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Le registre fossile récent des tortues de la plaine centrale de la Thaïlande révèle des extinctions locales

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Abstract:

With more than 50 extant turtle species, Southeast Asia is currently a hotspot of turtle biodiversity. However, the distribution areas of most species are decreasing as a consequence of human activities. The causes of this decline are multiple: habitat and natural resources destruction, introduction of invasive species, hunting, etc. Historical data are however still lacking for a detailed understanding of that regional trend as well as for forecasting its evolution in the future. Indeed, while oral testimonies and text data can provide a rather good appreciation of the decline of biodiversity over the last few decades; nothing is known about the dynamic of turtle biodiversity over the Holocene. This lack of data is especially damaging in area where human activities are interacting for a long time with the wild fauna, as the central plain of Thailand, which is now dominated by agricultural landscape.

In order to solve these issues, we investigated five Holocene localities in Thai central plain which provided assemblages of turtle remains ranging from Neolithic to Dvaravati periods (4000 to 1000 BP). The studied archaeological assemblages showed a very high species richness. Species such as *Malayemys macrocephala, Cuora amboinensis, Heosemys annandalii, Heosemys grandis, Siebenrockiella crassicolis, Amyda ornata* were among the most abundant. We also found several

plates and a cranial material belonging to a species of the genus *Batagur* and tortoise remains including *Indotestudo elongata* and a few plates belonging to the genus *Geochelone.* The *Batagur* and *Geochelone* genera are absent from living turtle assemblages in the central plain but are present in Myanmar, Cambodia, Indonesia or Southern Thailand for *Batagur* and far in the West for *Geochelone* (Myanmar) respectively. *Batagur* is usually found in coastal areas and its disappearance from central plain is interpreted as resulting from the destruction of a fragile habitat and possibly from the rapid geomorphological evolution of the Chao Phraya deltaic plain, the disappearance of tortoises could result from deforestation. Cutting traces showed that most turtles were used as food resources at these times, suggesting that turtle hunting was a common practise. Furthermore, occurrence of holes in the margin of the carapace of specimens from Kheed Khin (Saraburi Province) and Promthin Tai (Lopburi Province) suggests that turtles were sometimes kept captive alive or transported. This study shows that investigation of recent fossil localities allows for a better understanding of the role of past human populations in the alteration of the biodiversity through time, and for a more accurate estimation of the rates of species extinction.

Résumé:

L'Asie du Sud-Est est aujourd'hui le hotspot de biodiversité concentrant le plus grand nombre de vertébrés sauvages menacés par les activités humaines. Avec plus de 50 espèces présentes dans la région, l'ordre des tortues est fortement impacté. Les causes de leur déclin sont multiples, mais ce déclin est mal documenté durant l'Holocène. Les témoignages directs et les traces écrites sont limités aux dernières dizaines d'années ou au dernier siècle et ne permettent pas de donner une image satisfaisante de la biodiversité originelle de zones fortement anthropisées depuis plusieurs siècles comme c'est le cas de la plaine centrale de Thaïlande. Afin de combler ces lacunes, nous avons étudié les assemblages de restes subfossiles de tortues dans 5 localités archéologiques de la plaine centrale de Thaïlande sur une période s'étendant du Néolithique à la période Dvaravati (de -2000 à + 1000). Les assemblages étudiés montrent tous une diversité importante de taxons dominée par les espèces *Malayemys macrocephala, Cuora amboinensis, Heosemys annandalii, Heosemys grandis, Siebenrockiella crassicolis* et *Amyda ornata.* Des restes de tortues terrestres (*Indotestudo elongata*, *Geochelone sp.*) ainsi que du genre *Batagur* ont été également retrouvés. Ces trois derniers taxons sont aujourd'hui absents de la région et présentent pour certains une aire de distribution actuelle très éloignée de la plaine centrale. Ces absences actuelles peuvent être interprétées comme des extinctions locales. La disparition de la tortue fluviale

et estuarienne *Batagur* pourrait avoir été amorcée par les changements hydrologiques et géomorphologiques associés à la régression marine holocène dans le golfe de Thaïlande. Des traces de découpe sur les restes subfossiles et des trous pratiqués sur le bord de la carapace montrent que l'exploitation des tortues par l'Homme s'est poursuivie au moins depuis le Néolithique et que cette pratique a également pu altérer la biodiversité de ces animaux. Plus généralement les effets de la destruction d'habitats fragiles dès l'âge des métaux peuvent expliquer ce déclin.

1. Introduction

South-East Asia harbors the hotspot of biodiversity with a large number of reptiles and amphibians that is the most threatened today by human activities (Wilcove et al., 2013). Within this rich herpetofauna, more than 50 species of turtles can be found from Myanmar to Indonesia (Rhodin et al., 2017), most of them being threatened and protected, some being judged as the most endangered species in the world (Rhodin et al., 2017). In Thailand, based on oral testimonies and more systematic surveys, ecologists noticed that the decline of several species and populations was already dramatic in the 90's (Thirapukt and van Dijk, 1997). We know, however, very little about the original state of biodiversity and the evolution of turtle distribution before the 20th century in this area. The first data came from the middle of the 19th century with the first scientific explorations, and most of the turtle surveys in continental south-east Asia with relatively good geographical and taxonomic references only started late with the work of Bourret (1941) and Smith (1916, 1931). Accurate geographical distributions of living species started to be documented late in the 20th century. Even in 1994, Thirapukt and van Dijk noted that "the complete, accurate, recent distributional range is known for few species, since there has never been a comprehensive survey of the whole kingdom". In addition, molecular studies often allowed cryptic species to be recognized very recently (Fritz et al., 2008, 2014; Ilhow et al., 2016; Prashag et al., 2008, 2009), which makes interpretations of the old literature more complicated. Therefore, assessing trends concerning diversity decrease and human impact before the last century is extremely speculative.

