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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))

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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

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

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

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Introduction

56 The Hoabinhian has been a major topic in prehistoric research in Mainland Southeast Asia for
57 nearly 90 years. Since its first definition by the French archaeologist Madeleine Colani in the early 1930s
58 (Collectif 1932), the Hoabinhian has no doubt been one of the most debated topics of the field. A wide
59 range of subjects pertaining to the Hoabinhian populations have been discussed, such as their
60 distribution in space and time, their definition, the technological and functional characteristics of their
61 lithic industries, their economic organization, and their environmental context (Forestier *et al.* 2021). The
62 chronology of the Hoabinhian has been largely extended since the earliest known Hoabinhian sites.
63 Indeed, the occupation of the Xiaodong Rock shelter in Southwest China has been dated to about 43, 000
64 BP (Ji *et al.* 2016) and is considered to be the earliest occurrence of the Hoabinhian culture while the site
65 of Huai Hin in Northwest Thailand, dated to about 3700 BP is considered to be the last occurrence with a
66 lithic production associated with ceramic sherds (Zeitoun *et al.* 2008; Forestier *et al.* 2013). More than a
67 hundred Hoabinhian sites have been reported in Southeast Asia (Moser 2001; Chung 2008; Zeitoun *et al.*
68 2008; White 2011; Forestier *et al.* 2017) leading inevitably to the question of the variability of Hoabinhian
69 lithic assemblages with unexpected operational sequences on pebble matrix (Forestier *et al.* 2022, 2023).
70 Despite this, the Hoabinhian people remain, however, quite poorly understood from cultural and
71 material point of views. In fact, the homogeneity and lack of diversity of their lithic material culture,
72 probably related to their putative heavy use of objects made of perishable vegetal material (Forestier
73 2003) does not allow to characterize the precise uses of the sites by past populations, and it is difficult to
74 expect a cultural stasis over 30,000 years among different hunter-gatherer groups in such an extensive
75 region presenting diverse environmental, ecological and geographic settings.

76 White (2011) proposed that the emergence of cultural diversity in mainland Southeast Asia
77 began precisely in the late Late Pleistocene which is also suggested by burial practices (Imdirakphol *et al.*
78 2017). Forestier *et al.* (2013) argued that more analyses were still needed to evaluate the whole corpus of
79 Southeast Asian lithic industries to describe putative “cultural variations” and since then some patterns
80 started to emerge (Forestier *et al.* 2017, 2021). However, while a technological definition of the
81 Hoabinhian culture is in progress, the lack of detailed zooarchaeological analyses makes our knowledge
82 of the Hoabinhian paleoecology and subsistence strategies variability blurry. This is also an issue for the
83 characterization of the archaeological deposits as faunal data are of major importance to characterize the
84 use and occupation periods of the archaeological sites. The economic aspects of the Hoabinhian culture
85 were previously addressed by several authors (Gorman 1969, 1970, 1971; Glover 1977; Yen 1977; Vu
86 1994). Yet, the pioneering prehistoric zooarchaeological studies relying on occurrence data (Gorman
87 1971) offer only a poor understanding of the choices made by the hunters by focusing on qualitative data
88 and the diversity of the exploited animals rather than on quantitative information reflecting the intensity
89 of the exploitation of each species. These first works also lack the detailed taphonomic and taxonomic
90 analyses needed to describe past human behaviors and bone accumulation processes in more depth.
91 Because of these lacks, we currently have only a vague idea of the spatial and chronological variability of
92 the subsistence strategies of the Hoabinhian people. These problems impacting southeast Asian
93 zooarchaeology have previously been reviewed in depth by Conrad (2015). Among the identified issues is
94 the lack of detailed study of each animal group but especially of the non-mammal taxa including reptiles
95 and non-marine turtles that are often accounting for a large part of the animal bone assemblages found
96 in the archaeological record.

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

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

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

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Material and Methods

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

149 The genus *Indotestudo* currently includes three species: the Forsten's Tortoise *Indotestudo*
150 *forstenii* (Schlegel & Müller, 1845), the Travancore Tortoise *Indotestudo travancorica* (Boulenger, 1907),
151 and the Yellow-Headed tortoise *Indotestudo elongata* (Blyth, 1854), the two later being sister taxa
152 (Iverson *et al.* 2001). These species are currently distributed in India (*I. travancorica*), Sulawesi (*I.*
153 *forstenii*), and northern India and continental Southeast Asia (*I. elongata*) (Rhodin *et al.* 2021). This last
154 species is the only *Indotestudo* species present in continental Southeast Asia. It is nowadays present in
155 most areas of Thailand, Cambodia, Vietnam, and Laos (Ihlow *et al.* 2016; Rhodin *et al.* 2021). It is also
156 occurring in northwestern Malaysia but is absent from most of this country and from the insular Sunda
157 (Ihlow *et al.*, 2016). *I. elongata* is a medium size tortoise whose adult Straight Carapace Length (SCL)
158 reaches about 300 mm (Taylor 1970). The largest specimen ever recorded is a male of about 380 mm SCL
159 (Rhodin *et al.* 2021). It is possible that the sexual dimorphism in this species vary from one population to
160 another although males are generally larger than females (Ihlow *et al.* 2016). The size of the hatchlings
161 ranges from 50 to 55 mm SCL (Ihlow & Handschuh 2011). The specie is present in a wide variety of
162 environments including many forest types (Ihlow *et al.*, 2016). *I. elongata* is active during daytime mostly
163 in the early morning and late afternoon. It present seasonal activity patterns in order to avoid the highest
164 temperatures during the dry season during which it aestivate spending most of its time hiding in former
165 burrows of other animal species including porcupines (Van Dijk 1998; Som & Cottet 2016; Ihlow *et al.*
166 2016). In their active period the individuals spend most of their time in open areas during the rainy
167 season then move in more closed environment (mostly semi-evergreen and pine forests) when the
168 climate becomes dryer (Van Dijk 1998; Som & Cottet 2016). Depending of their sex, the individuals reach
169 sexual maturity between 175 mm and 240 mm SCL at an age of 6-8 years old (Van Dijk 1998; Eberling
170 2011; Sriprateep *et al.* 2013). Reproduction takes place during the rainy season.

171 **Presentation of the studied sites and assemblages**

172 *The Doi Pha Kan rockshelter*

173 The site of Doi Pha Kan is a rockshelter located in northern Thailand (E 99° 46' 37.2" ; N 18° 26'
174 57.0"). The site is studied since 2011 by P. Auetrakulvit and V. Zeitoun and its excavation is still in
175 progress. The site is mostly known for its three Hoabinhian sepultures dated between 11,170 ± 40 and
176 12,930 ± 50 BP (Imdirakphol *et al.* 2017; Zeitoun *et al.* 2019). Two of these sepultures contained turtle
177 shells elements in anatomical connection interpreted as funeral offerings. The site also provided a rich
178 archaeological assemblage corresponding to a Hoabinhian occupation older than the sepultures. The
179 stratigraphy of the site being homogeneous from a sedimentary point of view, its archaeological material
180 has been so far considered as a single assemblage.

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

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

195 *The Moh Khiew Cave*

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

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

222 *The Khao Tha Phlai cave*

223 The site of Khao Tha Phlai is a cave located in southern Thailand in the province of Chumphon (E
224 10°36'12.39"; N 99° 5'49.08"). It has been excavated by the 12th Regional Office of Fine Arts Department,
225 Nakhon Si Thammarat since 2014, and has so far been the object of two excavation campaigns with two
226 test-pits conducted in the deposit. A first test-pit of 9 m² (TP1) in 2014, and a second of 20 m² (TP2) in
227 2021-2022.

228 The archaeofaunal material collected in the TP1 has been the object of a preliminary study by S.
229 Jeawkok in the framework of a Bachelor thesis that remained unpublished. This first study conducted on
230 6945 bone remains indicated that the reptiles represent around 25% of the NISP of the complete
231 assemblage, the remaining bones being nearly all attributed to large mammals. In the present study we
232 considered the herpetofaunal material previously extracted by S. Jeawkok in the faunal samples collected
233 in the TP1. We also consulted the full archaeofaunal sample recovered from the TP2 in order to extract
234 the reptile and amphibian bones from it. We considered separately the samples collected in the two test-
235 pits and subdivided the samples in two assemblages corresponding to Metal Ages (between 75 and 130
236 cm of depth in the TP2 and between 65 and 180 cm in TP1), and Neolithic periods (between 130 and 320
237 cm of depth in the TP2 and between 180 and 320 in TP1). These layers have been dated on the basis of
238 the typology of the archaeological artifacts they have provided.

239 *The Laang Spean cave*

240 The site of Laang Spean is a large cave of more than 1000 m² located in northwest Cambodia, in
241 the Battambang province (E 102° 51' 00.0"; N 12°51' 00.0"). The site has been the object of a first
242 excavation between 1965 and 1968 by R. Mourer and C. Mourer-Chauviré (Mourer-Chauviré *et al.* 1970;
243 Mourer-Chauviré & Mourer 1970). The archaeofaunal material collected during these excavations has
244 been the object of a preliminary study but has never been studied in depth at the exception of the
245 rhinoceros remains (Guerin & Mourer-Chauviré 1969), and no zooarchaeological study have been
246 conducted. Following this first exploration, the site has been the object of a new detailed archaeological
247 excavation by H. Forestier between 2009 and 2019 aiming to document in more detail the Hoabinhian
248 occupation previously identified (Forestier *et al.* 2015; Sophady *et al.* 2016). These excavations conducted
249 on a surface of over 40 m² led to the discovery of an important undisturbed Hoabinhian layer dated
250 between 5018 ± 29 cal. BP and 10 042 ± 43 cal. BP as well as several Neolithic burials dug in the
251 Hoabinhian level (Zeitoun *et al.* 2012, 2021). These sepultures have been dated from 3335 ± 30 to 2960 ±
252 30 BP (Sophady 2016). Regarding the subdivision of the material, the archaeological remains collected in
253 the squares lacking traces of Neolithic perturbations (see Forestier *et al.*, 2015) have been associated to
254 the Hoabinhian occupation. There is no stratigraphic evidence suggesting a subdivision of this Hoabinhian
255 assemblage obviously representing several occupations over a time span of more than 5000 years.
256 Regarding the other squares, the squares in which sepultures were found are grouped together under the
257 term "Sepulture layer" and the first 120 cm of the disturbed squares are considered as being a "Neolithic
258 layer". These subdivisions are however very artificial and probably correspond to a mix of Neolithic and
259 Hoabinhian material as it has been evidenced on the lithic material these contexts provided (H.
260 Forestier, *com. pers.*).

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

271 **Quantification of the zooarchaeological data**

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

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

293 **Size estimation of archaeological *Indotestudo***

294 In order to reliably estimate the body size of the archaeological individuals of *Indotestudo* sp. we
295 build size estimation equations on the models of what was previously done for Southeast Asian monitor
296 lizards (Bochaton *et al.* 2019), and recently on the size and weight of species of tortoises (Esler *et al.*
297 2019; Codron *et al.* 2022). These approaches are more powerful than considering isolated measurement
298 (e. g. Klein and Cruz-Urbe 1983) to describe the size of subfossil animal populations because: 1) they
299 enable to take account on several measurements from different anatomical parts to reconstruct the body
300 size structure of a past population, and 2) it converts measurements taken on the skeleton into a variable
301 used to describe the size of modern individuals which make easier the comparisons needed to address
302 biological questions. To build the equations we defined a set of 86 measurements (See Supplementary
303 Table 1; Appendix 1) that we recorded on a sample of 34 museum specimens of *Indotestudo* sp. from the
304 Florida Museum of Natural History (UF), and the Comparative Anatomy collection of the Muséum
305 national d'Histoire naturelle (MNHN-ZA-AC) (see all details in Supplementary Table 1). In order to have
306 enough specimens to produce relevant and reliable predictive equations we pooled altogether the three
307 species currently includes in the genus *Indotestudo*: *I. forstenii* (Schlegel & Müller, 1845): 8 specimens, *I.*
308 *travancorica* (Boulenger, 1907): 14 specimens, and *I. elongata* (Blyth, 1854): 12 specimens. Differences of
309 body proportions among species were controlled before applying this strategy to avoid including bias
310 related to interspecific differences in the size estimations.

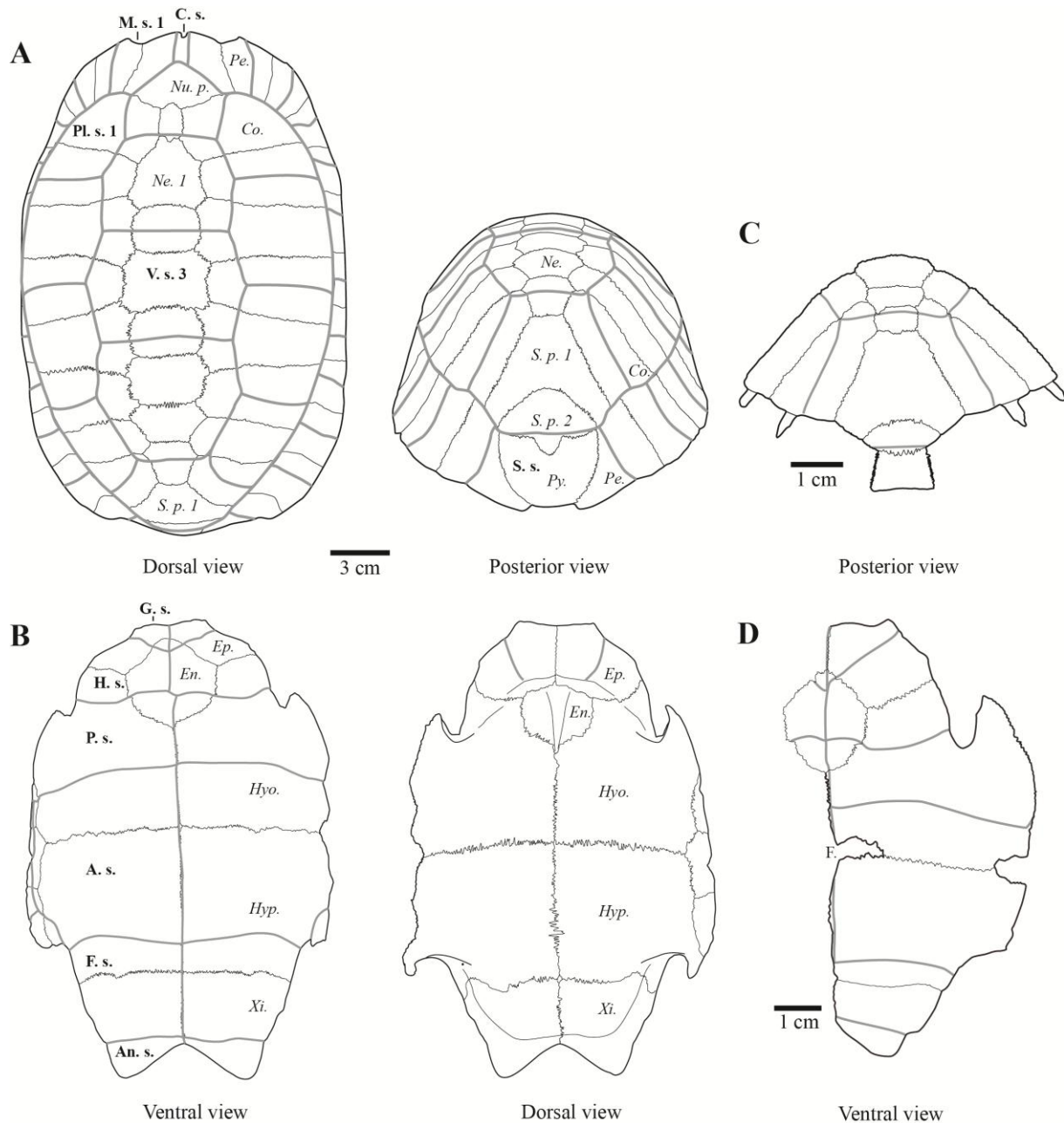
311 The measurements recorded were distributed on all the bones of the plastron and the carapace
312 as well as on the long bones. Vertebrae and skull elements were not taken into account as their
313 occurrences were too rare in the archaeological record. In addition to these measurements, in order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

$$326 \quad \text{Log (“size variable”)} = (\text{Beta1}) * \text{log (osteological measurement in mm)} + (\text{Beta0})$$

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

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

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



355
 356 **Figure 1** - A) Drawing of the carapace of an adult specimen of *Indotestudo elongata* (CUMZ-R-
 357 TT181); B) Drawing of the plastron of an adult specimen of *Indotestudo elongata* (CUMZ-R-TT181);
 358 C) Drawing of the carapace of a juvenile specimen of *Indotestudo elongata* lacking peripherals (UF-
 359 34760); D) Drawing of the plastron of a juvenile specimen of *Indotestudo elongata* showing central
 360 fontanel (UF-34760). **Abbreviations:** A. s.: Abdominal scute, An. s.: Anal scute, G. s.: Gular scute,
 361 Co.: Costal plate, F. s.: Femoral scute, Ep.: Epiplastron, En.: Entoplastron, F.: plastral fontanel, H. s.:
 362 Humeral scute, Hyo.: Hyoplastron, Hyp.: Hypoplastron, M. s.: Marginal scute, Ne.: Neural plate, Nu.
 363 p.: Nuchal plate, C. s.: Cervical scute, P. s.: Pectoral scute, Pe.: Peripheral plate, Pl. s.: Pleural scute,
 364 Py.: Pygal plate, S.p. 1: Supra-pygal 1, S.p. 2: Supra-pygal 2, S. s.: Supra-caudal scute, V. s.: Vertebral
 365 scute, Xi.: Xiphiplastron.

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Results

369 **Size predictive equations**

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

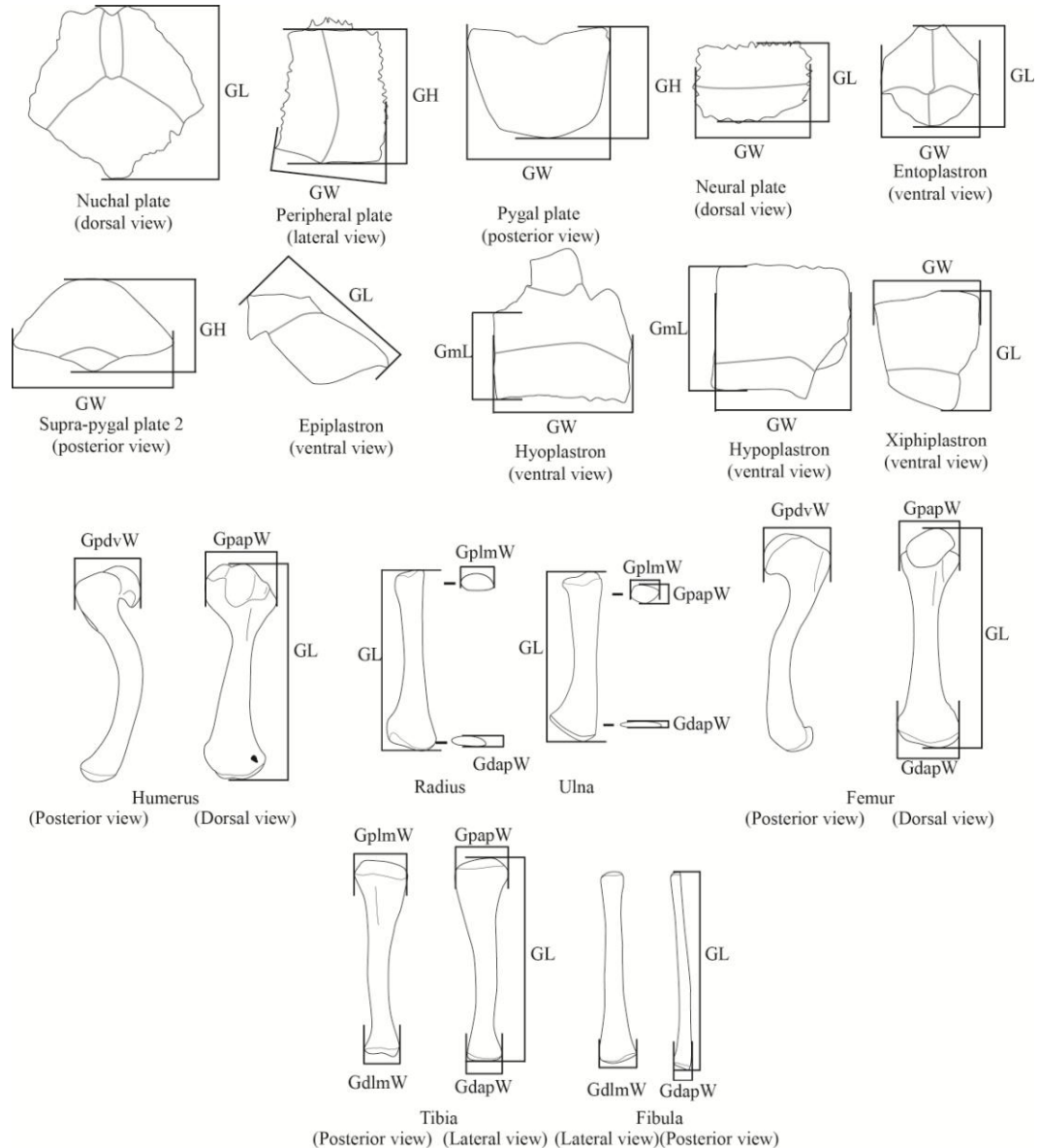
379 From our complete modern sample, a set of 86 equations corresponding to the 86 initial
380 recorded measurements has been produced. This set has been refined to keep only the equations
381 providing the most reliable (significant linear relationships) and precise (high R^2 linear relationships) SCL
382 estimations. This final set of equations include 52 equations from 52 measurements distributed on
383 epiplastron, entoplastron, hyoplastron, hypoplastron, xiphiplastron, nuchal plate, neural plates (ranks 1,
384 2, 3, 4, 6, and 7), peripheral plates (ranks 1, 2, 3, 8, 9, and 10), 2nd supra-pygal plate, pygal plate,
385 humerus, radius, ulna, femur, tibia, and fibula (Fig. 2; Table. 1).

