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First record of hybodont egg capsules from the Jurassic of Thailand

Découverte de capsules ovigères de requins hybodontes dans le Jurassique de Thaïlande

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ABSTRACT

Two egg capsules of *Palaeoxyris* sp. are reported from the Jurassic Phu Kradung Formation in the Khorat Plateau, northeastern Thailand. As the record of this genus remains rare in the Jurassic, it complements its stratigraphic distribution. Most importantly, it represents the first unambiguous evidence that some hybodont sharks from the Mesozoic of Thailand were able to reproduce in fresh waters, even if it is not yet possible to identify which species in particular.

RÉSUMÉ

Deux capsules ovigères de *Palaeoxyris* sp. ont été découvertes sur le plateau de Khorat dans le nord-est de la Thaïlande. Les spécimens proviennent de la Formation Phu Kradung, datée du Jurassique. Le registre fossile de ce genre demeurant mal connu au Jurassique, cette découverte permet de compléter sa distribution stratigraphique. Ces capsules ovigères représentent la première preuve indéniable que durant le Mésozoïque certains requins hybodontes se reproduisaient dans les eaux douces thaïlandaises, même s'il n'est pas encore possible d'identifier quelles espèces en particulier.

Keywords: Elasmobranchii, Hybodontiformes, Egg capsule, Jurassic, Thailand

Mots clés : Elasmobranchii, Hybodontiformes, Capsule ovigère, Jurassique, Thaïlande

1. Introduction

In the last forty years, the Mesozoic of the Khorat Plateau (northeastern Thailand) has yielded diverse assemblages of freshwater hybodont sharks consisting of isolated teeth,

dermal denticles and dorsal fin spines (Cappetta et al., 1990, 2006; Cuny et al., 2007, 2008, 2014; Khamha et al., 2016). In 2008, a site from the Jurassic Phu Kradung Formation called “Phu Noi” was discovered and excavated by the Department of Mineral Resources (DMR) and Mahasarakham University. It has yielded diverse vertebrate fossils including dinosaurs, crocodiles, turtles, bony fishes, lungfishes, temnospondyls, pterosaurs and freshwater sharks (Chanthasit et al., 2019; Nonsrirach et al., 2021; Manitkoon et al., 2023), of which seven new species have been described so far (Cuny et al., 2014; Deesri et al., 2014; Tong et al., 2015, 2019; Martin et al., 2019; Cavin et al., 2020; Johnson et al., 2020). According to Cuny et al. (2014), the shark assemblage from Phu Noi includes *Acrodus kalasinensis*, *Hybodus* sp., aff. *Hybodus* sp., *Jiaodontus* sp. and *Lonchidion* sp. based on isolated teeth, dorsal fin spines and dermal denticles. However, a new specimen found partly in connection and currently under study indicates the presence of a new genus and species to which the teeth described previously as *Hybodus* sp. should be referred.

During the last few years, the DMR, led by a team from Sirindhorn Museum has continued the excavation and many new well-preserved fossils were unearthed including two hybodont egg capsules, which represent the first occurrence of their kind in Thailand. The present work aims therefore at describing the first fossils unambiguously demonstrating that at least some Mesozoic hybodont sharks were reproducing in fresh waters in Thailand.

2. Geological setting

Phu Noi is situated in Kham Muang district, Kalasin province, Northeastern Thailand (See location map in Chanthasit et al. [2019]). It belongs to the middle part of the Phu

Kradung Formation of the Khorat Group (see Sattayarak and Polachan, 1990), although no formal stratigraphic criteria on which to subdivide this Formation can be currently defined (Booth and Sattayarak, 2011). This Formation is composed of maroon, reddish-brown mudstone, sandstone and gravelly conglomerate deposited in a lacustrine to fluvial environment, probably under a two seasons semi-arid/humid climate (Mouret, 1994; Racey et al., 1996; Racey, 2009). Fossils have been recovered from two main units in Phu Noi: a conglomerate in the lower part of the section and from siltstones in its middle part (Ditbanjong and Chanthasit, 2019) (Fig. 1). The two egg capsules were found from a maroon siltstone in the middle part, at a distance of approximately 5 m from each other. They were recovered a few centimetres above a layer that has yielded many dinosaur bones. The presence of *Jiaodontus* and other vertebrate remains such as a xinjiangcheliid turtle and a freshwater teleosaurid crocodile suggest a Middle to Late Jurassic age for Phu Noi (Cuny et al., 2014; Martin et al., 2019; Tong et al., 2019; 2021). Fossil woods recovered at Phu Por, a site overlying Phu Noi and located a couple of kilometres West to the latter confirm such an age (Boonchai et al., 2020).