The dynamic of that biodiversity and its interaction with humans can nevertheless be estimated by exploring the recent fossil record using the subfossil material in archaeological context. The recent fossil record in South-East Asia shows that extinction may have happen in Pleistocene with the disappearance of giant tortoises (Claude et al., 2011; Turtle extinctions working group 2017), but this record is still poorly documented in this area, especially during the Holocene. It is therefore difficult to draw a clear image of turtle biodiversity dynamic in the region. Most

archaeological surveys often lead to the recovering of bio-archaeological material (vegetal and animal subfossils) that was accumulated in anthropological contexts. These remains are mostly studied from a zooarchaeological point of view with a focus more on the past human activities and culture but not anatomy and systematic. The cattle and hunted fauna (mostly mammals) is therefore often studied, but identifications of the remaining biodiversity are rarely detailed and reliable enough to be used for studies about past biodiversity. On the other hand, the temporal context is often well established which is a good opportunity to document the dynamic in past distributions of organisms. In South-East Asia, turtles are often found in archaeological context, either because they were hunted and consumed by humans, or used as offering in burials, or because they were living at proximity of human settlements, or because humans settlements were accompanied by modifications of habitat that were suitable for them (by digging canals or moats for instance). Turtle bones are often abundant in archaeological collections and are usually correctly identified as turtles, but these bones are often very fragmentary and rarely assessed at the species level in zoo-archaeological studies. In addition, when detailed taxonomic identifications are provided, anatomical criteria used to perform these identifications are most of time not provided. Some works started to emerge in order to help solving this issue by providing osteological criteria for the identification of Southeast Asian reptiles (Pritchard et al., 2009; Bochaton et al., 2018), but much works remain to be done to uncover the osteological morphology of the modern taxa of this area and thus to perform reliable identifications of subfossil remains. In this study, we survey turtle remains from five archeological sites in the central plain of Thailand ranging in age from the Neolithic (3800-3500 BP) to the Dvaravati period (~1000 BP) (Fig. 1). In order to obtain detailed and reproducible taxonomic identifications useful to assess the evolution of turtle biodiversity through time in this region, we performed a detailed anatomical analysis of the remains based on explicit osteological characters and interpreted our results in regard of the up to date knowledge concerning the systematics and distribution of living turtles in South East Asia.

Figure 1 about here

2. Geographical and archaeological settings

The examined sites are shown on figure 1.. We selected the central plain because the archaeological sequence of this region is rather well known and documents a transition between hunting/gathering to development of agriculture (Rispoli et al, 2013). During the Iron age (~2500 BP – 1800 BP), agriculture started to develop, accompanied by controlled irrigation and deforestation; moated cities replaced isolated settlements and flourished from that time and

protohistoric periods (Dvaravati period). The moats offer a nice context for analyzing fossil turtle remains (either because they were living in the moat or because they were thrown away as rubbish in the moat). In this area, important economical exchanges started at large geographical scale probably late with the development of the Khmer Empire, although cultural exchanges started earlier with neighboring regions (India, China).

The context of the central plain is also very interesting in terms of rapid hydro and geomorphological changes. The coastline in this area has progressed forward more than 50 km during the Holocene. It was long believed that human settlements followed southwards the progression of the palaeo-gulf of Thailand during the delta progression (Supajanya and Vanasin, 1983). This context could have offered the opportunity to establish eventual spatial changes in fauna in relation with shift of marine, brackish and deltaic environments and to understand potential effect of anthropisation on fauna. Recent and precise palynological studies, however, revealed that the palaeo-shoreline was rather close to that of today during the Neolithic time and that cities were not necessary following the regression, but at some distance from the coastline (Hutangkura, 2014). The sites that we have investigated here were nevertheless much closer to the sea during the major Holocene transgression (8000 - 7000 BP), and hydrological changes in these sites are likely. Furthermore, documenting the past diversity a bit North of what was under the sea level can reveal how fast turtle fauna could colonize a new habitat in the South (region of Bangkok, Nakhon Pathom and Samut Songkhram), which has also rapidly been affected by human activities.

The five investigated sites are briefly presented in an ascending age order:

* Ban Hua Ud. This site is located in Suphan Buri Province at coordinates 100°00'05'' E/14°32'54''N. It corresponds to a small settlement and a burial, dated by 14C AMS dating on a necklace made by giant clam shells found in the sepulture as 3800-3500 years BP. It is possible that these clams represent subfossils collected by humans (see Ciarla et al., 2017), and that the age of the site could be younger. There is, however, no metal artifact indicating a younger age, whereas polished artifacts and pottery point all to a Neolithic age. Numerous vertebrates including fishes, reptiles and mammals have been found in this locality.

* Tha Kae. This site is located in Lopburi Province, in Muang District at coordinates 14°50'38''N/100°37'10'', the moated site covers an age span from the late Neolithic to Lopburi period and it is well known for past manufacturing of shell jewelry (Natapintu, 1984; Ciarla et al., 1992; Ciarla et al., 2017). Except mollusks, an important vertebrate fauna was discovered including crocodiles and turtles. The turtles examined here are from the Neolithic to Dvaravati periods.

