified pollen was detected (Fig. 8), but diversity and density were very low, pollen cannot be used to estimate plant diversity, plant community and paleoenvironment. Racey and Goodall (2009) considered the age of the Sao Khua Formation to be Early Cretaceous by using lithostratigraphy and biostratigraphy (especially *Dicheiropollis etruscus* pollen). In addition, the detection of *Corollina* and *Dicheiropollis* pollen indicates sediment accumulation at warm temperature and a dominantly seasonally dry subtropical climate. The key palynomorph, *D. etruscus* was not found in this study, possibly as a result of the low sample number, disappearance of pollen during the palynological analysis or because there is no key pollen in the red bed sandstone.

## DISCUSSION

This shell bed is a lime nodule conglomeratic sandstone of the Sao Khua Formation, which is exposed on the top of the small hill "Phu Kum Khao" in Roi Et Province. Total registered specimens are 6,637 individuals of nine species of freshwater bivalve, including *Pseudohyria* (*Matsumotoina*) *somanai*, 95.51%; *Yunnanoconcha* sp. cf. *Y. khoratensis*, 1.91%; *Trigonioides (Diversitrigonioides)* sp. cf. *T. (D.) diversicostatus*, 0.86%; *Nippononaia* sp. cf. *N. mekongensis*, 0.42%; and another five un-identified taxa, no specimens at hand of these taxa reveal the position of anterior pedal retractor scar and anterior adductor scar, therefore, we cannot exactly judge them into the precise Superfamily, therefore, we used Superfamily *incertae cedis* for these 5 taxa (Tables 1–3). The dominant species is *Pseudohyria* (*Matsumotoina*) *somanai*, which has a triangular shell shape similar to the modern analogue *Corbicula* spp. (Family Corbiculidae) which live in sand at the shallow side of the flowing rivers (near point bars); but the fossils are larger and have a thicker shell than recent species.

*Yunnanoconcha* sp. cf. *Y. khoratensis* has an oblong shell shape similar to modern species of *Namkongnaia* spp. living in mud substrate of stillwater (Jeratthitikul et al. 2021) such as ponds (Brandt, 1974) and mud substrate in still part of the river or in lenthic habitat such as pond and lakes (Morelet, 1875; Morlet, 1889: Brandt, 1974).

*Nippononaia* sp. cf. *N. mekongensis* has a size, shape, and surface ornamentation similar to the recent species *Scabies crispata*, which lives in the sandy bottom of shallow and flowing water.

Unionoida *superfam. indet.* 4 has a large trapezoid shell shape (approximately 11 cm shell length). It looks similar to the largest recent freshwater bivalve species of the Chao Praya and Mekong River Basins, *Chamberlainia hainessiana* and *C. somsakpanhai*, respectively. Both species live in the deep part of the river channel (Kongim et al., 2023)

Therefore, we assume that the bivalve assemblage of this shell bed is mixed, comprising of species that lived in sand near to point bars in a meandering river, in shallow flowing water, stagnant water (such as backswamp, pond, oxbow lake) and the deep river channels. Both articulated valves and disarticulated valves were found in almost all species (Table 2). The disarticulated valves comprise almost the similar number of right and left valves (Table 3).

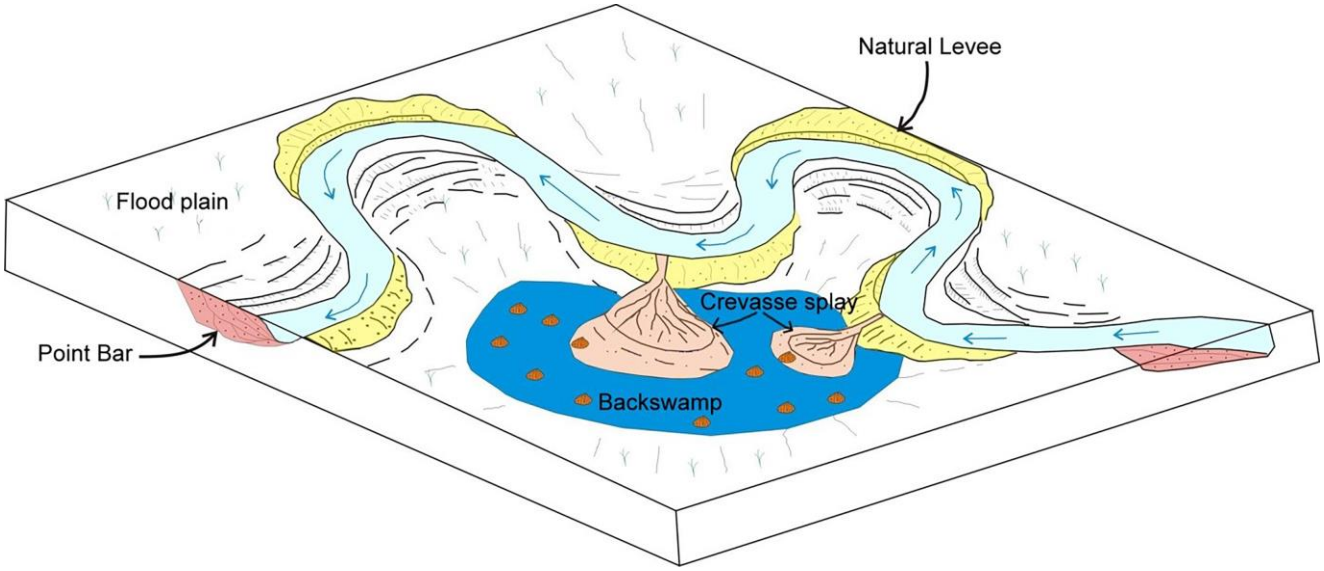


**FIGURE 9.** Reconstruction of palaeo-environment in Phu Kum Khao bivalve fossil locality, Pho Chai District, Roi Et Province**.** (Adapted after Nulay, 2023)