3. Material and methods

The terminology used to describe the specimens follows Fischer et al. (2010) and *Palaeoxyris* is here considered a form genus containing generically unrelated species (Zidek, 1976). However, for practical reasons, it is treated in accordance to the rules of the International Code of Zoological Nomenclature (ICZN, 1999).

The two egg capsules are housed in the collections of the Sirindhorn Museum (SM), Sahatsakhan, Kalasin Province, Thailand.

4. Description

Genus *Palaeoxyris* Brongniart, 1828

Palaeoxyris sp.

The first egg capsule, displaying part and counterpart, (SM 2023-1-014, fig. 2) is approximately 80 mm long and 22 mm wide. It is almost uncompressed but incomplete as its anterior part (beak) is missing. It shows a broad fusiform body with at least six visible segments made probably of six spiral bands turning clockwise around the body, three being visible on the exposed side of the pedicle. All bands display a similar width and a smooth surface. Six low raised, parallel ridges are also twisted around the body. The angle of the ridges with the cross axis is approximately 25°. The collarettes are poorly developed or preserved. A sharp constriction separates the pedicle from the body. The former is seemingly subequal to the body in length or slightly longer. It displays bands arranged parallel to the body axis.

The second specimen (SM 2023-1-015, fig. 3) is similar to the first one, but less complete. It also displays part and counterpart. It is 40 mm long and 23 mm wide as preserved. The upper part of the body and the beak are missing, and the pedicle is partly covered by sediment. On the latter, there is a change of orientation of the ridges that become parallel to the long axis of the egg capsule. In total, six segments and seven ridges are visible. The angle of the ridges with the cross axis of the body is approximately 25°. The collarettes are again poorly developed or preserved.

5. Discussion

5.1. Affinities of the specimens

According to Fischer et al. (2011), the genus *Palaeoxyris* can be diagnosed by the following characteristics: a three-fold division into beak, body and pedicle; a body broadly fusiform, gradually tapering towards each end, composed of three or more parallel helicoidally twisted bands; anterior end gradually tapering into shorter pointed beak; posterior end tapering to long, slender pedicle marked by either spiral or parallel ribbing; collarettes accompanying band margins; fine longitudinal striation on bands and collarettes; compressed specimens with transverse rhomboidal pattern, which allow to refer the two specimens described above to this genus, although they appear to lack the fine longitudinal striations on their bands usually present in this genus (Fischer et al., 2011; McLean, 2014). This, however, is likely to be a preservation artefact. The specimens not being much compressed, a rhomboidal pattern is not visible.

The subparallel arrangement of the ribs on the pedicle is a typical character of Mesozoic *Palaeoxyris*, whereas all Palaeozoic specimens show spiral/rhomboidal ribbing (Fischer et al., 2011). Moreover, almost all Mesozoic species are constructed with four or six bands, although many Palaeozoic specimens were not analysed to determine their number of bands (McLean, 2014).

SM 2023-1-014 and -015 were probably of a similar size, 100-120 mm long and 25 mm wide, although this is difficult to estimate as the shape of their beak is currently unknown (compare the reconstruction provided by Böttcher, 2010, Fischer et al., 2010 and McLean 2014). This represents a somewhat average size for *Palaeoxyris*, the largest specimens currently known being *P. friessi* from the Ladinian of Germany, reaching 270 mm in total length and the smallest ?*Palaeoxyris* sp. from the Cretaceous of Kansas probably not longer than 70 mm (Böttcher, 2010; McLean, 2014).