* Phromthin Tai. This site is located in Khok Samrong District in Lopburi Province at coordinates 14° 59' 26'' N/100° 37' 17'' E. It is a moated city of one square kilometer, which was occupied from the Bronze age to Dvaravati times based on artifacts and ESR dating (Lertcharnrit,

2014; Murphy, 2016). The layers we analyzed here correspond to iron age levels (2500 BP -1500 BP) and were dated using 14C AMS dating. Domesticated and hunted mammals were found, together with birds, reptiles, and fishes.

   * Kheed Khin. This site is a moated city in Ban Moh district in Saraburi Province at coordinates 14°37'13"N/100°44'08"E. It is dated from the Iron age to Dvaravati time (2500-1200 BP) based on 14C AMS dating; Murphy (2016) also provides a similar age range for the sequence in Kheed Khin. The fauna comes from the excavation of the moat and is composed of mammals (domesticated and hunted), reptiles (monitor lizards, turtles), and freshwater fishes.

   * Ban Ku Muang. It is located in Inburi district in Singburi Province at coordinates 100°16'52''/ 14°58'38''N . Its Thai name refers to the fact that it is a moated city dated from the Dvaravati time. Several mammal species (domesticated and hunted), birds, fishes, and reptiles were discovered. Reptiles include turtles, monitor lizards, and crocodiles.

3. Taxonomic identification

   Except for few articulated specimens, turtles had to be diagnosed from fragmentary material. Here we list a set of diagnostic features for each species which have allowed for their identification.

Testudinoidea Batsch, 1788

This group is represented by plastral and carapacial plates with a smooth surface, and plate contacts usually consisting in sutures. The inguinal and axillary buttresses are well developed (except in hinged forms) and reach the peripheral and costal plates.

Figure 2 somewhere here.

Geoemydidae Theobald, 1868

In Geoemydidae by comparison to Testudinidae, the pygal plate is shorter than wide. The sulcus between marginal and pleural scutes is located on peripheral plates. Epiplastral lips on the visceral surface are usually less thick or long in relation to the length of the epiplastral symphisis.

Batagur affinis (Cantor, 1847) Figure 2

In this species, the inguinal and axillary buttresses are extremely developed. Sutures between costal and neural plates are often fused, whereaslateral fontanelles persist between costal and peripheral plates in adults. Furthermore, visceral extension of scutes is extremely limited on the plastron (i.e scute-skin sulcus is located very close to the free borders of plastral lobes). The anterior plastral lobe is truncated and the gular scute is short. In *Batagur affinis* and *Batagur baska*, the first vertebral scute is usually wider anteriorly with straight lateral sides and its anterior margin is more convex forward by comparison to *Batagur trivittata* and *Batagur borneoensis.* In addition, the first marginal scute is shorter on the nuchal. In our current state of knowledge, it is difficult to estimate the osteological differences between *B. affinis* and *B. baska*, therefore, assignment to the species level is tentative and based on the distribution of modern species and recent phylogeographic studies (see Discussion).

Malayemys macrocephala (Gray, 1859) Figure 2

The costal plates in this genus are strongly keeled. The nuchal bone is covered by a trapezoid, rather wide cervical scute. The anterior plastral lobe is truncated. The visceral side of the epiplastron shows an anterolateral thickening at the level of the gular/humeral sulcus. The gular is wide anteriorly and intersects only the anteriormost part of the entoplastron. The entoplastron is usually wider than long and intersected by the humero-pectoral sulcus on its posterior part. Furthermore, the plates of this turtle often show a micro-ornamentation consisting of small reticulated furrows. Three species are now recognized in *Malayemys* genus according to the molecular investigations (Ihlow et al., 2016). Up to now, no studies have addressed osteological variation among species and only *Malayemys macrocephala* is recognized in the Chao-Phraya basin. We therefore tentatively assign all material of that genus from the investigated sites to this species.

Heosemys grandis (Gray, 1860) Figure 2

This is a large geoemydid species. The inguinal and axillary buttresses are moderately developed. Strong serrations on posterior peripheral plates are present in adult individuals. The entoplastron is intersected by the gulo-humeral and humero-pectoral sulci. The nuchal plate is emarginated. The cervical scute covers the dorsal side of the nuchal in a much narrower and longer extent than on the visceral side. The epiplastron displays a relatively long epiplastral lip on the dorsal side, but there is no laterodorsal thickening at the level ofthe gular/humeral sulcus. The anterior margin of the third vertebral scute is often strongly convex.

Heosemys annandalii (Boulenger, 1903) Figure 2

This is a large geoemydid species very similar to *H. grandis.* Its posterior peripheral plates are serrated, undulated or smooth (in very large individuals). The central carina is less pronounced in adults than in *H. grandis.* On the visceral side of the nuchal plate, one can observe two strong bulges from each side of the symmetry axis just behind the sulcus of the cervical and marginal scutes. This feature is much weaker or absent in *H. grandis;* furthermore the cervical scute is usually longer on the visceral side of the nuchal plate in *H. annandalii.*

Cuora amboinensis (Riche, 1801) Figure 3

In this species, the hyoplastron is articulated with the hypoplastron by a hinge. This articulation is made possible by the coincidence of the hyo/hypoplastral suture with the pectoro-abdominal sulcus. Furthermore, the plastron/carapace attachment is ligamentous and there is no suture between peripherals and plastral plates. The posterior peripherals are not or weakly serrated and they are thickened at midlength. By comparison to *Cyclemys* spp., the anterior margin of the first vertebral scute is wide and straight on the nuchal plate. The cervical scute is usually elongate. There is no strong carina on costal plates. Anterior and posterior plastral lobes are rounded. The anterolateral sides of the entoplastron are usually concave. An anal notch is absent. The epiplastral lip on the visceral surface of the epiplastron is present but very low. Gular scutes extend well posteriorly on the anterior end of the entoplastron, which is also crossed by the humeropectoral sulcus. The anal scutes are long on their midline and the sulcus between anal and femoral scutes is oblique.

