Zooarchaeological investigation of the Hoabinhian exploitation of reptiles and amphibians in Thailand and Cambodia with a focus on the Yellow-Headed tortoise (*Indotestudo elongata* (Blyth, 1854))

Corentin Bochaton[1,2*], Sirikanya Chantasri[3], Melada Maneechote[4], Julien Claude[2,5], Christophe Griggo[6], Wilailuck Naksri[7], Hubert Forestier[8], Heng Sophady[9], Prasit Auertrakulvit[4], Jutinach Bowonsachoti[3], and Valéry Zeitoun[1]

[1]UMR 7207. CR2P-CNRS-MNHN-SU, Sorbonne Université, campus Jussieu, T. 46-56, 5ème étage, case 104, 4, place Jussieu, 75 252 Paris Cedex 05, France.
[2]Institut des sciences de l'évolution de Montpellier, UMR 5554 CNRS/UM/IRD/EPHE, Université de Montpellier, Montpellier, France.
[3]12th Regional Office of Fine Art Department, Nakhon Si Thammarat, Thailand.
[4]Department of Archaeology, Faculty of Archaeology, Silpakorn University, Bangkok, Thailand.
[5]Faculty of Science, University of Chulalongkorn, Bangkok, Thailand.
[6]Laboratoire Environnements, DYnamiques et Territoires de Montagne, UMR 5204 – Université Grenoble Alpes, Le Bourget-du-Lac, France.
[7]Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand.
[8]Muséum national d'Histoire naturelle, Musée de l'Homme, UMR 7194 HNHP, Paris, France.
[9]Ministry of Culture and Fine Arts of Cambodia, Phnom Penh, Cambodia.
[*]Corresponding author: corentin.bochaton@cnrs.fr

ABSTRACT

Although non-marine turtles are nearly ubiquitous in the Southeast Asian archaeological record, their zooarchaeological study has been very poorly undertaken in that tropical region of the world. This lack of study makes the understanding of past human subsistence strategies very complex especially regarding the prehistoric hunter gatherer populations which may have massively exploited inland chelonian taxa. In order to try to start a new dynamic regarding the study of the past human-turtle interactions in Southeast Asia we propose here an in-depth zooarchaeological analysis of the turtle bone remains recovered

from four Hoabinhian Hunter-gatherer archaeological assemblages located in Thailand and Cambodia, and dated from the Late Pleistocene to the first half of the Holocene. Our study is focused on the bone remains attributed to the Yellow-Headed Tortoise (*Indotestudo elongata*) as they account for the majority of the turtle archaeological assemblages identified in the target area. For this species, we developed osteo-metric equations enabling the estimation of the carapace size of the archaeological individuals of this species. This allowed us to study the size structure of the archaeological populations in the different sites and to reveal the human exploitation strategies of these animals. We found a strong taphonomic homogeneity between the studied assemblages suggesting similarities of the subsistence behaviors in the different sites despite their very different environmental settings. We thus hypothesize putative cultural similarities across time and space. In addition, we also provide a baseline for future zooarchaeological studies as well as a methodological frame for the detailed studies of archaeological turtle bones in continental Southeast Asia.

Keywords: Reptiles, Hunter-gatherer, Southeast Asia, Turtle, Zooarchaeology

Introduction

The Hoabinhian has been a major topic in prehistoric research in Mainland Southeast Asia for nearly 90 years. Since its first definition by the French archaeologist Madeleine Colani in the early 1930s (Collectif 1932), the Hoabinhian has no doubt been one of the most debated topics of the field. A wide range of subjects pertaining to the Hoabinhian populations have been discussed, such as their distribution in space and time, their definition, the technological and functional characteristics of their lithic industries, their economic organization, and their environmental context (Forestier *et al.* 2021). The chronology of the Hoabinhian has been largely extended since the earliest known Hoabinhian sites. Indeed, the occupation of the Xiaodong Rock shelter in Southwest China has been dated to about 43, 000 BP (Ji *et al.* 2016) and is considered to be the earliest occurrence of the Hoabinhian culture while the site of Huai Hin in Northwest Thailand, dated to about 3700 BP is considered to be the last occurrence with a lithic production associated with ceramic sherds (Zeitoun *et al.* 2008; Forestier *et al.* 2013). More than a hundred Hoabinhian sites have been reported in Southeast Asia (Moser 2001; Chung 2008; Zeitoun *et al.* 2008; White 2011; Forestier *et al.* 2017) leading inevitably to the question of the variability of Hoabinhian lithic assemblages with unexpected operational sequences on pebble matrix (Forestier *et al.* 2022, 2023). Despite this, the Hoabinhian people remain, however, quite poorly understood from cultural and material point of views. In fact, the homogeneity and lack of diversity of their lithic material culture, probably related to their putative heavy use of objects made of perishable vegetal material (Forestier 2003) does not allow to characterize the precise uses of the sites by past populations, and it is difficult to expect a cultural stasis over 30,000 years among different hunter-gatherer groups in such an extensive region presenting diverse environmental, ecological and geographic settings.

White (2011) proposed that the emergence of cultural diversity in mainland Southeast Asia began precisely in the late Late Pleistocene which is also suggested by burial practices (Imdirakphol *et al.* 2017). Forestier et al. (2013) argued that more analyses were still needed to evaluate the whole corpus of Southeast Asian lithic industries to describe putative “cultural variations” and since then some patterns started to emerge (Forestier *et al.* 2017, 2021). However, while a technological definition of the Hoabinhian culture is in progress, the lack of detailed zooarchaeological analyses makes our knowledge of the Hoabinhian paleoecology and subsistence strategies variability blurry. This is also an issue for the characterization of the archaeological deposits as faunal data are of major importance to characterize the use and occupation periods of the archaeological sites. The economic aspects of the Hoabinhian culture were previously addressed by several authors (Gorman 1969, 1970, 1971; Glover 1977; Yen 1977; Vu 1994). Yet, the pioneering prehistoric zooarchaeological studies relying on occurrence data (Gorman 1971) offer only a poor understanding of the choices made by the hunters by focusing on qualitative data and the diversity of the exploited animals rather than on quantitative information reflecting the intensity of the exploitation of each species. These first works also lack the detailed taphonomic and taxonomic analyses needed to describe past human behaviors and bone accumulation processes in more depth. Because of these lacks, we currently have only a vague idea of the spatial and chronological variability of the subsistence strategies of the Hoabinhian people. These problems impacting southeast Asian zooarchaeology have previously been reviewed in depth by Conrad (2015). Among the identified issues is the lack of detailed study of each animal group but especially of the non-mammal taxa including reptiles and non-marine turtles that are often accounting for a large part of the animal bone assemblages found in the archaeological record.

This limit is not proper to continental Southeast Asia but is more impactful here than in many other areas. Zooarchaeological studies fully focused on non-marine turtles have been conducted in non-tropical areas as Europe (Blasco 2008; Nabais & Zilhão 2019; Nabais *et al.* 2019), Near East (Speth & Tchernov 2002; Blasco *et al.* 2016; Biton *et al.* 2017), South Africa (Avery *et al.* 2004; Thompson &

Henshilwood 2014), and Northern America (Rhodin 1992). Such studies remained, however, limited in tropical areas including in South-East Asia despite the fact that turtle bones are way more common in tropical settings than in the temperate regions where there is a strong tradition of prehistoric studies. In Southeast Asia, this problem is partly rooted in the facts that there is a general lack of detailed anatomical data allowing for the identification of the taxa on the basis of isolated plate remains, and that appropriate methodological framework were never developed to analyze this material. Several works have been conducted regarding the osteology of Southeast Asian turtles most of which focusing on the Geoemydidae family in order to address questions related to the phylogeny and the paleo-biodiversity of the group (Naksri 2007, 2013; Naksri *et al.* 2013; Garbin *et al.* 2018). However, only few works have been interested in the study of the isolated elements found in the archaeological record (Pritchard *et al.* 2009; Claude *et al.* 2019). Despite these limitations several zooarchaeological studies of Hoabinhian archaeological deposits in mainland Southeast Asia have started to characterize the exploitation of the non-marine turtles by these prehistoric populations. In the few existing studies, turtle remains are often left unidentified: Ban Rai Rockshelter (Treerayapiwat 2005); Banyan Valley Cave (Higham 1977); Gua Gunung Runtuh (Zuraina 1994); Gua Harimau (Bulbeck 2003); Gue Kechil (Dunn 1964; Medway 1969); Gua Ngaum (Bulbeck 2003); Gua Peraling (Adi 2000); Gua Teluk Kelawar (Bulbeck 2003); Tham Lod Rockshelter (Amphansri 2011); Lang Kamnan Cave (Shoocongdej 1996); Khao Toh Chong Rockshelter (Van Vlack 2014); Moh Khiew II Rockshelter (Auetrakulvit 2004); Spirit Cave (Higham 1977); Tham Phaa Can (Higham 2002); Thung Nong Nien Rockshelter (Auetrakulvit 2004). In some studies they are identified but not quantified by species for instance in the Lang Rongrien Rock Shelter assemblage (Anderson 1990; Mudar & Anderson 2007). In the rare studies in which turtle bones are identified and quantified, the most abundant species is often by far the Yellow-Headed tortoise (*Indotestudo elongata* (Blyth, 1854)) -Doi Pha Kan Rockshelter (Frère *et al.* 2018); Laang Spean Cave (Frère *et al.* 2018); Spirit Cave (Conrad *et al.* 2016)- at least in its modern distribution area as Geoemydidae turtles are the best represented in the Malaysian sites Gua Sagu (Rabett 2012), and Gua Tenggek (Rabett 2012). There is also a site in Vietnam (Hiem Cave) where the tortoise *Manouria* is the most abundant turtle taxa but the small size of the faunal assemblage does not allow drawing conclusions from this observation (Masojc *et al.* 2023). However, even in the quantified above mentioned studies, the study of the turtle bone remains is still superficial. For instance, a detailed analysis of the taphonomy of the bone assemblages is not conducted and the population of turtle exploited is not characterized further than from the aspect of its species composition.

To start proposing solutions to these issues and also to provide the first detailed data regarding the prehistoric exploitation of Southeast Asian turtles we conducted an in-depth zooarchaeological analysis of the turtle bone remains recovered from four hunter-gatherer archaeological assemblages. These sites are located in Thailand and Cambodia and dated from the Late Pleistocene to the first half of the Holocene. They are the Doi Pha Kan rockshelter, the Moh Khiew Cave, and the Khao Tha Phlai Cave located in Thailand, and the Laang Spean Cave located in Cambodia. In addition, in order to be able to characterize with more precision the exploitation strategies of the non-marine turtles by the archaeological human populations, we developed osteo-metric equations enabling to estimate the carapace size of the archaeological individuals of *Indotestudo elongata*. We choose to focus our methodological approach on this species as most of the rich assemblages of turtle bones collected in the four considered sites correspond to this species (Frère *et al.* 2018; C. B., J. C. preliminary observations). This analytical tool allows for the study of the size structures of the archaeological populations in the different sites, and the characterization the choices made by the hunters. Altogether these data provide the first characterization of the exploitation of non-marine turtle by Pleistocene and Holocene hunter-gatherer populations of continental Southeast Asia.

Material and Methods

Main characteristics of *Indotestudo elongata*, the Yellow-Headed tortoise

The genus *Indotestudo* currently includes three species: the Forsten's Tortoise *Indotestudo forstenii* (Schlegel & Müller, 1845), the Travancore Tortoise *Indotestudo travancorica* (Boulenger, 1907), and the Yellow-Headed tortoise *Indotestudo elongata* (Blyth, 1854), the two later being sister taxa (Iverson *et al.* 2001). These species are currently distributed in India (*I. travancorica*), Sulawesi (*I. forstenii*), and northern India and continental Southeast Asia (*I. elongata*) (Rhodin *et al.* 2021). This last species is the only *Indotestudo* species present in continental Southeast Asia. It is nowadays present in most areas of Thailand, Cambodia, Vietnam, and Laos (Ihlow *et al.* 2016; Rhodin *et al.* 2021). It is also occurring in northwestern Malaysia but is absent from most of this country and from the insular Sunda (Ihlow et al., 2016). *I. elongata* is a medium size tortoise whose adult Straight Carapace Length (SCL) reaches about 300 mm (Taylor 1970). The largest specimen ever recorded is a male of about 380 mm SCL (Rhodin *et al.* 2021). It is possible that the sexual dimorphism in this species vary from one population to another although males are generally larger than females (Ihlow *et al.* 2016). The size of the hatchlings ranges from 50 to 55 mm SCL (Ihlow & Handschuh 2011). The specie is present in a wide variety of environments including many forest types (Ihlow et al., 2016). *I. elongata* is active during daytime mostly in the early morning and late afternoon. It present seasonal activity patterns in order to avoid the highest temperatures during the dry season during which it aestivate spending most of its time hiding in former burrows of other animal species including porcupines (Van Dijk 1998; Som & Cottet 2016; Ihlow *et al.* 2016). In their active period the individuals spend most of their time in open areas during the rainy season then move in more closed environment (mostly semi-evergreen and pine forests) when the climate becomes dryer (Van Dijk 1998; Som & Cottet 2016). Depending of their sex, the individuals reach sexual maturity between 175 mm and 240 mm SCL at an age of 6-8 years old (Van Dijk 1998; Eberling 2011; Sriprateep *et al.* 2013). Reproduction takes place during the rainy season.

Presentation of the studied sites and assemblages

The Doi Pha Kan rockshelter

The site of Doi Pha Kan is a rockshelter located in northern Thailand (E 99° 46' 37.2'' ; N 18° 26' 57.0''). The site is studied since 2011 by P. Auetrakulvit and V. Zeitoun and its excavation is still in progress. The site is mostly known for its three Hoabinhian sepultures dated between 11,170 ± 40 and 12,930 ± 50 BP (Imdirakphol *et al.* 2017; Zeitoun *et al.* 2019). Two of these sepultures contained turtle shells elements in anatomical connection interpreted as funeral offerings. The site also provided a rich archaeological assemblage corresponding to a Hoabinhian occupation older than the sepultures. The stratigraphy of the site being homogeneous from a sedimentary point of view, its archaeological material has been so far considered as a single assemblage.

Samples of the lithic material and of the animal bone assemblages collected on the site have already been the object of studies (Celiberti *et al.* 2018; Frère *et al.* 2018) but most of the material is still under study. In this paper we will present zooarchaeological data collected on the herpetofaunal taxa bone remains recovered on the site until 2019. To collect this dataset the whole archaeofaunal material has been observed to extract and then study the reptile and amphibian bone remains. The material screened this way corresponds to the material previously studied by S. Frère (Frère *et al.* 2018) with the addition of the material collected following this first study. In the first study, S. Frère analyzed 4256 animal remains among which 2541 were attributed to vertebrate species. So far, no complete study of this faunal assemblage has been completed and no Minimal Number of Individual (MNI) data have ever been published. In these conditions, the overall weight of the herpetofauna we collected in respect to the full sample cannot be assessed with precision. However, the existing data indicates it could account for a very significant part of the full assemblage as it corresponds to 17.1% of the total bone weight and 51% of

the vertebrate total Number of Indentified Skeletal Parts (NISP) analyzed in the previous study (Frère *et al.* 2018).

The Moh Khiew Cave

The site of Moh Khiew Cave is a 30m long archaeological rock-shelter located in southern Thailand in the Krabi Province (E 98° 55’ 49.27’’; N 08° 09’ 36.32’’). It was first excavated by S. Pookajorn between 1991 and 1994 (Pookajorn 2001) before being the object of a later excavation in 2008 by P. Auetrakulvit in order to clarify its stratigraphy (Auetrakulvit *et al.* 2012). The stratigraphy of the site is composed of several archaeological layers dated from the Holocene to the Late Pleistocene, most of which corresponding to Hoabinhian occupations. Five sepultures were also discovered, one during the first excavations, and four in 2008.

Regarding the zooarchaeological data, the complete assemblages of the first excavations was studied by P. Auetrakulvit (Auetrakulvit 2004). In this assemblage, MNI data indicate that herpetofaunal species account for 24.9% of the assemblage. This proportion dramatically increases to more than 70% of the material if the NISP is considered with nearly 60% for the non-marine turtles bone alone. Unfortunately, the turtle remains were not identified further at the moment of this first study and we were not able to locate this material in order to study it again in the framework of the present analysis. We however had access to the material collected during the 2008 excavation but only to previously studied herpetofaunal bone samples that were extracted from the complete bone samples by several master students. These bones were recovered from the four different layers identified during the 2008 excavation of Moh Khiew Cave (Auetrakulvit et al., 2012). The first layer (Layer 1) is composed of the upper first 90 cm of the sequence. It is a disturbed layer that has not been dated and which corresponds to the levels 1 and 2 identified by S. Pookajorn in the first excavations. The second layers include the sediment collected between 90 and 170 cm of depth. It has been the object of three radiocarbon dates between 7520+-420 BP. and 8660+-480 BP. This layer corresponds to the level 3 identified in the previous excavations. The third layer correspond to a depth between 170 and 210 cm and has been dated with two radiocarbon dates of 8730+-480 BP. and 9270+-510 BP. It was also identified as corresponding to the level 3 previously described by S. Pookajorn. The last layer corresponds to the remaining of the stratigraphy. It is a layer of scree and was not dated but associated to the level 4 described in the previous excavations.

The Khao Tha Phlai cave

The site of Khao Tha Phlai is a cave located in southern Thailand in the province of Chumphon (E 10°36'12.39"; N 99° 5'49.08"). It has been excavated by the 12th Regional Office of Fine Arts Department, Nakhon Si Thammarat since 2014, and has so far been the object of two excavation campaigns with two test-pits conducted in the deposit. A first test-pit of 9 m² (TP1) in 2014, and a second of 20 m² (TP2) in 2021-2022.

The archaeofaunal material collected in the TP1 has been the object of a preliminary study by S. Jeawkok in the framework of a Bachelor thesis that remained unpublished. This first study conducted on 6945 bone remains indicated that the reptiles represent around 25% of the NISP of the complete assemblage, the remaining bones being nearly all attributed to large mammals. In the present study we considered the herpetofaunal material previously extracted by S. Jeawkok in the faunal samples collected in the TP1. We also consulted the full archaeofaunal sample recovered from the TP2 in order to extract the reptile and amphibian bones from it. We considered separately the samples collected in the two test-pits and subdivided the samples in two assemblages corresponding to Metal Ages (between 75 and 130 cm of depth in the TP2 and between 65 and 180 cm in TP1), and Neolithic periods (between 130 and 320 cm of depth in the TP2 and between 180 and 320 in TP1). These layers have been dated on the basis of the typology of the archaeological artifacts they have provided.

The Laang Spean cave

The site of Laang Spean is a large cave of more than 1000 m² located in northwest Cambodia, in the Battambang province (E 102° 51‘ 00.0‘‘; N 12°51‘ 00.0‘‘). The site has been the object of a first excavation between 1965 and 1968 by R. Mourer and C. Mourer-Chauviré (Mourer-Chauviré *et al.* 1970; Mourer-Chauviré & Mourer 1970). The archaeofaunal material collected during these excavations has been the object of a preliminary study but has never been studied in depth at the exception of the rhinoceros remains (Guerin & Mourer-Chauviré 1969), and no zooarchaeological study have been conducted. Following this first exploration, the site has been the object of a new detailed archaeological excavation by H. Forestier between 2009 and 2019 aiming to document in more detail the Hoabinhian occupation previously identified (Forestier *et al.* 2015; Sophady *et al.* 2016). These excavations conducted on a surface of over 40 m² led to the discovery of an important undisturbed Hoabinhian layer dated between 5018 ± 29 cal. BP and 10 042 ± 43 cal. BP as well as several Neolithic burials dug in the Hoabinhian level (Zeitoun *et al.* 2012, 2021). These sepultures have been dated from 3335 ± 30 to 2960 ± 30 BP (Sophady 2016). Regarding the subdivision of the material, the archaeological remains collected in the squares lacking traces of Neolithic perturbations (see Forestier et al., 2015) have been associated to the Hoabinhian occupation. There is no stratigraphic evidence suggesting a subdivision of this Hoabinhian assemblage obviously representing several occupations over a time span of more than 5000 years. Regarding the other squares, the squares in which sepultures were found are grouped together under the term “Sepulture layer” and the first 120 cm of the disturbed squares are considered as being a “Neolithic layer”. These subdivisions are however very artificial and probably correspond to a mix of Neolithic and Hoabinhian material has it has been evidenced on the lithic material these contexts provided (H. Forestier, com. pers.).

A sample of the complete faunal assemblage collected in the Hoabinhian squares has been the object of a first zooarchaeological study by S. Frère (Frère *et al.* 2018). In this first study, among the 5885 vertebrate remains identified, turtle account for 44% of the NISP, monitor lizards for 1%, and large mammals for 37%. Unfortunately no MNI data were reported and the fact that most of the small fragments were not attributed to a least a size class of animal make these results difficult to interpret. The study presented in this paper corresponds to the herpetofaunal material collected in the complete assemblage of bones recovered during all the excavations since 2009. This material has been extracted by C. B. upon the consultation of all the bone samples collected on the site. The zooarchaeological study of the other groups of vertebrate for the complete Hoabinhian assemblage of Laang Spean is currently in progress and the final results are not available at the moment.