The ridges of SM 2023-1-014 and -015 are equidistant, which allows to distinguish them from the Mesozoic species *P. alterna* and *P. gilewii*, the latter displaying bands of different, alternating widths (Fischer et al., 2011). The body of SM 2023-1-014 appears to be more bulged than in *Palaeoxyris duni*, *P. friessi*, *P. humblei*, *P. jugleri*, *P. muensteri*, *P. regularis*, *P. sinocoreana* (corrected spelling according to article 32.5.2.3 of the International Code of Zoological Nomenclature, ICZN [1999]) and *Palaeoxyris* sp. from the lowermost Jurassic of Sweden and the Neocomian of Spain, and closer to *Palaeoxyris taurica* from the Middle Jurassic of Crimea, *?Palaeoxyris* sp. from the middle Cretaceous of Kansas or to *Palaeoxyris* sp. from the Cenomanian of France (Sauvage, 1903; Kawasaki, 1925; Crookall, 1930, 1932; Khabakov, 1949; Sze, 1954; Gomez Pallerola, 1982, 1988; Wenz, 1991; Böttcher, 2010; Fischer et al., 2010; Vullo et al., 2013; McLean, 2014; Austen et al., 2018; Néraudeau et al., 2020; Brignon, 2021, fig. 12; Krüger et al., 2021) although this character appears to be quite variable and depends probably on taphonomic processes (See Schenk, 1871, plates XIX and XX; Khabakov, 1949). However, SM 2023-1-014 displaying moderate compression, it is reasonable to state that the bulged aspect of its body is unlikely to be a taphonomic artefact. This character is more difficult to evaluate on SM 2023-1-015 as it is less well-preserved. Anyway, the *?Palaeoxyris* from Kansas is easily separated from the Phu Noi specimens by an angle of the bands with the cross axis of 60°, whereas it is only 25° in the studied specimens. The angle of the bands with the cross axis is also more important in *Palaeoxyris taurica* than in SM 2023-1-014 and -015. In addition, the bulged body of one of the two specimens illustrated by Khabakov (1949, pl. IX, fig. 7b) appears to be the result of a taphonomic deformation. All in all, the Thai specimens appear closer to the specimens from the Cenomanian of France (Vullo et al., 2013), although the collarettes appear to be more developed in the latter, as well as in most species of *Palaeoxyris*, than in SM 2023-1-014

and -015. Conversely, *Palaeoxyris duni* and the Thai specimens share no obvious flanged collarette extensions from the ribs, but these structures can be easily removed during the taphonomic process (McLean, 2014).

In conclusion, the morphology of their pedicle is typical of Mesozoic *Palaeoxyris*, but the two specimens being incomplete, a more precise identification would necessitate additional material, all the more since the unusual characters of the Thai specimens (lack of surface striation and no obvious flanged collarette) might be related to the quality of their preservation. Mesozoic *Palaeoxyris* have hitherto being recovered mostly in the Triassic and Cretaceous (McLean, 2014) but remain rare in the Jurassic, being limited to *P. sinocoreana* in the Lower Jurassic of Korea and China (Sze, 1954), *P. taurica* from the Bajocian-Bathonian of Crimea (Khabakov, 1949; Fischer and Kogan, 2008; Böttcher, 2010) and *Palaeoxyris* sp. from the lowermost Jurassic of Sweden (Krüger et al., 2021). Precise dating of continental series is always delicate, but the record of the Thai *Palaeoxyris* could be the only one from the Upper Jurassic (Tong et al., 2019) and is not older than the Bathonian (Cuny et al., 2014; Boonchai et al., 2020).

5.2. *Environment of deposition and reproduction of the Phu Noi hybodont sharks*

The main fossiliferous layer at Phu Noi, where the egg capsules have been found, was reconstructed as floodplain deposits in an oxbow part of a complex river system (Cuny et al., 2014; Liard et al., 2015; Martin et al., 2016). Moreover, desiccation cracks were observed at the base of the bone bed (Liard et al., 2015) as well as rosette type marks attributable to pupation chambers of dermestid beetles or similar insects on some bones of dinosaurs and crocodiles (Martin et al., 2016, 2019). These suggest that the fossils were exposed under aerial conditions for extended periods of at least a few weeks before burial. According to

Martin et al. (2019), the fossils sustained limited transport on a short distances after carcasses had decayed, with possible scattering by scavengers. The most parsimonious hypothesis explaining the deposition of the egg capsules in an oxbow is probably that they were transported together with the plants to which they were attached and the diverse already dead animal carcasses during flooding in the monsoon season. The egg capsule and plants being less dense than bones, they were transported in the upper part of the flood and therefore avoided damages from the transportation until deposition in the oxbow where they were buried together with the bone remains by deposition of layers of silt following less severe flood events. However, such a hypothesis will need more detailed sedimentary and taphonomic studies to be tested. The difference in colour between the two specimens is due to a secondary iron crust that is often observed around dinosaur bones in Phu Noi sites. SM 2023-1-15 was indeed found closer to a dinosaur bone than SM 2023-1-14.