386

387 **Table 1** - Equations retained for the prediction of the Straight Carapace Length (SCL) of the
388 archaeological *Indotestudo* specimens. Are indicated: the measurement used (to be recorded on
389 the archaeological specimen, the slope X (“Beta1” to integrate in the equation indicated in the
390 Material and Method section), and the intercept Y (“Beta0” to integrate in the equation indicated in
391 the Material and Method section). Is also indicated the coefficient of determination (R^2) of each
392 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

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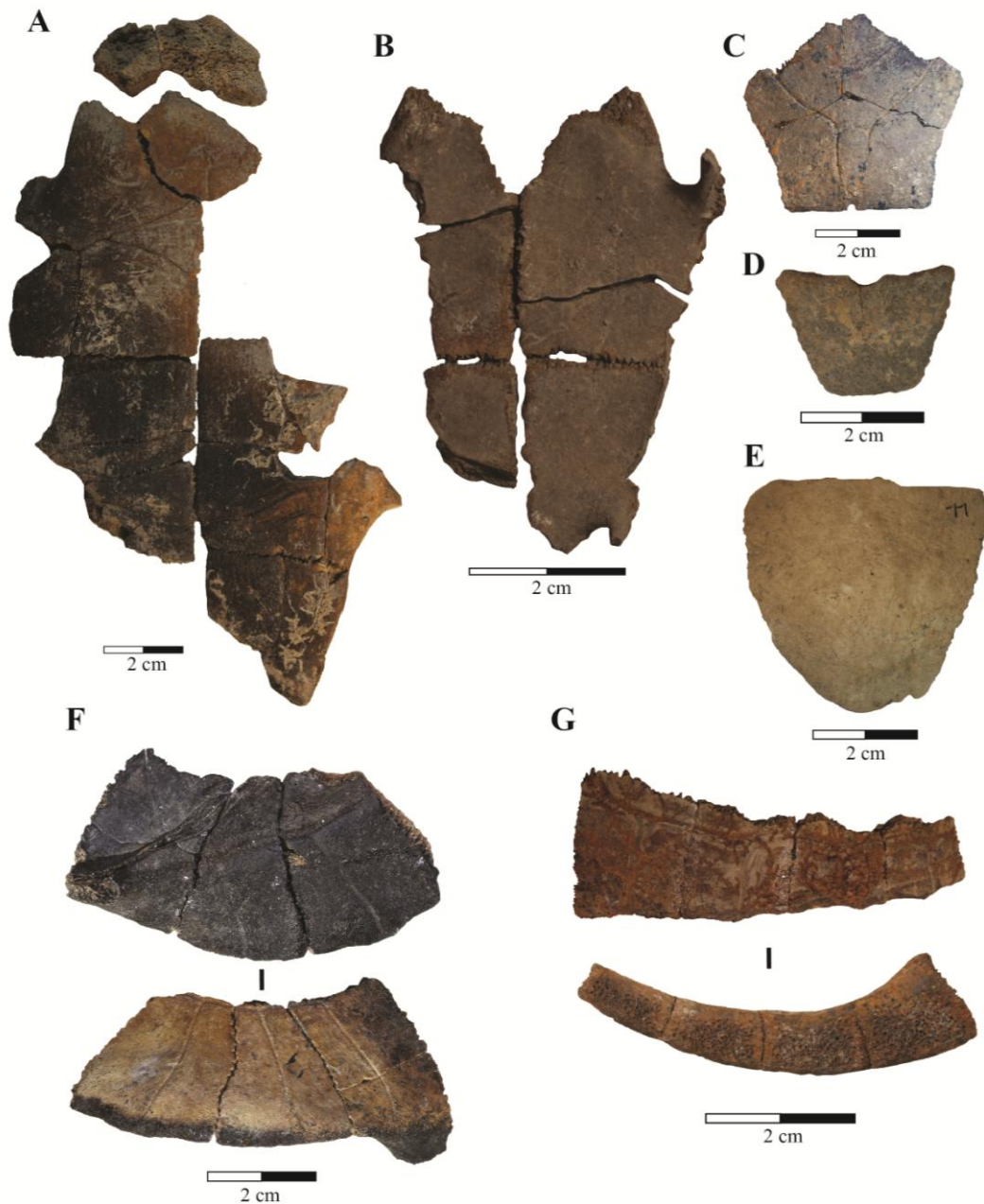
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Figure 2 - Measurements corresponding to the 52 equations retained to predict the SCL of our archaeological sample of *Indotestudo elongata* bone remains. Measurements names: GB: Greatest Width (on the latero-medial axis), GdapW: Greatest distal antero-posterior 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.

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404 **Zooarchaeological and taphonomic analyses of the herpetofaunal assemblages**



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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.

418 *Doi Pha Kan Rockshelter*
419 Composition of the herpetofaunal assemblages

420 The herpetofaunal assemblage of Doi Pha Kan consist of 8414 bone remains weighting a total of
 421 6875 gr. and representing a least 115 individuals. Most of these bones correspond to non-marine turtles
 422 (Fig. 3; Table. 2) in term of WR (74%), NISP (56%), and MNI (47%) with the second most represented
 423 group being Monitor lizards (23% of the WR, 38% of the NISP, and 38% of the MNI) followed by rare
 424 snakes, amphibians, and small lizards bone remains.

425 **Table 2** - Weight of the Remains (WR), Number of Identified Skeletal Parts (NISP), and Minimal
 426 Number of Individual (MNI) corresponding to the different taxa identified in the complete Doi Pha
 427 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

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430 Regarding the bones attributed to turtles and tortoises (Table. 3), 66.8% of them (50.8% of the
 431 WR) could not be attributed to a given family. Among the fragments that were identified to at least the
 432 family level, 71 % of them were attributed to *Indotestudo elongata* (71% of the WR and 76% of the MNI),
 433 28% (28% of the WR and 18% of the MNI) to Geoemydidae, and less than 1% (0.6% of the WR and 5% of
 434 the MNI) to Trionychidae. Note that for Trionychids remains from all localities, attribution can be done
 435 for all the plates because of their ornamentation, they are therefore not underrepresented because they
 436 cannot be easily identified.

437

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

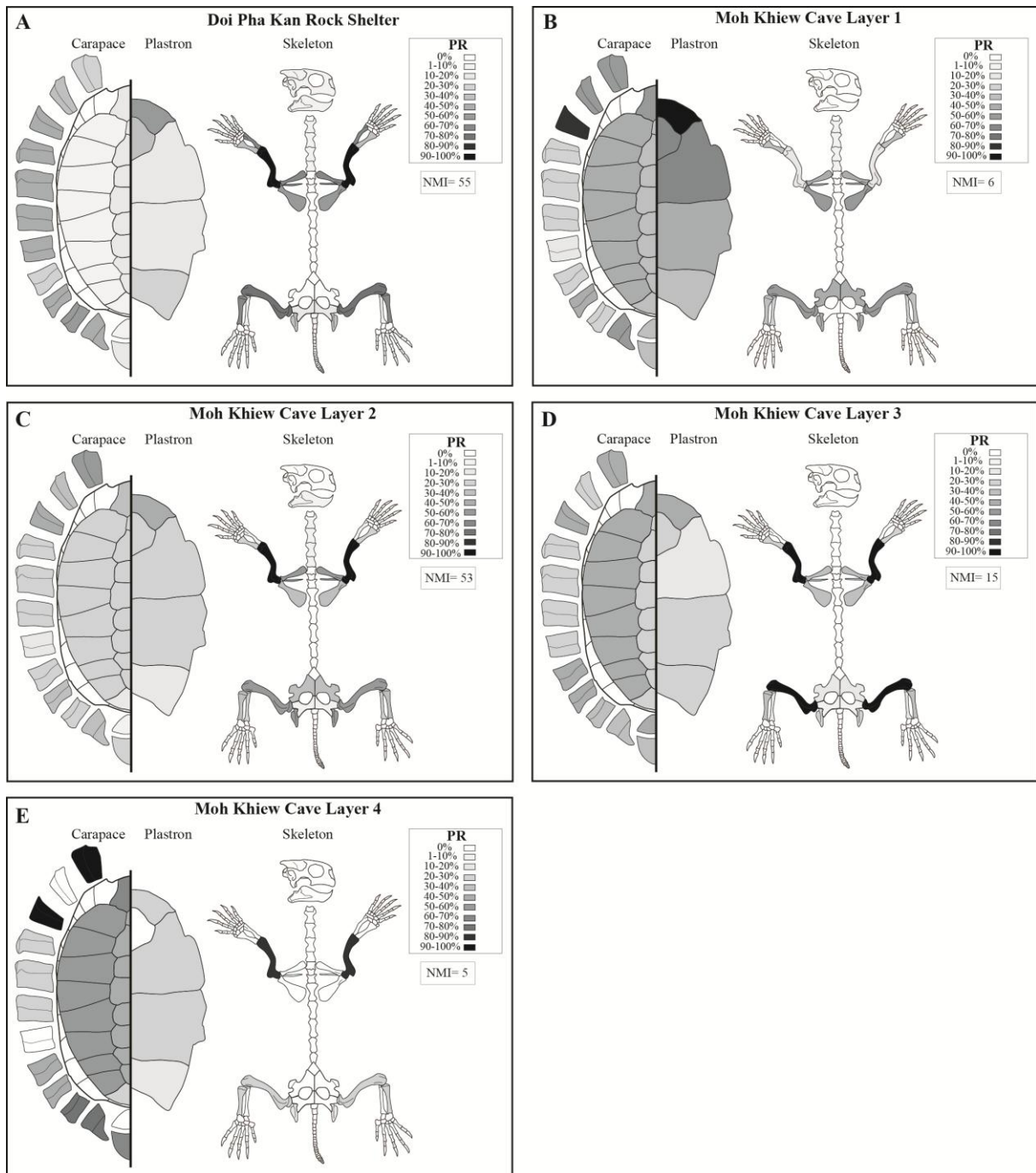
	NISP	WR	NMI
<i>Indotestudo elongata</i>	1122	1787.17	42
Geoemydidae	447	711.34	10
Trionychidae	12	14.13	3
Turtle ind.	3181	2600.38	
Total	4762	5113.02	55

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443 Taphonomy of the turtle/tortoise bone assemblage

444 Among the 4762 bone fragments attributed to turtle/tortoises, 303 are complete elements
 445 (6.3%), and 249 are nearly complete (at least 90% of the bone is preserved) while 1389 (29%) are small
 446 fragments representing less than 5% of the complete anatomical part. The average percentage of
 447 completion of the bones is 32%. The overall PR is 28%. The best represented bones (Fig. 4 – A) are the
 448 stylopods (humerus and femur with PR>75%) followed by the tibia, the radius, the scapula, the coracoid,
 449 and the epiplastron (PR>50%). Then follow the rest of the long bones, and most of the plates that are the
 450 easiest to identify. The peripheral plates of the bridge are less represented (PR=10%) than all the other
 451 peripheral plates (PR=39%). The skull, vertebrae and all small elements of the hands and foot are nearly
 452 absent. The largest plates (hyoplastron and hypoplastron) are the most fragmented with completion
 453 means of less than 26%. The peripheral plates corresponding to the bridge are also more heavily

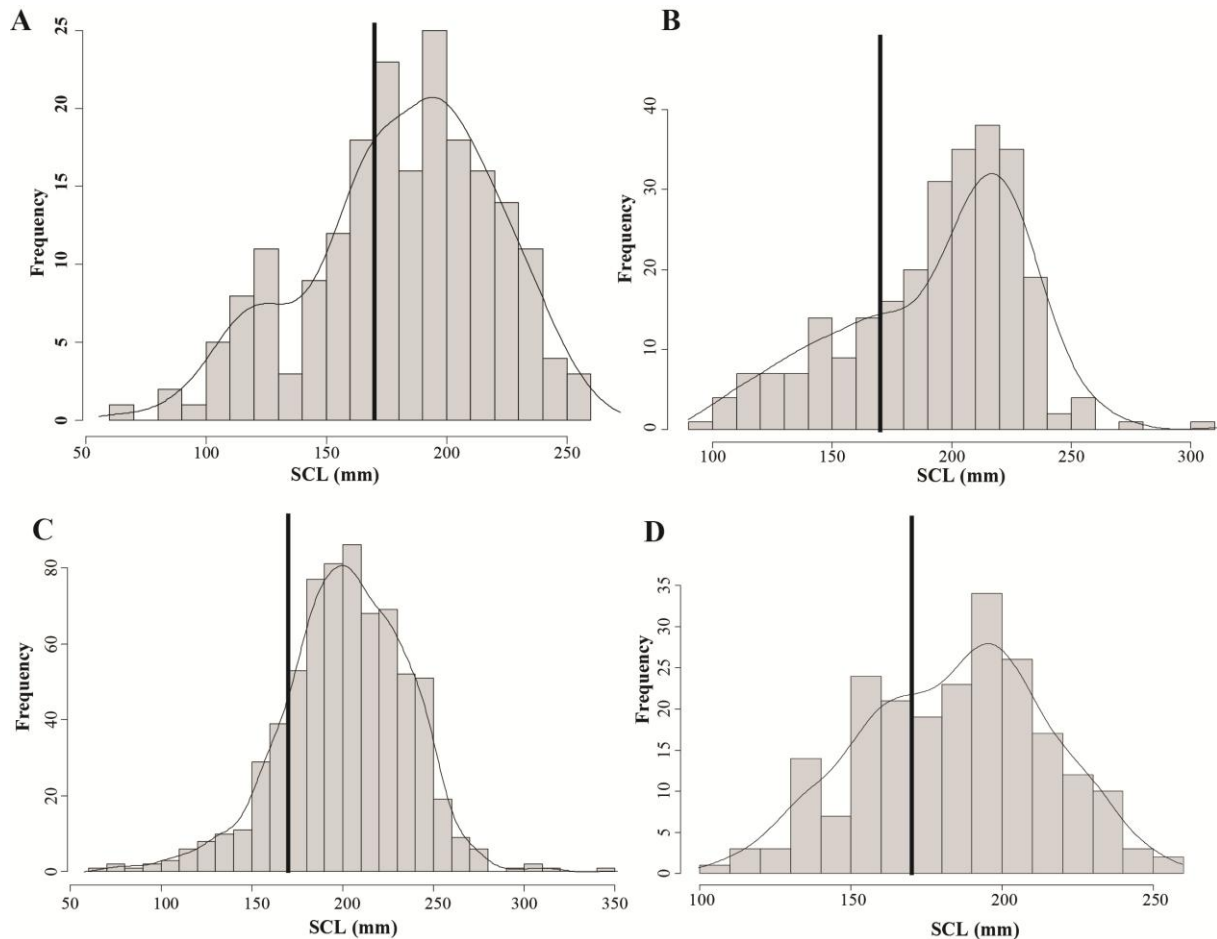
454 fragmented (completion mean of 59%) compare to the other peripheral plates (completions means 67-
455 89%). Burning (black) and carbonization (grey/white) traces were observed on 690 bones (14% of the
456 total NISP). Such traces were present indiscriminately on every anatomical element of the carapace and
457 skeleton. Cut marks were observed on only five bones, six peripheral plates, and one hypoplastron. A
458 series of peripheral plates attributed to a Geoemydidae turtle bears clear traces of a clean cut aiming to
459 cut the ventral part of the carapace (Fig. 3-G). Lastly, 120 bones have been observed as corresponding to
460 preserved anatomical connections on the field between unfused plates. This indicates that at least a part
461 of the assemblage was undisturbed prior to the excavation.
462



463
464 **Figure 4** - Anatomical distributions of the turtle/tortoise remains collected in the sites of Doi Pha
465 Kan rockshelter (A), and Moh Khiew Cave (B-E). The percentage of representation (PR) is considered
466 here to provide a graphical visualization of the different values observed for the different
467 anatomical elements.

468 Size of *Indotestudo elongata* archaeological individuals

469 The measurements recorded on the *I. elongata* archaeological material of Doi Pha Kan enabled
470 for the reconstruction of 201 SCL estimations included between 64 and 292 mm with a mean of 182 mm
471 (Figure. 5-A) and corresponding to at least 42 individuals. The distribution of these sizes was not
472 unimodal (Hartigans' dip test, $p.val>0.05$) but could be bi-modal with a population of small individuals
473 around 120 mm, and a second one between 140 and 260 mm.
474



475 **Figure 5** - Histograms of the *Indotestudo elongata* size reconstructions (Standard Carapace Length)
476 obtained from the different herpetofaunal bone assemblages studied: A) Doi Pha Kan Rock-shelter
477 (NMI=42); B) Moh Khiew Cave (NMI=59); C) Laang Spean Cave (NMI=75); D) Khao Ta Phlai Cave
478 (NMI=26). The black bars represent the minimal size of the sexually mature specimens based on
479 modern data collected on modern *I. elongata* populations.
480

481 Moh Khiew cave

482 Composition of the herpetofaunal assemblages

483 The herpetofaunal assemblage of Moh Khiew consists in 9 108 bone remains weighting 8351 gr.
484 Those bones are mostly distributed in the layers 2 (51% of the NISP, and 52% of the WR), 1 (26% of the
485 NISP, and 24% of the WR), and 3 (17% of the NISP, and 18% of the WR) (Table. 4). The complete
486 assemblage includes bone fragment from a least 152 individuals.
487 The full sample mostly correspond to non-marine turtle remains (63% of the NISP, 74% of the WR, and
488 52% of the MNI), followed by Monitor lizards (25% of the NISP, 16% of the WR, and 24% of the MNI), and
489 snakes (8% of the NISP, 8% of the WR, and 4% of the MNI). The small size lizards (excluding snakes),
490 amphibians and crocodile remains altogether represent less than 5% of the assemblage in term of NISP
491 and WR. The distribution of these groups among the layers is however far from homogenous. Indeed,

492 turtle bone remains represent more than 75% of the NISP, 85% of the WR, and 60% of the MNI in the
 493 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,
 494 Monitor lizards represent 46% of the NISP, 31% of the WR, and 35% of the MNI in the layer 1 but less
 495 than 20% of NISP, 13% of the WR, and 25% of the MNI in the other layers. Snakes are also better
 496 represented in the layer 1 (23% of the NISP) than in the subsequent levels (less than 2.6% of the NISP).
 497 Chi² tests performed on the NISP indicate that the faunal composition of the layer 1 significantly differs
 498 (P.val< 0.01) from the layers 2 and 3, the effective of the layer 4 being too low to conduct a statistical
 499 test.