Siebenrockiella crassicolis (Gray, 1830) Figure 3

This turtle is characterized by its gingko leave shaped second to fourth vertebral scutes. Posteriorly, the first to fourth vertebral scutes are very narrow with the lateral margin located very close or even covering neural plates. On the visceral side of the nuchal plate, the posterior sulcus of the cervical and marginal scutes form a clear V shape, contrary to *Malayemys* spp. for which the incurvation is more rounded. Posterior peripherals can be serrated (as in *Malayemys* spp. or *Heosemys* spp.). Lateral and central carinae may be present but they are never as strong as in *Malayemys* spp. The sulcus between the gular and humeral scutes is more oblique than in *Malayemys* and the gular extends more on the entoplastron. The humero-pectoral sulcus intersects the entoplastron at mid-length.

Testudinidae Batsch, 1788

In Testudinidae, the sulcus between the pleural and marginal scutes coincides with the costo-peripheral suture (except in *Manouria impressa*; which can be recognised by its very thin bony plates and presence of fontanelles). The pygal plate is longer or as long as wide. Neural plates are often octogonal or square in shape and their attachment with dorsal vertebra is not as strong as in geoemydids or trionychids. There are no keels on neural and costal plates.

Indotestudo elongata (Blyth, 1853) Figure 3

This species can be recognized by its very short anal scute, its long and narrow cervical scute with convex posterior sulcus. The first vertebral scute is convex anteriorly and narrower than the nuchal plate. The first neural plate is long, quadrangular with lateral side convergent anteriorly. The epiplastral lips are well developed. The entoplastron is intersected by the gulo-humeral sulcus very anteriorly and by the humero-pectoral sulcus at the midlength. The femoro-anal sulcus is perpendicular to the symmetry axis (it is oblique in *Geochelone elegans* or *G. platynota*).

Geochelone platynota (Blyth, 1863) Figure 3

In this species, the entoplastron is not intersected by the humero-pectoral sulcus, this one being located far behind. There is no cervical scute. The femoro-anal sulcus runs parallel to the margin of the anal notch. Because few plates could be assigned to that genus, assignment to the species level is tentative here and was done on the basis of the distribution of the modern species of that genus in Asia (see Discussion).

Manouria emys phayrei (Schlegel et Müller, 1840) Figure 3

This species is potentially present in one site based on two xiphiplastra belonging to the same individual; however, its presence has to be confirmed by more material. As in *Geochelone*, the femoro-anal sulcus is parallel to the margin of the anal notch. The anal scute is longer than in *Geochelone* spp. It extends greatly on the visceral side of the xiphiplastron. The hyoplastral plate or nuchal plate are distinct from other Testudinidae in the large cervical scute, the humero-pectoral sulcus barely reaching the posterior end of the entoplastron, a pectoral scute that is very short at the midline, with a contact between the abdominal and humeral scutes in the subspecies *M. emys phayrei*.

Figure 3 somewhere here.

Trionychidae Gray, 1825

Trionychid plates are easily recognizable by their typical ornamentation which consists of vermiculate sculpturing. Only one species could be identified in that study.

Amyda ornata (Gray, 1861) Figure 3

This relatively large trionychid species exhibits anteroposterior discontinuous and irregular ridges on the costal plates (these ridges are absent in the other large trionychid species from South-East Asia, but can be present in the relatively small species *Palea steindachneri* from China, Laos and Vietnam). The first neural plate is elongated with a straight anterior margin (it is convex anteriorly in *Pelochelys spp.* and *Chitra spp.*), the eighth costal plate is wider than in *Pelochelys spp.* or *Rafetus spp*. The hyo- and hypoplastra are short and show few lateral and medial pikes with moderately developed callosities by comparison to *Chitra spp.* and *Pelochelys spp.*, which have more pikes and more developed hyo-hypoplastral callosities. *Amyda* currently occupies an area including India, Myanmar, Thailand, Cambodia, Vietnam, Malaysia and Indonesia (Rhodin et al., 2017). The genus comprises two species *A. ornata* in the North and *A. cartilaginea* in the South. These two taxonomic entities have been recently identified thanks to molecular analyses (Fritz et al., 2014) and no clear diagnostic characters are currently available on the skeleton. Since *A. cartilaginea* is restricted to Malaysia, Brunei, and Indonesia, and *A. ornata* is still observable in the central plain of Thailand, we assign the specimens from the central plain to *A. ornata*, based on parsimony principle.

4. Faunal composition by site

In this section, a systematic list is established for every studied site. Skeletal elements that have allowed identification are listed, and a Minimal Number of Individuals (MNI) is estimated for each species. The number of specimens corresponds to the bone remains diagnostic at the family level (small fragments are discarded).

Ban Hua Ud. More than 300 turtle specimens have been examined by us in this site.

- *Amyda ornata.* Hyoplastron, lower jaw, and other isolated plastral and carapacial elements including costal plates. MNI = 2.

- *Batagur affinis.* Epiplastron, costal, peripheral, neural plates and the posterior portion of a skull. MNI=2

- *Cuora amboinensis.* Epiplastron, entoplastron, hyoplastron, hypoplastron, xiphiplastron, peripheral, suprapygal, costal, nuchal plates and scapulae. MNI=13

- *Heosemys annandalii.* Nuchal and posterior peripheral plates. MNI=1.