So far, the capacity of Thai Mesozoic hybodont sharks to reproduce in fresh waters has been suggested from the discovery of possible juveniles and adults of *Heteroptychodus steinmanni* at at the same spot in the Lower Cretaceous Khok Kruat Formation (Cuny, 2012). On the other hand, *Paleoxyris* is a shark egg capsule known from the Carboniferous to the Cretaceous for which Hybodontiformes are considered to be the most probable producers (Crookall, 1932; Fischer and Kogan, 2008; Fischer et al., 2007, 2010; Krüger et al., 2021). Their recovery in a site yielding various hybodont taxa offers therefore the first direct evidence that at least some hybodonts were reproducing in fresh waters in the Mesozoic of Thailand. At least five different taxa have been recovered from Phu Noi so far (*Acrodus kalasinensis*, “*Hybodus*” sp., aff. *Hybodus* sp., *Jiaodontus* sp. and *Lonchidion* sp.), so that identifying the owner of the egg capsules is difficult. However, aff. *Hybodus*, *Jiaodontus* sp. and *Lonchidion* sp. have been recovered only

from the basal conglomeratic layer at the base of the sequence (Fig. 1) whereas only teeth of *Acrodus kalasinensis* and “*Hybodus*” sp. (these teeth belongs in fact to a new genus in the process of being described, see introduction) have been recovered in the same fossiliferous layers as the egg capsules. So the two latter genera are the most likely to be the producers of the egg capsules.

Although coming from the same layer, the two specimens have been recovered at approximately 5 m from each other. As a result, whether they formed a single clutch (see for example Schenk, 1871, P. XIX and XX) transported and separated by the current or correspond to two independent egg laying events cannot be demonstrated. Therefore, it cannot be demonstrated either whether SM 2023-1-14 and SM 2023-1-15 were produced by the same species. However, the fact they were found well separated from each other could indeed hint at the fact that the egg capsules were transported over a short distance by flooding.

The palaeoenvironment in which all *Palaeoxyris* egg capsules had been found is considered to be one of either freshwater fluvial or lacustrine or deltaic conditions, so that the discovery of the Thai specimens in a large river system is not unusual (Fischer et al., 2011; McLean, 2014; Krüger et al., 2021). On the contrary, no recent oviparous sharks is known to lay egg capsules in freshwater environments. The few elasmobranchs that are today adapted to more or less permanent life in fresh waters are viviparous (Schultze and Soler Gijón, 2004). This could actually hint at a major difference in reproductive strategy between modern neoselachians (sharks, skates and rays) and hybodonts. Patterson (1966) and Rees and Underwood (2008) conjectured that hybodonts might have radiated and diversified within wholly freshwater environments under pressure of the developing marine neoselachians in the Jurassic and Cretaceous (See McLean, 2014), whereas neoselachians are not recovered in fresh waters before the Barremian (Sweetman and Underwood, 2006). Their capacity to lay

eggs in freshwater environments might therefore have represented a major advantage over neoselachians in this process.

6. Conclusion

Although the specimens described above appear to be devoid of striation on the surface of their bands and do not display obvious flanged collarettes, they show all the other diagnostic features of *Palaeoxyris* and are therefore assigned to this genus. Their rather bulged body is quite reminiscent of specimens from the Cenomanian of France, but with only two incomplete specimens, it is impossible to reach a more precise identification or to erect a new species. Nevertheless, Jurassic records of *Palaeoxyris* remaining rare, its record at Phu Noi, possibly the highest so far in the Jurassic, allows to complement its known stratigraphic distribution. Most importantly, the report of *Palaeoxyris* at Phu Noi is the first indisputable evidence that at least some Mesozoic hybodont sharks from Thailand were able to reproduce in fresh waters, even if it is not yet possible to precisely identify them. The capacity of hybodont sharks to laying eggs in freshwater environment might have represented a major advantage over neoselachian sharks, allowing their radiation in such environments during the Jurassic and the Cretaceous.

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Captions for figures

Fig. 1. Diagrammatic section of Phu Noi synthesizing the flora and fauna recovered from this site.

The horizontal black arrow on the top indicates the direction in which the excavation progressed from 2008 to 2022. PBB1: Phu Noi 'Bone Bed' 1; PBB2: Phu Noi 'Bone Bed' 2, where *Palaeoxyris* egg capsules were retrieved.

Coupe simplifiée du site de Phu Noi synthétisant la flore et la faune fossiles découvertes jusqu'à présent. La flèche noire horizontale indique la progression du chantier de fouille entre 2008 et 2022. PBB1 : Niveau fossilifère 1 ; PBB2 : niveau fossilifère 2 ayant livré les capsules ovigères de Palaeoxyris.