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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

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

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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
<i>Indotestudo elongata</i>	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

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521 Taphonomy of the turtle/tortoise bone assemblage

522 The fragmentation of the 5740 bone fragments analyzed increase with the depth. In the layer 1,
 523 8.9% of the bones are complete, and 12.9% nearly complete, in layer 2 these percentages falls to 7.5 and
 524 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
 525 completeness of the bones is also slightly higher in layers 1 and 2 (36 and 37%) than in the layers 3 and 4
 526 (34 and 28%). These differences are only significant between the layers 1 and 4 (Chi² test; p.
 527 value<0.01).The anatomical distribution of the remains present strong variations between the layers (Fig.

528 4) but the sizes of the assemblages are also very dissimilar with the bone samples of the layers 1 and 4
529 containing only 503 and 439 remains and those of the layers 2 and 3 containing 3614 and 1184 bone
530 fragments. Distributions in small samples could be more strongly impacted by random effects than larger
531 assemblages and a strict comparison of the four layers might not make sense at all. Some general trends
532 can, however, still be noted just as the overall PR which is between 27 and 24% in all the layers at the
533 exception of the first in which it is slightly higher (36%). Nearly all the anatomical parts are present in
534 every layer but the skulls, vertebrae, and extremities are nearly absent. The stylopods (humerus and
535 femur) are the best represented bones in the richest layers. They are also well represented in layers 1
536 and 2 but are outnumbered by some specific carapace plates. Girdles and zeugopods are also present but
537 in smaller number. Regarding the carapace and the plastron, no clear pattern emerges at the exception
538 of the nearly systematic lower representation of the peripheral plates of the bridge (PR=25-21%) in
539 respect to the other peripheral plates (mean PR=52-29%). This could be explained by an identification
540 bias related to the lower mean completion rate of peripheral plates of the bridge in respect to the others.
541 Burning (black) and carbonization (grey/white) traces were observed on 325 bones (5.7% of the total
542 NISP). Such traces were present indiscriminately on every anatomical element and every side of the
543 carapace and skeleton parts. They were recorded on the internal side of several peripheral plates that
544 were still in anatomic connection at the moment of the excavation (Fig. 3-F). Such observations were,
545 however, not repeated on the rest of the material. Cut marks were observed on only three bones: one
546 peripheral plate, one nuchal plate, and one xiphiplastron. Among the full assemblage 61 fragments of
547 carapaces were still in anatomical connection at the moment of the excavation. These elements were
548 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.

549

550 Size of *Indotestudo elongata* individuals

551 The measurements recorded on the *I. elongata* archaeological material of Moh Khiew Cave
552 enabled for the reconstruction of 201 SCL estimations included between 98 and 310 mm and with a mean
553 of 193 mm (Figure. 5-B) and corresponding to at least 59 individuals. The mean size of the tortoises is
554 similar in all layers and no statistically significant differences was noted (student T-test; p.val>0.01). In
555 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
556 finally 195 mm in layer 4 (N=19). The largest observed specimen was in the layer 1. The global
557 distribution of these sizes was not unimodal (Hartigans' dip test, p.val>0.01) and mixture models indicate
558 it is most likely bimodal with a best represent group of individuals around 220 mm and a second group of
559 smaller specimens around 150 mm.

560

561 *Khao Ta Phlai Cave*

562 Taxonomic composition

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

569

570 **Table 6** - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), Number of
571 Remains (NR), and Minimal Number of Individual (MNI) corresponding to the different
572 herpetofaunal taxa identified in the herpetofaunal bone assemblages collected in the two test-pits
573 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

574
575

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

581 The distribution of the main herpetofaunal taxa across the layers does not present strong
582 variations (Tab. 7) as only the very poor metal age layer of the TP2 significantly differ from the other
583 levels (Chi²; p.value <0.01). Turtle bones are always the best represented (between 71 and 87% of the
584 NISP) but Monitor lizards seems a bit better represented in Metal Ages layers from TP1 and 2 (18 and
585 20% compared to Neolithic layers (14 and 11% of the NISP). These tendencies are, however, not
586 statistically significant and difficult to interpret in the absence of a study of the complete faunal
587 assemblages.

588

589 **Table 7** - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal
590 Number of Individual (MNI) corresponding to the different herpetofaunal taxa identified in the
591 herpetofaunal bone assemblages of the two periods identified in the two test-pits of the site of
592 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

593
594

595 The identification rate of non-marine turtles bones was lower in the TP1 (41% of the WR and 25%
596 of the NR) than in TP2 (57% of the WR and 35% of the NR). Regarding the bones attributed to a given
597 family (Tab. 8), TP1 provided nearly as much Testudinidae as Geoemydidae in terms of WR and NISP
598 while *Indotestudo elongata* is much more represented than the latter in the TP 2 (61% of the WR and
599 69% of the NISP). These differences are statistically significant (Chi² test; p.value<0.01). Trionychidae are
600 present in the two TPs. If the chronological phases are considered (Tab. 9), Geoemydidae and
601 Trionychidae are significantly better represented in the upper layers of the TP2 and TP1 corresponding to
602 the metal ages. These two layers do not significantly differ in term of family composition (Chi² test;
603 p.value>0.01) but significantly differ from the two Neolithic layers (Chi² test; p.value<0.01). This trend to
604 a more important exploitation of freshwater turtles during the metal ages in regard to the Neolithic
605 period is for now difficult to interpret considering the possible issues of chronological associations
606 between the layers of the two TPs and the possibility of a spatial variation in the distribution of the
607 remains inside the site. Indeed freshwater turtles are also better represented in the Neolithic layer of the
608 TP1 compare to TP2.

609

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

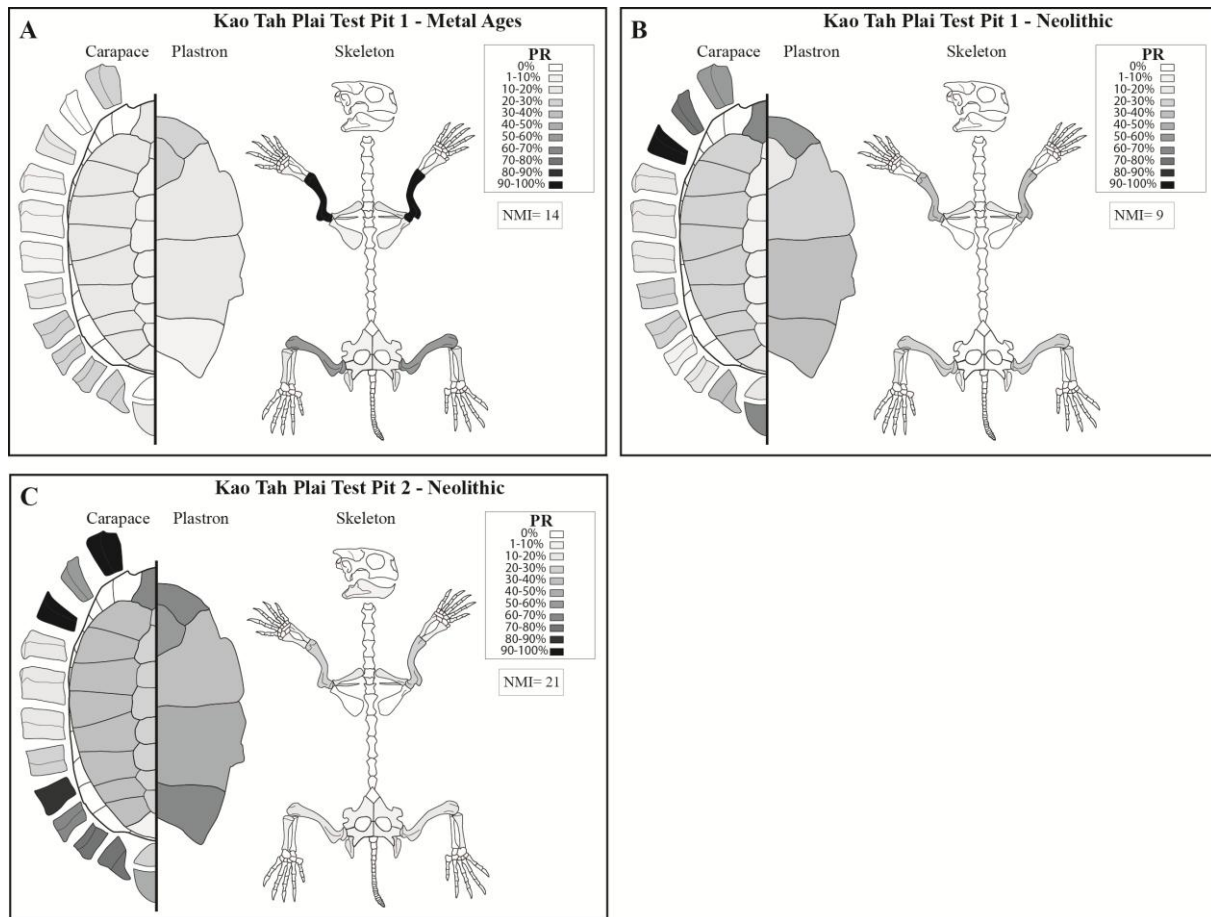
	TP1			TP2		
	NISP	WR	NMI	NISP	WR	NMI
<i>Indotestudo elongata</i>	175	435.5	8	441	1357	14
Geoemydidae	150	581.9	5	191	838.6	3
Trionychidae	10	14.1	1	9	32.2	1
Turtle ind.	1000	1478		1184	1673	
Total	1335	2510	14	1825	3901	18

613
 614
 615 **Table 9** - Number of Identified Skeletal Parts (NISP), Weight of the Remains (WR), and Minimal
 616 Number of Individual (MNI) corresponding to the different turtle/tortoise taxa identified in the
 617 bone assemblages collected in the different chronological phases of the two test-pits of the site of
 618 Khao Ta Phlai.

	TP1-MA			TP1-NE			TP2-MA			TP2-NE		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
<i>Indotestudo elongata</i>	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

619
 620
 621 Taphonomy of the turtle/tortoise bone assemblage

622 Among the 3 160 bone fragments attributed to turtle/tortoises in the material of Khao Ta Phlai,
 623 221 were complete elements (6.9%), and 370 were nearly complete (at least 90% of the complete bone)
 624 while 760 (24%) were small fragments representing less than 5% of the complete anatomical part. The
 625 average percentage of completion of the bones is 29%. This value is similar in the Neolithic layers of TP1
 626 and TP2 (29%). It is slightly lower in the metal ages layer of the TP1 (25%), and higher in the same period
 627 layers from TP2 (39%) but the small size of this assemblage does not allow to consider this result as
 628 significant.



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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.

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

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

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

660

661 Size of *Indotestudo elongata* individuals

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

672

673 Laang Spean Cave

674 Composition of the herpetofaunal assemblage

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

684

685 **Table 10** - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal
 686 Number of Individuals (MNI) studied in the complete herpetofaunal assemblage from the different
 687 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

688

689

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

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

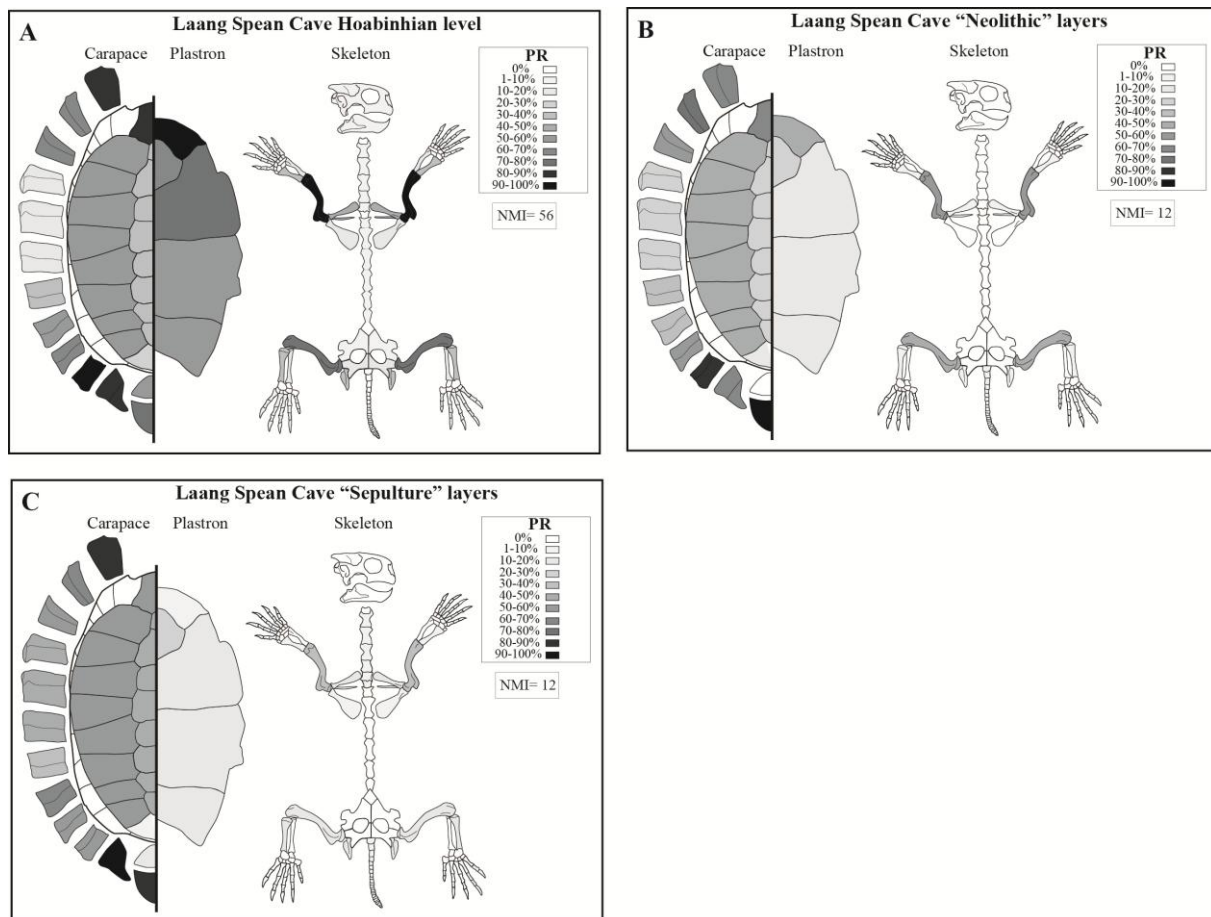
695 **Table 11** - Number of Identified Skeletal Parts (NISP), Weight of the remains (WR), and Minimal
696 Number of Individuals (MNI) identified in the turtle/tortoise bones assemblage from the different
697 layers of Laang Spean Cave.

	Hoabinhian layer			Neolithic layer			Sepulture layers			Total		
	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI	NISP	WR	NMI
<i>Indotestudo elongata</i>	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

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700 Taphonomy of the turtle/tortoise bone assemblage

701 Regarding the taphonomy of the turtle bones collected in the different squares, the mean
702 completion rate is slightly lower in the “sepulture” assemblage (32%) than in the “Neolithic” and
703 “Hoabinhian” assemblages (39.2 and 36.7%). The general fragmentation pattern is otherwise similar in all
704 layers. The complete bones constitute between 9.3% of the assemblages for the Hoabinhian assemblage,
705 and 7.2-6.2% for the “Neolithic” and “Sepulture” assemblages while nearly complete elements account
706 for 14.2% of the “Hoabinhian”, 13.8% of the “Neolithic”, and 11% of the “Sepulture” assemblages. Most
707 anatomical parts are represented in the different assemblages but the extremities, vertebrae, and skull
708 remains are very rare with a PR below 4% in all assemblages (Fig. 7). There is also a global tendency to
709 the lower representation of the peripheral plates of the bridge (11%-31%) in respect to the other
710 peripheral plates (58-70%) although this trend is more strongly marked in the Hoabinhian layer (11% vs.
711 70%). The peripheral plates of the bridge are also systematically more fragmented (59-67% of mean
712 completion) than the others (83-87% of mean completion). Outside of these common trends, significant
713 strong differences emerge between the “Hoabinhian” assemblages and the two other layers. Indeed,
714 although the general PR is similar in the different assemblages (41% for the Hoabinhian assemblage, 37%
715 for the Neolithic assemblage, and 34% for the Sepulture assemblage) the carapace elements are
716 dramatically better represented in the Hoabinhian bones (Fig. 7-A) compare to the two other
717 assemblages (Fig. 7-B, C) (Chi² test; p.value<0.01). Indeed, although the PR of the carapace and plastron
718 bones are more or less similar in the Hoabinhian assemblage (57.8% vs. 67%) the plastron elements are
719 mostly missing in the other assemblages (54% vs. 20.8% in the Neolithic assemblage and 53% vs. 15.1% in
720 the Sepulture assemblage). The stylopods are also better represented in the Hoabinhian squares (84%)
721 compare to the other assemblages (50.4% and 28%).



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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.

726 The observation of traces on the bones is made very challenging by the fact that 61% of them are covered
727 by a veil of calcite. Interestingly, this calcite deposit was more frequent in the Hoabinhian squares where
728 it covered 65% of the bones but was scarcer in the Neolithic and sepulture squares where it covered
729 respectively 56% and 38% of the bones. This is probably related to the position of the remains in the
730 cave, more or less close to the walls, which influenced their exposition to water flows during the rainy
731 season. There is also a possibility that the calcite veil might be more frequent on the oldest remains. The
732 presence of water flow in the site is also indicated by the occurrence of 61 bones having been polished by
733 water flows. Porcupine gnawing traces were observed on only 13 elements distributed in several areas
734 and layers of the site and digestion traces on only one. This clearly indicates a minor impact of animal
735 species on the integrity of the archaeological assemblage. Putative burning traces were observed 10% of
736 the remains. These traces were better represented in the Hoabinhian squares where they were present
737 on 12% of the bones while they only occur on 2.8 and 3.8% of the bones recovered in the Neolithic and
738 Sepulture squares. The characterization of burning traces was made very difficult by the fact that the
739 material present a strong variability of surface color probably related to post-depositional chemical
740 alteration. The occurrence of these traces might thus have been underestimated given the fact that we
741 choose to record them only when their nature was undisputable. No cut mark was observed.
742 Among the full assemblage 327 fragments of carapaces (3.7% of the NR) were still in anatomical
743 connection at the moment of the excavation. These elements are mostly from the Hoabinhian squares
744 (N=292) where they account for 4.3% of the turtle remains. Elements in anatomical connection are
745 scarcer in the other assemblages with only 35 occurrences (1.7% of the turtle NR). This indicates that the
746 Hoabinhian squares have been indeed less disturbed than the "Neolithic" and "Sepulture" squares.