Quantification of the zooarchaeological data

The basic units of quantification considered are the Number of Indentified Skeletal Parts (NISP) and the Weight of the Remains (WR). The fragmentation of each bone has been recorded by describing the Percentage of Completion (PC) of the anatomical elements represented by the fragment. The laterality of the bones has been registered when possible for the best represented and easiest to identify anatomical elements (i. e. peripheral plates, and all paired elements of the plastron). A Minimal Number of Elements (MNE) has been compute for each anatomical part in order to study the anatomical distribution of the remains in the different archaeological contexts. To do so, we have added the PCs of a given element and divided the result by 100. The results were rounded to the superior unit to obtain the MNEs. The Minimal Number of Individual (MNI) is defined using the anatomical element with the highest MNE. The anatomical distributions are represented by the Percentage of Representation (PR) of Dodson and Wexlar (1979) using the MNE of each anatomical elements and the MNI of the considered assemblage. All the archaeological bones have been weighted individually. In order to avoid a potential impact of taxonomic identification bias on the anatomical distribution of the remains we considered all

the turtle/tortoises taxa in these analyses and not only the bone fragments attributed to *Indotestudo*. As tortoises are by far the best represent taxa in the different assemblage most of the unidentified turtle bones likely represents *Indotestudo*. The positions of the peripheral plates have been identified but only for *Indotestudo* remains. The peripheral plates for which it was not possible to give a position have been posteriorly assigned to the different ranks following the distribution of those for which a position was determined. Regarding the size estimations (see below), the mean of the obtained size estimation is considered in the case several measurements were recorded on a single bone. Chi² tests were performed on the Microsoft Excel software 2007 version.

Size estimation of archaeological Indotestudo

In order to reliably estimate the body size of the archaeological individuals of *Indotestudo* sp. we build size estimation equations on the models of what was previously done for Southeast Asian monitor lizards (Bochaton *et al.* 2019), and recently on the size and weight of species of tortoises (Esker *et al.* 2019; Codron *et al.* 2022). These approaches are more powerful than considering isolated measurement (e. g. Klein and Cruz-Uribe 1983) to describe the size of subfossil animal populations because: 1) they enable to take account on several measurements from different anatomical parts to reconstruct the body size structure of a past population, and 2) it converts measurements taken on the skeleton into a variable used to describe the size of modern individuals which make easier the comparisons needed to address biological questions. To build the equations we defined a set of 86 measurements (See Supplementary Table 1; Appendix 1) that we recorded on a sample of 34 museum specimens of *Indotestudo* sp. from the Florida Museum of Natural History (UF), and the Comparative Anatomy collection of the Muséum national d'Histoire naturelle (MNHN-ZA-AC) (see all details in Supplementary Table 1). In order to have enough specimens to produce relevant and reliable predictive equations we pooled altogether the three species currently includes in the genus *Indotestudo*: *I. forstenii* (Schlegel & Müller, 1845): 8 specimens, *I. travancorica* (Boulenger, 1907): 14 specimens, and *I. elongata* (Blyth, 1854): 12 specimens. Differences of body proportions among species were controlled before applying this strategy to avoid including bias related to interspecific differences in the size estimations.

The measurements recorded were distributed on all the bones of the plastron and the carapace as well as on the long bones. Vertebrae and skull elements were not taken into account as their occurrences were too rare in the archaeological record. In addition to these measurements, in order to be able to choose a variable accounting for the "body size" of each individual, we took three measurements considered as "size variables" on the complete carapace of the modern specimens: the Carapace Straight Length (CSL), the Shell Height (SH), and the Plastron Length (PL). All the measurements collected on modern and archaeological specimens were recorded using a digital dial calliper [IP 67 (Mitutoyo Corporation, Japan)]. All the measurements recorded are included in the Supplementary Table 1. All statistical analyses were performed using the basic library Stats of the open-source software R (R Core Team 2020). Each size estimation equation produced is the result of a linear regression between a given log transformed measurement recorded on a bone/plate and the log transformed "size variable" of the specimens. The variables are log transformed in order to make linear the simple allometric relationship between the used variables (Huxley 1932; Gould 1966). Consequently, the obtained CSL estimation has to be log reversed using an exponential function to be obtained in the same unit as the used measurements. Obtained equations are of the form:

Log ("size variable") = (Beta1)* log (osteological measurement in mm) + (Beta0)

From this initial set of equations we choose to discard all the equation that were not significant (p.value above 0.01) and/or with a low coefficient of determination (R2) (below 0.85) in order to keep only the best equations to estimate the size of the archaeological individuals.

Specific identification of the *I. elongata* archaeological bone sample

The archaeological bones attributed to *I. elongata* have been identified on the basis of a direct comparison with pictures of the skeletal specimens of this species used to build the SCL estimation equations. The fact that the family of the Testudinidae is only represented by very few species in Southeast Asia (*Geochelone platynota*, *Indotestudo elongata*, *Manouria emys*, and *Manouria impressa*) (Das 2010) presenting different sizes, morphologies, and distribution areas allowed to attribute with relative ease nearly all of the studied Testudinidae remains to *I. elongata*. Among the *Indotestudo* genus, as the only currently available qualitative diagnostic criteria for *I. elongata* is located on the nuchal plate (presence of a long and narrow cervical scute), we based most of our identification obtained from other plates/bones on the exact similarity between the archaeological bone remains and the morphologies present on the modern specimens of different ages we observed. An overview of the carapace morphologies of juvenile and adult *I. elongata* is provided here (Fig. 1). The remains attributed to this species also present the morphological traits common to most Testudinidae: a carapace lacking lateral keels, a costal pattern of odd costal plates with short distal end and long medial end, and even costal plates with long distal end and short medial end, octagonal and squared neural plates, peripheral plates without musk ducts, a costo-marginal sulcus superimposed to the costo-peripheral suture, a pygal plate not intersected by the posterior sulcus of the fifth vertebral scute, thickened epiplastra, and thin and vertical inguinal and axillary buttresses. Among Testudinidae the genus *Indotestudo* is characterized by the fact that the humeropectoral sulcus is crossing the entoplastron (Auffenberg 1974). The establishment of robust and quantified diagnostic criteria for the identification of isolated bones of Southeast Asian turtles has still to be performed. As a comment, we signal that the characteristic nuchal scute morphology of *I. elongata* was present on all the nuchal plate (N=109) attributed to this species at the exception of a single remain from Laang Spean cave. It has been previously signaled that the nuchal scute could be absent on some specimens (Ihlow *et al.* 2016) and our data indicate a frequency of such feature inferior to 1%.

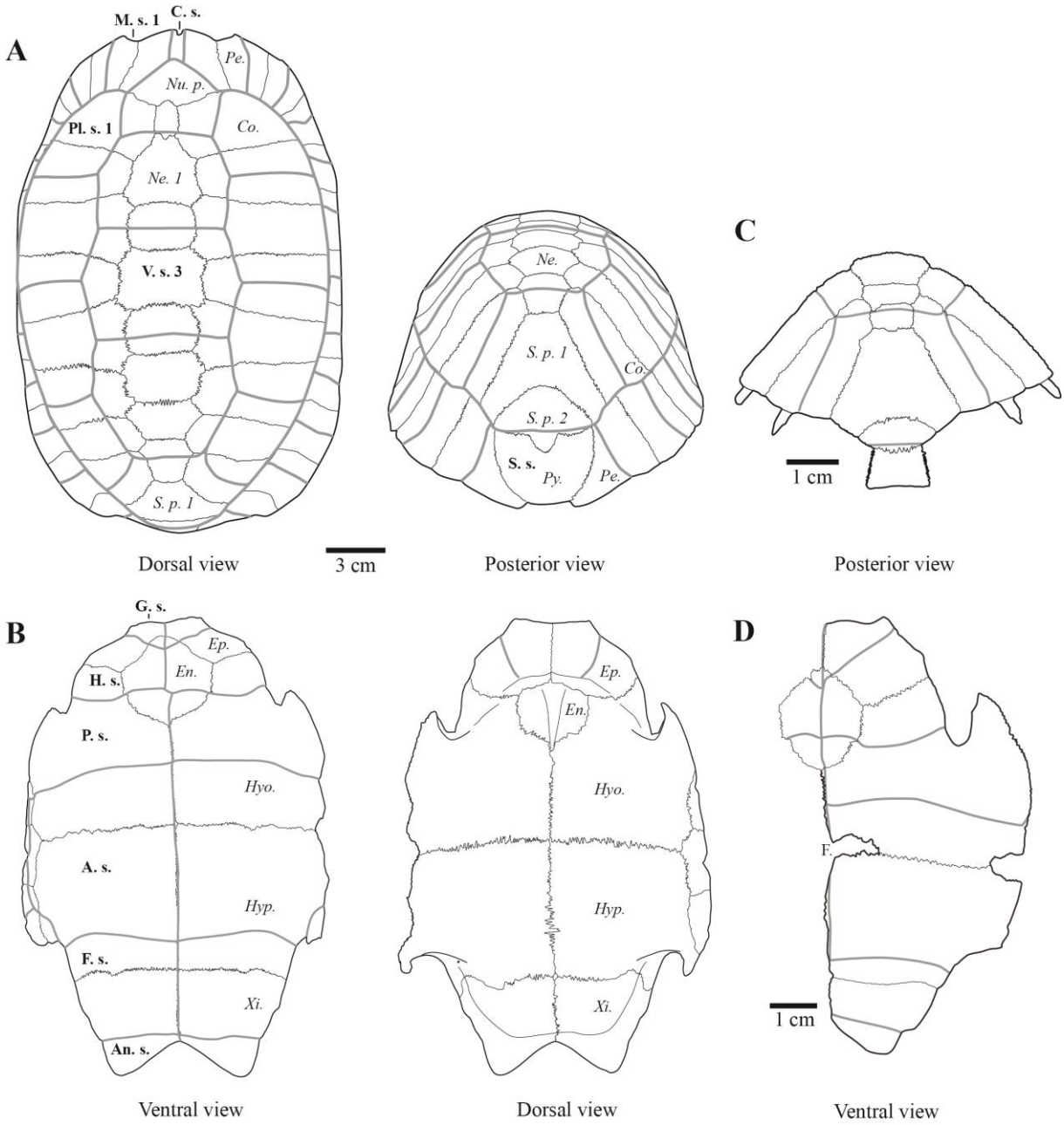

Figure 1 - A) Drawing of the carapace of an adult specimen of Indotestudo elongata (CUMZ-R-TT181); B) Drawing of the plastron of an adult specimen of Indotestudo elongata (CUMZ-R-TT181); C) Drawing of the carapace of a juvenile specimen of Indotestudo elongata lacking peripherals (UF-34760); D) Drawing of the plastron of a juvenile specimen of Indotestudo elongata showing central fontanel (UF-34760). **Abbreviations:** A. s.: Abdominal scute, An. s.: Anal scute, G. s.: Gular scute, Co.: Costal plate, F. s.: Femoral scute, Ep.: Epiplastron, En.: Entoplastron, F.: plastral fontanel, H. s.: Humeral scute, Hyo.: Hyoplastron, Hyp. : Hypoplastron, M. s.: Marginal scute, Ne.: Neural plate, Nu. p.: Nuchal plate, C. s.: Cervical scute, P. s.: Pectoral scute, Pe.: Peripheral plate, Pl. s.: Pleural scute, Py.: Pygal plate, S.p. 1: Supra-pygal 1, S.p. 2: Supra-pygal 2, S. s.: Supra-caudal scute, V. s.: Vertebral scute, Xi.: Xiphiplastron.

Results

Size predictive equations

In order to choose the variable we will use as our "size" variable we tested the correlations between the three "body size" measurements taken on the complete carapaces of our *Indotestudo* spp. modern specimens. Our results indicate that the Straight Carapace Length (SCL) is strongly correlated to the Plastron Length (PL) (R^2=0.97), and that the Shell Height is more weakly correlated to the two other measurements (R^2=0.93 and 0.92). This could be related to sex specific or interspecific differences regarding the height of the carapace among the considered specimens but these hypotheses are not possible to test considering the small size of our sample. As a result and because the carapace length is the most used variable to describe the size of a turtle we choose the SCL as our size scalar but the PL could have been equally considered.

From our complete modern sample, a set of 86 equations corresponding to the 86 initial recorded measurements has been produced. This set has been refined to keep only the equations providing the most reliable (significant linear relationships) and precise (high R^2 linear relationships) SCL estimations. This final set of equations include 52 equations from 52 measurements distributed on epiplastron, entoplastron, hyoplastron, hypoplastron, xiphiplastron, nuchal plate, neural plates (ranks 1, 2, 3, 4, 6, and 7), peripheral plates (ranks 1, 2, 3, 8, 9, and 10), 2nd supra-pygal plate, pygal plate, humerus, radius, ulna, femur, tibia, and fibula (Fig. 2; Table. 1).

Table 1 - Equations retained for the prediction of the Straight Carapace Length (SCL) of the archaeological Indotestudo specimens. Are indicated: the measurement used (to be recorded on the archaeological specimen, the slope X ("Beta1" to integrate in the equation indicated in the Material and Method section), and the intercept Y ("Beta0" to integrate in the equation indicated in the Material and Method section). Is also indicated the coefficient of determination (R2) of each relation, the p.values, and the degree of freedom of each linear regression.

Measurement Used	Y	X	R^2	P. value	Freedom degree
Greatest Length Nuchal plate (GL)	1.44	1.05	0.89	2.48E-14	27
Greatest Heigth Peripheral plate 1 (GH)	2.30	0.91	0.89	2.77E-14	27
Greatest Width Peripheral plate 1 (GW)	1.95	1.01	0.90	3.43E-15	27
Greatest Heigth Peripheral plate 2 (GH)	1.68	1.11	0.92	4.10E-16	26
Greatest Width Peripheral plate 3 (GW)	1.96	1.06	0.88	5.70E-14	27
Greatest Heigth Peripheral plate 3 (GH)	2.42	0.84	0.93	2.20E-16	27
Greatest Width Peripheral plate 8 (GW)	2.45	0.89	0.86	5.22E-13	27
Greatest Heigth Peripheral plate 8 (GH)	2.19	0.91	0.94	2.20E-16	27
Greatest Width Peripheral plate 9 (GW)	2.58	0.86	0.89	1.47E-14	27
Greatest Heigth Peripheral plate 9 (GH)	2.27	0.89	0.90	7.29E-15	27
Greatest Width Peripheral plate 10 (GW)	2.26	0.95	0.89	3.04E-14	27
Greatest Heigth Peripheral plate 10 (GH)	2.69	0.77	0.90	3.55E-15	27
Greatest Length Neural plate 2 (GL)	2.54	0.91	0.87	2.82E-13	27
Greatest Width Neural plate 2 (GW)	1.55	1.14	0.92	3.36E-16	27
Greatest Length Neural plate 3 (GL)	2.20	1.07	0.90	4.73E-15	27
Greatest Length Neural plate 4 (GL)	2.52	0.93	0.85	1.09E-12	27
Greatest Width Neural plate 4 (GW)	1.82	1.05	0.92	2.20E-16	27
Greatest Width Neural plate 6 (GW)	2.10	0.98	0.91	6.00E-16	27
Greatest Width Neural plate 7 (GW)	2.23	0.96	0.86	3.95E-13	27
Greatest Width Supra-pygal plate 2 (GW)	2.19	0.86	0.88	1.61E-13	26
Greatest Heigth Pygal plate (GH)	2.98	0.68	0.93	2.20E-16	26
Greatest Length Epiplastron (GL)	1.48	1.06	0.95	2.20E-16	27
Greatest Length Entoplastron (GL)	1.54	1.09	0.86	3.09E-13	27
Greatest Width Entoplastron (GW)	1.76	1.02	0.92	4.25E-16	27
Greatest medial Length Hyoplatron (GmL)	1.81	0.96	0.87	1.14E-13	27
Greatest Width Hyoplastron (GW)	0.02	1.29	0.94	2.20E-16	25
Greatest medial Length Hypoplastron (GmL)	0.44	1.25	0.90	7.32E-15	27
Greatest Width Hypoplastron (GW)	-0.09	1.32	0.95	2.20E-16	25
Greatest Length Xiphiplastron (GL)	1.53	1.02	0.88	6.69E-14	27
Greatest Width Xiphiplastron (GW)	1.09	1.15	0.92	2.20E-16	27
Greatest Length Humerus (GL)	1.16	1.08	0.95	2.20E-16	24
Greatest proximal antero-posterior Width Humerus (GpapW)	2.74	0.99	0.91	3.32E-14	24
Greatest proximal dorso-ventral Width Humerus (GpdvW)	2.59	1.00	0.94	8.45E-16	24
Greatest Length Ulna (GL)	1.52	1.12	0.96	2.20E-16	23
Greatest distal antero-posterior Width Ulna (GdapW)	3.60	0.93	0.90	4.69E-13	26
Greatest proximal latero-medial Width Ulna (GplmW)	3.13	1.02	0.87	1.22E-11	23
Greatest Length Radius (GL)	1.34	1.17	0.94	1.82E-15	23
Greatest proximal latero-medial Width Radius (GplmW)	3.18	1.10	0.92	3.64E-14	23
Greatest proximal antero-posterior Width Radius (GpapW)	3.96	0.89	0.89	1.20E-12	23
Greatest distal antero-posterior Width Radius (GdapW)	3.91	0.99	0.86	2.08E-11	23
Greatest Length Femur (GL)	1.41	1.03	0.96	2.20E-16	23
Greatest proximal antero-posterior Width Femur (GpapW)	3.15	0.86	0.93	1.89E-14	23
Greatest proximal dorso-ventral Width Femur (GpdvW)	2.91	0.90	0.97	2.20E-16	23
Greatest distal antero-posterior Width Femur (GdapW)	3.46	0.77	0.86	2.91E-11	23
Greatest Length Fibula (GL)	1.57	1.06	0.94	1.81E-14	21
Greatest distal latero-medial Width Fibula (GdlmW)	3.59	0.94	0.89	1.06E-11	21
Greatest distal antero-posterior Width Fibula (GdapW)	3.92	0.96	0.90	9.30E-12	21
Greatest Length Tibia (GL)	1.39	1.09	0.95	1.25E-15	22
Greatest proximal latero-medial Width Tibia (GplmW)	3.06	1.01	0.92	2.16E-13	22
Greatest proximal antero-posterior Width Tibia (GpapW)	3.20	1.02	0.94	3.03E-15	22
Greatest distal latero-medial Width Tibia (GdlmW)	3.45	1.00	0.92	1.99E-13	22
Greatest distal antero-posterior Width Tibia (GdapW)	3.60	0.97	0.91	9.04E-13	22

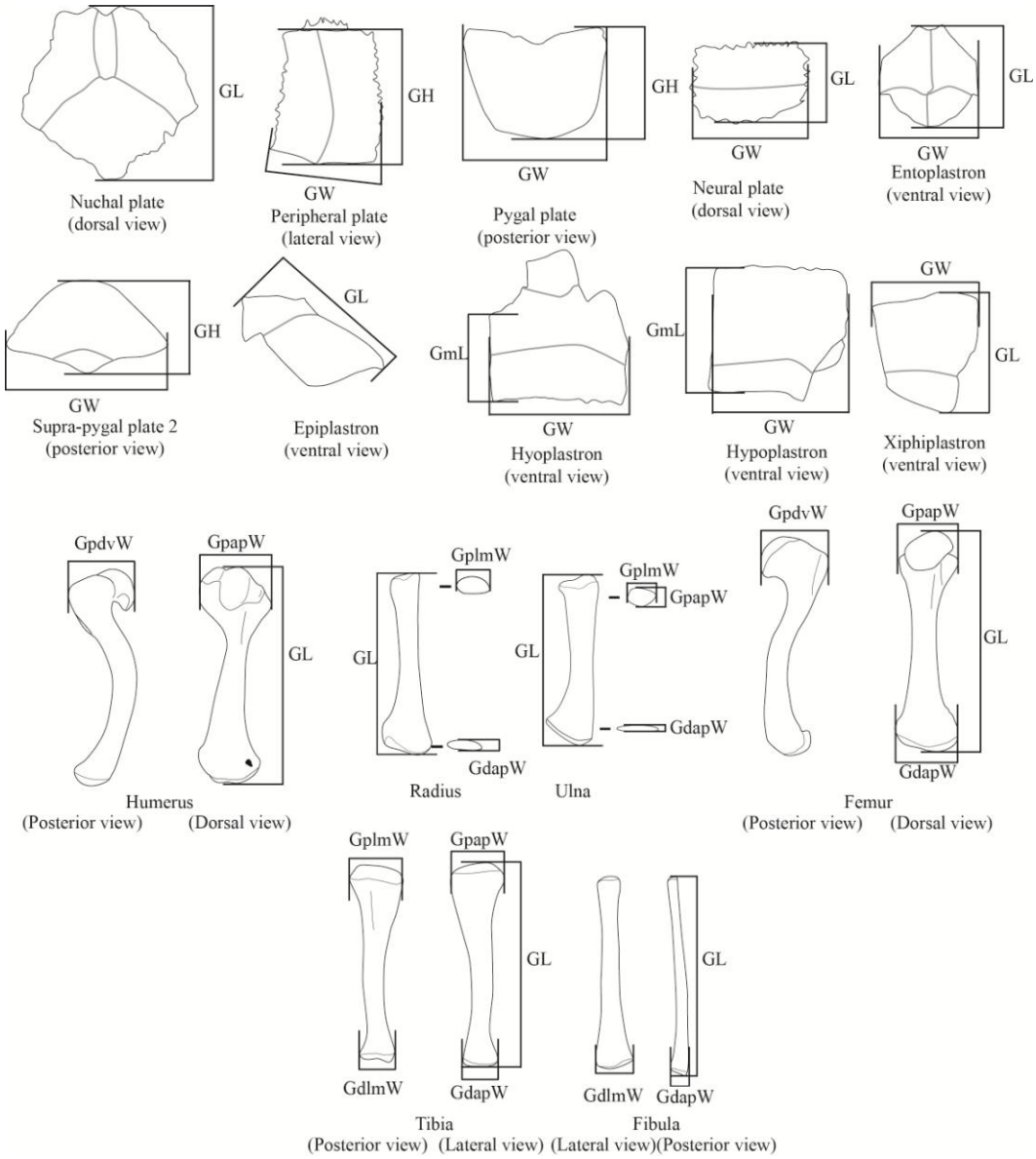

Figure 2 - Measurements corresponding to the 52 equations retained to predict the SCL of our archaeological sample of Indotestudo elongata bone remains. Measurements names: GB: Greatest Width (on the latero-medial axis), GdapW: Greatest distal antero-posterior Width, GddvW: Greatest distal dorso-ventral Width, GdlvW: Greatest distal latero-ventral Width, GH: Greatest Height (on the dorso-ventral axis), GL: Greatest Length (on the antero-posterior axis), GmL: Greatest medial Length(on the antero-posterior axis), GpapW: Greatest proximal antero-posterior Width, GpdvW: Greatest proximal dorso-ventral Width, GplvW: Greatest proximal latero-ventral Width.