- *Heosemys* spp. Epiplastron, xiphiplastron, hyoplastron, hypoplastron, peripheral, neural and costal plates. MNI=2.

- *Malayemys macrocephala.* Nuchal, peripheral, neural, costal, epiplastron, hyoplastron, hypoplastron, xiphiplastron plates and mandibles. MNI=4.

- *Siebenrockiella crassicolis.* Nuchal, costal, hyoplastron and neural plates. MNI=3

- Testudinidae indet. Peripheral plates. MNI=1.

Phromthin Tai: About 300 specimens could be referred to a given turtle taxon.

- *Amyda ornata.* Costal plates, fragmentary plastral plates. MNI=1.

- *Batagur affinis.* Partially articulated carapace. MNI=1.

- *Cuora amboinensis.* Xiphiplastron and peripheral plates. MNI=1.

- *Heosemys annandalii.* Neural plates. MNI=1.

- *Heosemys sp.* Epiplastron, Peripheral, costal, neural plates, dentary. MNI=1.

- *Indotestudo elongata.* Peripheral, suprapygal, nuchal, first neural, hypoplastron, epiplastron, entoplastron, pygal plates. MNI=3.

- *Malayemys macrocephala.* Isolated plastral and carapacial plates, mandibles. MNI=10.

- *Siebenrockiella crassicolis.* First neural plate. MNI=1.

Tha Kae. Of the 700 specimens observed in this site, half could be assigned to a given turtle taxon.

- *Amyda ornata*. Costal plates. MNI=1.

- *Batagur affinis.* Entoplastron, epiplastron, hyoplastron, peripheral plates. MNI=2.

- *Cuora amboinensis.* Hypoplastron, peripheral, epiplastron plates. MNI=1.

- *Geochelone* sp. Hyoplastron, xiphiplastron. MNI=2.

- *Heosemys grandis.* Nuchal plate. MNI=1.

- *Heosemys* sp. Neural, costal, peripheral, entoplastron, hypoplastron plates. MNI=1.

- *Indotestudo elongata. X*iphiplastron plate. MNI=1.

- *?Manouria emys.* Partial xiphiplastra. MNI=1.
- Testudinidae indet. Peripheral plates. MNI=1.
- *Malayemys macrocephala.* Plastral and carapacial elements, mandibles, partial skulls. MNI=5.
- *Siebenrockiella crassicolis.* First neural and first costal plates. MNI=2.

Kheed Kin. About 140 individuals are examined in this site. Several carapaces or plastra were partially or completely articulated.
- *Batagur affinis.* Dorsal carapace. MNI=1.
- *Heosemys annandalii.* Partial carapaces and plastrons. MNI=2.
- *Heosemys grandis.* Partial carapaces and plastrons. MNI=2.
- *Malayemys macrocephala.* Partial shells, isolated plates, jaw and partial skulls. MNI=7.
- Trionychidae indet. Hypoplastron, costal plates. MNI=1.

Ban Ku Muang: About 400 specimens were examined from that site. They consist mostly of isolated plates, few of them are partially articulated.

- *Amyda ornata.* Partial carapace and plastral plates, MNI=1.
- *Batagur cf. affinis.* Peripheral, costal, neural plates. MNI=1.
- *Cuora amboinensis.* Xiphiplastron, hyoplastron, hypoplastron, peripheral plates. MNI=2.
- *Heosemys annandalii.* Nuchal plates. MNI=2.
- *Heosemys grandis.* Posterior peripheral plates. MNI=1.
- *Heosemys* sp. Epiplastron, hyoplastron, hyoplastron*,* costal, peripheral, xiphiplastron plates MNI=1.
- *Malayemys macrocephala.* Hyoplastron, hypoplastron, costal, peripheral, nuchal, xiphiplastron, neural, epiplastron plates and lower jaws. MNI=23.
- Testudinidae indet. Peripheral plates MNI=1.

Figure 4 somewhere here.

5. Discussion

Today, in the investigated area, 11 species of turtles are present based on the work of Rhodin et al. (2017): *Malayemys macrocephala, Heosemys annandalii, Cuora amboinensis, Siebenrockiella crassicolis, Heosemys grandis*, *Amyda ornata*, *Cyclemys oldhamii*, *Chitra chitra, Pelochelys cantorii, Pelodiscus sinensis* and *Trachemys scripta.* Among them, the first six occur in

most studied archaeological sites and the last two represent recent introductions (for the pet trade or as food resource) which are believed to date back at least from the 70's (Welcomme and Vidthayanon, 2003). *Pelochelys* is now considered extinct in this area and its past occurrences in the Chao-Phraya or Mae Klong system are based on museum specimens (van Dijk and Palasuwan, 2000; Thirakupt and Van Dijk, 1994). *Cyclemys oldhamii* has been recorded in the North of Suphan Buri Province but it might be rare since it is out of the distribution presented by Chan-Ard et al. (2015). *Chitra chitra* is currently only clearly recorded in the Mae Klong Basin and we are not aware of any clear record in the Chao Phraya. If we base on the work of Chan-Ard et al. (2015), *Cyclemys oldhamii*, *Chitra chitra*, *Pelochelys cantorii* should be removed from that list and *Heosemys grandis* would have a restricted distribution on the West of the area we investigated.