747 Size of *Indotestudo elongata* individuals

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

756 **Discussion**

757 **Taxonomic composition of the herpetofaunal assemblages**

758 In all the assemblages the distribution of the herpetofaunal groups in the four investigated sites
759 present strong similarities. Non-marine turtles are nearly systematically the best represented
760 herpetofaunal group (between 59 and 91% of the NISP) before Monitor lizards (between 6 and 25% of
761 the NISP), snakes (below 3.5% of the NISP), and amphibians. The only exception to this trend is the layer
762 1 of Moh Khiew cave in which Monitor Lizards (25% of the NISP), and snakes (23% of the NISP) bone
763 remains are more numerous than turtle skeletal elements (20% of the NISP). This layer is disturbed and
764 not dated so interpreting this observation is impossible for now. However, the other sites follow a clear
765 pattern showing that hunter-gatherers groups have preferentially exploited turtles over other reptile and
766 amphibian taxa. This follow the general regional pattern previously observed in similar zooarchaeological
767 assemblages (Conrad 2015). Regarding the proportion of the turtle/tortoise families in the assemblages,
768 Testudinidae (*Indotestudo elongata*) is always the most represented group as it account for between 52
769 and 89% of the turtle bones NISPs. The proportions of Geoemydidae turtles vary a lot between 48 and
770 11% of the same NISPs. As most of the species from this group are aquatic freshwater turtles this
771 variability could be explained by the accessibility of streams, rivers, and lakes by the inhabitants of the
772 sites. In most sites the proportion of Geoemydidae is around 30% of the NISP but these turtles are much
773 less prevalent in Laang Spean cave, and the best represented in the TP1 of the site of Khao Ta Phlai. The
774 published data regarding the faunal assemblage from Laang Spean indicate a weak contribution of
775 freshwater taxa (mussels and fish) to the overall diet (Forestier *et al.* 2015; Frère *et al.* 2018) which is in
776 accordance with our observation of the scarcity of freshwater turtles in the site. Regarding the
777 prevalence of Geoemydidae species in the TP1 of Khao Ta Phlai, this could indicate a stronger reliance on
778 freshwater resources than in the other sites. However, considering the chronology of the two test-pits of
779 the site is not yet fully resolved and that general importance of aquatic resources in this assemblage still
780 need to be estimated, this fact cannot be related to a cultural/chronological trend for now. From a
781 general point of view, the data regarding the herpetofaunal assemblages, however, point to strong
782 similarities between assemblages of different ages and from very different environmental settings. This
783 should be considered at the light of the studies regarding the mammal bone assemblages of the same
784 sites to test the hypothesis of a putative homogeneity of the Hoabinhian subsistence strategies in
785 continental Southeast Asia.

786 **Taphonomy of the turtle assemblages**

787 The fragmentation rate of the bones is fairly homogenous among the sites. The average
788 percentage of completeness of the bones is between 37 and 28%. The material from three first layers of
789 Moh Khiew Cave and Laang Spean are the less fragmented (average percentage of completeness above
790 33%). The layer 4 of Moh Khiew cave provided the most fragmented material (average percentage of
791 completeness of 28%). The presence of large limestone blocks in this layer may be indicative of crumbling

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

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

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

846 **Size of *Indotestudo elongata* archaeological specimens**

847 The size of *I. elongata* individuals observed in the four archaeological deposits (Fig. 5) shows
848 common patterns but also some differences. The distributions of the estimated sizes are bimodal in all
849 sites except Laang Spean. In all the sites, most of the estimations correspond to adult size specimens
850 above 170 mm SCL reaching maximums of 270-345 mm SCL. These specimens all fall in the size range of
851 the modern representatives of the species. Yet, all sites present a variable proportion of smaller, likely
852 immature individuals. The representation of this second group is the lowest in Laang Spean (16% of the
853 total number of estimations) but is important enough in the other sites to make their distributions
854 bimodal with 35%-33% in Doi Pha Kan and Khao Ta Phlai, and 24% in Moh Khiew cave. Specimens below
855 140mm SCL are rare in all sites as they account for less than 10% of the estimations in all sites but
856 represent more than 15% of the Doi Pha Kan population.

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

884 The site of Laang Spean presents a unimodal size distribution in which juvenile specimens are mostly
885 excluded. In that sense, this distribution is very different from that of a natural population and indicates a
886 strong selection on adult specimens of moderate to large size. This is clearly indicative of a very selective
887 hunting strategy that may have been enabled by the abundance of resources in the vicinity of the site.
888 Such a selection, although visible in other deposits is less marked as juvenile specimens composed more
889 important parts of the assemblages, especially in Doi Pha Kan. In these sites, it is impossible to estimate
890 whether or not the proportions of juvenile specimens present in the assemblages are similar to those of
891 the exploited natural populations and thus to estimate the exact intensity of the selection toward large
892 size individuals. In any case, it is the sign of an opportunistic foraging as such a combination of juvenile
893 specimens has been observed on modern hunter-gatherer population actively collecting tortoises this
894 way (Mena *et al.* 2000). But this might also be influenced by the hunting method in the case a direct
895 selection by the hunter is not made, for instance with the use of trapping that was also hypothesized in
896 Doi Pha Kan for the hunting of monitor lizards (Bochaton *et al.* 2019). This technique is also the most
897 used to hunt tortoise in the Amazon as it is the most efficient method before active searching (Santos *et al.*
898 2020). This implies no selection on the specimens in the wild although the type of trap used (i. e. size
899 of the ground hole) might induce some size bias. The use of traps could thus explain the strong
900 representation of smaller individuals present in the archaeological assemblages and indicate a very
901 opportunistic strategy indicative of either a poor selection by the hunter and/or a relative scarcity of the
902 tortoises in the environments making harder the collect of large individuals. The hunting season could
903 also be an explanation to the stronger or weaker presence of juvenile specimens in the assemblages.
904 Indeed, during the dry season tortoises are less active and harder to find which could led the hunter to be
905 less selective especially in the case of a use of non-selective hunting methods allowing to find these
906 animals. Theobald (1868) mentions the hunts of tortoises by Burmese hunters in the dry season by
907 clearing grass lands and forests with fire in order to destroy their shelters and locate them. At the
908 opposite, smaller tortoises are more active in the rainy season during which dogs are more used to track
909 them (Blythe 1854; Theobald 1868). Ultimately, both seasonal hypotheses could explain the occurrence
910 of small individual using different explanations (hunting method vs. activity season). Only the use of non-
911 traditional approaches such as skeletochronology (Ehret 2007) could help to clarify this question by
912 estimating the season of death of the tortoise individuals as well as the occupation seasonality of the
913 different sites given the absence of other seasonality makers in the materials.

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

928

Conclusion and perspective

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

953
954

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960

Data, scripts, code, and supplementary information availability

961 Supplementary information is available online: XXXXDOI of the webpage hosting the data
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963

964

Conflict of interest disclosure

965 The authors declare that they comply with the PCI rule of having no financial conflicts of interest
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974