Zooarchaeological and taphonomic analyses of the herpetofaunal assemblages

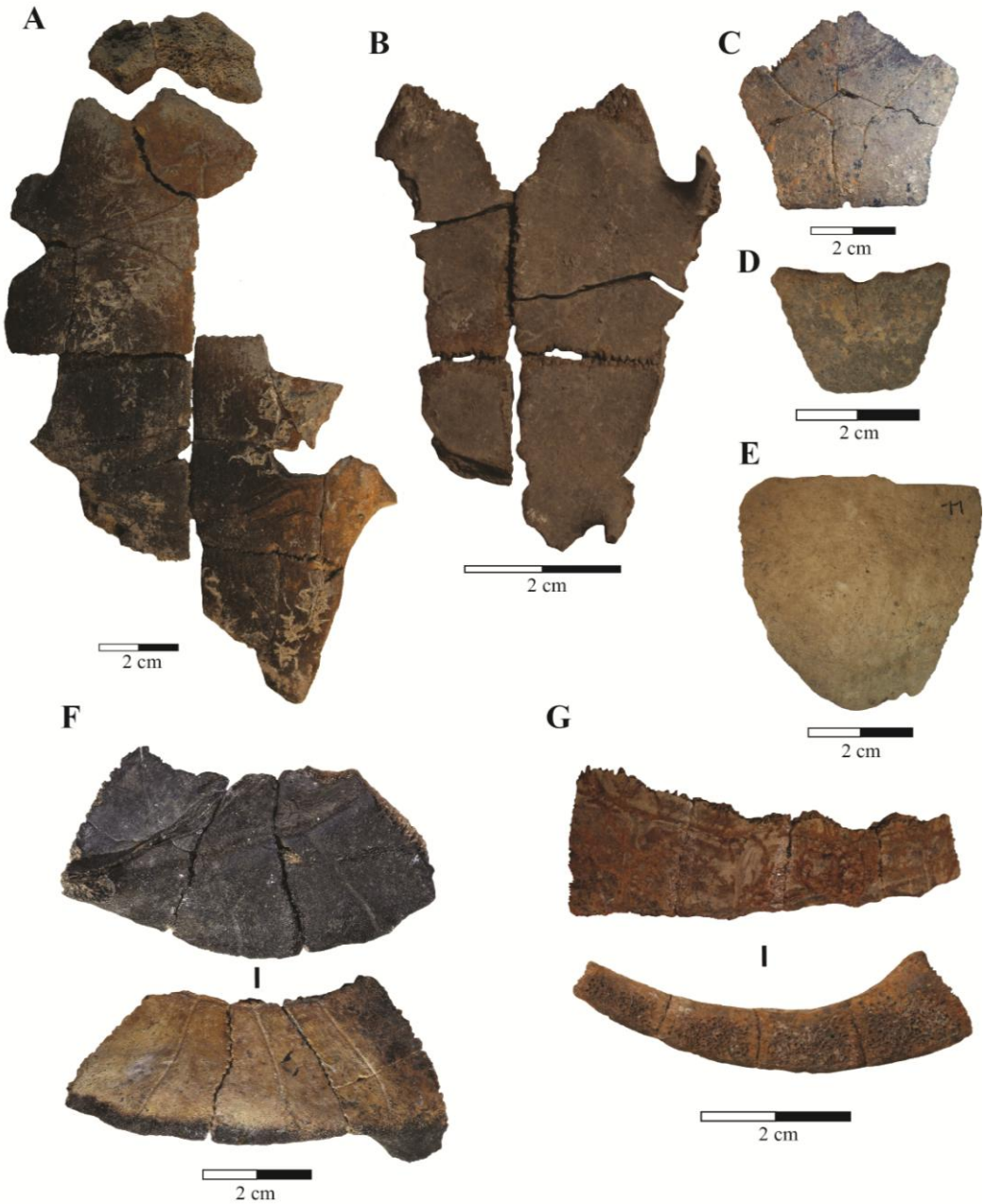

Figure 3 - Examples of the turtle bone remains studied. A) Plastron of an adult *I. elongata* in anatomical connection from the Hoabinhian layer of Laang Spean Cave (ventral view); B) Plastron of a juvenile *I. elongata* in anatomical connection from the Hoabinhian layer of Laang Spean Cave (ventral view); C) Nuchal plate of *I. elongata* from the Hoabinhian layer of Laang Spean Cave (dorsal view); D) Pygal plate of a juvenile *I. elongata* from the Neolithic layer of Laang Spean Cave (posterior view); E) Pygal plate of an adult *I. elongata* from the Neolithic layer of Laang Spean Cave (posterior view); F) Left peripheral plates (1st to 3rd) of *I. elongata* in anatomical connection from the layer 2 of Moh Khiew Cave presenting burning traces limited to the internal side of the carapace; G) Left peripheral plates (8th to 11th) of a Geoemydidae in anatomical connection whose ventral part has been cut-down from the site of Doi Pha Kan.

Doi Pha Kan Rockshelter

<u>Composition of the herpetofaunal assemblages</u>

The herpetofaunal assemblage of Doi Pha Kan consist of 8414 bone remains weighting a total of 6875 gr. and representing a least 115 individuals. Most of these bones correspond to non-marine turtles (Fig. 3; Table. 2) in term of WR (74%), NISP (56%), and MNI (47%) with the second most represented group being Monitor lizards (23% of the WR, 38% of the NISP, and 38% of the MNI) followed by rare snakes, amphibians, and small lizards bone remains.

Table 2 - Weight of the Remains (WR), Number of Identified Skeletal Parts (NISP), and Minimal Number of Individual (MNI) corresponding to the different taxa identified in the complete Doi Pha Kan Rock-shelter herpetofaunal assemblage.

	NISP	WR	NMI
Turtle/Tortoise	4762	5113.02	55
Monitor lizard	3203	1610.39	44
Snake	375	141	3
Amphibian	67	10.57	10
Small lizards	7	0.82	3
Total	**8414**	**6875.8**	**115**

Regarding the bones attributed to turtles and tortoises (Table. 3), 66.8% of them (50.8% of the WR) could not be attributed to a given family. Among the fragments that were identified to at least the family level, 71 % of them were attributed to *Indotestudo elongata* (71% of the WR and 76% of the MNI), 28% (28% of the WR and 18% of the MNI) to Geoemydidae, and less than 1% (0.6% of the WR and 5% of the MNI) to Trionychidae. Note that for Trionychids remains from all localities, attribution can be done for all the plates because of their ornamentation, they are therefore not underrepresented because they cannot be easily identified.

Table 3 - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal Number of Individual (MNI) corresponding to the different turtle/tortoise taxa identified in the complete Doi Pha Kan Rock-shelter assemblage.

	NISP	WR	NMI
Indotestudo elongata	1122	1787.17	42
Geoemydidae	447	711.34	10
Trionychidae	12	14.13	3
Turtle ind.	3181	2600.38	
Total	**4762**	**5113.02**	**55**

Taphonomy of the turtle/tortoise bone assemblage

Among the 4762 bone fragments attributed to turtle/tortoises, 303 are complete elements (6.3%), and 249 are nearly complete (at least 90% of the bone is preserved) while 1389 (29%) are small fragments representing less than 5% of the complete anatomical part. The average percentage of completion of the bones is 32%. The overall PR is 28%. The best represented bones (Fig. 4 – A) are the stylopods (humerus and femur with PR>75%) followed by the tibia, the radius, the scapula, the coracoid, and the epiplastron (PR>50%). Then follow the rest of the long bones, and most of the plates that are the easiest to identify. The peripheral plates of the bridge are less represented (PR=10%) than all the other peripheral plates (PR=39%). The skull, vertebrae and all small elements of the hands and foot are nearly absent. The largest plates (hyoplastron and hypoplastron) are the most fragmented with completion means of less than 26%. The peripheral plates corresponding to the bridge are also more heavily

fragmented (completion mean of 59%) compare to the other peripheral plates (completions means 67-89%). Burning (black) and carbonization (grey/white) traces were observed on 690 bones (14% of the total NISP). Such traces were present indiscriminately on every anatomical element of the carapace and skeleton. Cut marks were observed on only five bones, six peripheral plates, and one hypoplastron. A series of peripheral plates attributed to a Geoemydidae turtle bears clear traces of a clean cut aiming to cut the ventral part of the carapace (Fig. 3-G). Lastly, 120 bones have been observed as corresponding to preserved anatomical connections on the field between unfused plates. This indicates that at least a part of the assemblage was undisturbed prior to the excavation.

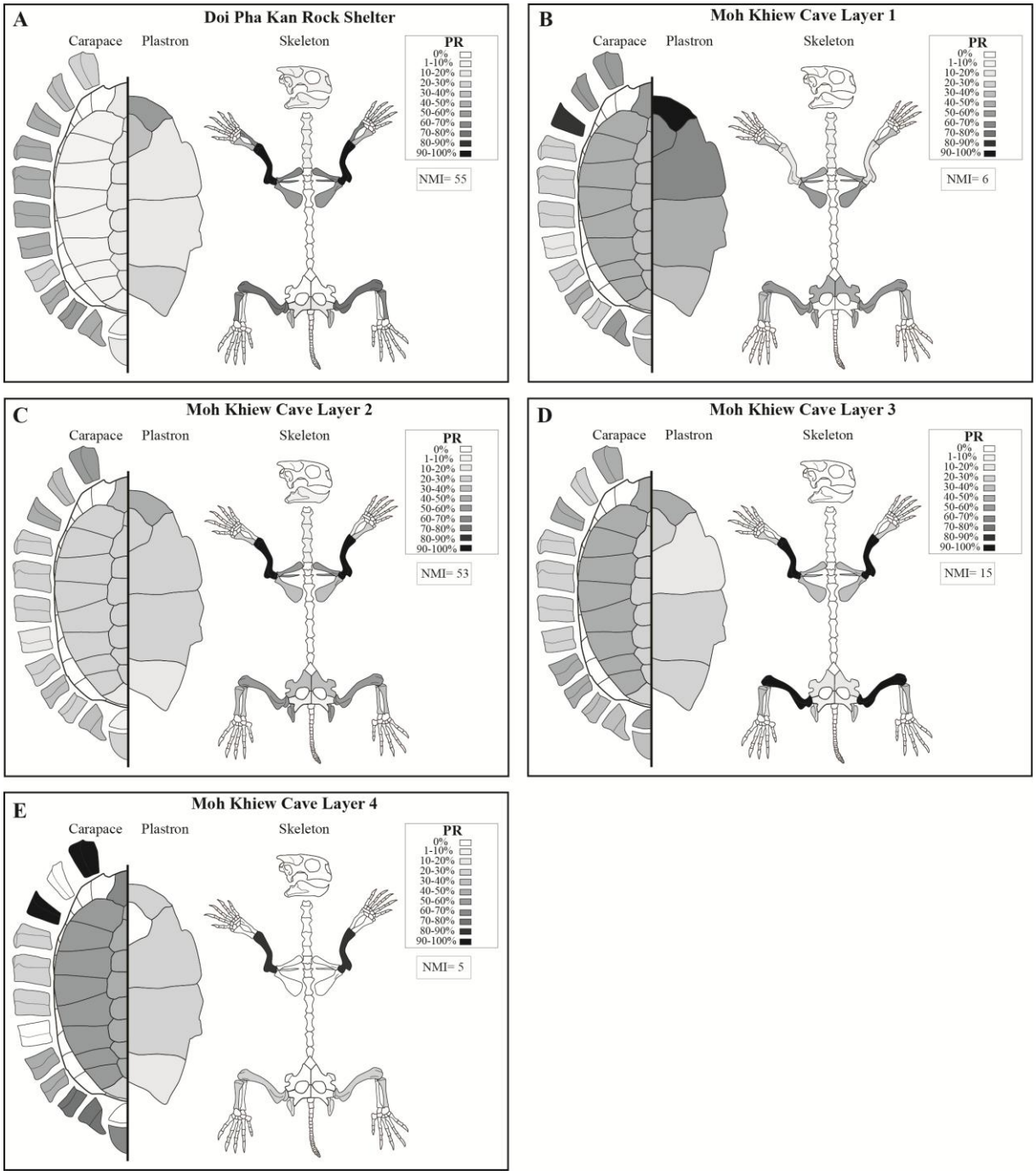

Figure 4 - Anatomical distributions of the turtle/tortoise remains collected in the sites of Doi Pha Kan rockshelter (A), and Moh Khiew Cave (B-E). The percentage of representation (PR) is considered here to provide a graphical visualization of the different values observed for the different anatomical elements.

Size of *Indotestudo elongata* archaeological individuals

The measurements recorded on the *I. elongata* archaeological material of Doi Pha Kan enabled for the reconstruction of 201 SCL estimations included between 64 and 292 mm with a mean of 182 mm (Figure. 5-A) and corresponding to at least 42 individuals. The distribution of these sizes was not unimodal (Hartigans' dip test, p.val>0.05) but could be bi-modal with a population of small individuals around 120 mm, and a second one between 140 and 260 mm.

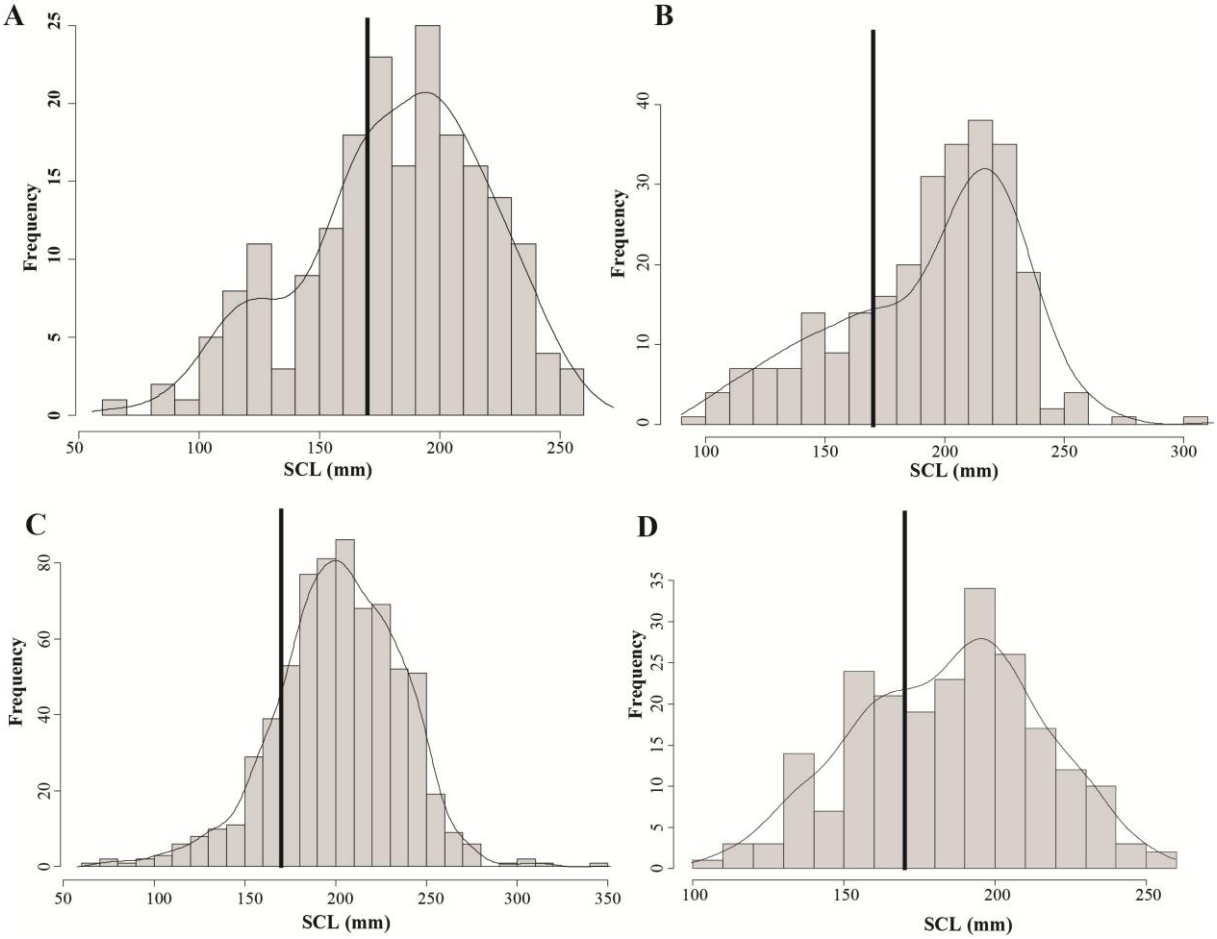

Figure 5 - Histograms of the *Indotestudo elongata* size reconstructions (Standard Carapace Length) obtained from the different herpetofaunal bone assemblages studied: A) Doi Pha Kan Rock-shelter (NMI=42); B) Moh Khiew Cave (NMI=59); C) Laang Spean Cave (NMI=75); D) Khao Ta Phlai Cave (NMI=26). The black bars represent the minimal size of the sexually mature specimens based on modern data collected on modern *I. elongata* populations.

Moh Khiew cave

Composition of the herpetofaunal assemblages

The herpetofaunal assemblage of Moh Khiew consists in 9 108 bone remains weighting 8351 gr. Those bones are mostly distributed in the layers 2 (51% of the NISP, and 52% of the WR), 1 (26% of the NISP, and 24% of the WR), and 3 (17% of the NISP, and 18% of the WR) (Table. 4). The complete assemblage includes bone fragment from a least 152 individuals.

The full sample mostly correspond to non-marine turtle remains (63% of the NISP, 74% of the WR, and 52% of the MNI), followed by Monitor lizards (25% of the NISP, 16% of the WR, and 24% of the MNI), and snakes (8% of the NISP, 8% of the WR, and 4% of the MNI). The small size lizards (excluding snakes), amphibians and crocodile remains altogether represent less than 5% of the assemblage in term of NISP and WR. The distribution of these groups among the layers is however far from homogenous. Indeed,

turtle bone remains represent more than 75% of the NISP, 85% of the WR, and 60% of the MNI in the layers 2 to 4 but only 20% of the NISP, 35% of the WR, and 21% of the MNI in the layer 1. At the opposite, Monitor lizards represent 46% of the NISP, 31% of the WR, and 35% of the MNI in the layer 1 but less than 20% of NISP, 13% of the WR, and 25% of the MNI in the other layers. Snakes are also better represented in the layer 1 (23% of the NISP) than in the subsequent levels (less than 2.6% of the NISP). Chi² tests performed on the NISP indicate that the faunal composition of the layer 1 significantly differs (P.val< 0.01) from the layers 2 and 3, the effective of the layer 4 being too low to conduct a statistical test.

Table 4 - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal Number of Individuals (MNI) identified in the complete herpetofaunal assemblage of the different layers of the 2008 excavation of Moh Khiew Cave.

	Layer 1			Layer 2			Layer 3			Layer 4			Total		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Turtle/Tortoise	503	702.8	6	3614	3789	53	1184	1288	15	439	481.3	5	**5740**	**6261**	**79**
Monitor lizard	1111	641.4	17	872	463.8	12	298	190.1	5	43	25.4	2	**2324**	**1321**	**36**
Snake	560	612.2	3	117	52.8	1	37	29.15	1	7	6.4	1	**721**	**700.6**	**6**
Amphibian	144	38.45	14	34	6.5	4	22	3.92	3	0	0	0	**200**	**48.87**	**21**
Small lizards	89	8.27	7	4	0.3	1	28	3.1	1	**0**	0	**0**	**121**	**11.67**	**9**
Crocodile	2	8.5	1	0	0	0	0	0	0	0	0	0	**2**	**8.5**	**1**
Total	**2409**	**2012**	**48**	**4641**	**4312**	**71**	**1569**	**1514**	**25**	**489**	**513.1**	**8**	**9108**	**8351**	**152**

Regarding the identification of non-marine turtle taxa (Table 5), between 66 and 79% of the bone fragment have not been associated with at least a family rank identification. Regarding the identified families, Testudinidae (*Indotestudo elongata*) represent a stable major part of the identified bone remains (between 68 and 63% of the NISP, 70-56% of the WR, and 86-50% of the MNI depending of the layer). The other fragments have been attributed to Geoemydidae turtles (36-29% of the NISP, 36-28% of the WR, and 33-12% of the MNI), and Trionychidae (0-2% of the NR and WR). The composition of the turtle assemblages in term of families seems then to be fairly stable across the layers as indicated by results of Chi² tests that did not indicated significant differences in the distribution of the NISP from the different testable layers (P.val> 0.01).