At least three species (and possibly four) present in the studied subfossil assemblages are no more present today in the central plain of Thailand. Among them, tortoises have been recorded in the West near the border with Myanmar and, for *Indotestudo elongata* in the forested area east to Saraburi town. These tortoises became rare in the sites dating from Dvaravati time onwards. The disappearance/rarefaction of Testudinidae in the central plain is therefore an event that occurred during the last millennium and that may have started before. Considering their modern occurrences in forested environment, it is possible that the rarefaction or disappearance of *Indotestudo elongata* and ?*Manouria emys* today are related to habitat alteration and hunting. It is in the archaeological locality of Tha Kae, that we found the largest diversity of Testudinidae with the unexpected occurrence of *Geochelone* sp. This occurrence is based on the presence of hyoplastral material showing that the humero-pectoral sulcus was located far behind the entoplastron. These are characters not found in any Thai living testudinid species, but that we could observe in the Asian species *Geochelone platynota* or *Geochelone elegans*. The current distribution range of *G. elegans* corresponds to India, Pakistan and Bangladesh, and *G. platynota* is restricted geographically in the Irrawaddy Basin, Myanmar (Rhodin et al., 2017). It is difficult to distinguish these two species based on skeletal elements with the rare material identified here. Since *G. platynota* is closer geographically, we tentatively assign the material to that species, supposing it was naturally occurring in this area, but we cannot completely exclude that this presence could come from a potential trade with Myanmar. Further evidences from older sites is needed to confirm our hypothesis. Today, *Geochelone platynota* is still harvested in Myanmar and is threatened by extinction in the wild (Platt et al., 2000). It is probable that hunting of that species started early and that its area of distribution was much larger in the past.

In addition to the tortoises, we discovered in all archaeological sites the remains of *Batagur* spp. with carapacial and plastral elements matching with the species *Batagur baska* and *B. affinis*. *B. affinis* and *B. baska* are estuarine turtles nesting ever on estuary bank or on beaches and

the last marine regression may have further isolated populations around the Sunda shelf. These two species are nowadays restricted to Cambodia, southernmost Thailand, Sumatra and Malaysia for *B. affinis*, Bengladesh, India, Myanmar and possibly Ranong Province of Thailand for *B. baska* respectively (Rhodin et al., 2017). *Batagur baska* is present as scattered populations along the Andaman Sea and Bay of Bengal. *Batagur affinis* has scattered populations bordering the gulf of Thailand which are gathered in the subspecies *B. affinis edwardmolli*, while the nominal subspecies is restricted to the margin of the Malacca Strait. The differentiation between the two subspecies with *B. affinis* could potentially be related to a vicariant event, isolating the populations of river systems in the east from those of the west. This vicariant event could have been fostered during the major regression occurred during the last glacial optimum 21 000 years ago. Since the species is estuarine, its distribution may have followed the coastline evolution, with populations in the the palaeo estuaries of the Mekong and Siam river system on the East, and population in the palaeo Malacca river estuaries system on the West. Populations may have later partially been isolated from each other during the marine transgression, a phenomenon that may have been accentuated by humans in harvesting of adults or eggs but also by river canalisation and sand extraction (destruction of natural river banks). Because of these considerations, we refer the specimens from the Holocene sites in the central plain of Thailand to *B. affinis edwardmolli* although we acknowledge that recognizing *B. baska* from *B. affinis* can be tough with fragmentary skeletal remains. Interpreting these remains as resulting from a trade would be unlikely since we found them also before metal ages in the Neolithic. Our study suggests rather that the decline of *B. affinis* is dramatic and does not concern only rarefaction in its current range (Moll and Moll, 2004) but also concern extinction of local populations. It is not completely excluded that *B. affinis* was still present in the Chao-Phraya Basin in the 19th century but it needs to be tested. Indeed, in its list of reptiles of 1899, Flower mentioned that "One species (apparently *Callagur picta*) is also found in Siam; we have seen it at Bangkok". Smith in 1916, however, who recognized the presence of *Batagur* in Pattani area, formulated doubts about that presence in Bangkok, which means that it was no more common or that the animals identified by Flower were not *Batagur* or *Callagur*, or that they were imported. Platt et al. (2003) wrote that the species was also probably present at the beginning of the 20th century in the Tonle Sap in Cambodia, while now in this country, it is only recorded in the South in the Sre Ambel River system. It seems therefore that it was certainly much more widely distributed throughout South-East Asia than today. Finally, one should note that *Heosemys grandis* is now extremely rare and just found on the East side of the distribution investigated if we refer to Chan-Ard et al. (2015) and to our field observations. This species may also have seen its distribution reduced as a consequence of human activities (probably deforestation and river canalisation).

In all investigated sites, we found evidence that turtles were used by past human populations. In all sites where metallurgy was present (Tha Kae, Promthin Tai, Ban Ku Muang, Kheed Kin), we could identify cutting marks on several fragments. These cutting marks indicate that turtles were used as food resources in the investigated sites. Some cutting marks were done for separating the plastron from the carapace (plate 3 E), while others certainly reflect the breakage of the animal in small pieces. Cutting marks were observed on *Amyda ornata*, Testudinids, *Malayemys macrocephala* and *Heosemys spp.* These species are still consumed nowadays in some places or at least recently were. In Ban Hua Ud, we found two plates of turtles transformed as tools or ornaments (plate 3). One of these artifacts was polished and sharpened on one side (plate 3 F), the other was polished to give a pointed shape (plate 3G). In the sites of Promthin Tai, Ban Ku Muang and Kheed Kin, we found drilled anterior peripheral plates. This practice was certainly done while the turtle was alive since carapaces were still articulated. Since drilling the carapace margin would not have killed the turtle, this hole may have been used to attach the specimen and to keep it captive, possibly as a food provision (plate 3 A and B). At least *Malayemys macrocephala*, and *Heosemys sp.* were subject of that practice. It is certain that humans participated in turtle rarefaction by the destruction of their habitat and also by direct predation. Habitat destruction (deforestation, modification of the hydrologic system, urbanization, river canalisation) possibly started to alter the diversity of turtle faunas in South-East Asia well before the more dramatic environmental changes occurring during the last decades. With the intensification of deforestation and urbanization, human activities will inexorably extirpate the few remaining wildlife in weakened and altered ecosystems.