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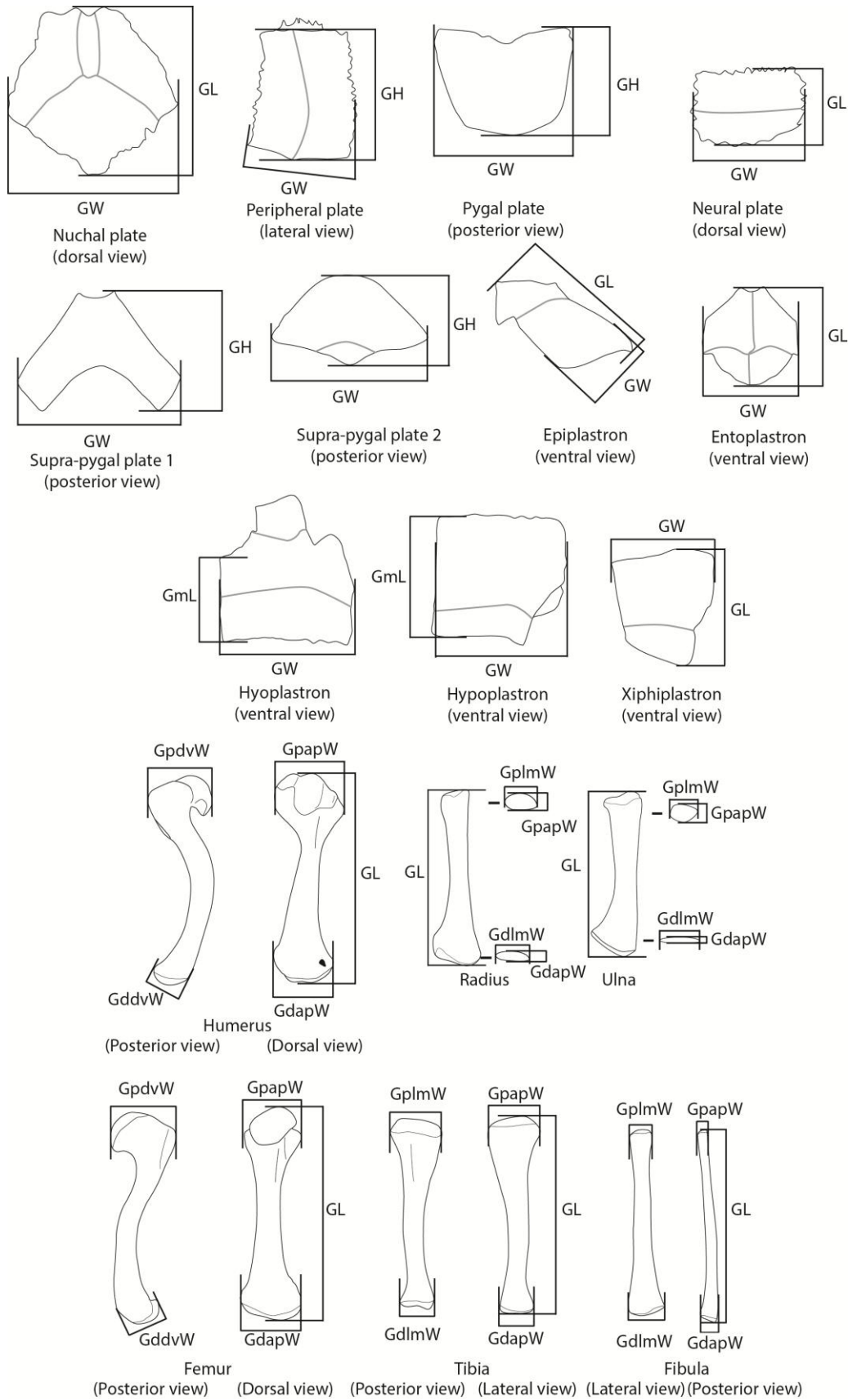
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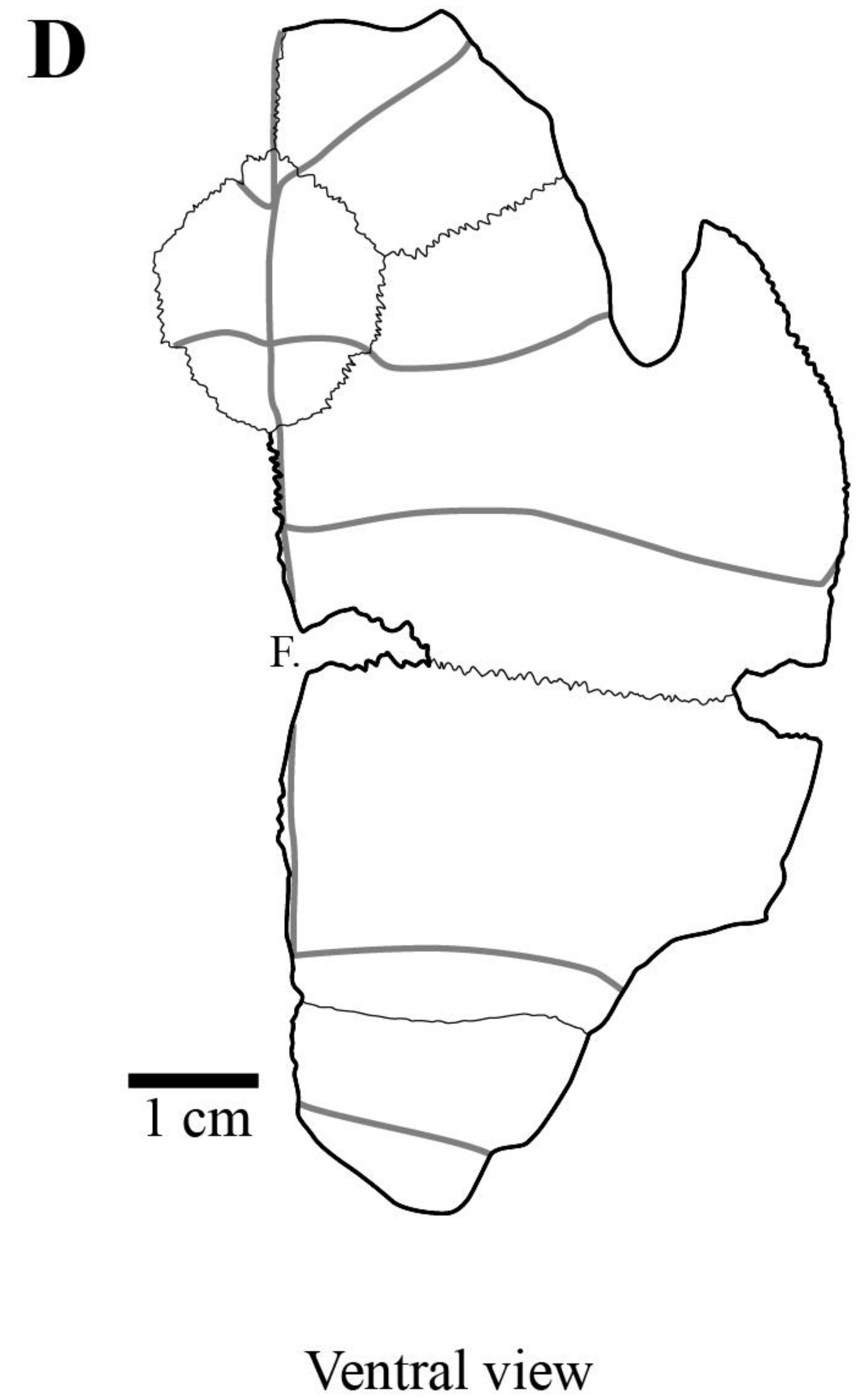
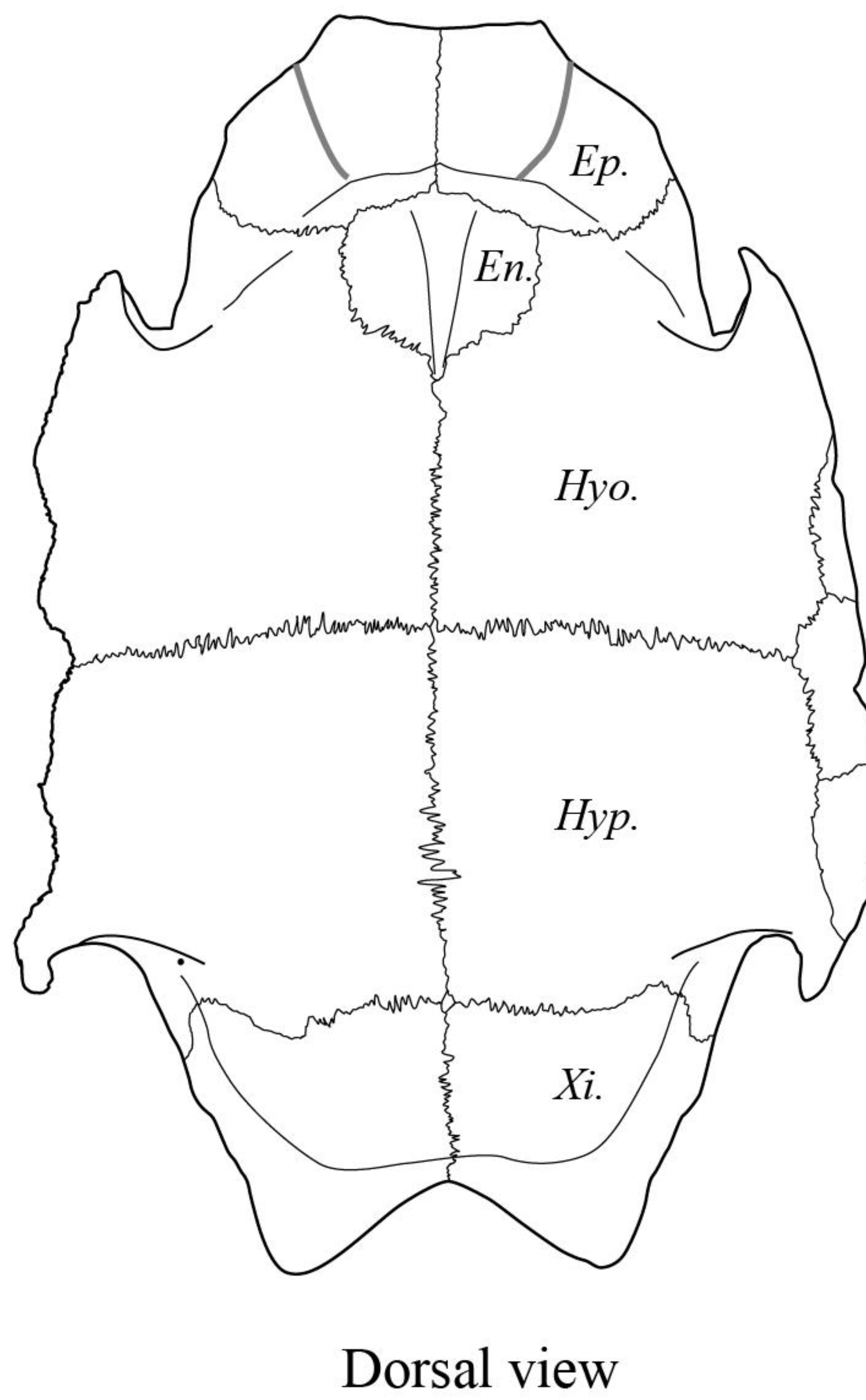
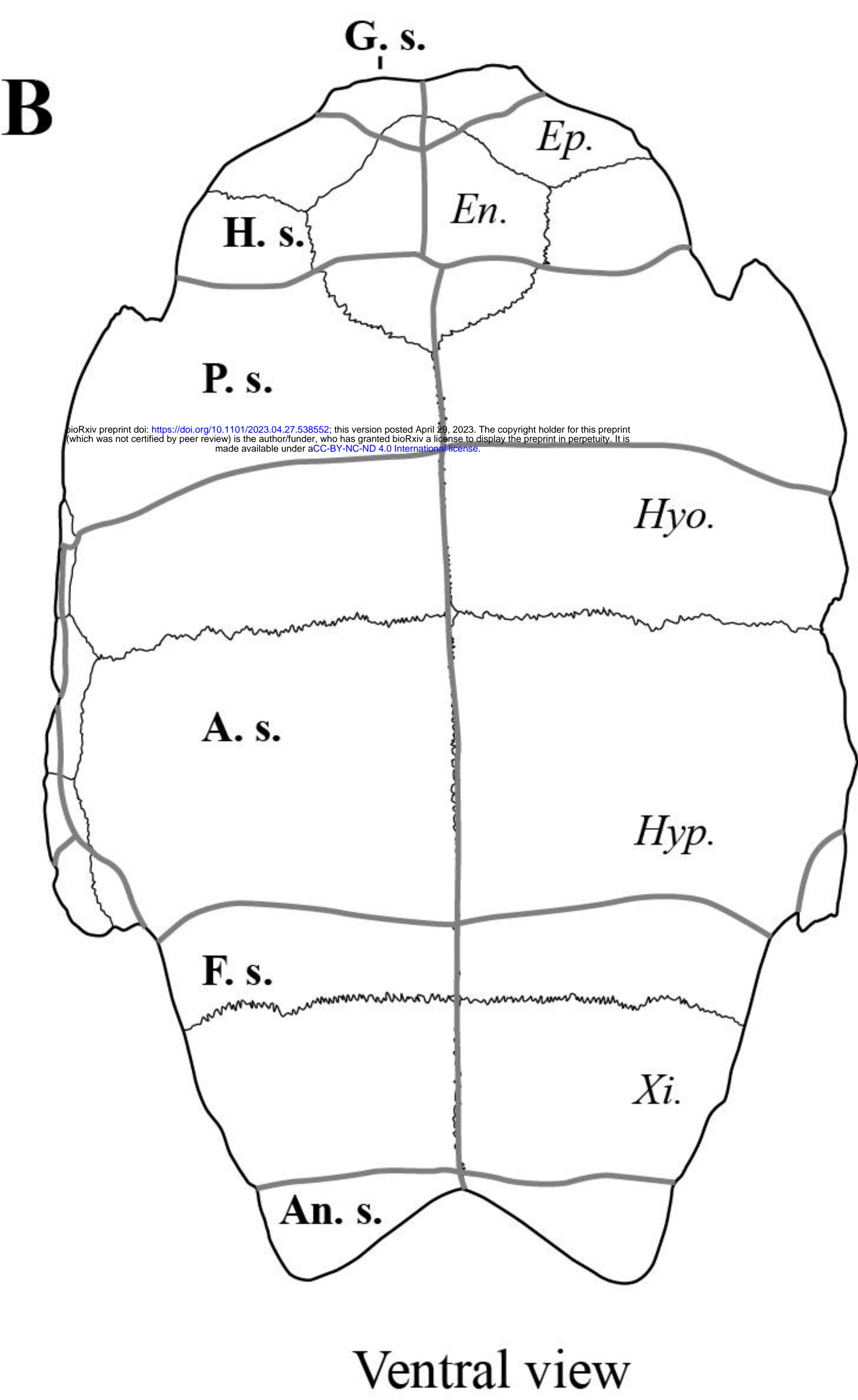
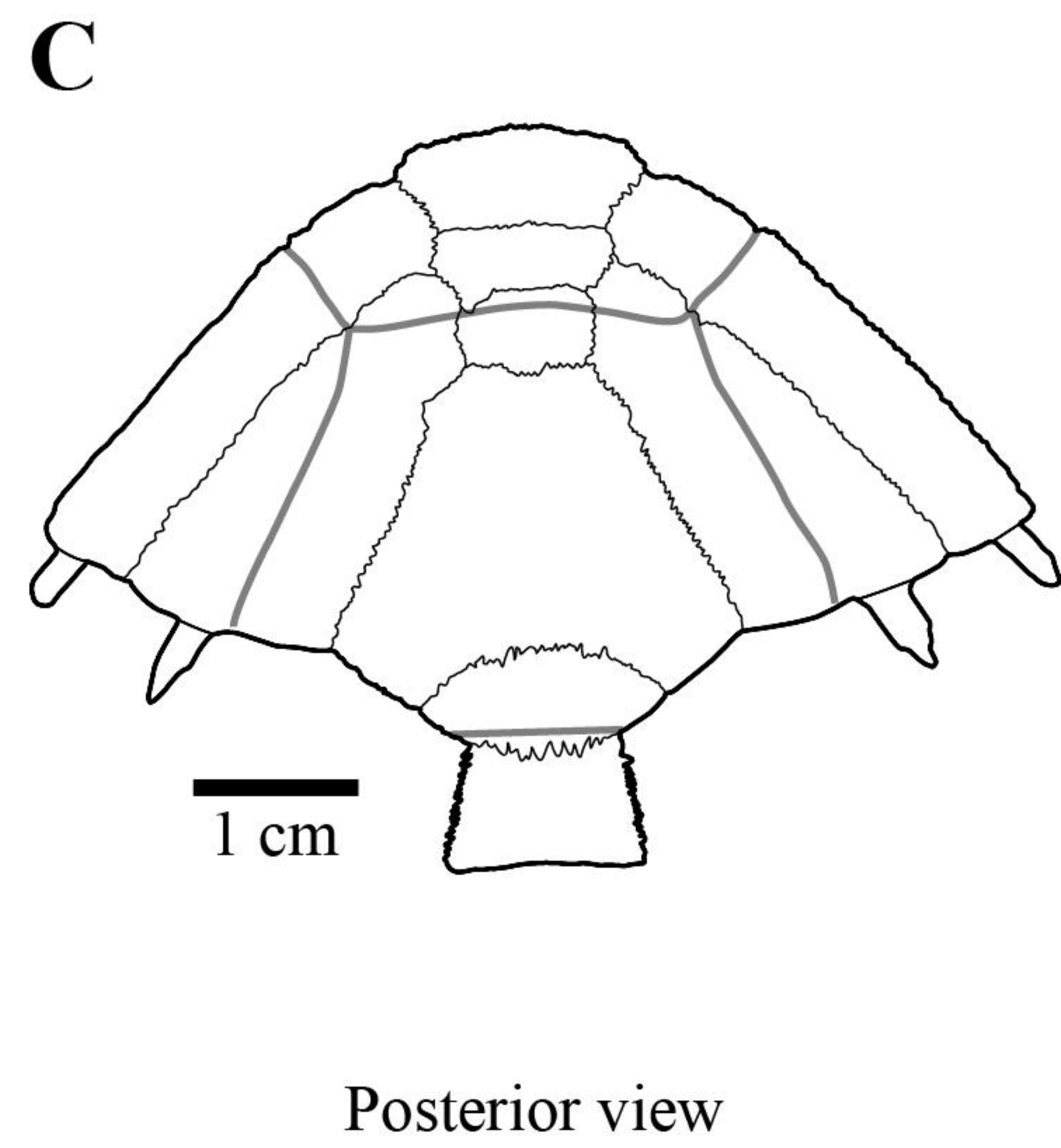
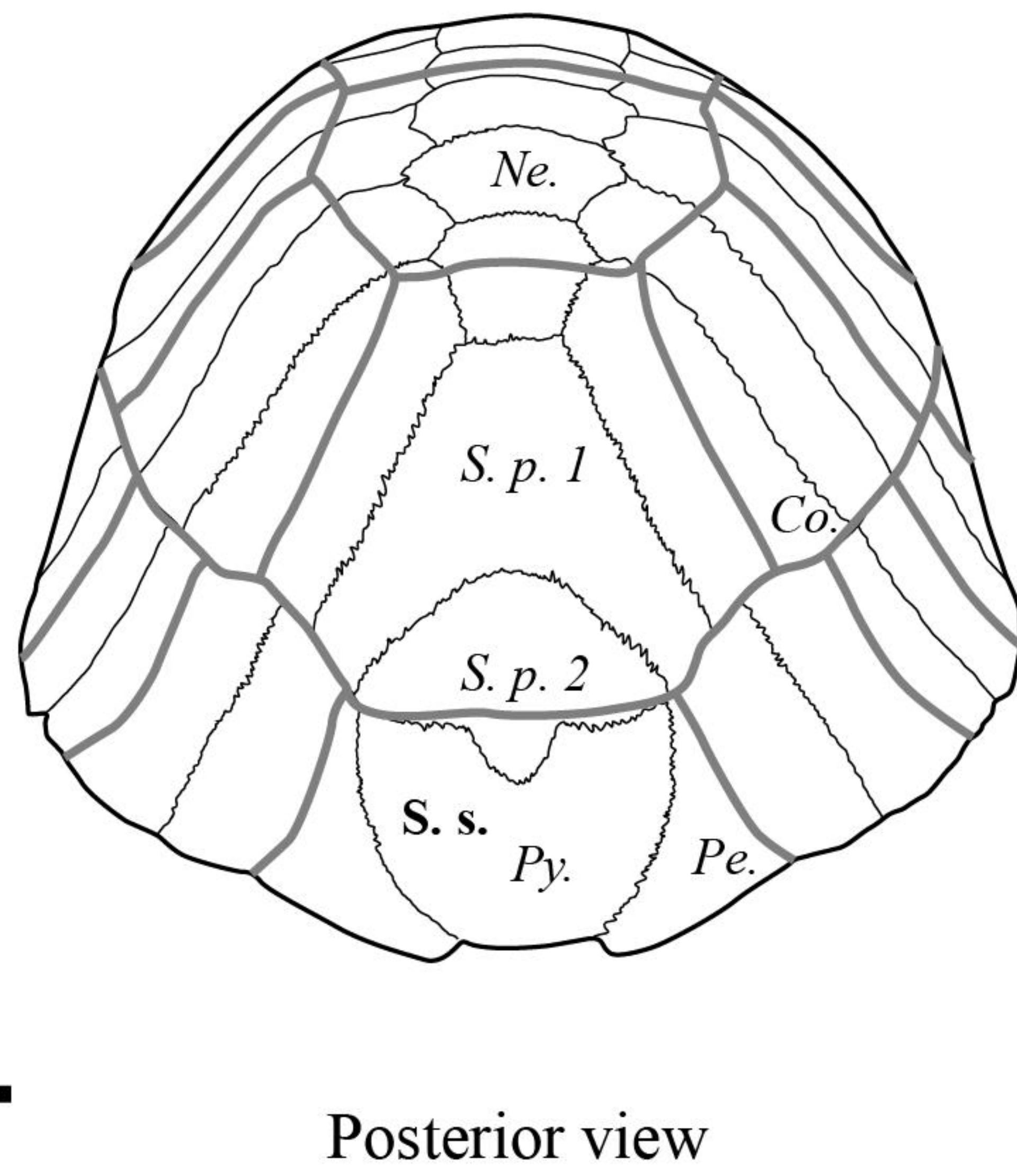
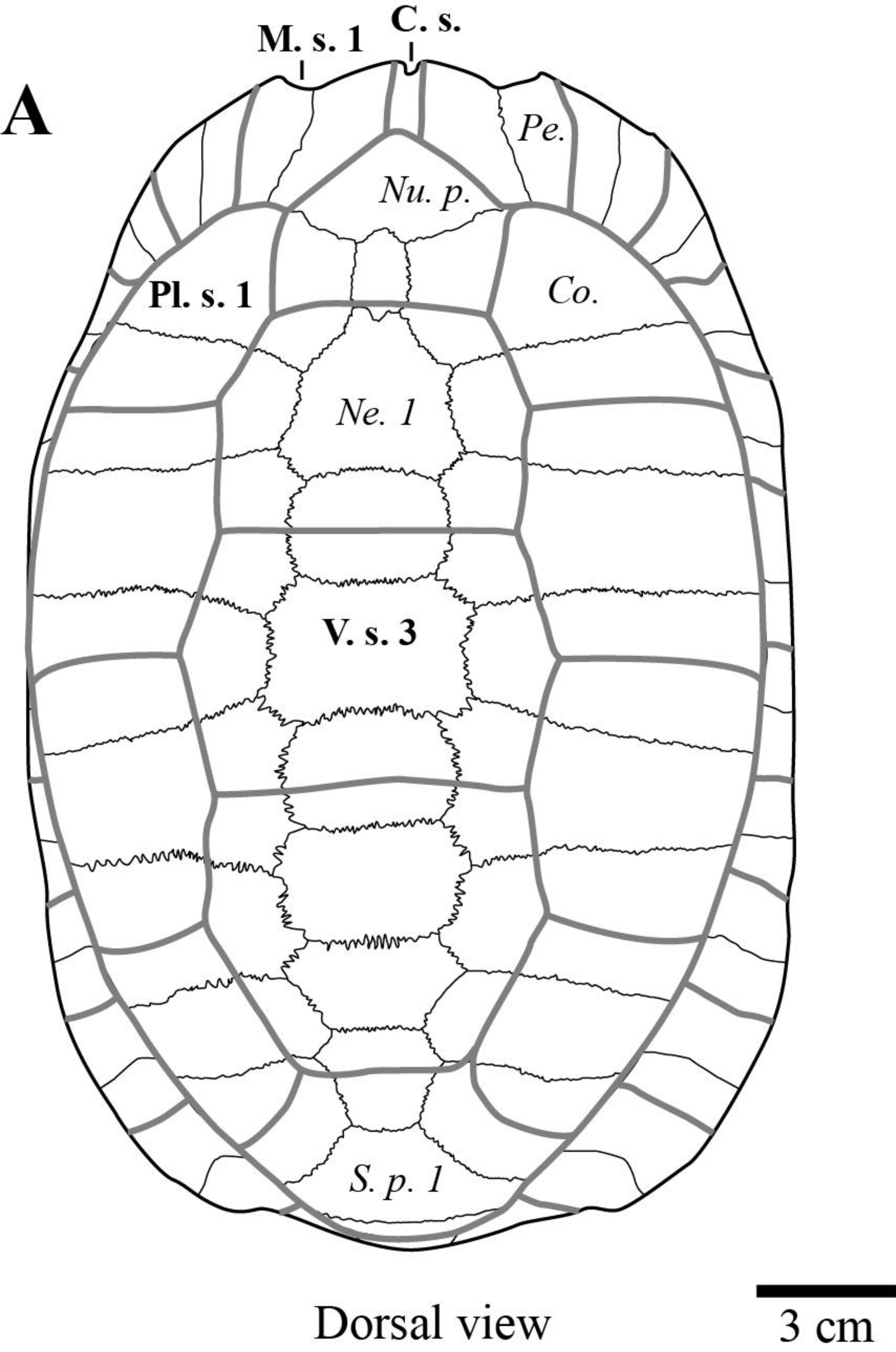
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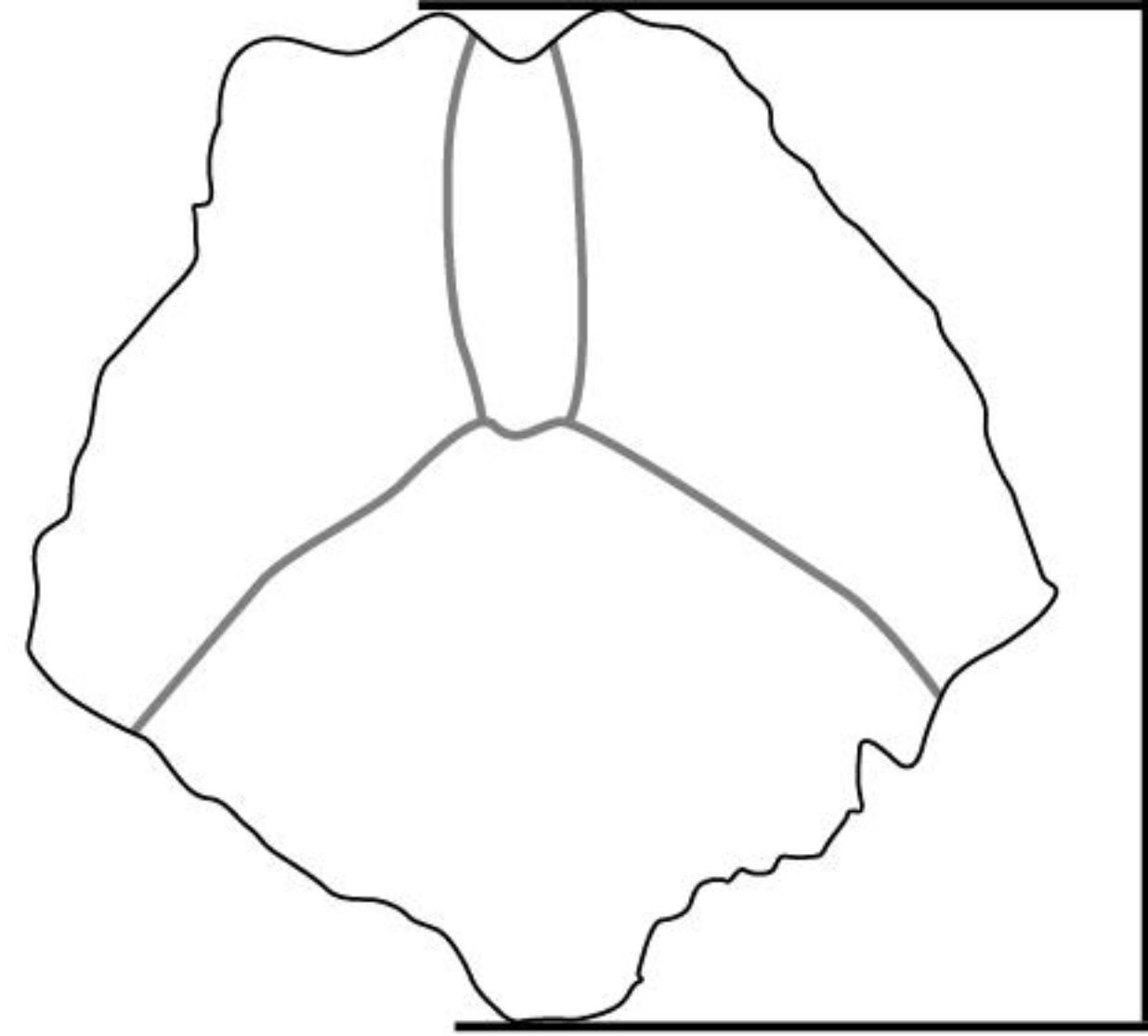
1263 Appendix

1264 Appendix 1: All measurements recorded on the modern turtle skeletons.



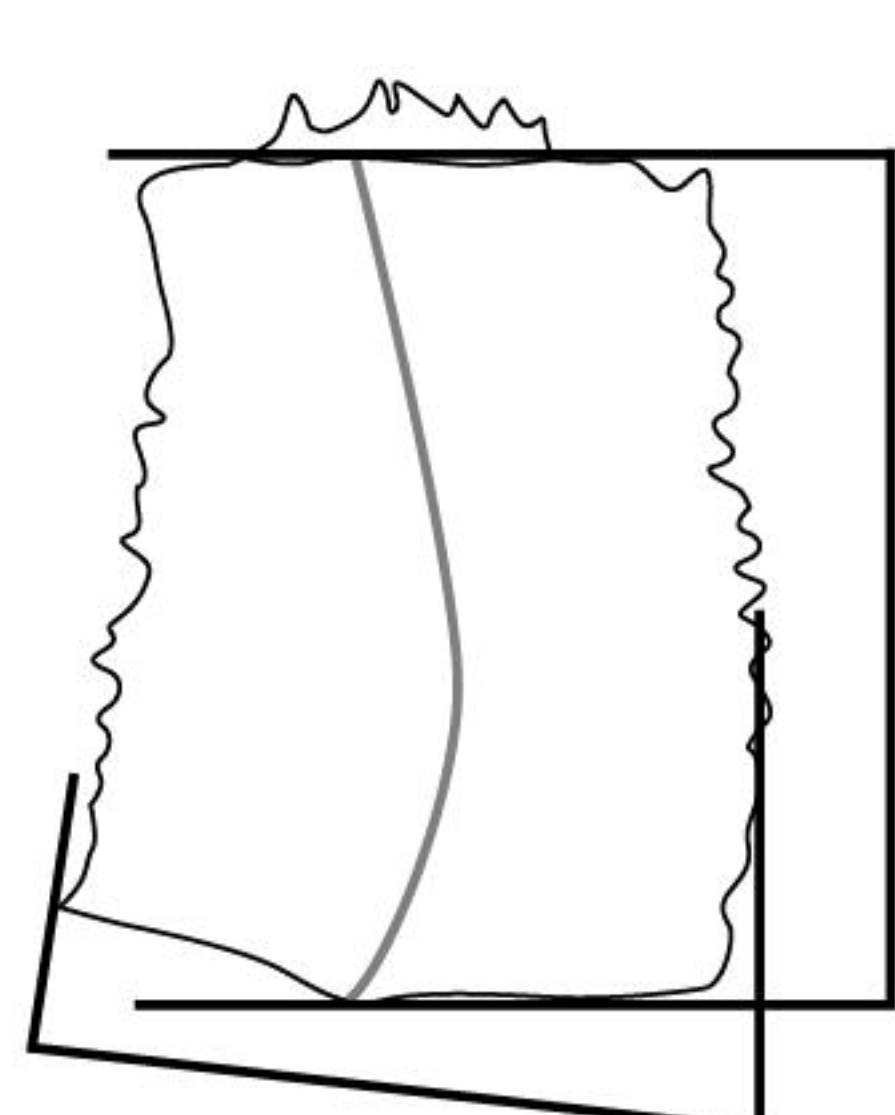
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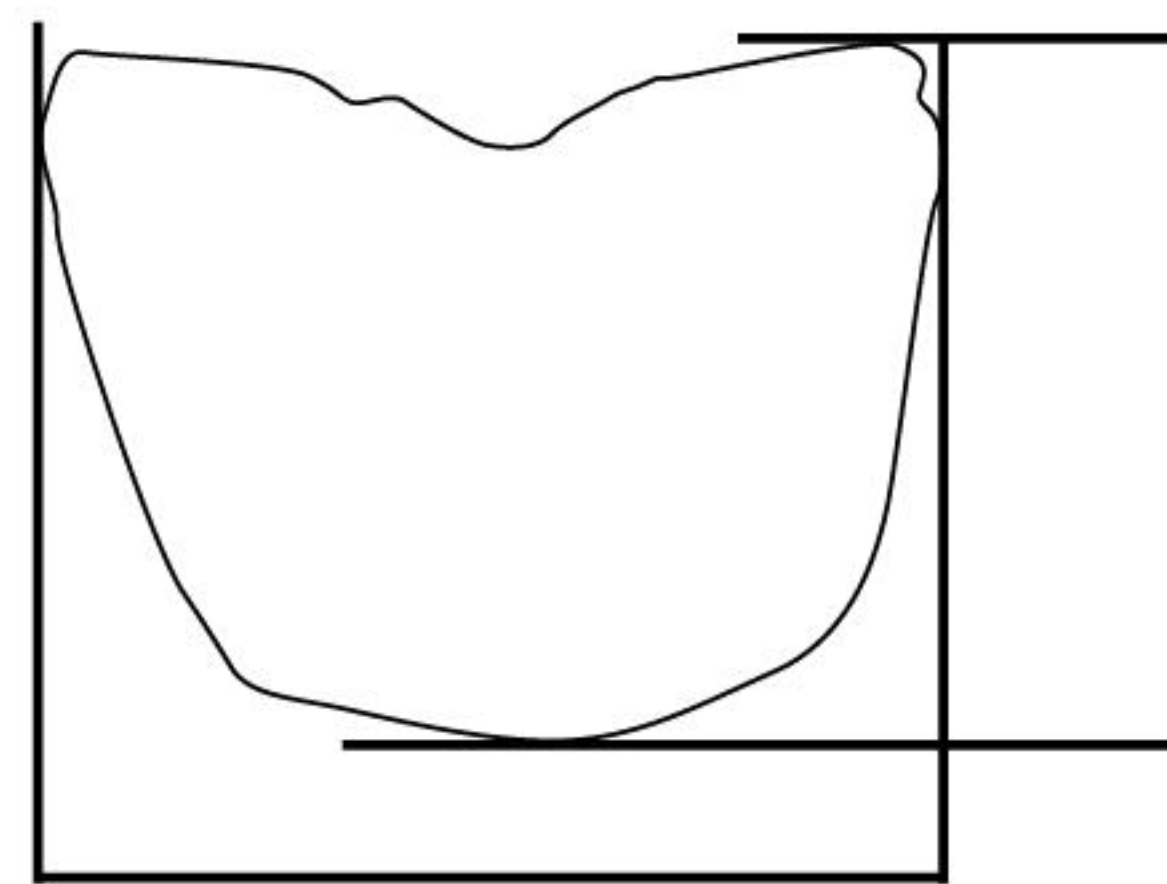
Nuchal plate
(dorsal view)