The combination of geometry, lithology, palaeo-current pattern, sedimentary structure of the shell bed and the underlying bed, and the information of fossil assemblage and fossil occurrence might be interpreted as this shell bed having been deposited in a crevassed splay depositional environment in a meandering river system (Fig. 9) by a flash flood or overbank flood on a floodplain, It is feasible to conclude this because clasts in lime nodule conglomeratic sandstone possesss mixed assemblage of bivalves from many micro habitats of the meandering river system, and several kinds of rock, with no size sorting.

The articulated valves were preserved *in situ* in various size and with good preservation indicating that they died suddenly in life positions when thick sediment buried them during big flooding events.

For enormous number of specimens of disarticulated shells, especially *Pseudohyria* (*Matsumotoina*) *somanai*, there are twice time more than articulate valves. Among disarticulated valves of the same species, the numbers of left and right valves are nearly equal (Table 3) indicating that these disarticulated valves died before transportation and were transported and buried in this shell bed not far from the habitat they used when alive.

In contrast, in *Yunnanoconcha* sp. cf. *Y. khoratensis*, more (almost 2x) articulated valves were found than disarticulated valves. This indicates that most of them were suddenly buried *in situ* in a floodplain pond by sediment when a flash flood occurred after overbank flow and collapse of the natural levee. Large amount of sediment from flooding spread on the floodplain as crevasse splay.

This eroded lime nodule conglomerattic sandstone bed contained numerous bivalve and vertebrate fossils, such as archosauria teeth, a dermal skull bone of a bony fish, a vertebra of a sauropod dinosaur, and theropod dinosaur teeth. Fragments of freshwater hybodont shark teeth *Heteroptychodus steinmanni* were found as microremains. These teeth are of a durophagus shark, suitable for crushing animals with hard shells, such as bivalves and crabs. This shark might have hunted for bivalves, crushing their shells with blunt durophagous type teeth and eating the soft part inside, and spitting out shell fragments to the substrate.

The results of palynological study of the samples from the underlaying red purple mudstone indicates both very low abundance and diversity and cannot be used as evidence for estimating population size, plant assemblage or the palaeodepositional environment. Due to the red purple mudstone being deposited in an oxidating environment, almost all pollen and palynomorphs were degraded and destroyed. Unfortunately, the key palynomorphs *Dicheiropollis etruscus* or others were not found in this study, therefore, we cannot use pollen and palynomorphs for a precise age determination of this shell bed.

According to the radiometric dating of detrital zircons studied by Tucker et al. (2022), they suggest 133.8 (±1.8) Ma (late Valanginian) for the middle part of the Sao Khua Formation, 136.0 (±5.5) Ma (middle Valanginian) for the upper part of the Sao Khua Formation, and 132.4 (±2.0) Ma (early Hauterivian) for the lowermost part of the Phu Phan Formation. Zircon is a mineral that, commonly crystallized in igneous rocks, and the crystals grow between the

temperature of 600–1,100 °C, when zircon has cooled below 800 °C it retains all the lead (Pb) from the radioactive decay. Therefore, U-Pb age can be treated as the age of crystallization in igneous rock (Wikipedia, 2024). Normally, after the igneous rock wherthered and eroded, the detrital zircon grains were transported and deposited as sedimentary rocks, which the time that sedimentary rock deposited cannot older than the youngest detrital zircon grain, this application is name "Maximum depositional age" (Dickinson and Gehrels, 2009; Gehrels, 2014), that is especially valuable for strata lacking fossils for biostratigraphic age control (Dickinson and Gehrels, 2009).

## CONCLUSIONS

1. The fossil assemblage in the Phu Khum Khao bivalve fossil locality at Pho Chai District, Roi Et Province comprised nine taxa of freshwater bivalves, and one taxon of the following: freshwater hybodont shark, ray finned fish, archosaur, theropod dinosaur, and sauropod dinosaur.
2. It represents the highest abundance and diversity of freshwater bivalve assemblages in the Sao Khua Formation of Thailand.
3. The site is characterized by the dominance of the Late Barremian *Pseudohyria (Matsumotoina) somani* deposited in lime nodule conglomeratic sandstone.
4. The middle to late Valanginian Age derived from detrital zircon studied from the middle and the upper Sao Khua Formation is the Maximum Depositional Age, which the true depositional age might be younger than Valanginian.
5. The pollen assemblage comprised Poales and unidentified pollen. Diversity and density were very low, and the assemblage cannot be used for estimation of plant diversity, community and paleoenvironments.
6. According to the molluscan assemblage, their occurrence and orientation and the stratigraphic results, this shell bed was interpreted as crevasse play deposited in the flood plain of a meandering river system.

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