6. Conclusions

The current decrease in biodiversity observed in South-East Asia is more dramatic when the recent fossil record is taken into account. In our study, we found evidences that *Batagur affinis* and tortoises were present in the central plain of Thailand two thousand years ago, while humans started to modify heavily their environment. Deforestation, mangrove destruction, sand extraction in rivers, water drainage and river canalisation are multiple causes certainly responsible for the extirpation of these species from part of their original range. In addition, we found evidence that hunting turtles was a current practice. This may explain why turtle material is abundant in archaeological sites especially in places with symbolic funeral practices. This study demonstrated that Holocene systematic and palaeontological analysis certainly helps to better document the faunal dynamics related to the undergoing 6th extinction. Other similar developments are desirable for older and more recent archaeological periods and in different environmental contexts. Yet, much

work remains to be done especially in tropical areas where the biodiversity is the richest and the works are the fewest, especially concerning non-mammal taxa.

Acknowledgments

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Figure and Plate captions

Fig. 1. Location of the five sites, with reconstruction of the shoreline from the maximum transgression of the Holocene based on the work of Hutangkura (2014). In light gray, maximum extension of the palaeo-gulf of Thailand at the maximum transgression (7000 BP), in gray during metal ages (3000-2000 BP), in dark gray during Dvaravati period (1500 BP-1000 BP). Abbreviations for main cities in yellow (Sb: Singburi, Lo: Lopburi, Sa: Saraburi, Su: Suphan Buri, Ay: Ayutthaya, Pt: Pathum Tani, NP: Nakhon Phanom, Ss: Samut Songkhram) and for sites studied in red (BKM: Ban Ku Muang, PTT: Promthin Tai, TK: Tha Kae, BHU: Ban Hua Ud, KK: Kheed Khin)

Localisation des 5 sites, avec reconstruction de la ligne de rivage depuis le maximum de transgression holocène basée sur le travail de Hutangkura (2014). En gris clair, extension maximum du paléo-golf de Thaïlande durant le maximum de transgression (7000 BP); en gris : extension durant l'âge des métaux (3000-2000 BP) ; en gris foncé, extension du golfe durant la période Dvaravati (1500-1000BP). Les abréviations pour les villes en jaune sont : Sb : Singburi, Lo : Lopburi, Sa : Saraburi, Su : Suphan Buri, Ay : Ayutthaya, Pt : Pathum Tani, NP : Nakhon Phanom, Ss: Samut Songkhram) et pour les sites étudiés en rouge : BKM : Ban Ku Muang, PTT : Promthin Tai, TK : Tha Kae, BHU : Ban Hua Ud, KK : Kheed Khin.

Fig. 2. A and A': *Batagur affinis* partial carapace from Promthin Tai S4, West section (A: dorsal view, A': ventral view); B: *Batagur affinis* partial skull from Ban Hua Ud 2.74.65 (B: ventral view, B': dorsal view); C: *Batagur affinis* right first peripheral plate from Ban Ku Muang TP3.9082; D: *Malayemys macrocephala* nearly complete shell in dorsal view from Kheed Khin 125/104; E: *Malayemys macrocephala* partial plastron from Ban Ku Muang, TP3.8186; F: *Malayemys macrocephala* right maxillary bone from Kheed Kin kk08.94.1-unnumbered; G: *Malayemys macrocephala* dentaryfrom Ban Ku Muang TP3.8383 (dorsal view) ; H: *Heosemys grandis* partial

posterior carapace from Kheed Khin kk08.94.1-001/046; I: *Heosemys grandis* associated nuchal, first peripheral, and first costal plates from Kheed Khin kk008-unnumbered; J and J': *Heosemys annandalii* associated nuchal, first costal and first peripheral plates from Ban Ku Muang TP3.7106,7107,7144 (J: dorsal view, J': ventral view); K: *Heosemys sp.* isolated dentary from Promthin Tai S4, West section (lingual view). Scale graduations = 1 cm.

A and A' : Carapace partielle de Batagur affinis *de Promthin Tai S4, section ouest (A : vue dorsale, A': vue ventrale) ; B : Crâne partiel de* Batagur affinis *de Ban Hua Ud 2.74.65 (B : vue ventrale, B' : vue dorsale) ; C : Première plaque périphérique de* Batagur affinis *de Ban Ku Muang TP3.9082 ; D : Carapace quasi complète de* Malayemys macrocephala *en vue dorsale de Kheed Khin 125/104 ; E : Plastron partiel de* Malayemys macrocephala *de Ban Ku Muang, TP3.8186 ; F : Maxillaire droit de* Malayemys macrocephala *de Kheed Kin kk08.94.1-unnumbered ; G : Dentaire de* Malayemys macrocephala *de Ban Ku Muang TP3.8383 vue dorsale ; H : Carapace postérieure partielle de* Heosemys grandis *de Kheed Khin kk08.94.1-001/046 ; I : Plaques nucale, première périphérique et première costale associées de* Heosemys grandis *de Kheed Khin kk008-unnumbered ; J et J': Plaques nucale, première périphérique et première costale associées de* Heosemys annandalii *de Ban Ku Muang TP3.7106,7107,7144 (J : vue dorsale, J' : vue ventrale) ; K : Dentaire isolé de* Heosemys *sp. de Promthin Tai S4, section ouest (vue linguale). Graduations d'échelle = 1 cm.*