GL



Peripheral plate
(lateral view)

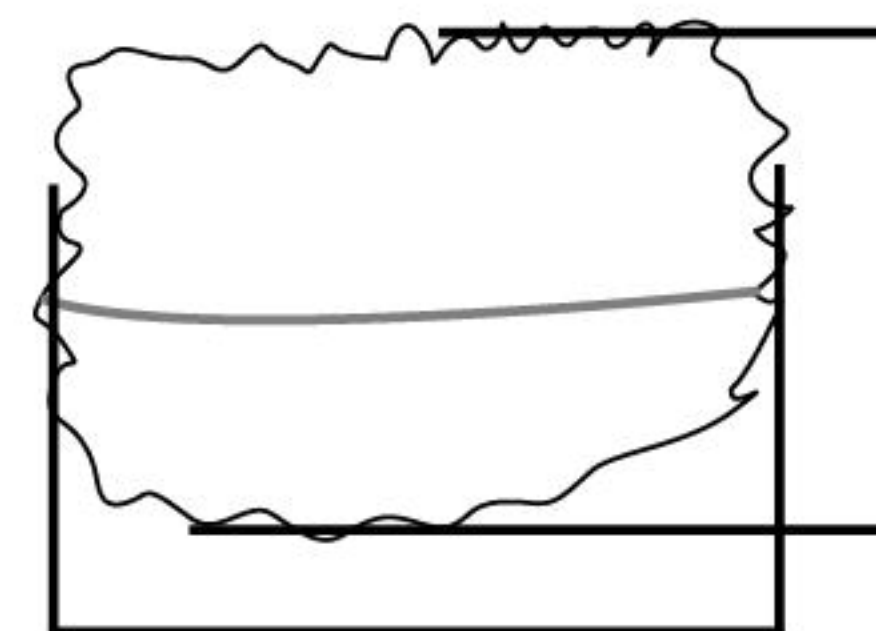
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Pygal plate
(posterior view)

GW

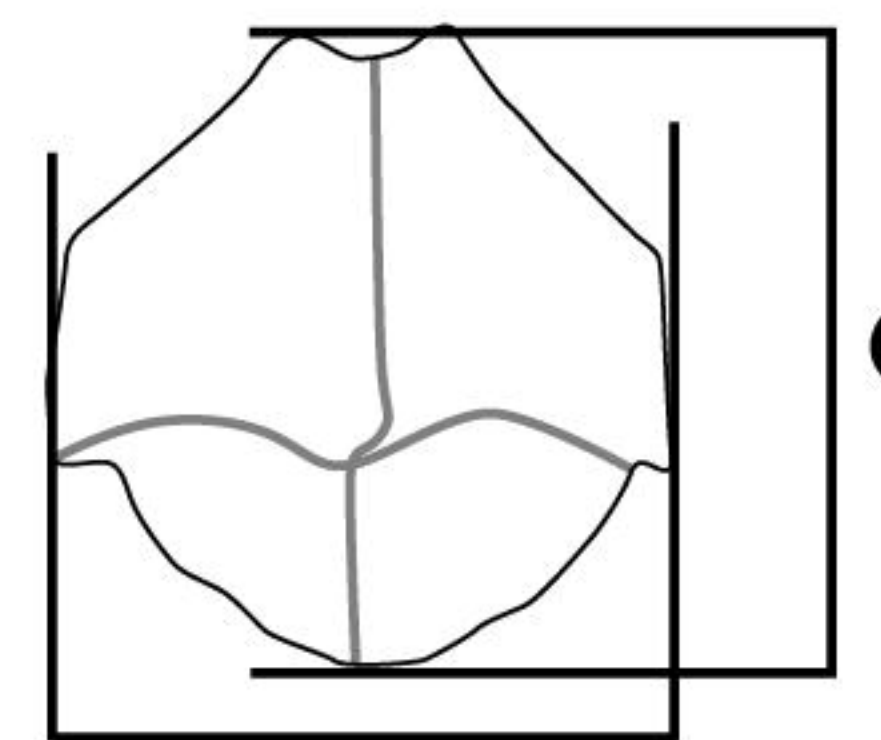
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Neural plate
(dorsal view)

GW

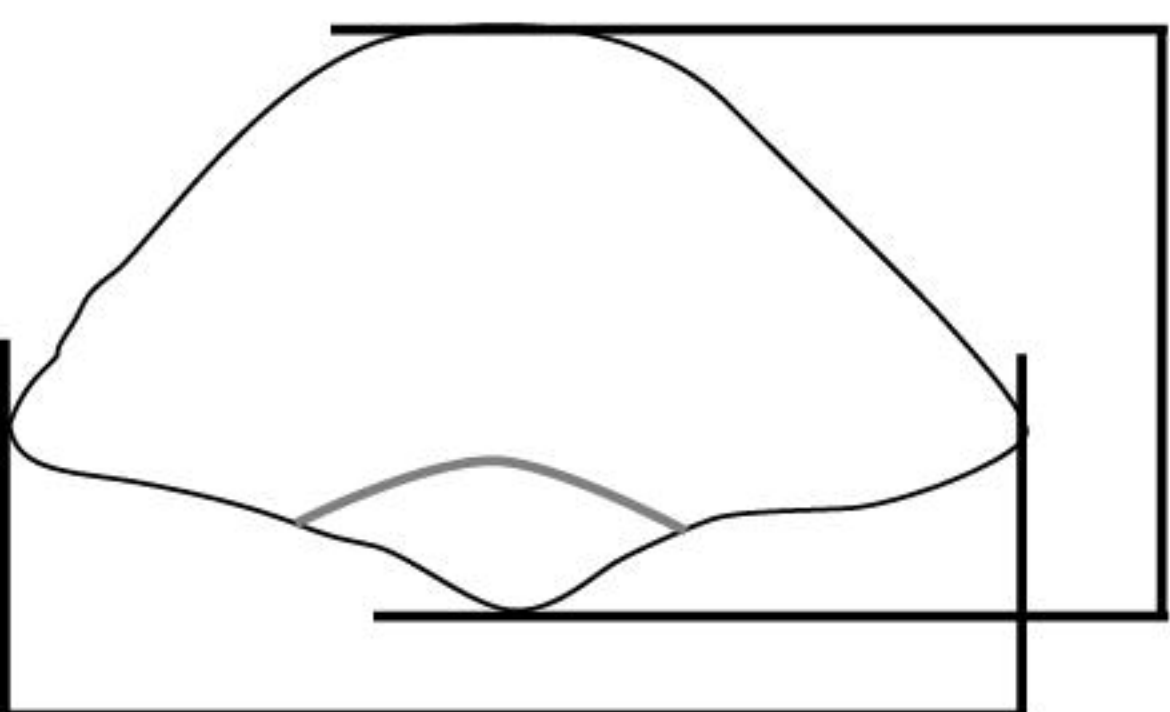
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Entoplastron
(ventral view)

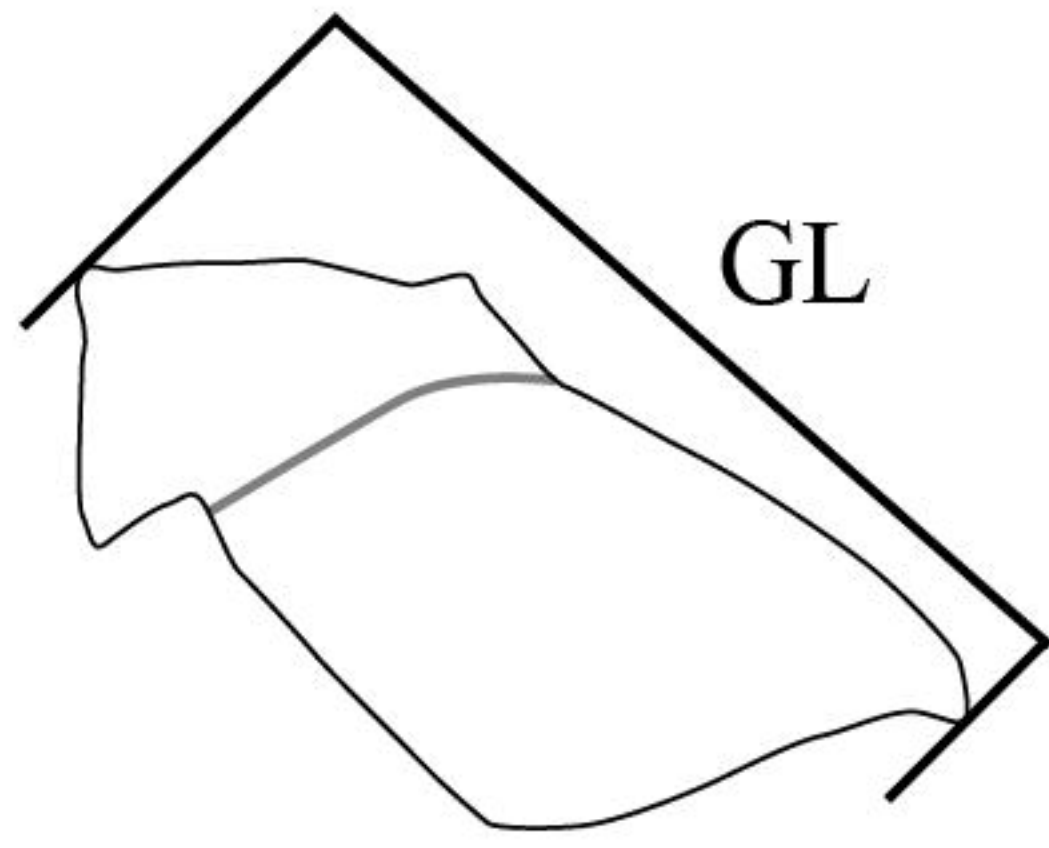
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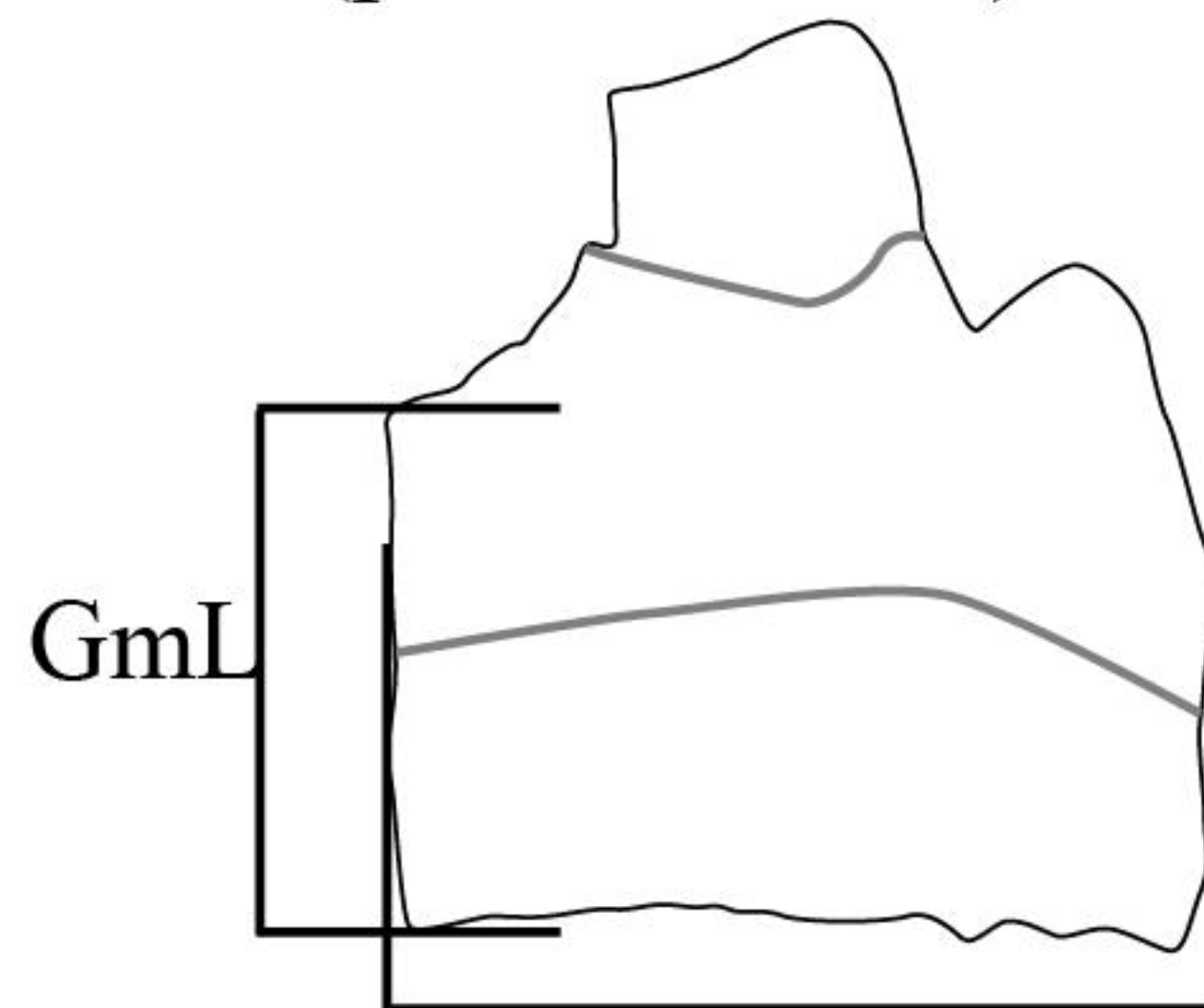
Supra-pygal plate 2
(posterior view)

GH



Epiplastron
(ventral view)

GL

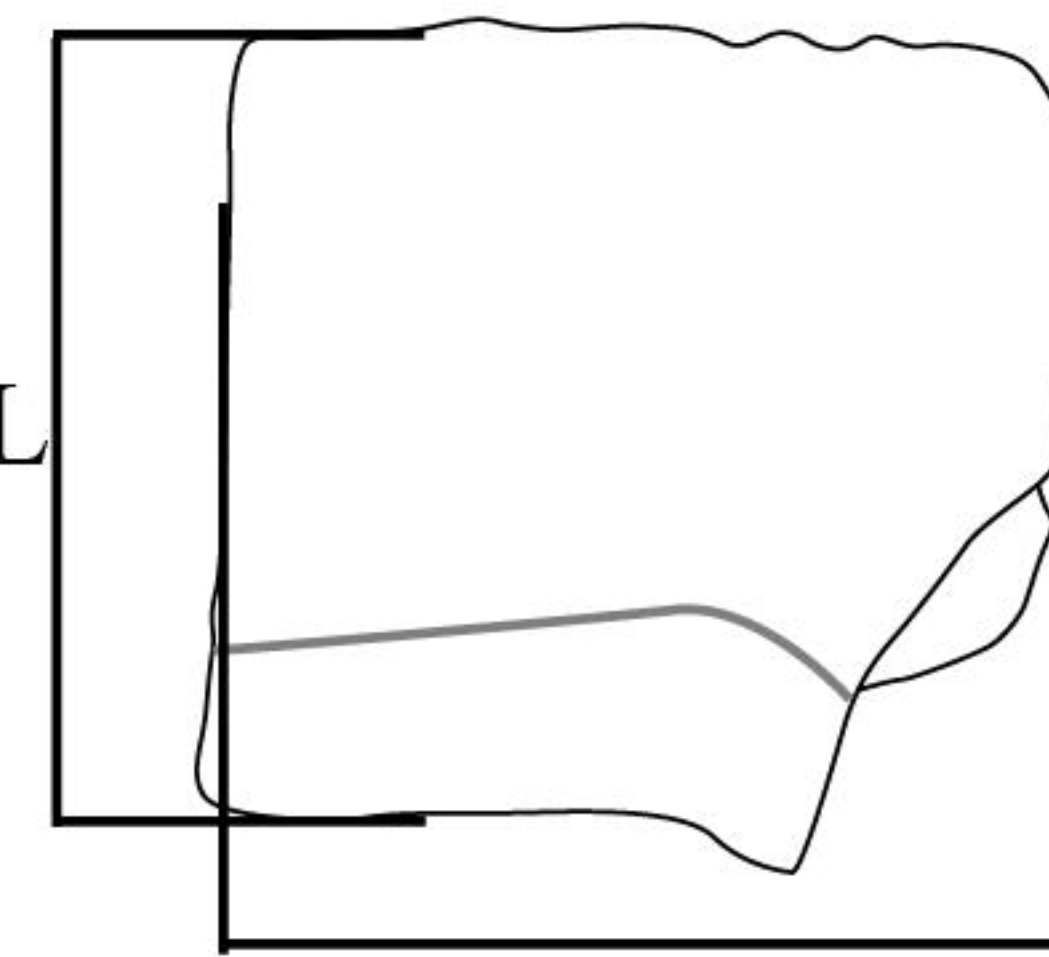


Hyoplastron
(ventral view)