Table 5 - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal Number of Individuals (MNI) in the non-marine turtle assemblage from the different layers of the 2008 excavation of Moh Khiew Cave.

	Layer 1			Layer 2			Layer 3			Layer 4			Total		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Indotestudo elongata	109	239.9	4	853	1274	43	193	323.9	10	60	105	2	**1215**	**1943**	**59**
Geoemydidae	61	107.3	2	386	512.9	6	111	253.9	3	26	62.2	1	**584**	**936**	**12**
Trionychidae	1	0.7	0 (1)	16	37.8	1	0	0	1	2	2.5	1	**19**	**41**	**3**
Turtle ind.	332	354.9	0	2359	1964	3	880	709.9	1	351	311.6	1	**3922**	**3340**	**5**
Total	**503**	**703**	**6**	**3614**	**3789**	**53**	**1184**	**1288**	**15**	**439**	**481**	**5**	**5740**	**6261**	**79**

Taphonomy of the turtle/tortoise bone assemblage

The fragmentation of the 5740 bone fragments analyzed increase with the depth. In the layer 1, 8.9% of the bones are complete, and 12.9% nearly complete, in layer 2 these percentages falls to 7.5 and 12.1%, then to 5.6 and 9.6% in layer 3, and finally to 3.9 and 7.7% in layer 4. The average percentage of completeness of the bones is also slightly higher in layers 1 and 2 (36 and 37%) than in the layers 3 and 4 (34 and 28%). These differences are only significant between the layers 1 and 4 (Chi² test; p. value<0.01).The anatomical distribution of the remains present strong variations between the layers (Fig.

4) but the sizes of the assemblages are also very dissimilar with the bone samples of the layers 1 and 4 containing only 503 and 439 remains and those of the layers 2 and 3 containing 3614 and 1184 bone fragments. Distributions in small samples could be more strongly impacted by random effects than larger assemblages and a strict comparison of the four layers might not make sense at all. Some general trends can, however, still be noted just as the overall PR which is between 27 and 24% in all the layers at the exception of the first in which it is slightly higher (36%). Nearly all the anatomical parts are present in every layer but the skulls, vertebrae, and extremities are nearly absent. The stylopods (humerus and femur) are the best represented bones in the richest layers. They are also well represented in layers 1 and 2 but are outnumbered by some specific carapace plates. Girdles and zeugopods are also present but in smaller number. Regarding the carapace and the plastron, no clear pattern emerges at the exception of the nearly systematic lower representation of the peripheral plates of the bridge (PR=25-21%) in respect to the other peripheral plates (mean PR=52-29%). This could be explained by an identification bias related to the lower mean completion rate of peripheral plates of the bridge in respect to the others. Burning (black) and carbonization (grey/white) traces were observed on 325 bones (5.7% of the total NISP). Such traces were present indiscriminately on every anatomical element and every side of the carapace and skeleton parts. They were recorded on the internal side of several peripheral plates that were still in anatomic connection at the moment of the excavation (Fig. 3-F). Such observations were, however, not repeated on the rest of the material. Cut marks were observed on only three bones: one peripheral plate, one nuchal plate, and one xiphiplastron. Among the full assemblage 61 fragments of carapaces were still in anatomical connection at the moment of the excavation. These elements were distributed mostly in the layers 2 and 3 but also in the lower part of the layer 1 at a depth of 70-80 cm.

Size of *Indotestudo elongata* individuals

The measurements recorded on the *I. elongata* archaeological material of Moh Khiew Cave enabled for the reconstruction of 201 SCL estimations included between 98 and 310 mm and with a mean of 193 mm (Figure. 5-B) and corresponding to at least 59 individuals. The mean size of the tortoises is similar in all layers and no statistically significant differences was noted (student T-test; p.val>0.01). In layer 1 (N=25) the mean size was 198 mm, 194 mm in layer 2 (N=169), 187 mm in layer 3 (N=52), and finally 195 mm in layer 4 (N=19). The largest observed specimen was in the layer 1. The global distribution of these sizes was not unimodal (Hartigans' dip test, p.val>0.01) and mixture models indicate it is most likely bimodal with a best represent group of individuals around 220 mm and a second group of smaller specimens around 150 mm.

Khao Ta Phlai Cave

Taxonomic composition

A total of 3763 bone remains of herpetofauna weighting 7239 gr. and representing at least 43 individuals were analyzed from the two excavated test-pits of the site of Khao Ta Phlai (Table. 6). Most of these bones correspond to turtle or tortoises in term of WR (87% in TP1 and 90% in TP2), NISP (81% in TP1 and 86% in TP2), and MNI (65% in TP1 and 70% in TP2). The second most represented herpetofaunal group is the Monitor lizards (12 and 9% of the WR, 16 and 12% of the NISP, and 23 and 22% of the MNI) followed by some rare remains of snakes as well as few amphibian bones in the TP2 only.

Table 6 - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), Number of Remains (NR), and Minimal Number of Individual (MNI) corresponding to the different herpetofaunal taxa identified in the herpetofaunal bone assemblages collected in the two test-pits of the site of Khao Ta Phlai.

	TP1			TP2		
	NISP	WR	NMI	NISP	WR	NMI
Amphibians				3	0.51	1
Snakes	38	33.4	2	37	69.3	2
Turtle/Tortoise	1335	2509.7	19	1825	3901	18
Monitor lizards	274	347.7	6	251	377.9	6
Total	**1647**	**2891**	**27**	**2116**	**4349**	**27**

Although the distribution of the material between the two TPs is somewhat homogenous, the repartition of the bones across the two main periods documented (metal ages and Neolithic) is quite different. Indeed, in the TP2, most of the material (95% of the NISP) is located in the Neolithic layers while in TP1 the bone are more evenly distributed (55% of the NISP in the Metal Ages layers and 44% of the NISP in the Neolithic levels).

The distribution of the main herpetofaunal taxa across the layers does not present strong variations (Tab. 7) as only the very poor metal age layer of the TP2 significantly differ from the other levels (Chi^2; p.value <0.01). Turtle bones are always the best represented (between 71 and 87% of the NISP) but Monitor lizards seems a bit better represented in Metal Ages layers from TP1 and 2 (18 and 20% compared to Neolithic layers (14 and 11% of the NISP). These tendencies are, however, not statistically significant and difficult to interpret in the absence of a study of the complete faunal assemblages.

Table 7 - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal Number of Individual (MNI) corresponding to the different herpetofaunal taxa identified in the herpetofaunal bone assemblages of the two periods identified in the two test-pits of the site of Khao Ta Phlai.

	TP1-Metal Age			TP1-Neolithic			TP2-Metal Age			TP2-Neolithic		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Amphibians										3	0.51	1
Snakes	33	22.4	2	5	11	2	9	13.4	2	28	55.9	2
Turtle/Tortoise	720	1011.8	14	615	1497.8	9	70	131.2	2	1755	3769.8	21
Monitor lizards	166	146.2	1	108	201.5	1	20	36.2	1	231	341.7	3
Total	**919**	**1180**	**17**	**728**	**1710**	**12**	**99**	**180.8**	**5**	**2017**	**4168**	**27**

The identification rate of non-marine turtles bones was lower in the TP1 (41% of the WR and 25% of the NR) than in TP2 (57% of the WR and 35% of the NR). Regarding the bones attributed to a given family (Tab. 8), TP1 provided nearly as much Testudinidae as Geoemydidae in terms of WR and NISP while *Indotestudo elongata* is much more represented than the latter in the TP 2 (61% of the WR and 69% of the NISP). These differences are statistically significant (Chi^2 test; p.value<0.01). Trionychidae are present in the two TPs. If the chronological phases are considered (Tab. 9), Geoemydidae and Trionychidae are significantly better represented in the upper layers of the TP2 and TP1 corresponding to the metal ages. These two layers do not significantly differ in term of family composition (Chi^2 test; p.value>0.01) but significantly differ from the two Neolithic layers (Chi^2 test; p.value<0.01). This trend to a more important exploitation of freshwater turtles during the metal ages in regard to the Neolithic period is for now difficult to interpret considering the possible issues of chronological associations between the layers of the two TPs and the possibility of a spatial variation in the distribution of the remains inside the site. Indeed freshwater turtles are also better represented in the Neolithic layer of the TP1 compare to TP2.

Table 8 - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal Number of Individual (MNI) corresponding to the different turtle/tortoise taxa identified in the bone assemblages collected in the two test-pits of the site of Khao Ta Phlai.

	TP1			TP2		
	NISP	WR	NMI	NISP	WR	NMI
Indotestudo elongata	175	435.5	8	441	1357	14
Geoemydidae	150	581.9	5	191	838.6	3
Trionychidae	10	14.1	1	9	32.2	1
Turtle ind.	1000	1478		1184	1673	
Total	**1335**	**2510**	**14**	**1825**	**3901**	**18**

Table 9 - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal Number of Individual (MNI) corresponding to the different turtle/tortoise taxa identified in the bone assemblages collected in the different chronological phases of the two test-pits of the site of Khao Ta Phlai.

	TP1-MA			TP1-NE			TP2-MA			TP2-NE		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Indotestudo elongata	86	149	7	89	286.5	6	14	40.2	1	427	1316.6	12
Geoemydidae	81	243.2	2	69	338.7	3	13	28.7	1	178	809.9	4
Trionychidae	10	14.1	1				3	5.2	1	6	27	1
Turtle ind.	543	605		457	872.63		70	57.1		1144	1616.3	
Total	**720**	**1011**	**10**	**615**	**1498**	**9**	**100**	**131.2**	**3**	**1755**	**3770**	**17**

Taphonomy of the turtle/tortoise bone assemblage

Among the 3 160 bone fragments attributed to turtle/tortoises in the material of Khao Ta Phlai, 221 were complete elements (6.9%), and 370 were nearly complete (at least 90% of the complete bone) while 760 (24%) were small fragments representing less than 5% of the complete anatomical part. The average percentage of completion of the bones is 29%. This value is similar in the Neolithic layers of TP1 and TP2 (29%). It is slightly lower in the metal ages layer of the TP1 (25%), and higher in the same period layers from TP2 (39%) but the small size of this assemblage does not allow to consider this result as significant.

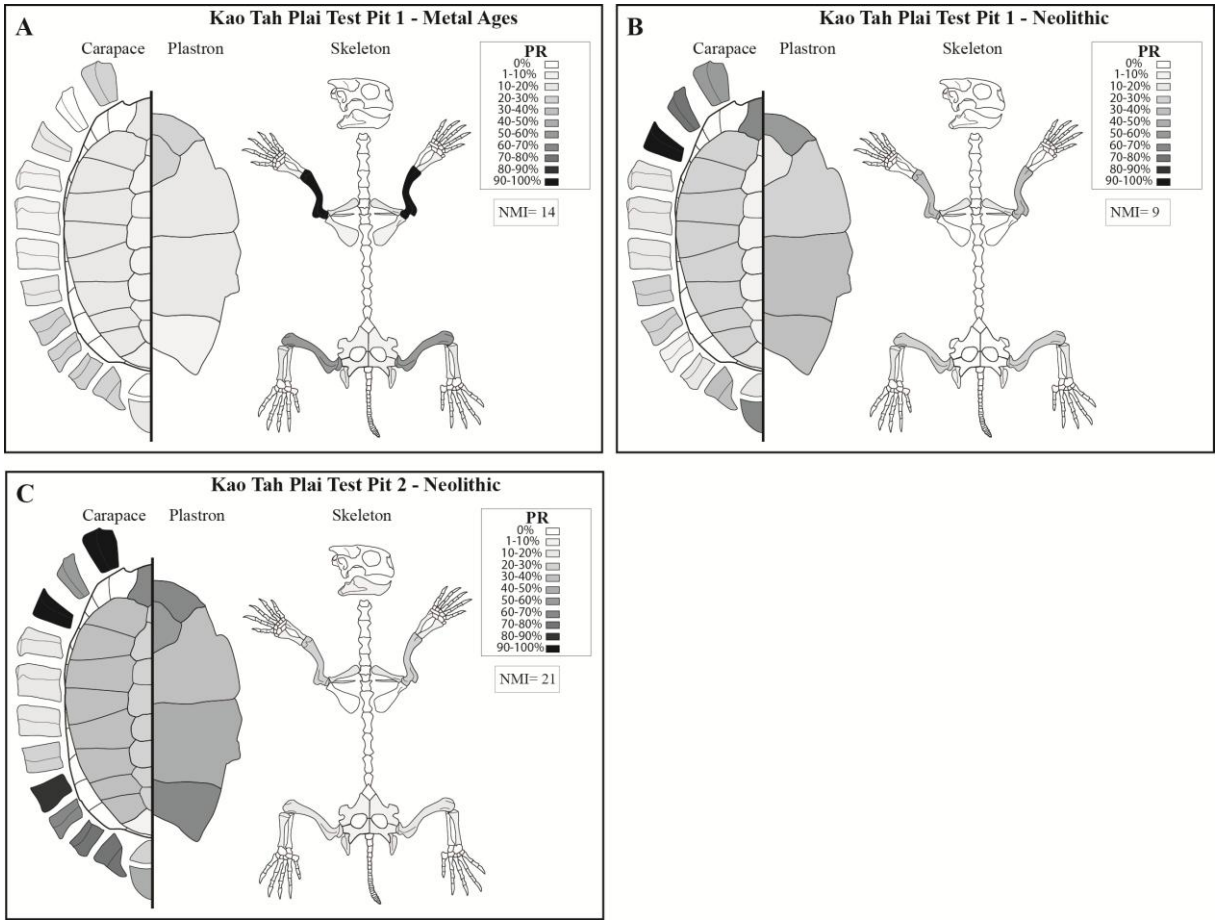

Figure 6 - Anatomical distributions of the non-marine turtle remains collected in the different test-pits and layers of the site of Khao Ta Phlai: (A) Test-pit 1 – Metal Ages, (B) Test-pit 1– Neolithic, (C), Test-pit 2– Neolithic. The percentage of representation (PR) is considered here to provide a graphical visualization of the different values observed for the different anatomical elements.

The anatomical distributions of the turtle bone elements present strong variations among the different layers (Fig. 6). The distribution observed in the Neolithic layers of the TP2 is fairly homogenous (mean PR=33%) with a representation of all the anatomical part at the exception of the smallest elements (phalanges, carpal and tarsal articulations, and vertebrae), and the skull. The most robust anatomical parts are the best represented (peripheral plates, epiplastron, entoplastron, and nuchal plate -PR>38%-) and the most fragile the least represented (zeugopods, and most girdles elements - PR<5%-). The only exception to that pattern is the peripheral plates of the bridge (PR=15%) which are least represented than the other elements of the carapace and other peripherals (mean PR=73%). The distribution pattern is quite less homogenous in TP1 where the mean PR is lower (24% in the Neolithic layers and 15% in the metal ages layers) but the Neolithic layers follow the same general pattern as the one of the TP2 with a lower global representation due to the strong presence of a single peripheral plate rank. In this last layer, another difference with TP2 is that the stylopods are also better represented than the elements from the carapace. The anatomical distribution of the bones collected in the metal ages layers of TP1 is very different with a very strong representation of the stylopods (mean PR=76%) compare to the most robust elements of the carapace (PR=29-15%). Otherwise, the same general observations applies with a lack of skull and extremities elements, a better representation of the most robust elements of the carapace, and a lower representation of the peripheral plates of the bridge (PR=5%) in regard of other peripheral plates (Mean PR=18%).

Most of the material (72% of the NISP) was covered by a veil of calcite which made very difficult the observation of the surface alterations of the bones. Despite this important limitation, nine bones

were recorded as presenting traces of dissolution under the effect of flowing water, and 182 as bearing traces of burning and carbonization. During the study we also recorded 22 associations of bones from the same context being in anatomical connection in the two TPs below 120 cm of depth in the TP 2 and 135 cm in the TP 1. This indicates that the material from the deepest layers was not strongly disturbed since its deposition. Nine combination of bone in anatomical connection linked together by concretion were also found in the same layers.

Size of *Indotestudo elongata* individuals

The measurements recorded on the *I. elongata* archaeological material of the Khao Ta Phlai site have enabled for the reconstruction of 219 SCL estimations included between 108 and 252 mm and with a mean of 184 mm (Figure. 5-D) and corresponding to at least 26 individuals. Most of the size estimations are from the Neolithic layers of the TP2 (n=158) and TP1 (n=31) while only 29 estimations were obtained from the metal ages layers (mean size = 178 mm). The strong disparities of the distributions of the size estimations between the archaeological contexts do not allow for an individual comparison of the different layers. The Neolithic layers provided mean SCL values of 185 and 186 mm. The global distribution of these sizes was not unimodal (Hartigans' dip test, p.val>0.01) and mixture models indicate it is most likely bimodal with a group of individuals around 210 mm and a second group of smaller specimens around 165 mm.

Laang Spean Cave

Composition of the herpetofaunal assemblage

The complete herpetofaunal assemblage of Laang Spean consists of 9533 bone fragments weighting 18 804 gr. and representing at least 115 individuals (Tab. 10). Most of them come from the Hoabinhian layer accounting for 76% of the NISP, 78% of the WR, and 62% of the MNI. The “Neolithic” and “sepulture” assemblages are of similar sizes and account respectively for 10.5 and 13.2% of the NR. The material corresponds nearly exclusively to non-marine turtle remains which account for 92% of the NISP, 95% of the WR, and 70% of the MNI. Monitor lizards represent 5% of the NISP of the assemblage, snakes are rare (2% of the NISP), and the occurrence of amphibians and smaller lizards is insignificant (below 1%). The distribution of the taxa is not statistically different across the sub-assemblages (Chi² test; p.value>0.01).

Table 10 - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal Number of Individuals (MNI) studied in the complete herpetofaunal assemblage from the different layers of the Laang Spean Cave.

	Hoabinhian layer			Neolithic layer			Sepulture layers			Total		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Turtle/Tortoise	6650	13893	56	904	1854	12	1195	2057	12	**8749**	**17804**	**80**
Monitor lizard	406	497	3	30	48	2	39	56	3	**475**	**601**	**8**
Snake	158	311	3	16	37	1	19	30	2	**193**	**378**	**6**
Amphibian	45	9	7	33	6	5	6	1	2	**84**	**16**	**14**
Small lizards	13	2	3	16	2	3	3	1	1	**32**	**5**	**7**
Total	**7272**	**14712**	**72**	**999**	**1947**	**23**	**1262**	**2145**	**20**	**9533**	**18804**	**115**

Regarding the identifications of the turtle and tortoise bone fragments (Tab. 11), only 33% of the NISP and 52% of the WR have been attributed at least to a family. *Indotestudo elongata* bone remains account for most of the identified turtle/tortoise bones with 86% of the NISP, 86% of the WR, and 87% of

the MNI. Geoemydidae are rare with only 14% of the NISP, 13% of the WR, and 9% of the MNI, while the occurrence of Trionychidae is anecdotic (less than 1% of the NR and WR, and 3.5% of the MNI).

Table 11 - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal Number of Individuals (MNI) identified in the turtle/tortoise bones assemblage from the different layers of Laang Spean Cave.

	Hoabinhian layer			Neolithic layer			Sepulture layers			Total		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
Indotestudo elongata	2046	6706	51	204	649	12	260	692	12	2510	8047	75
Geoemydidae	325	955	4	34	115	2	47	162	2	406	1232	8
Trionychidae	7	20.5	1	2	7	1	5	16	1	14	43.5	3
Turtle ind.	4272	6212		664	1084		883	1187		5819	8483	0
Total	**6650**	**13894**	**56**	**904**	**1855**	**15**	**1195**	**2057**	**15**	**8749**	**17806**	**86**

Taphonomy of the turtle/tortoise bone assemblage

Regarding the taphonomy of the turtle bones collected in the different squares, the mean completion rate is slightly lower in the “sepulture” assemblage (32%) than in the “Neolithic” and “Hoabinhian” assemblages (39.2 and 36.7%). The general fragmentation pattern is otherwise similar in all layers. The complete bones constitute between 9.3% of the assemblages for the Hoabinhian assemblage, and 7.2-6.2% for the “Neolithic” and “Sepulture” assemblages while nearly complete elements account for 14.2% of the “Hoabinhian”, 13.8% of the “Neolithic”, and 11% of the “Sepulture” assemblages. Most anatomical parts are represented in the different assemblages but the extremities, vertebrae, and skull remains are very rare with a PR below 4% in all assemblages (Fig. 7). There is also a global tendency to the lower representation of the peripheral plates of the bridge (11%-31%) in respect to the other peripheral plates (58-70%) although this trend is more strongly marked in the Hoabinhian layer (11% vs. 70%). The peripheral plates of the bridge are also systematically more fragmented (59-67% of mean completion) than the others (83-87% of mean completion). Outside of these common trends, significant strong differences emerge between the “Hoabinhian” assemblages and the two other layers. Indeed, although the general PR is similar in the different assemblages (41% for the Hoabinhian assemblage, 37% for the Neolithic assemblage, and 34% for the Sepulture assemblage) the carapace elements are dramatically better represented in the Hoabinhian bones (Fig. 7-A) compare to the two other assemblages (Fig. 7-B, C) (Chi^2 test; p.value<0.01). Indeed, although the PR of the carapace and plastron bones are more or less similar in the Hoabinhian assemblage (57.8% vs. 67%) the plastron elements are mostly missing in the other assemblages (54% vs. 20.8% in the Neolithic assemblage and 53% vs. 15.1% in the Sepulture assemblage). The stylopods are also better represented in the Hoabinhian squares (84%) compare to the other assemblages (50.4% and 28%).