Fig. 3. A and A': *Cuora amboinensis* left xiphiplastron from Ban Hua Ud 2.79.8. (A: dorsal view, A': ventral view); B and B': *Cuora amboinensis* right hyoplastron from Ban Hua Ud 2.64.2 (B: ventral view, B':dorsal view); C and C': *Cuora amboinensis* right epiplastron from Tha Kae 123.11336/4 (C: ventral view, C': dorsal view); D and D': *Siebenrockiella crassicolis* nuchal and first right peripheral plates from Ban Hua Ud 2.113.49,53 (D: dorsal view, D': ventral view); E: *Siebenrockiella crassicolis* first left costal plate from Promthin Tai S4 NWS unnumbered ; F: *?Geochelone platynota* partial left hyoplastron from Tha Kae 202.11337/1; G: *?Manouria emys* partial left xiphiplastron from Tha Kae 116.11397/1; H: *Indotestudo elongata* nuchal plate from Promthin Tai S4, West section; I; *Indotestudo elongata* left xiphiplastron from Promthin Tai S4, West section; J: *Amyda ornata* costal plate from Ban Hua Ud 2.87.126 showing ridges in addition to the vermiculated ornamentation; K: *Amyda ornata* posterior skull from Ban Hua Ud in dorsal view 2.86.41; L: *Amyda ornata* dentary from Ban Hua Ud 2.032.12; M and M': *Amyda ornata* partial carapace from Ban Ku Muang TP3.7277,7279,7284,7285, 7287,7288,7289/ (M: dorsal view, M': ventral view); N: *Amyda ornata* right hypoplastron from Kheed Khin TP6'090/001. Scale graduations = 1 cm.

A and A' : Xiphiplastron gauche de Cuora amboinensis *de Ban Hua Ud 2.79.8. (A : vue dorsale, A' : vue ventrale) ; B et B' : Hyoplastron droit de* Cuora amboinensis *de Ban Hua Ud 2.64.2 (B : vue ventrale, B': vue dorsale) ; C and C' : épiplastron droit de* Cuora amboinensis *de Tha Kae 123.11336/4 (C : vue ventrale, C' : vue dorsale) ; D and D' : Nucale et première plaque périphérique droite de* Siebenrockiella crassicolis *de Ban Hua Ud 2.113.49,53 (D : vue dorsale, D': vue ventrale) ; E : Première plaque costale gauche de* Siebenrockiella crassicolis *de Promthin Tai S4 NWS unnumbered ; F : Hyoplastron partiel gauche de ?*Geochelone platynota *de Tha Kae 202.11337/1; G: Xiphiplastron partiel gauche de ?*Manouria emys *de Tha Kae 116.11397/1 ; H : Plaque nucale de* Indotestudo elongata *de Promthin Tai S4, section ouest ; I ; Xiphiplastron gauche de* Indotestudo elongata *de Promthin Tai S4, section ouest ; J : Plaque costale de* Amyda ornata *de Ban Hua Ud 2.87.126 présentant l'ornementation par rides en plus de l'ornementation vermiculée ; K : Arrière crâne de* Amyda ornata *de Ban Hua Ud en vue dorsale 2.86.41 ; L : Dentaire de* Amyda ornata *de Ban Hua Ud 2.032.12 ; M et M' : Carapace partielle de* Amyda ornata *de Ban Ku Muang TP3.7277,7279,7284,7285, 7287,7288,7289/ (M : vue dorsale, M': vue ventrale) ; N : Hypoplastron droit de* Amyda ornata *de Kheed Khin TP6'090/001. Barres d'échelle = 1 cm.*

Fig. 4. A: *Heosemys grandis*, partial carapace from Kheed Kin with drilled first peripheral plate kk108-132/004; B and B': *Malayemys macrocephala*, drilled first right peripheral plate from Promthin Tai – S4, East section (B: dorsal view, B': ventral view); C: Trionychid hyoplastron with cutting marks from Ban Ku Muang 3.8755; D: testudinid costal plate with cutting mark in visceral view from Ban Ku Muang TP3.8841; E: peripheral plates from the buttress area of *Heosemys sp.* showing that they were cut to separate the carapace from the plastron from Ban Ku Muang TP5.16.unnumbered; F: polished plastral fragment from Ban Hua Ud 1.65.2 (F: dorsal view, F': ventral view, F'': lateral view); G: polished turtle plate from Ban Hua Ud 2.86.68 (G: lateral view; G': another view of the same artifact). Scale graduations = 1 cm

*A : Carapace partielle d'*Heosemys grandis *de Kheed Kin avec la première plaque périphérique perforée kk108-132/004; B et B': Première plaque périphérique droite perforée de* Malayemys macrocephala *de Promthin Tai – S4, section Est (B : vue dorsale, B' : vue ventrale) ; C : Plastron de Trionychidae présentant des traces de découpes de Ban Ku Muang 3.8755 ; D : Plaque costale de Testudinidae présentant des traces de découpes sur la face viscérale à Ban Ku Muang TP3.8841 ; E : Plaques périphériques découpées au niveau du pont de* Heosemys *sp. montrant que la dossière a été séparée du plastron à Ban Ku Muang TP5.16.unnumbered ; F : Fragment poli de plastron de Ban Hua Ud 1.65.2 (F : vue dorsale, F': vue ventrale, F": vue latérale); G : Plaque de tortue polie de Ban Hua Ud 2.86.68 (G: vue latérale; G': autre vue du même artéfact). Barres d'échelle = 1 cm.*