GmL

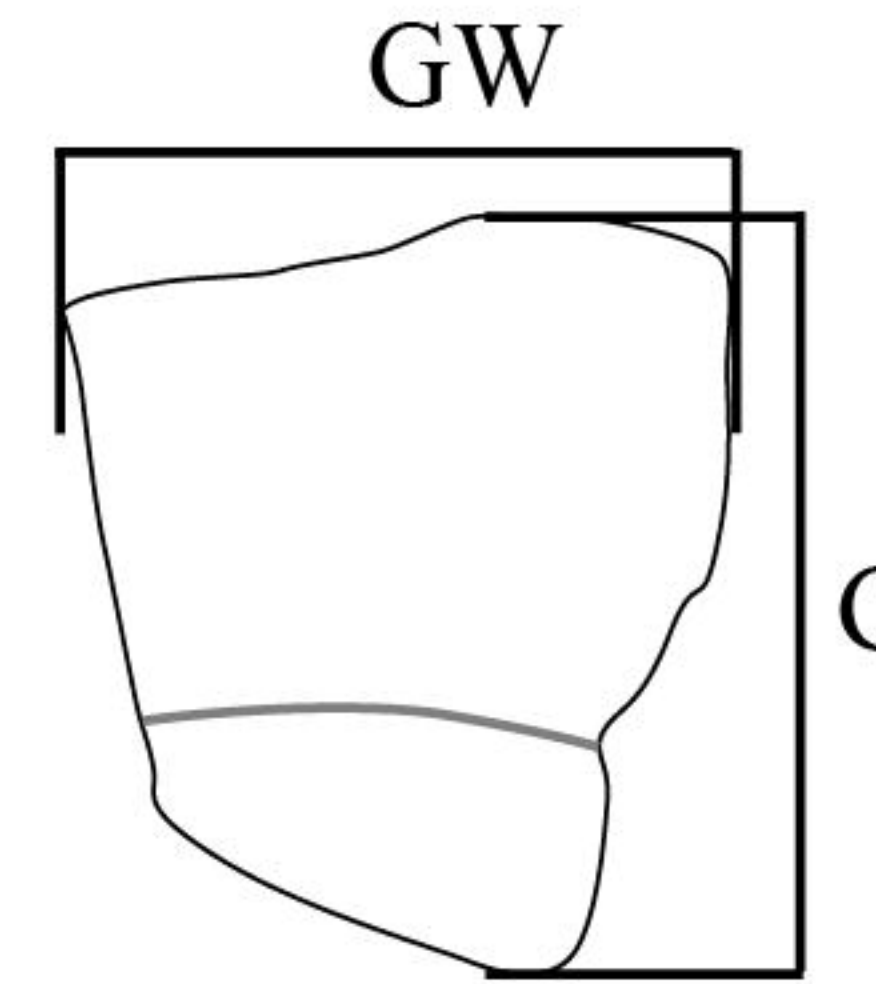
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Hypoplastron
(ventral view)

GW



Xiphiplastron
(ventral view)

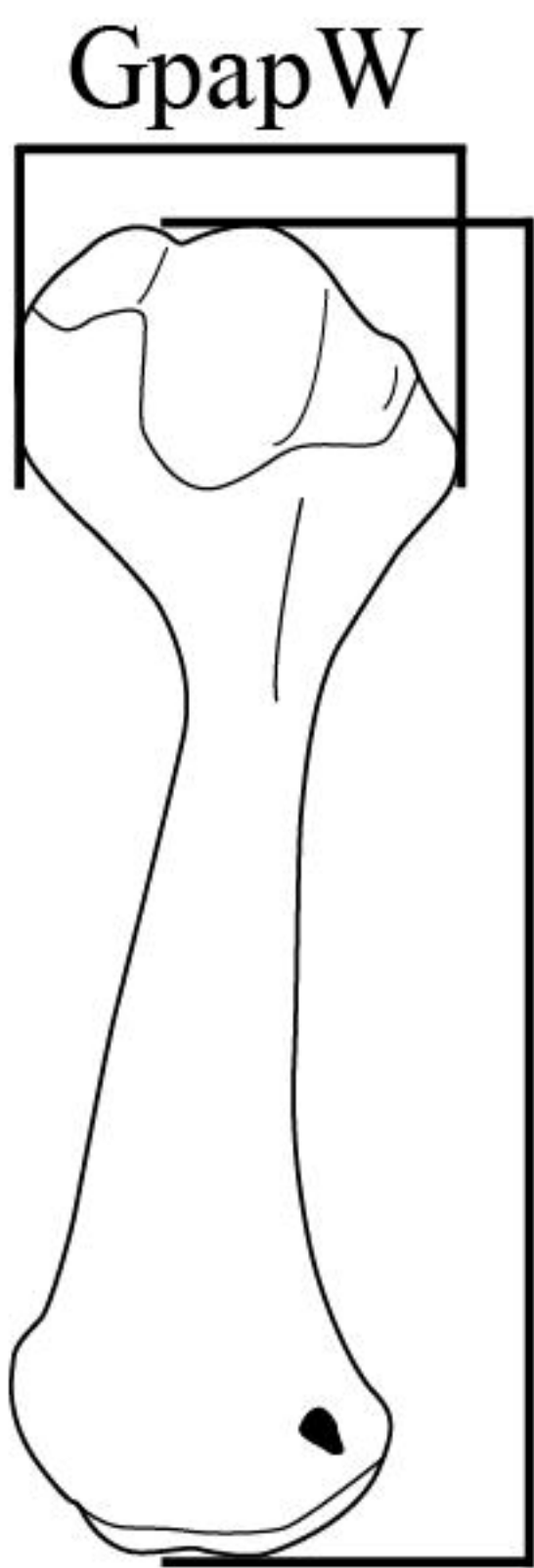
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Humerus
(Posterior view)

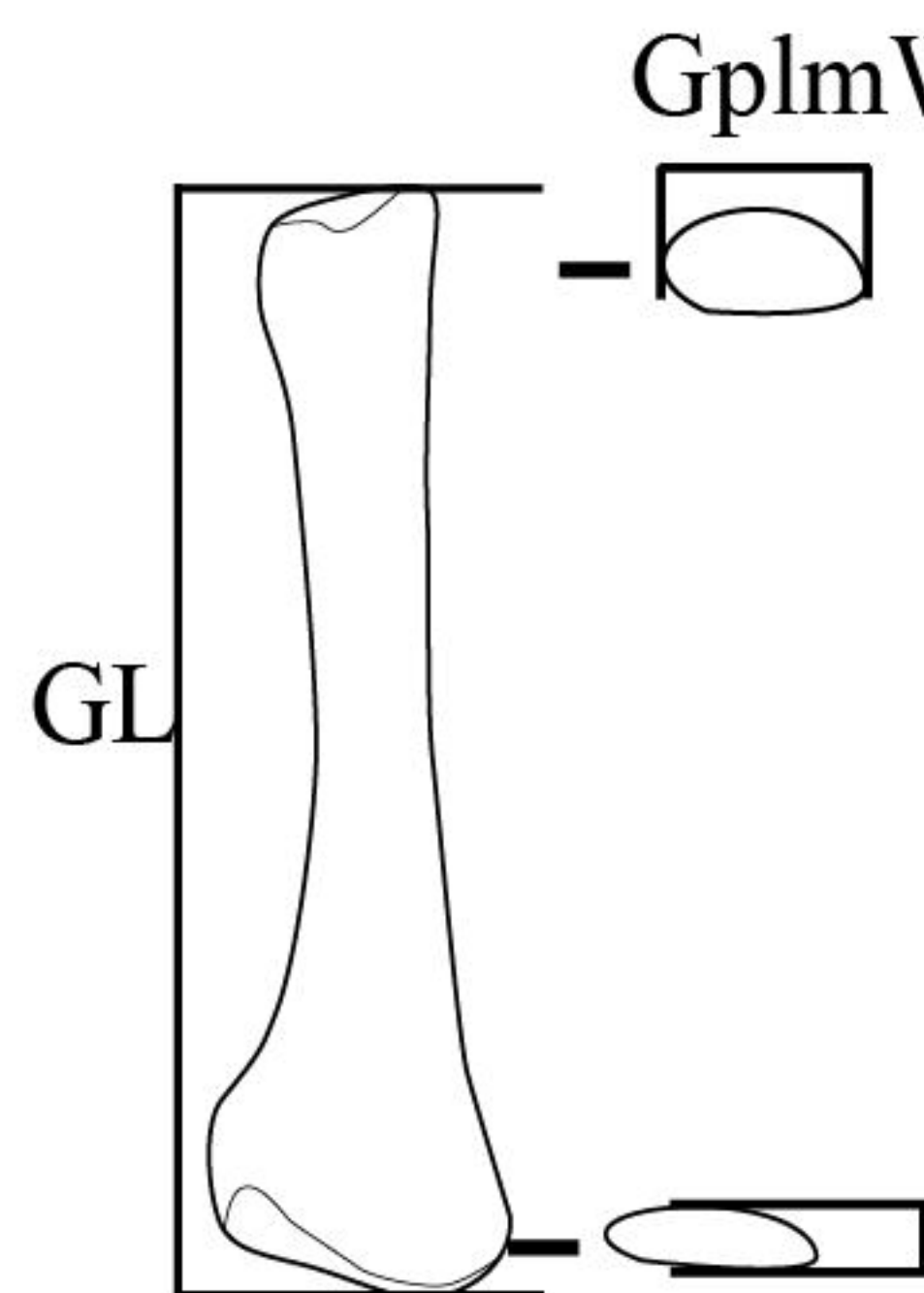
GpdvW



Humerus
(Dorsal view)

GpapW

GL

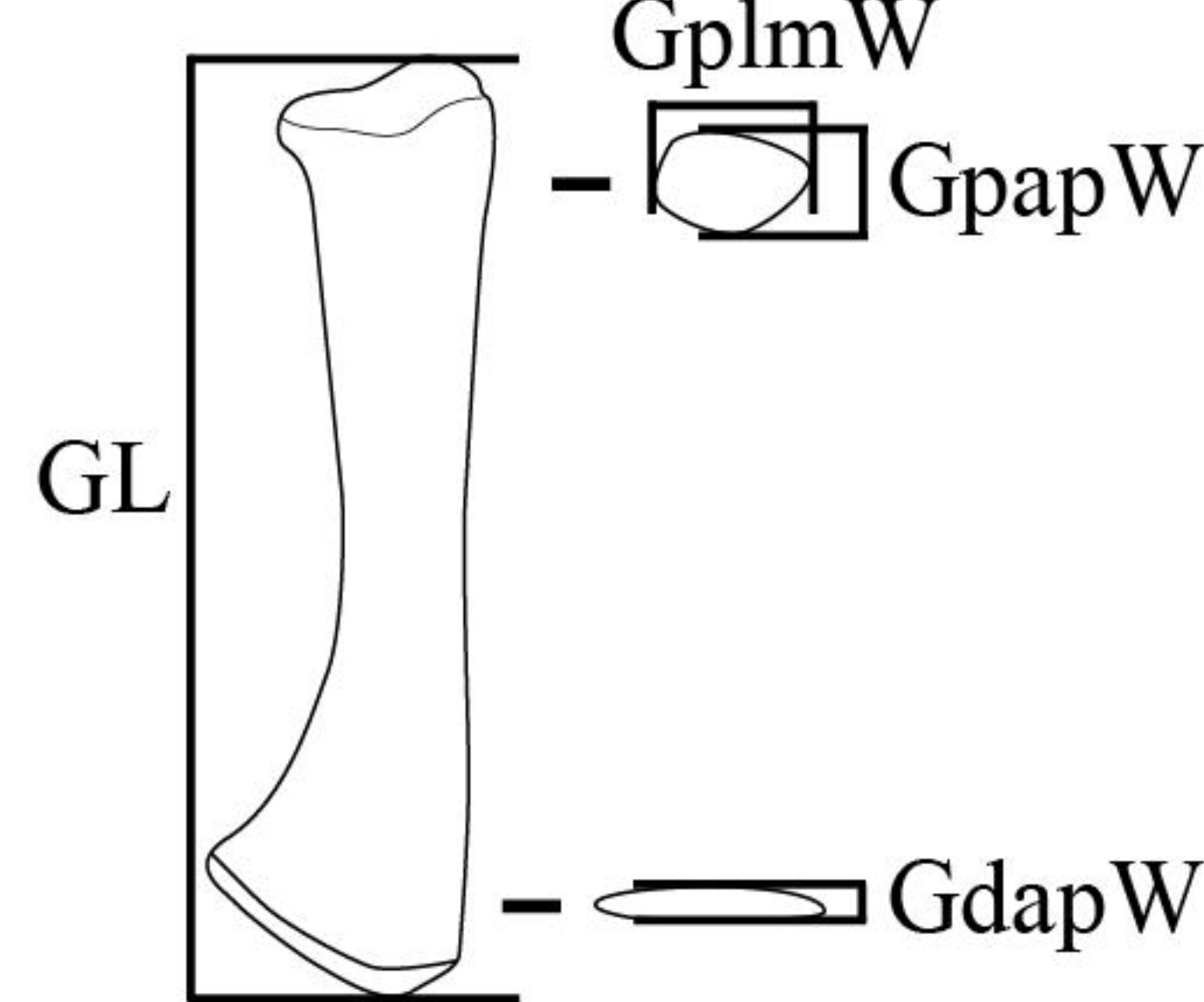


Radius

GL

GplmW

GdapW



Ulna

GL

GplmW

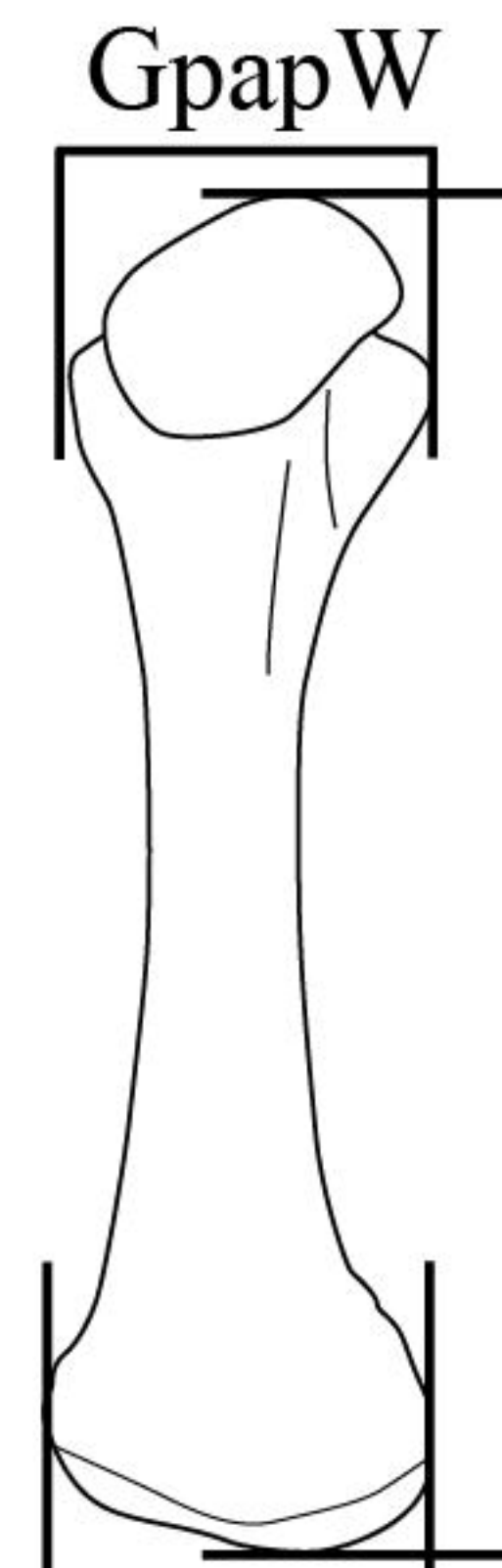
GpapW

GdapW



Femur
(Posterior view)

GpdvW



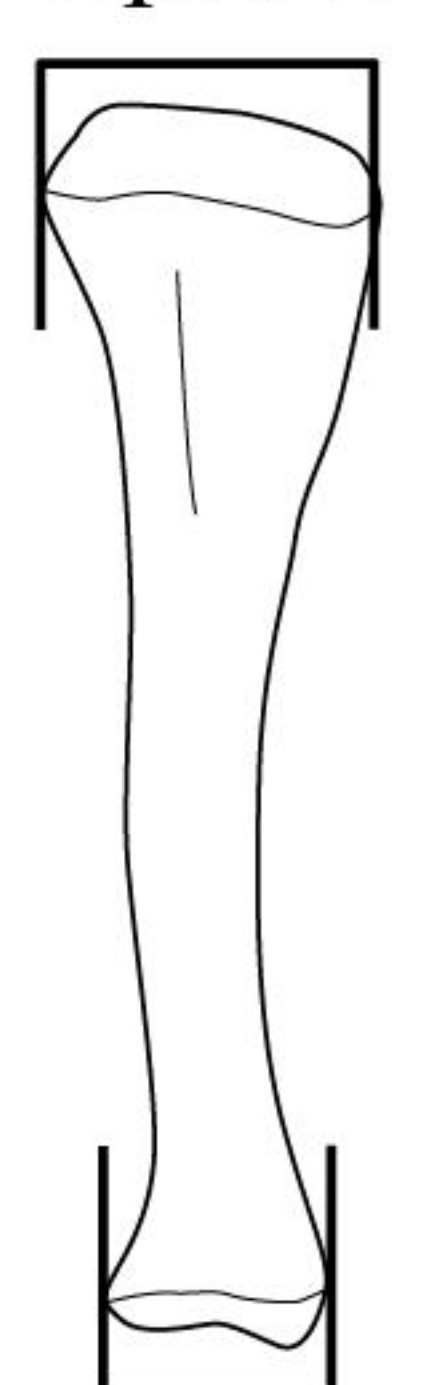
Femur
(Dorsal view)

GpapW

GdapW

GL

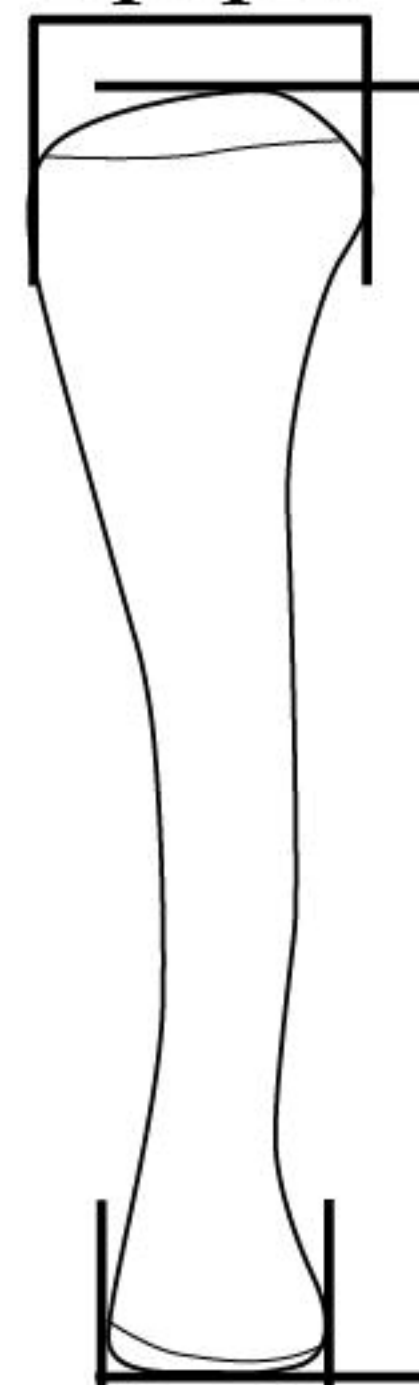
GplmW



Tibia
(Posterior view)

GdlmW

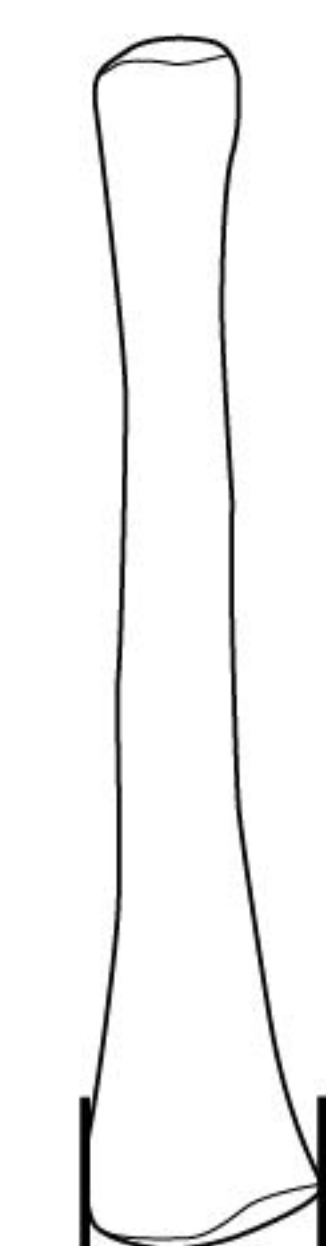
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Tibia
(Lateral view)