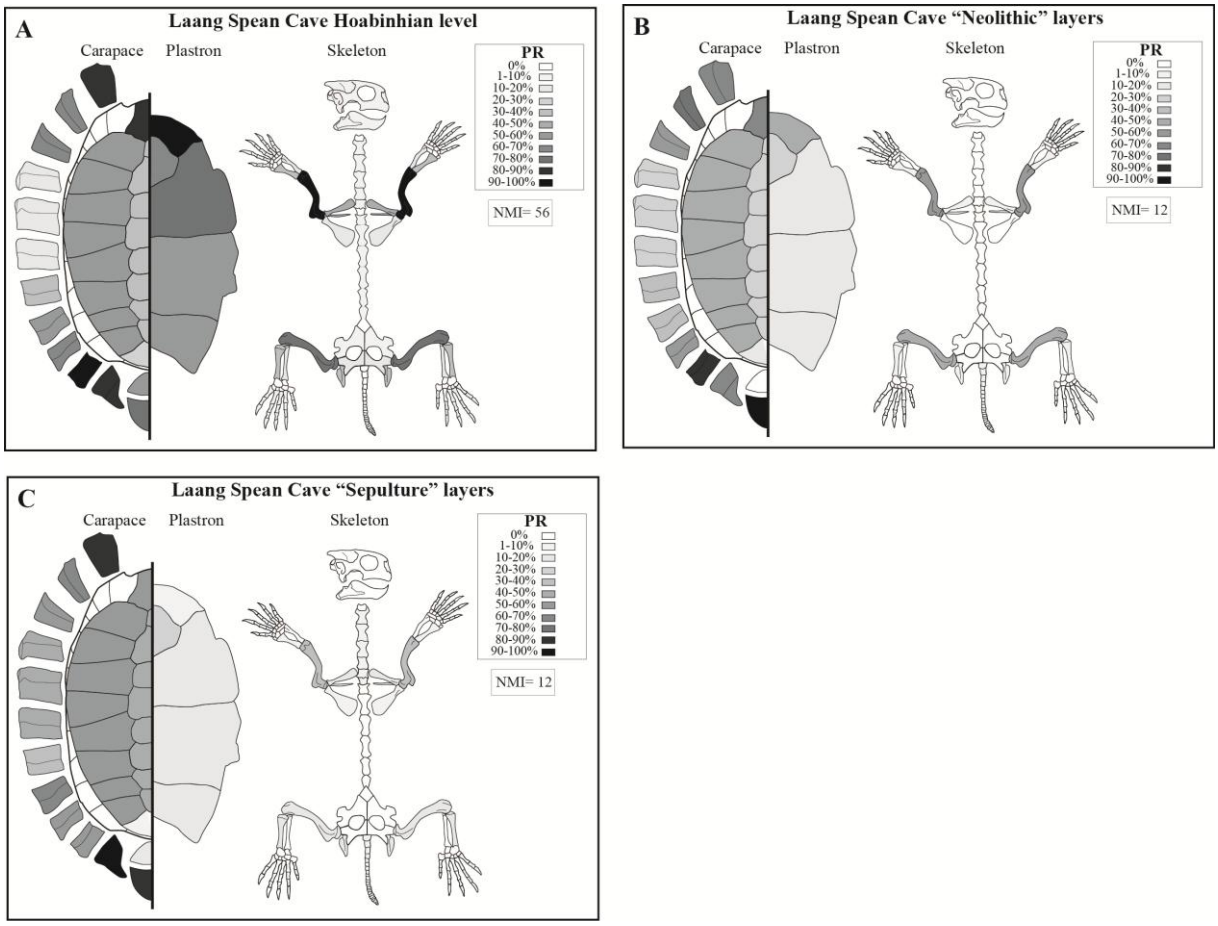

Figure 7 - Anatomical distributions of the turtle remains collected in the different layers of the site of Lang Spean. The percentage of representation (PR) is considered here to provide a graphical visualization of the different values observed for the different anatomical elements.

The observation of traces on the bones is made very challenging by the fact that 61% of them are covered by a veil of calcite. Interestingly, this calcite deposit was more frequent in the Hoabinhian squares where it covered 65% of the bones but was scarcer in the Neolithic and sepulture squares where it covered respectively 56% and 38% of the bones. This is probably related to the position of the remains in the cave, more or less close to the walls, which influenced their exposition to water flows during the rainy season. There is also a possibility that the calcite veil might be more frequent on the oldest remains. The presence of water flow in the site is also indicated by the occurrence of 61 bones having been polished by water flows. Porcupine gnawing traces were observed on only 13 elements distributed in several areas and layers of the site and digestion traces on only one. This clearly indicates a minor impact of animal species on the integrity of the archaeological assemblage. Putative burning traces were observed 10% of the remains. These traces were better represented in the Hoabinhian squares where they were present on 12% of the bones while they only occur on 2.8 and 3.8% of the bones recovered in the Neolithic and Sepulture squares. The characterization of burning traces was made very difficult by the fact that the material present a strong variability of surface color probably related to post-depositional chemical alteration. The occurrence of these traces might thus have been underestimated given the fact that we choose to record them only when their nature was undisputable. No cut mark was observed.

Among the full assemblage 327 fragments of carapaces (3.7% of the NR) were still in anatomical connection at the moment of the excavation. These elements are mostly from the Hoabinhian squares (N=292) where they account for 4.3% of the turtle remains. Elements in anatomical connection are scarcer in the other assemblages with only 35 occurrences (1.7% of the turtle NR). This indicates that the Hoabinhian squares have been indeed less disturbed than the "Neolithic" and "Sepulture" squares.

Size of *Indotestudo elongata* individuals

The measurements recorded on the *I. elongata* archaeological material of Laang Spean Cave enabled for the reconstruction of 688 SCL estimations included between 68 and 345 mm and with a mean of 201 mm (Figure. 5-C) and corresponding to at least 75 individuals. Most of the data (N=564) are from Hoabinhian layers while the Neolithic squares only provided 124 SCL data but no significant difference emerged from the comparison of these two assemblages (Student t-test, p.val>0.05). The global distribution (all squares) of these sizes is unimodal (Hartigans' dip test, p.val>0.05) with a peak of specimens around 200 mm SCL. In this site, small specimens below 170 mm represent only 16% of the population, and specimens below 140 mm only 4.7%.

Discussion

Taxonomic composition of the herpetofaunal assemblages

In all the assemblages the distribution of the herpetofaunal groups in the four investigated sites present strong similarities. Non-marine turtles are nearly systematically the best represented herpetofaunal group (between 59 and 91% of the NISP) before Monitor lizards (between 6 and 25% of the NISP), snakes (below 3.5% of the NISP), and amphibians. The only exception to this trend is the layer 1 of Moh Khiew cave in which Monitor Lizards (25% of the NISP), and snakes (23% of the NISP) bone remains are more numerous than turtle skeletal elements (20% of the NISP). This layer is disturbed and not dated so interpreting this observation is impossible for now. However, the other sites follow a clear pattern showing that hunter-gatherers groups have preferentially exploited turtles over other reptile and amphibian taxa. This follow the general regional pattern previously observed in similar zooarchaeological assemblages (Conrad 2015). Regarding the proportion of the turtle/tortoise families in the assemblages, Testudinidae (*Indotestudo elongata*) is always the most represented group as it account for between 52 and 89% of the turtle bones NISPs. The proportions of Geoemydidae turtles vary a lot between 48 and 11% of the same NISPs. As most of the species from this group are aquatic freshwater turtles this variability could be explained by the accessibility of streams, rivers, and lakes by the inhabitants of the sites. In most sites the proportion of Geoemydidae is around 30% of the NISP but these turtles are much less prevalent in Laang Spean cave, and the best represented in the TP1 of the site of Khao Ta Phlai. The published data regarding the faunal assemblage from Laang Spean indicate a weak contribution of freshwater taxa (mussels and fish) to the overall diet (Forestier *et al.* 2015; Frère *et al.* 2018) which is in accordance with our observation of the scarcity of freshwater turtles in the site. Regarding the prevalence of Geoemydidae species in the TP1 of Khao Ta Phlai, this could indicate a stronger reliance on freshwater resources than in the other sites. However, considering the chronology of the two test-pits of the site is not yet fully resolved and that general importance of aquatic resources in this assemblage still need to be estimated, this fact cannot be related to a cultural/chronological trend for now. From a general point of view, the data regarding the herpetofaunal assemblages, however, point to strong similarities between assemblages of different ages and from very different environmental settings. This should be considered at the light of the studies regarding the mammal bone assemblages of the same sites to test the hypothesis of a putative homogeneity of the Hoabinhian subsistence strategies in continental Southeast Asia.

Taphonomy of the turtle assemblages

The fragmentation rate of the bones is fairly homogenous among the sites. The average percentage of completeness of the bones is between 37 and 28%. The material from three first layers of Moh Khiew Cave and Laang Spean are the less fragmented (average percentage of completeness above 33%). The layer 4 of Moh Khiew cave provided the most fragmented material (average percentage of completeness of 28%). The presence of large limestone blocks in this layer may be indicative of crumbling

that may have altered the faunal material. Regarding the anatomical distribution of the turtle remains the sites present strong differences with mean PR between 41% (Laang Spean) and 15% (Khao Ta Phlai metal ages layer from TP1). This means that the anatomical representation of the bone remains is more or less biased toward some elements. Two main cases occur in the assemblages: sites in which stylopds are the best represented parts (Khao Ta Phlai metal ages layer from TP1, Doi Pha Kan, layers 2 to 4 of Moh Khiew cave), and sites in which the most robust parts of the carapace are the best represented elements. The mean PR is systematically higher in the assemblages where the stylopds are the most numerous. This indicates that these assemblages are the least altered by post-depositional phenomena. Indeed, a natural alteration would rather lead to the situation observed in the other assemblages in which the elements that are the most often founds are the most robust and thus would have the highest survival rates. However this is not sufficient to explain an overrepresentation of long bones that are supposed to preserve less well than carapaces elements. Considering that all the sediment of the studied deposit has been screened, a major recovery bias is unlikely although some of the smallest elements might have been missed. A post-depositional sorting of the material could also be ruled out as we shown no evidence of differential fragmentation and no abundant trace of water circulation in the different deposits studied. The most likely hypothesis is thus that human inhabitants of some of the sites discarded or transported for further use some of the carapaces of the consumed animals and left on place the smallest elements among which the largest and toughest (humerus and femurs) have been recovered and identified. This behavior would in any case not be systematic as the anatomical distributions indicate that complete individuals have been brought on the sites. The absence of the head of the specimens could be either related to an identification bias or a removal of these parts outside of the site. Humerus and femur put apart, the anatomical distributions of turtle bones follow a global pattern where the most robust anatomical elements are better represented than the more fragile ones. The only exception to this trend concern the peripheral plates of the bridge which are always less represented than the other peripheral. This is very likely to be related to an identification bias itself related to the nearly complete absence of complete pieces of such element in the material. This is undoubtedly linked to the separation of the carapace from the plastron by the inhabitants of the sites who have broken the bones in the area that links both part of the shell, a step that is mandatory to access to most of the meat content of the animal.

The observations of the surface traces on the bones indicate a nearly complete lack of predation and digestion traces which combined with the general weak fragmentation of the material allow to completely ruling out a putative role of non-human predators in the constitution of the studied assemblages. This is not surprising as although some predators, including Monitor lizards, are known to hunt juvenile tortoise individuals, adults' specimens probably have few non-human predators although some modern specimen bear traces of predation attempts (Ihlow *et al.* 2016) and that predation on other Southeast Asian tortoises species have been reported (Platt *et al.* 2021). Large felids (Emmons 1989), and eagles (Gil-Sánchez *et al.* 2022) are known to be able to hunt adults tortoises but such predator would undoubtedly have left predation traces on the subfossil bone assemblages we studied. Some very rare bones bearing porcupine traces indicate that these animals had a minor impact on some of the assemblages but not enough to impact the zooarchaeological interpretations. However, although it seems fairly evident that the animals present in the sites have been hunted to be consumed as there is no trace of bone industry in the assemblages, finding direct traces of culinary preparation on the bones is very challenging. Indeed, in Khao Ta Phlai and Laang Spean, some remains (72 and 37%) were covered by a veil of calcite making impossible to observe the surface of the bones. In addition, very few cut marks have been characterized on the bones of the different sites. Many burned bones were observed in all the sites but linking these to a cooking technique is very questionable. Indeed, these traces do not seem to be located on specific part of the bones (i. e. external side of the carapace) and appear randomly on

every area of every anatomical part. It is likely that these traces are related to post-depositional events unrelated to the cooking of the animals. The frequency of fire traces combined with the strong fragmentation of the large vertebrate remains in most sites (C. Griggo; C. Bochaton pers. obs) could indicate the use of the bones as combustible (Villa *et al.* 2002). Such a use is unlikely for the turtle skeletons considering their small size and the very good preservation stage of their remains but a proximity to the fire places (Bennett 1999) could explain the random occurrence of fire traces on their bone elements.

Size of Indotestudo elongata archaeological specimens

The size of *I. elongata* individuals observed in the four archaeological deposits (Fig. 5) shows common patterns but also some differences. The distributions of the estimated sizes are bimodal in all sites except Laang Spean. In all the sites, most of the estimations correspond to adult size specimens above 170 mm SCL reaching maximums of 270-345 mm SCL. These specimens all fall in the size range of the modern representatives of the species. Yet, all sites present a variable proportion of smaller, likely immature individuals. The representation of this second group is the lowest in Laang Spean (16% of the total number of estimations) but is important enough in the other sites to make their distributions bimodal with 35%-33% in Doi Pha Kan and Khao Ta Phlai, and 24% in Moh Khiew cave. Specimens below 140mm SCL are rare in all sites as they account for less than 10% of the estimations in all sites but represent more than 15% of the Doi Pha Kan population.

Interpreting the size distribution of the archaeological tortoises is a difficult task as it first requires an idea of what the size structure of a wild population would look like and basic biological data (season of birth, activity pattern, growth speed…) regarding modern and past *I. elongata* populations. However, these data are currently mostly missing which make very challenging a detailed interpretation of the collected archaeological data. The recovery of size distribution data in a natural modern population is always challenging as it could be influenced by many factors (i. e. climate, environment, seasonality, behaviors, and sizes of the individuals) that could bias the observations by making one or several size classes more difficult to observe than the others. In addition, the history and specific conditions of a wild population itself could have a dramatic impact on its size structure. In these conditions, defining a modern comparison point to the documented archaeological populations is difficult. To our knowledge, the only data collected on *I. elongata* concern the population of the Ban Kok Village (Khon Kaen Province, Thailand). This study shows that the pre-adult individuals have a low survivability rate as their population was mostly composed of newly born and old adult individuals (Sriprateep *et al.* 2013). The authors suggest that this strongly biased structure could be related to an absence of predation on the large individuals, and partly to several phenomena having a stronger impact on small specimens (e. g. predation, trampling of domestic bovids) but admit the main cause is still unknown while not discussing a potential poaching of the smaller individuals. Similarly, another publication about *I. travancorica* indicates a lack of juvenile specimen in the population but highlight that it could be related to a seasonal activity specific pattern. Indeed, juvenile specimens were much more commonly found at the beginning of the rainy season than during the dry season when their study has been conducted (Ramesh 2008). Other published distributions from other tortoises' species also indicate a strong representation of adult size individuals of different ages having completed their growth but also a much more balanced distribution of juvenile specimens of all sizes (Hailey & Coulson 1999; Znari *et al.* 2005; Rouag *et al.* 2007). In all these distributions the juvenile specimens are way scarcer than adult ones which make sense as adult class specimens correspond to individuals of very different ages having reached their final size. The only case in which this situation would be reversed is a population in which adult individuals would be subject to a strong predation pressure superior to the pressures imposed on the smaller individuals.

The site of Laang Spean presents a unimodal size distribution in which juvenile specimens are mostly excluded. In that sense, this distribution is very different from that of a natural population and indicates a strong selection on adult specimens of moderate to large size. This is clearly indicative of a very selective hunting strategy that may have been enabled by the abundance of resources in the vicinity of the site. Such a selection, although visible in other deposits is less marked as juvenile specimens composed more important parts of the assemblages, especially in Doi Pha Kan. In these sites, it is impossible to estimate whether or not the proportions of juvenile specimens present in the assemblages are similar to those of the exploited natural populations and thus to estimate the exact intensity of the selection toward large size individuals. In any case, it is the sign of an opportunistic foraging as such a combination of juvenile specimens has been observed on modern hunter-gatherer population actively collecting tortoises this way (Mena *et al.* 2000). But this might also be influenced by the hunting method in the case a direct selection by the hunter is not made, for instance with the use of trapping that was also hypothesized in Doi Pha Kan for the hunting of monitor lizards (Bochaton *et al.* 2019). This technique is also the most used to hunt tortoise in the Amazon as it is the most efficient method before active searching (Santos *et al.* 2020). This implies no selection on the specimens in the wild although the type of trap used (i. e. size of the ground hole) might induce some size bias. The use of traps could thus explain the strong representation of smaller individuals present in the archaeological assemblages and indicate a very opportunistic strategy indicative of either a poor selection by the hunter and/or a relative scarcity of the tortoises in the environments making harder the collect of large individuals. The hunting season could also be an explanation to the stronger or weaker presence of juvenile specimens in the assemblages. Indeed, during the dry season tortoises are less active and harder to find which could led the hunter to be less selective especially in the case of a use of non-selective hunting methods allowing to find these animals. Theobald (1868) mentions the hunts of tortoises by Burmese hunters in the dry season by clearing grass lands and forests with fire in order to destroy their shelters and locate them. At the opposite, smaller tortoises are more active in the rainy season during which dogs are more used to track them (Blythe 1854; Theobald 1868). Ultimately, both seasonal hypotheses could explain the occurrence of small individual using different explanations (hunting method vs. activity season). Only the use of non-traditional approaches such as skeletochronology (Ehret 2007) could help to clarify this question by estimating the season of death of the tortoise individuals as well as the occupation seasonality of the different sites given the absence of other seasonality makers in the materials.

Tortoise populations are vulnerable to intensive exploitation focused on the larger mature individuals. As such, and their exploitation has been considered as a marker of small scale hunting and thus of small human groups (Stiner *et al.* 2000). In the studied sites, the strong focus on a single turtle species (*I. elongata*) and the focus placed on large individuals would undoubtedly damage the natural populations and lead to a size reduction of the individuals (Close & Seigel 1997). Such exploitation would be sustainable only if it was not intensive meaning that not many individuals were collected in order to feed a putatively small size human group. It is difficult to address the question of the overall importance of the tortoises in the diet of the studied Southeast Asian hunter-gatherer groups as we still lack a complete and quantified study of the mammal fauna of the sites as well as strong data regarding the use of the studied sites. It is, however, clear that the investigated prehistoric population have exploited tortoises which composed a significant part of their meat diet. This is not surprising as turtle species are supposed to represent an important biomass in the ecosystems (Iverson 1982) and are also fairly easy to collect. This behavior have subsisted until nowadays in continental Southeast Asia (Hansel 2004) although all population does not choose to exploit reptile species (Tungittiplakornl & Dearden 2002).

Conclusion and perspective

The present work has been built as a stepping stone to provide the basic data and study tools enabling the study of tortoise's assemblages from continental Southeast Asia. As an effect, the true potential of this work will only be reached through the use of its analytical protocol for future studies and comparison with additional assemblages. We were however able to reach several conclusions as we demonstrated a putative strong similarities between the exploitation of the herpetofaunal taxa in the different sites as well as in the taphonomy of the non-marine turtle assemblages in different chronological and environmental settings. These data thus open many interesting questions regarding the trends of hunter-gatherer subsistence strategies in continental Southeast Asia during the Pleistocene and through the Holocene. However, much work remains to be done to reach a satisfactory zooarchaeological documentation level regarding these prehistoric human groups. As we demonstrate it in the introduction of this paper, many of the previously excavated Hoabinhian archaeological deposits of continental Southeast Asia, including sites which are known to have provided rich assemblages of non-marine turtle bone remains (i. e. Lang Rongrien), have not benefited from quantified zooarchaeological analyses. The complete study of these sites will be important to provide additional relevant comparison points to the present study. The non-herpetofaunal taxa of the sites included in this study should also be investigated to estimate the relative part of the reptile and amphibian exploitation in the global diet of these hunter-gatherer populations. Such studies should however be carried out in combination with the elaboration of appropriate study protocols regarding the estimation of the size/weight of the exploited individuals of large mammal species. Much needed is also the elaboration of identification methods, should they be morphological or molecular, designed for Southeast Asian species to complement the existing works (Pritchard *et al.* 2009; Bochaton *et al.* 2019). Only at the cost of such investment the zooarchaeology of Southeast Asia will be on par with the rich literature existing on the material productions of prehistoric groups but this will also require the local development of a strong research community interested in that discipline that is still lacking at the present.