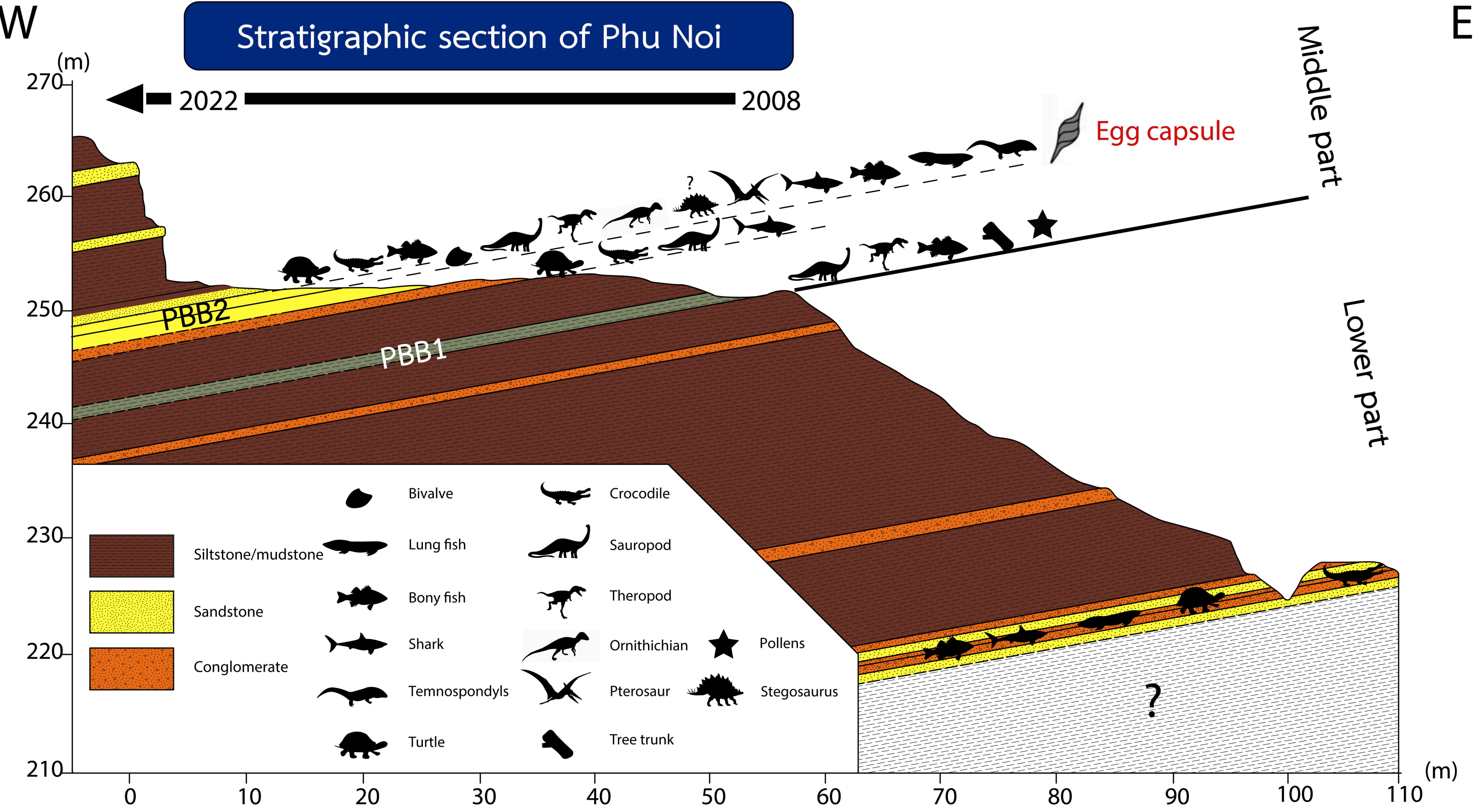
Fig. 2. Photograph of the *Palaeoxyris* sp. egg capsule SM 2023-1-014 (part on the left, counterpart on the right).

Photographie de la capsule ovigère de Palaeoxyris sp. SM 2023-1-014 (empreinte à gauche, contre-empreinte à droite).

Fig. 3. Photographs of the *Palaeoxyris* sp. egg capsule SM 2023-1-015 (part on the left, counterpart on the right).

Photographies de la capsule ovigère de Palaeoxyris sp. SM 2023-1-015 (empreinte à gauche, contre-empreinte à droite).

Stratigraphic section of Phu Noi



2022 ← 2008

Egg capsule

Middle part

Lower part

PBB2

PBB1

- | | | | | | |
|--|--------------------|--|---------------|--|--------------|
| | Siltstone/mudstone | | Bivalve | | Crocodile |
| | Sandstone | | Lung fish | | Sauropod |
| | Conglomerate | | Bony fish | | Theropod |
| | | | Shark | | Ornithichian |
| | | | Temnospondyls | | Pterosaur |
| | | | Turtle | | Tree trunk |
| | | | | | Pollens |
| | | | | | Stegosaurus |

(m)



1 cm



1 cm