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Data, scripts, code, and supplementary information availability

Supplementary information is available online: XXXXDOI of the webpage hosting the data https://doi.org/10.5802/fake3.doi

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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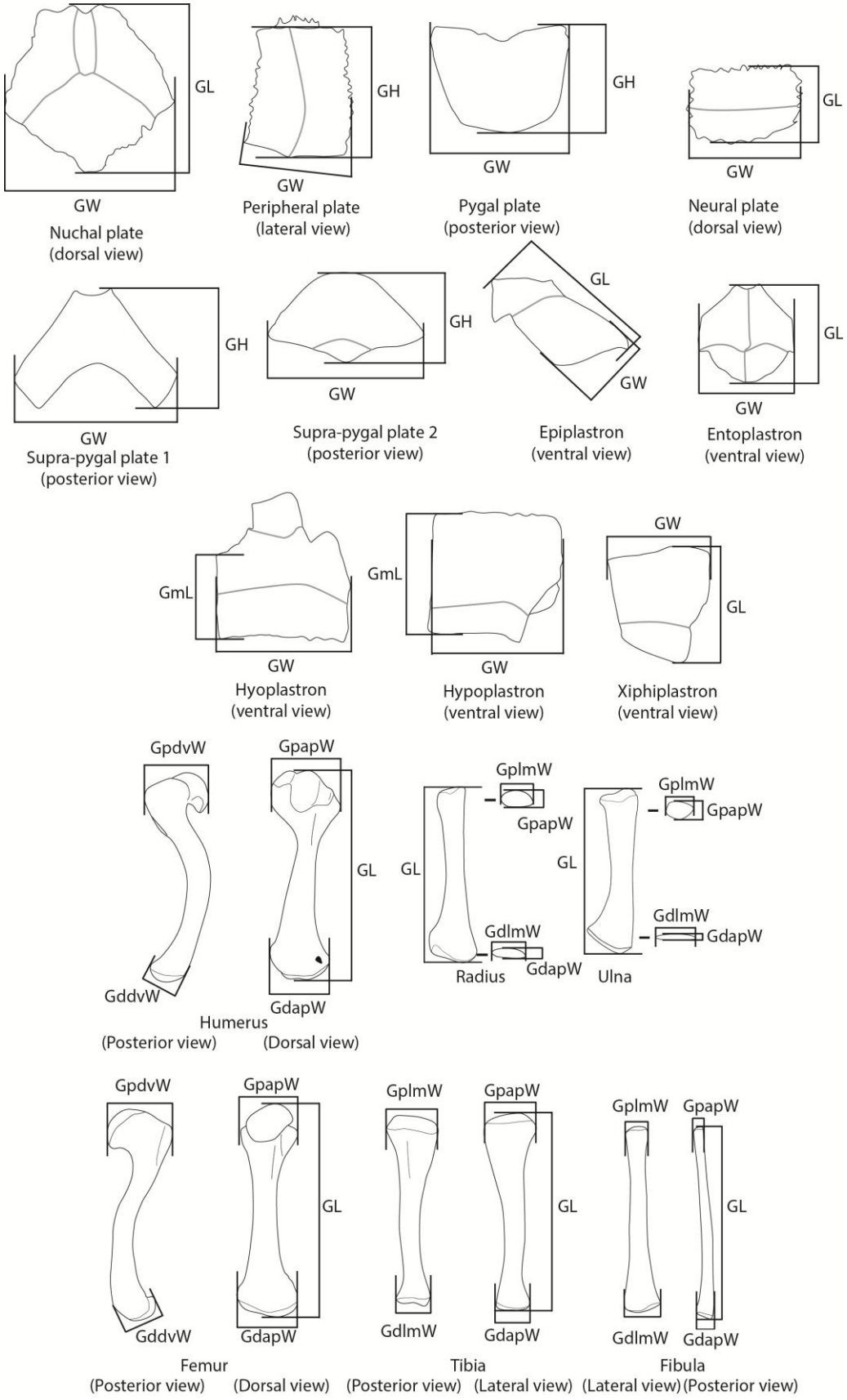
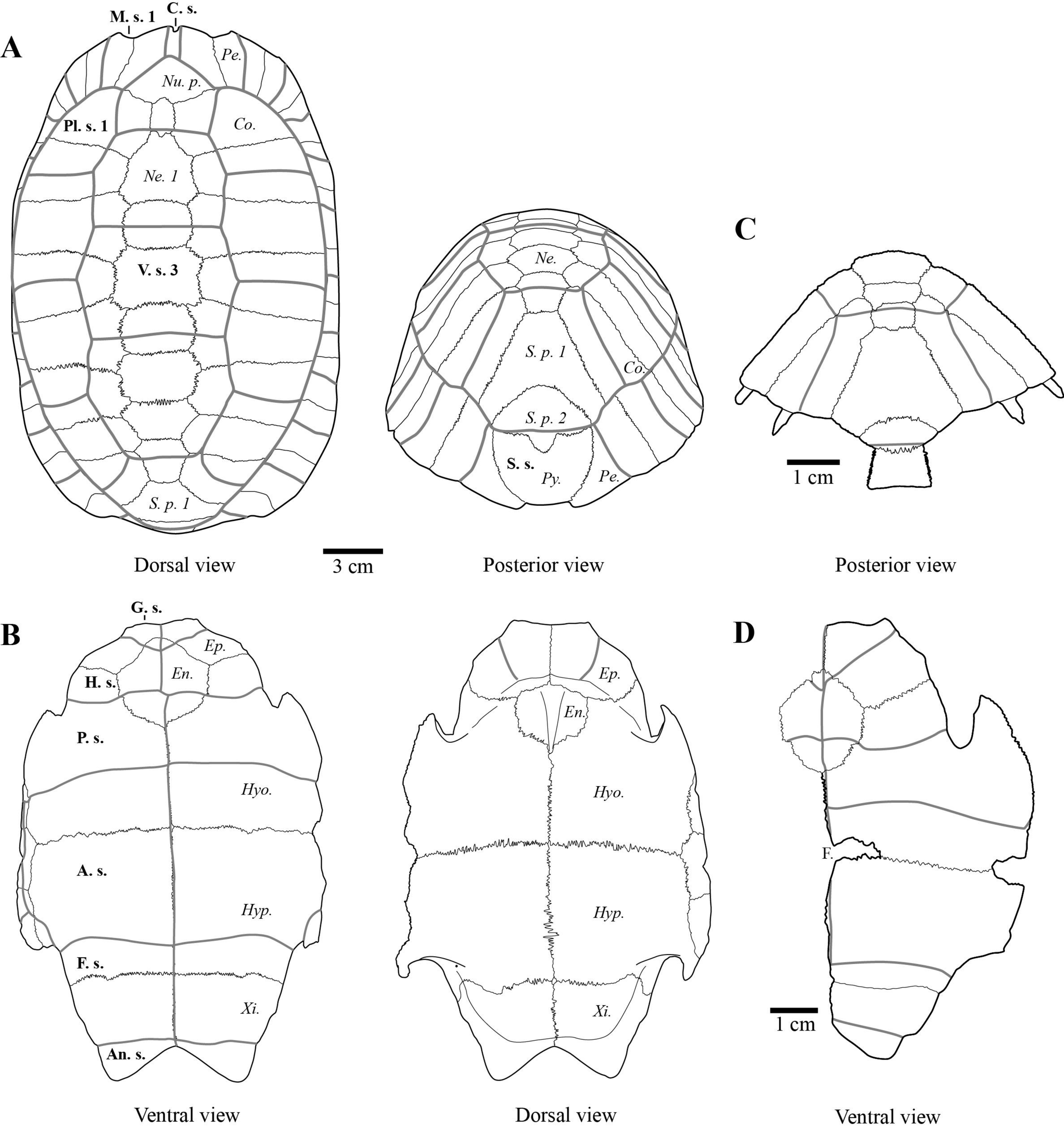
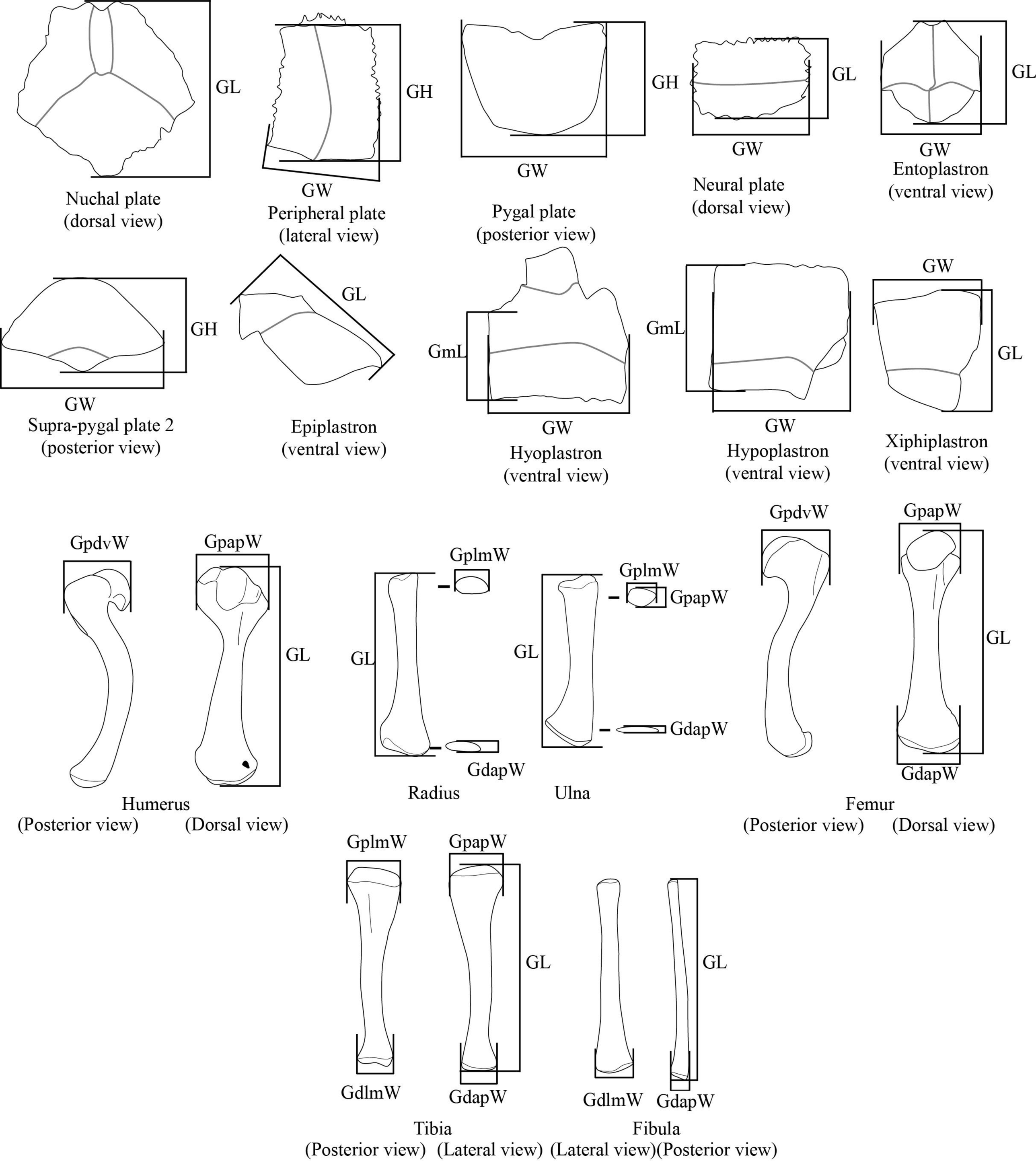
Appendix

Appendix 1: All measurements recorded on the modern turtle skeletons.


GL
GW
Nuchal plate
(dorsal view)
GH
GW
Peripheral plate
(lateral view)
GH
GW
Pygal plate
(posterior view)
GL
GW
Neural plate
(dorsal view)
GH
GW
Supra-pygal plate 1
(posterior view)
GH
GW
Supra-pygal plate 2
(posterior view)
GL
GW
Epiplastron
(ventral view)
GL
GW
Entoplastron
(ventral view)
GmL
GW
Hyoplastron
(ventral view)
GmL
GW
Hypoplastron
(ventral view)
GW
GL
Xiphiplastron
(ventral view)
GpdvW
GddvW
GpapW
GL
GdapW
Humerus
(Posterior view)
(Dorsal view)
GplmW
GpapW
GL
GdlmW
GdapW
Radius
GplmW
GpapW
GL
GdlmW
GdapW
Ulna
GpdvW
GddvW
GpapW
GL
GdapW
Femur
(Posterior view)
(Dorsal view)
GplmW
GdlmW
GpapW
GL
GdapW
Tibia
(Posterior view)
(Lateral view)
GplmW
GdlmW
GpapW
GL
GdapW
Fibula
(Lateral view)
(Posterior view)

1265


A
M. s. 1
C. s.
Pe.
Nu. p.
Pl. s. 1
Co.
Ne. 1
V. s. 3
S. p. 1
Dorsal view
3 cm
Ne.
S. p. 1
Co.
S. p. 2
S. s.
Py.
Pe.
Posterior view
C
1 cm
Posterior view
B
G. s.
Ep.
En.
H. s.
P. s.
Hyo.
A. s.
Hyp.
F. s.
Xi.
An. s.
Ventral view
Ep.
En.
Hyo.
Hyp.
Xi.
Dorsal view
D
F.
1 cm
Ventral view


GL
Nuchal plate
(dorsal view)
GH
GW
Peripheral plate
(lateral view)
GH
GW
Pygal plate
(posterior view)
GL
GW
Neural plate
(dorsal view)
GL
GW
Entoplastron
(ventral view)
GH
GW
Supra-pygal plate 2
(posterior view)
GL
Epiplastron
(ventral view)
GmL
GW
Hyoplastron
(ventral view)
GmL
GW
Hypoplastron
(ventral view)
GW
GL
Xiphiplastron
(ventral view)
GpdvW
GpapW
GL
Humerus
(Posterior view)
(Dorsal view)
GplmW
GL
GdapW
Radius
GplmW
GpapW
GL
GdapW
Ulna
GpdvW
GpapW
GL
GdapW
Femur
(Posterior view)
(Dorsal view)
GplmW
GpapW
GL
GdlmW
GdapW
Tibia
(Posterior view)
(Lateral view)
GL
GdlmW
GdapW
Fibula
(Lateral view)
(Posterior view)

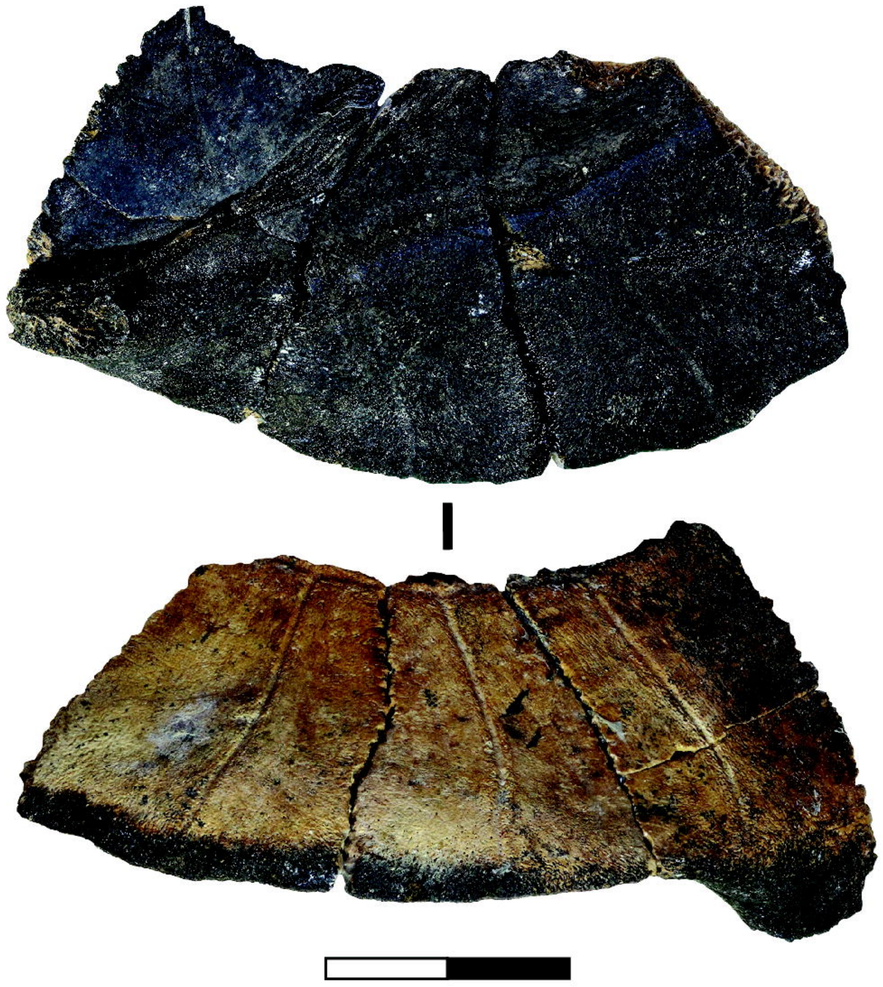
A
2 cm

B
2 cm

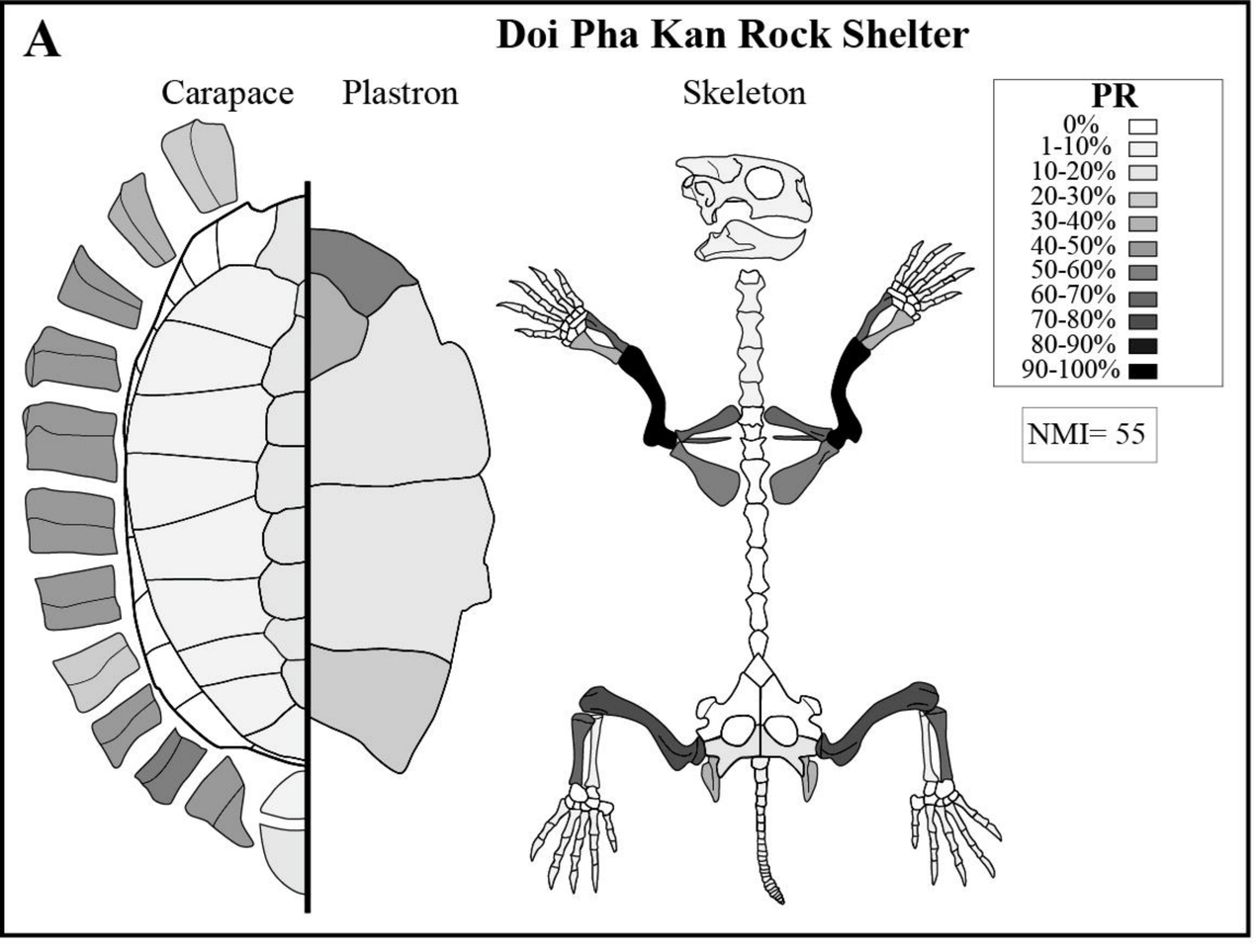
C
2 cm

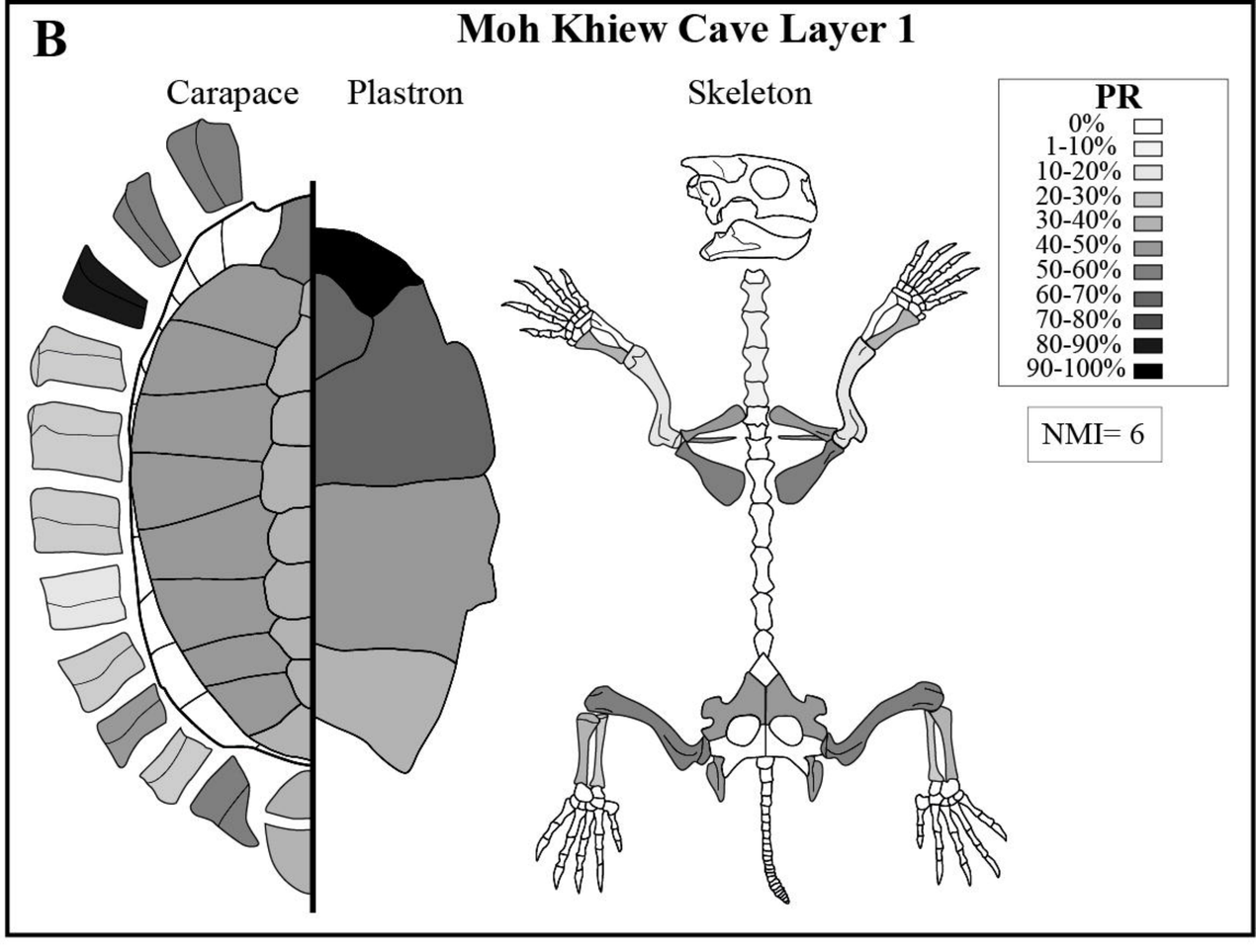
D
2 cm

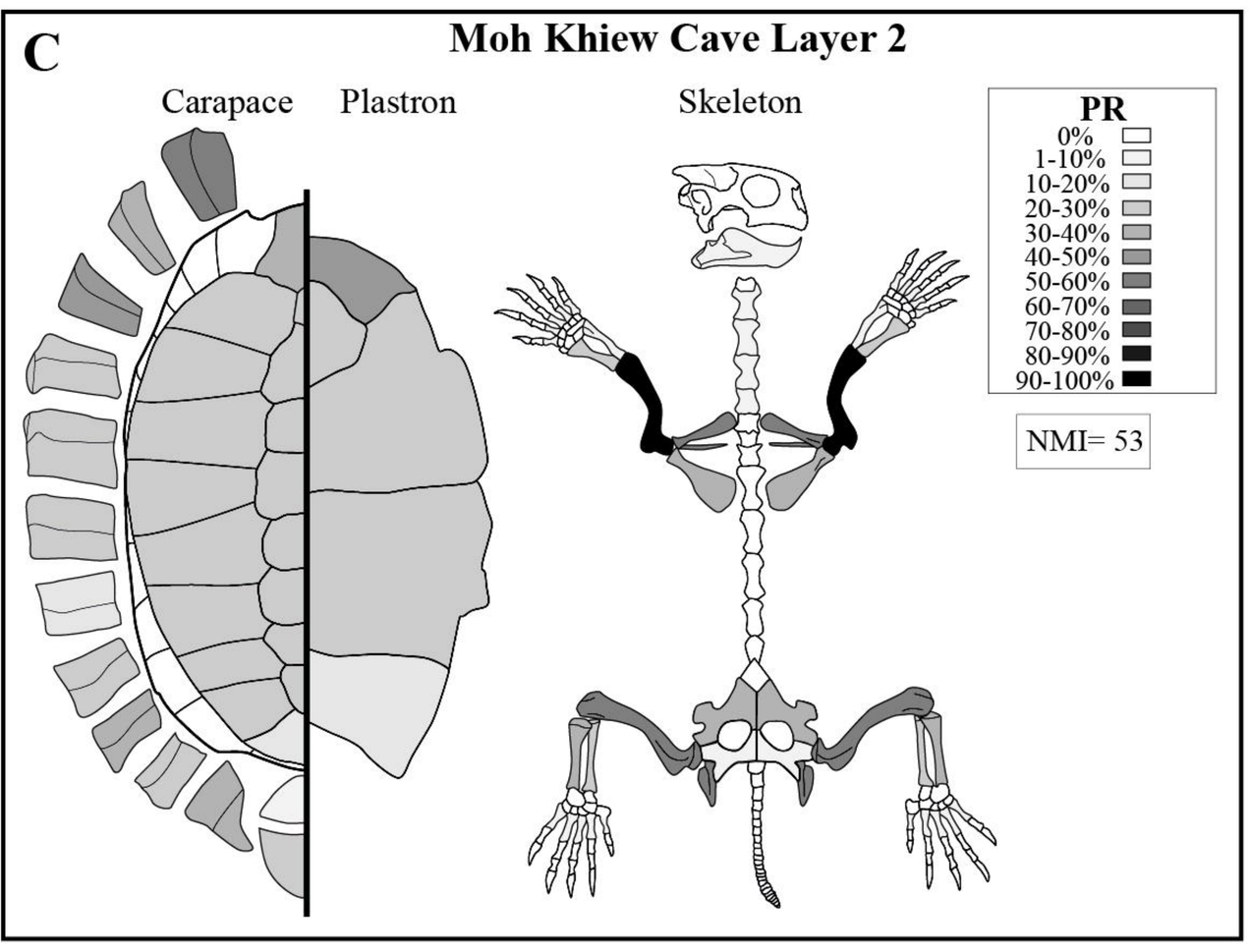
E
2 cm

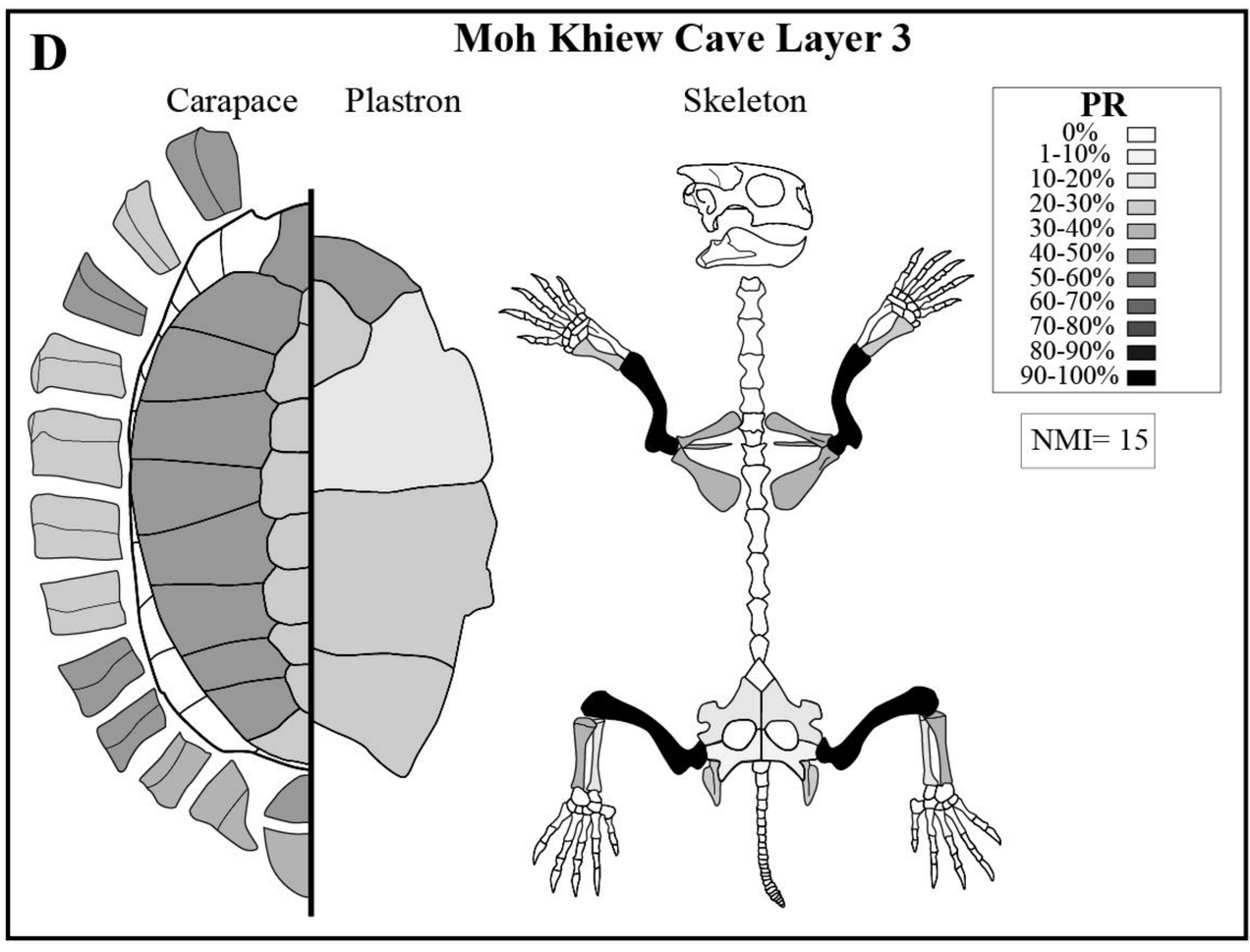

F
2 cm

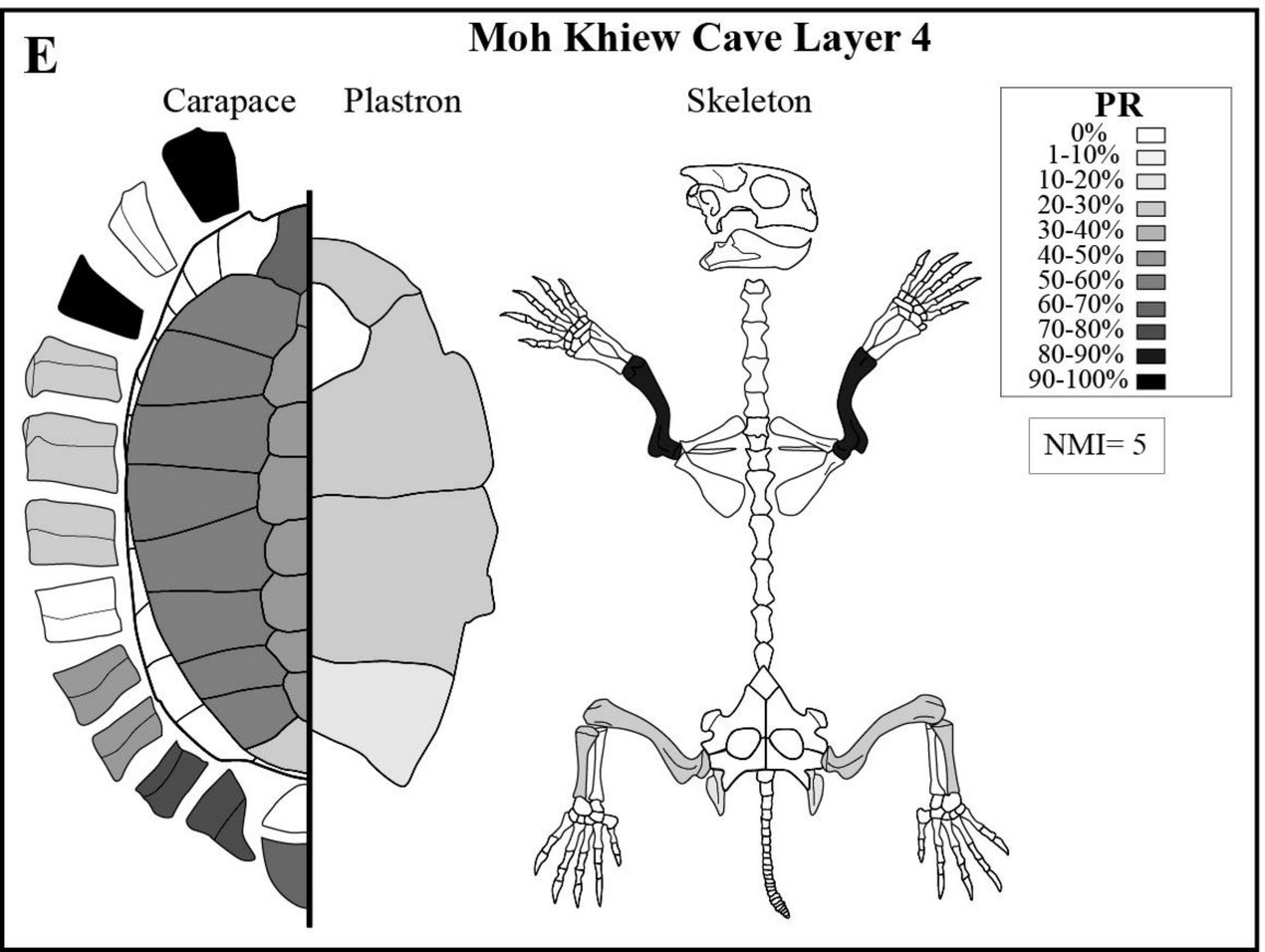
G
2 cm

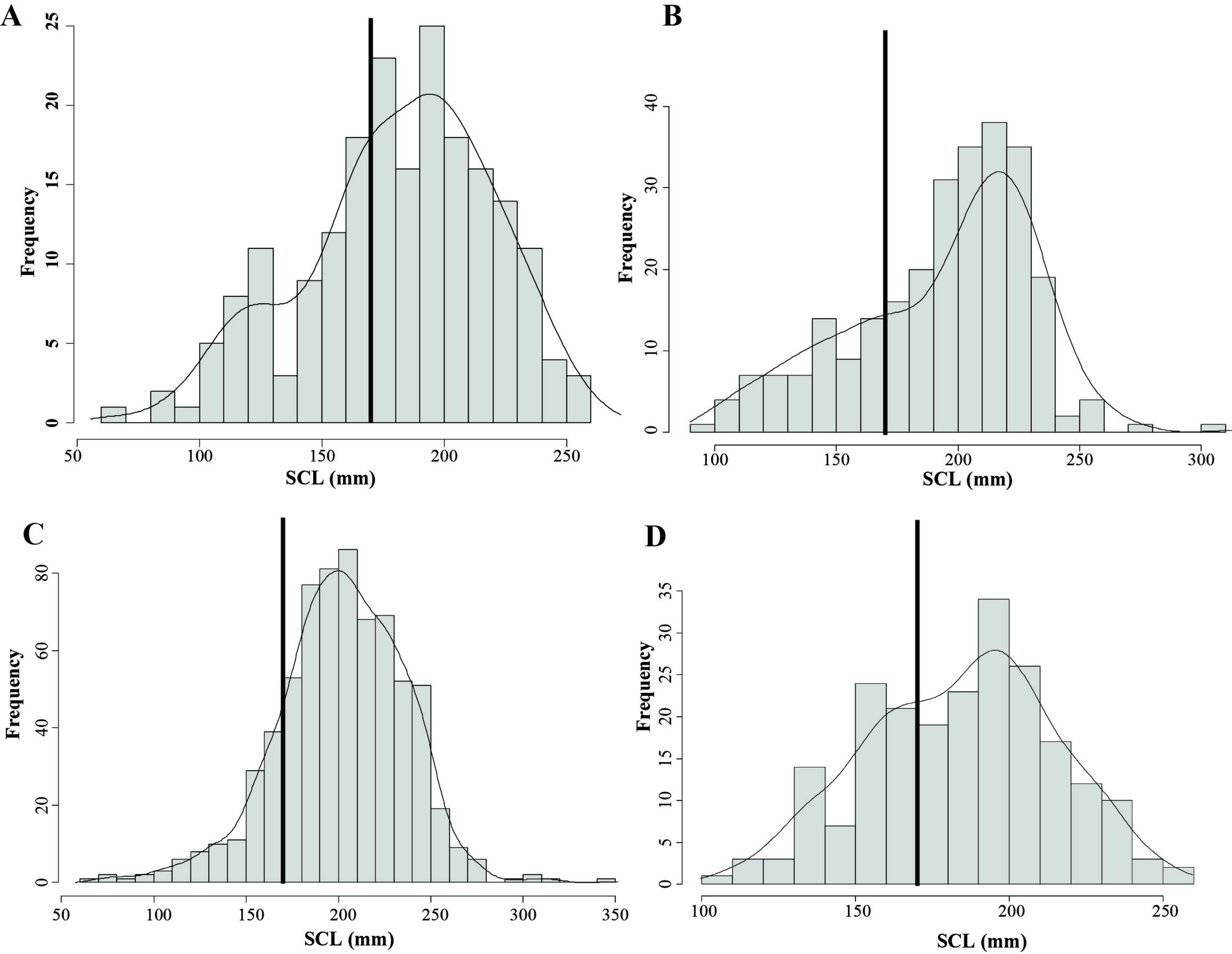

A
Doi Pha Kan Rock Shelter
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 55

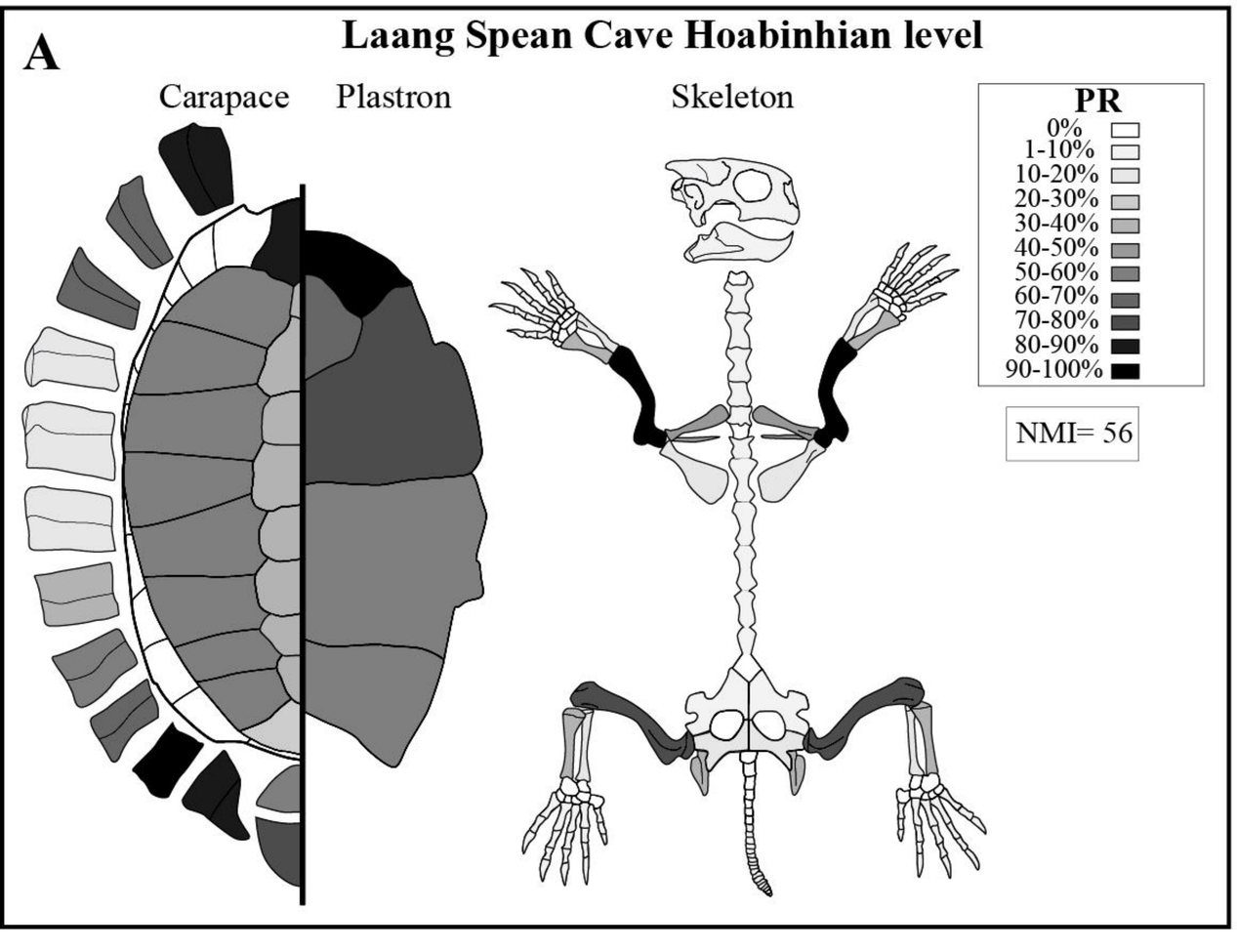

B
Moh Khiew Cave Layer 1
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 6

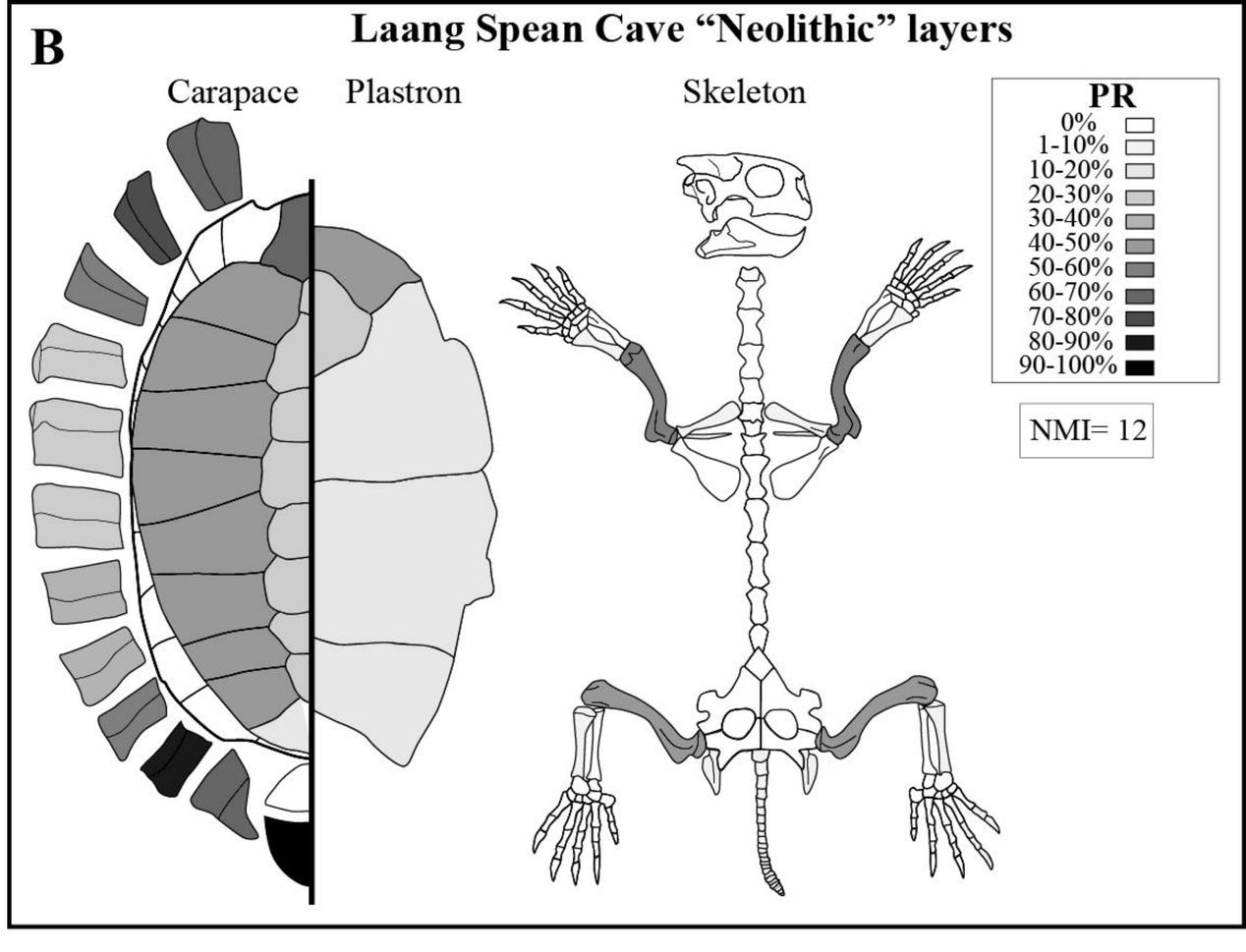

C
Moh Khiew Cave Layer 2
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 53

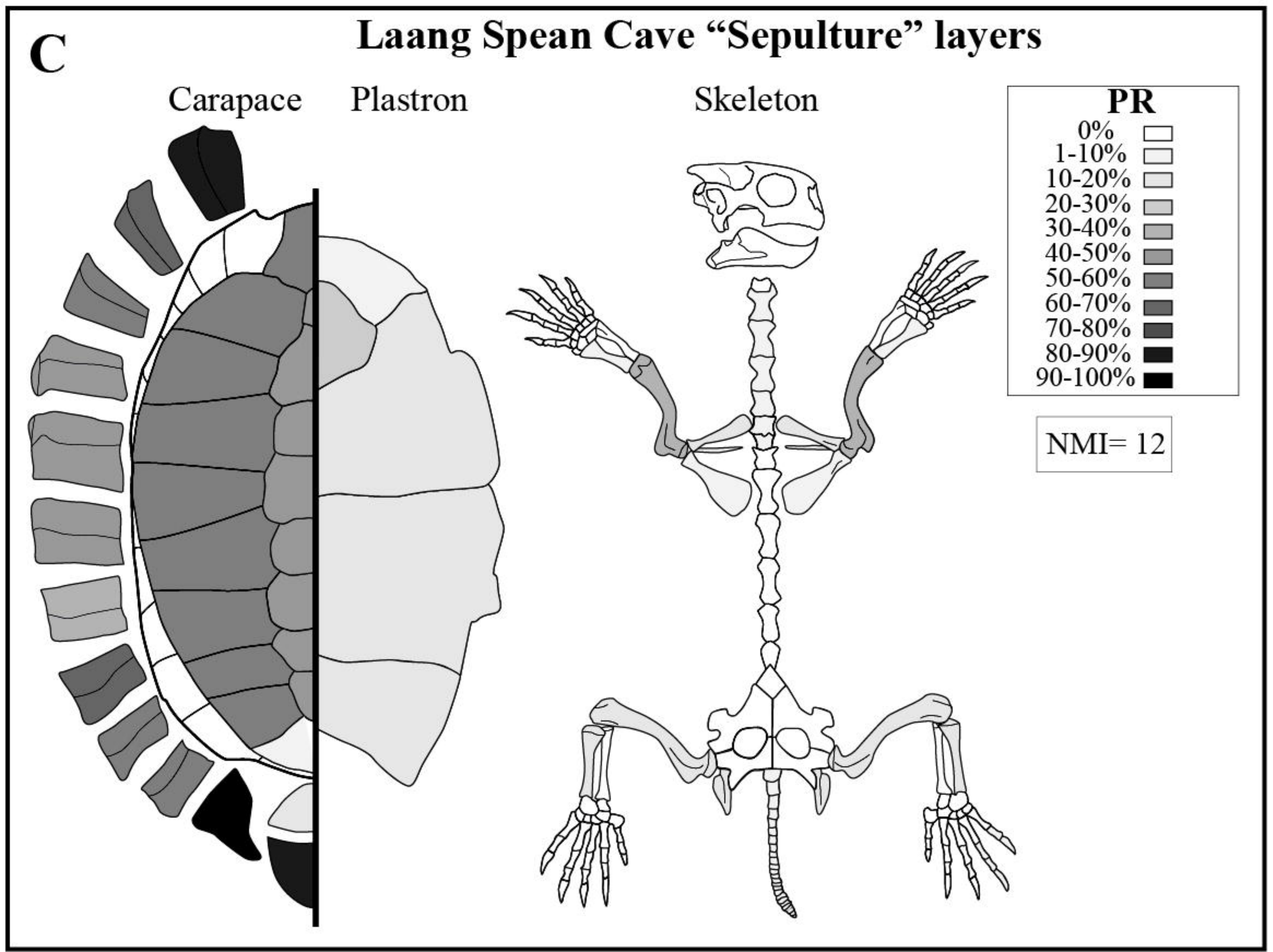

D
Moh Khiew Cave Layer 3
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 15

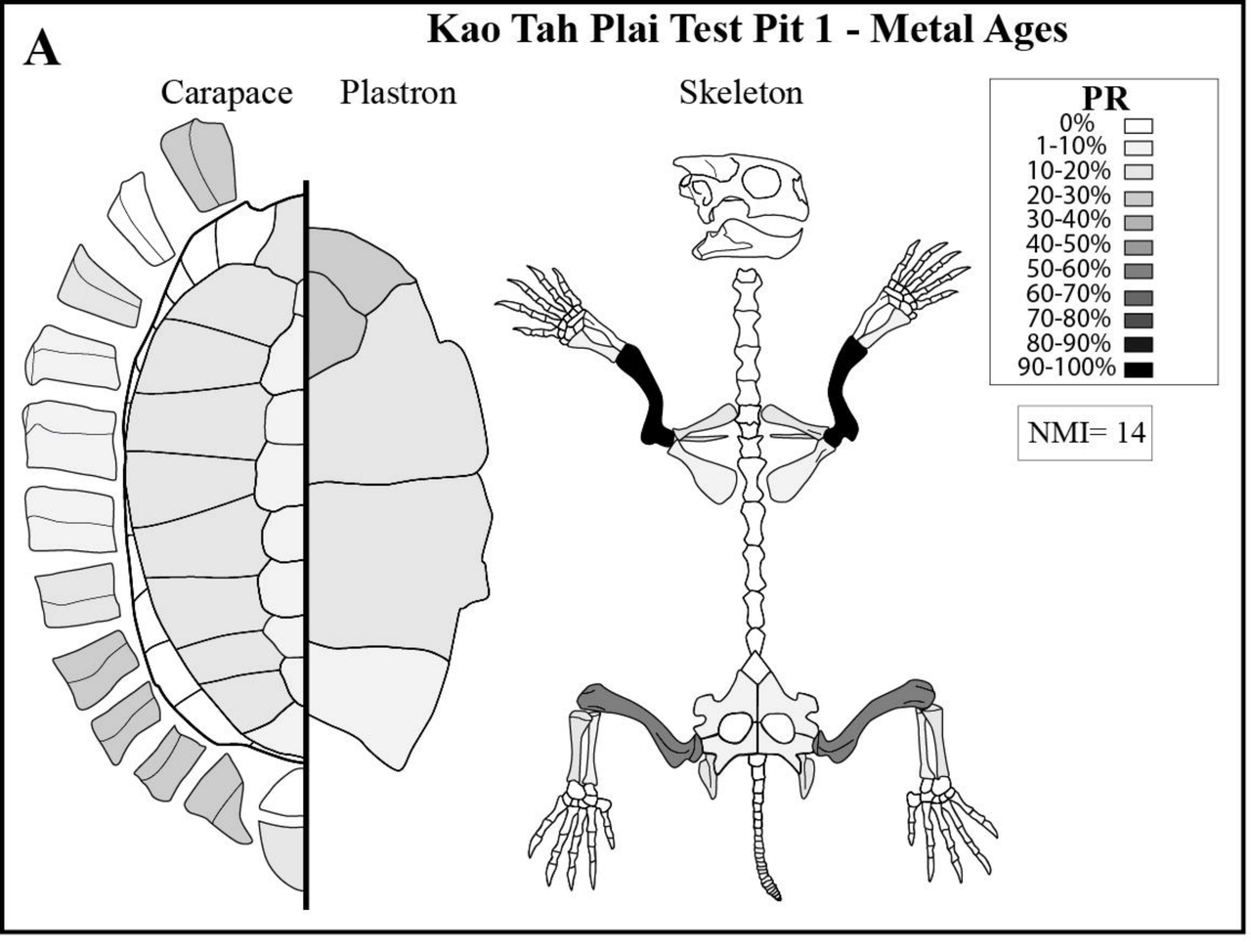

E
Moh Khiew Cave Layer 4
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 5

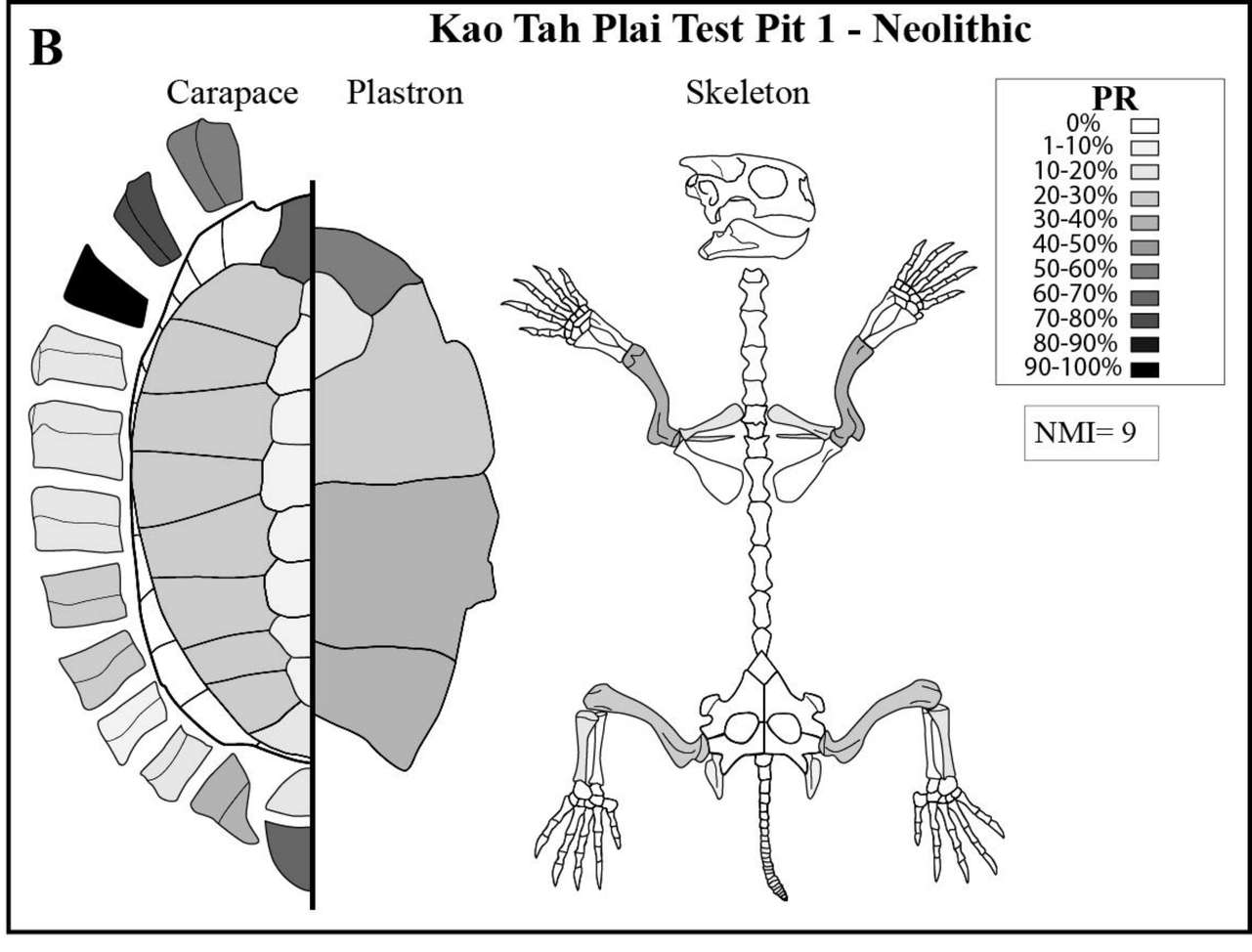

A
Frequency
0
5
10
15
20
25
50
100
150
200
250
SCL (mm)
B
Frequency
0
10
20
30
40
100
150
200
250
300
SCL (mm)
C
Frequency
0
20
40
60
80
50
100
150
200
250
300
350
SCL (mm)
D
Frequency
0
5
10
15
20
25
30
35
100
150
200
250
SCL (mm)

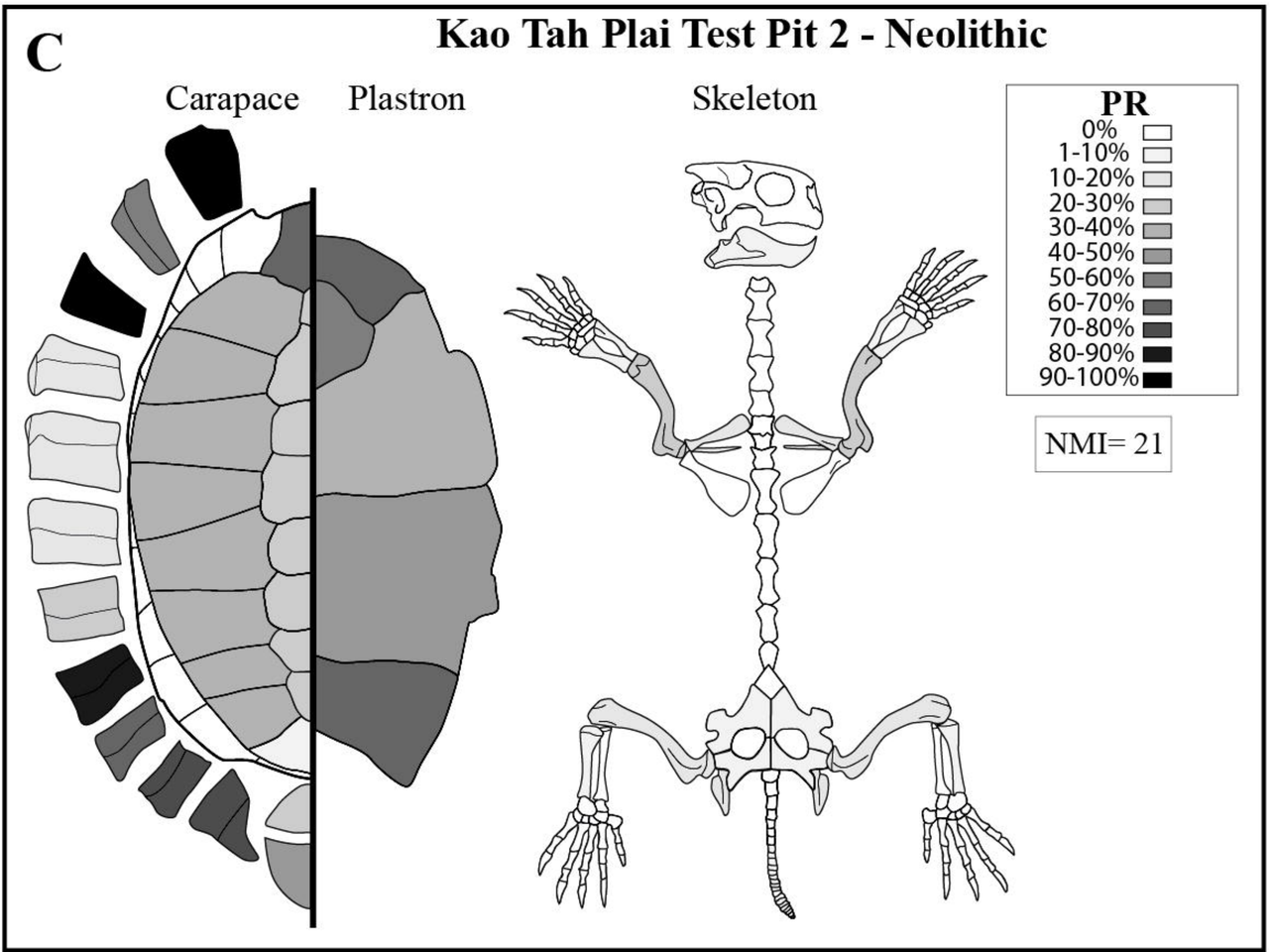

A
Laang Spean Cave Hoabinhian level
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 56


B
Laang Spean Cave "Neolithic" layers
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 12


C
Laang Spean Cave "Sepulture" layers
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 12


A
Kao Tah Plai Test Pit 1 - Metal Ages
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 14


B
Kao Tah Plai Test Pit 1 - Neolithic
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 9


C
Kao Tah Plai Test Pit 2 - Neolithic
Carapace
Plastron
Skeleton
PR
0%
1-10%
10-20%
20-30%
30-40%
40-50%
50-60%
60-70%
70-80%
80-90%
90-100%
NMI= 21