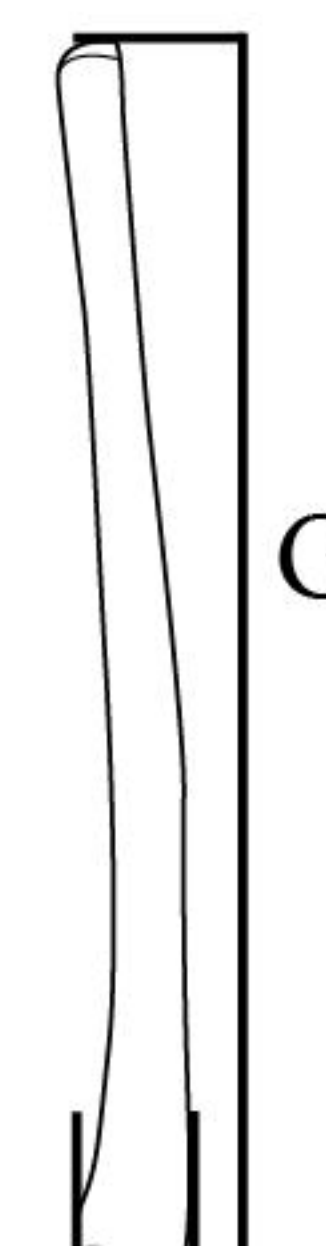
GdapW

GL



Fibula
(Lateral view)

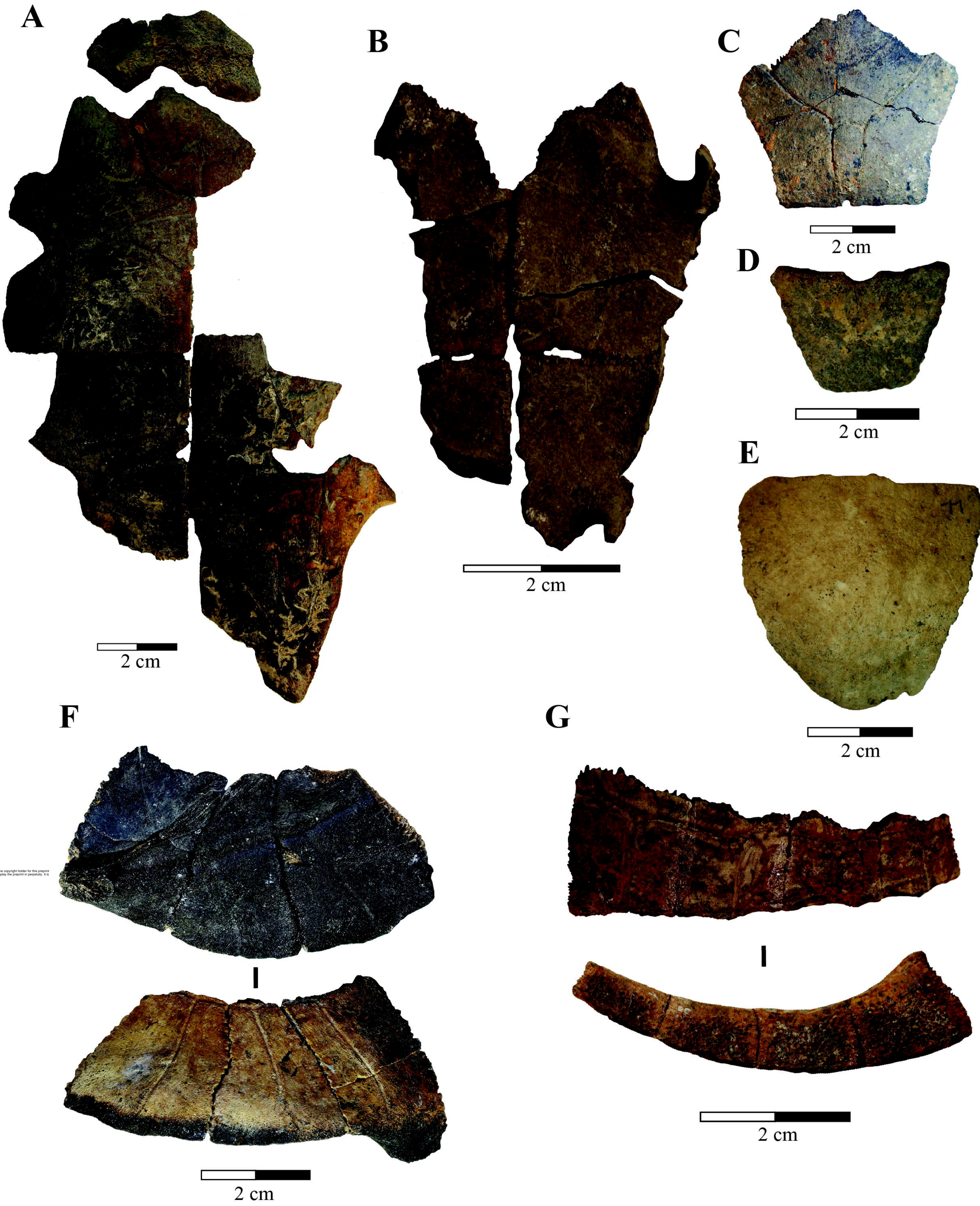
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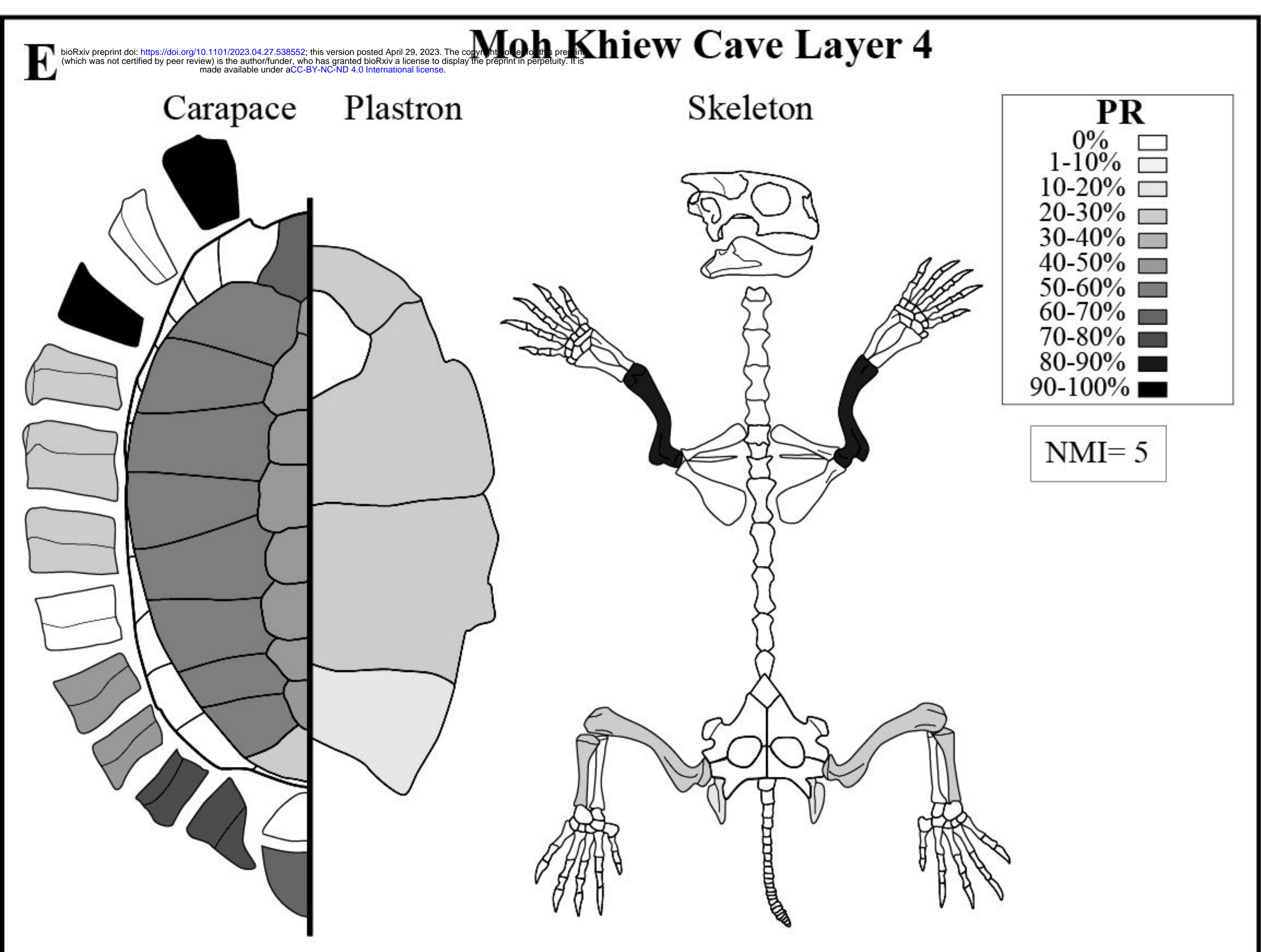
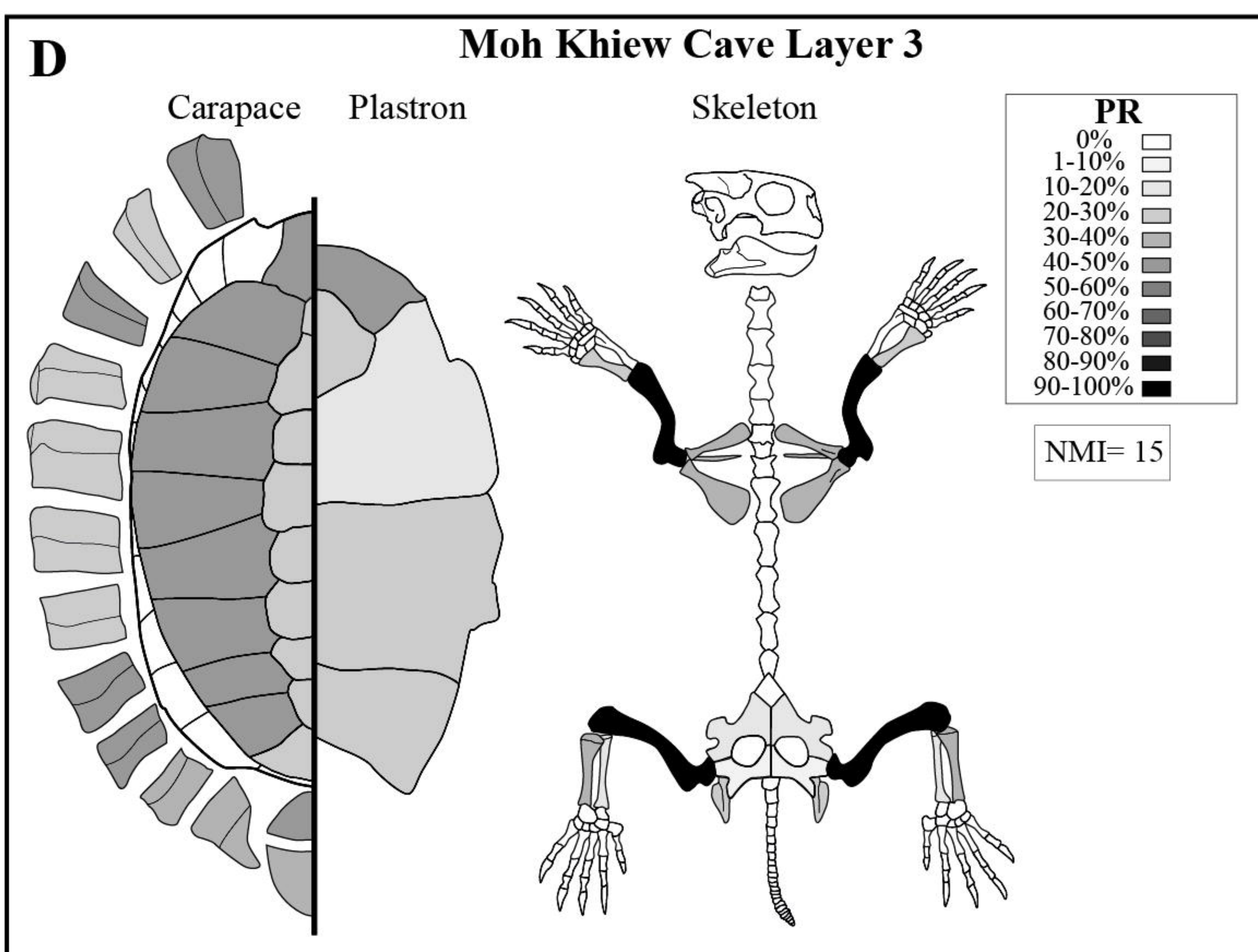
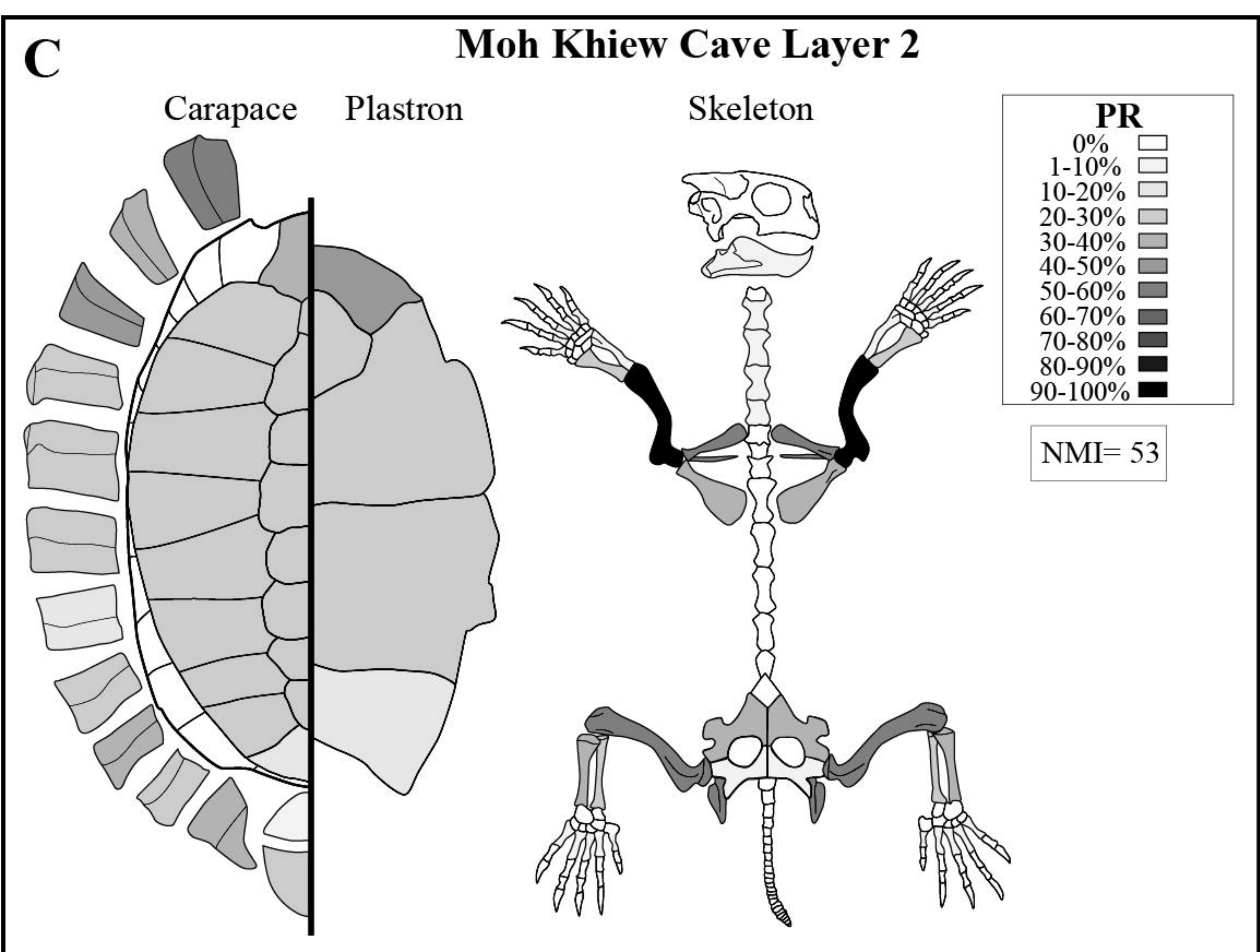
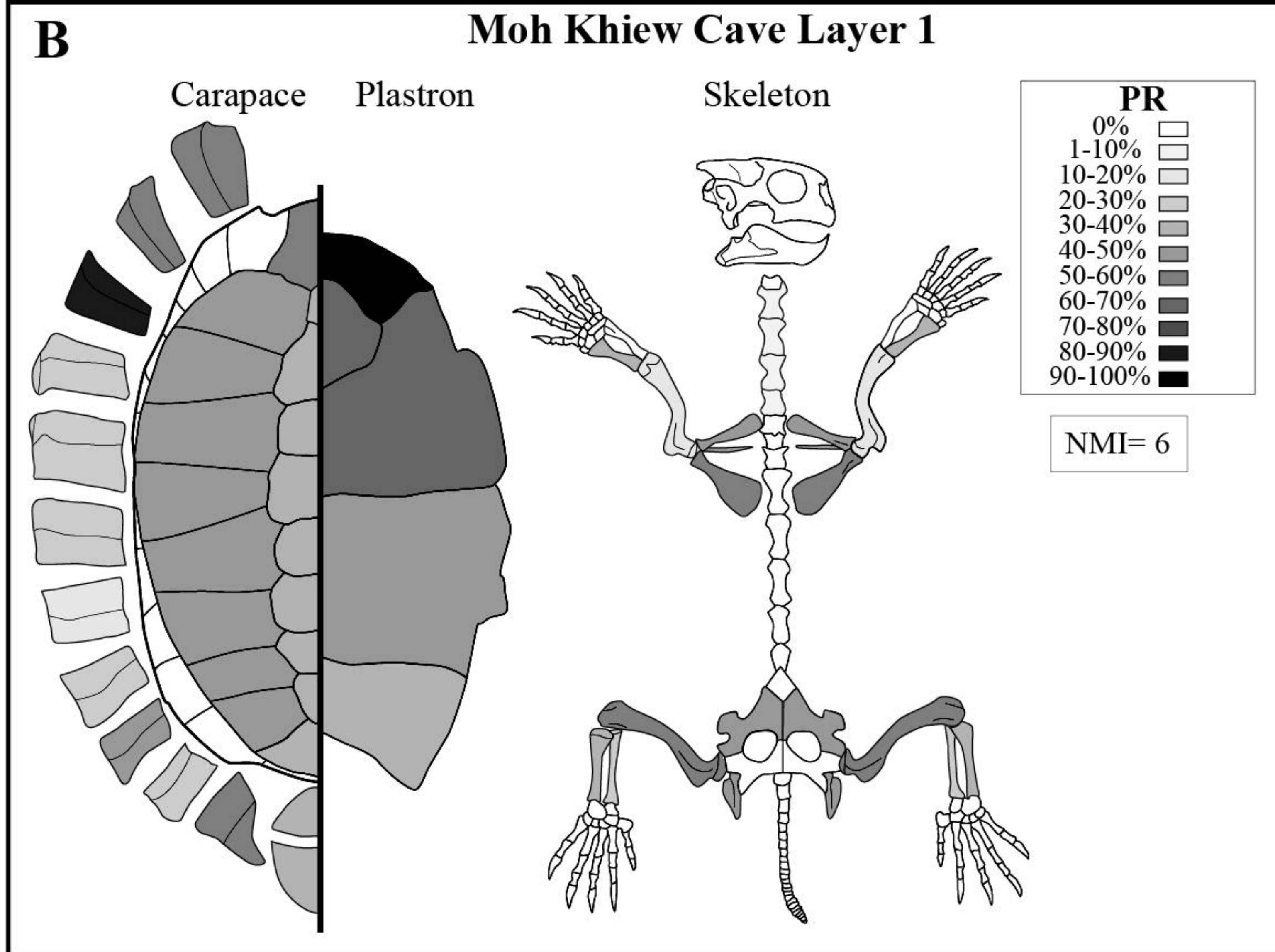
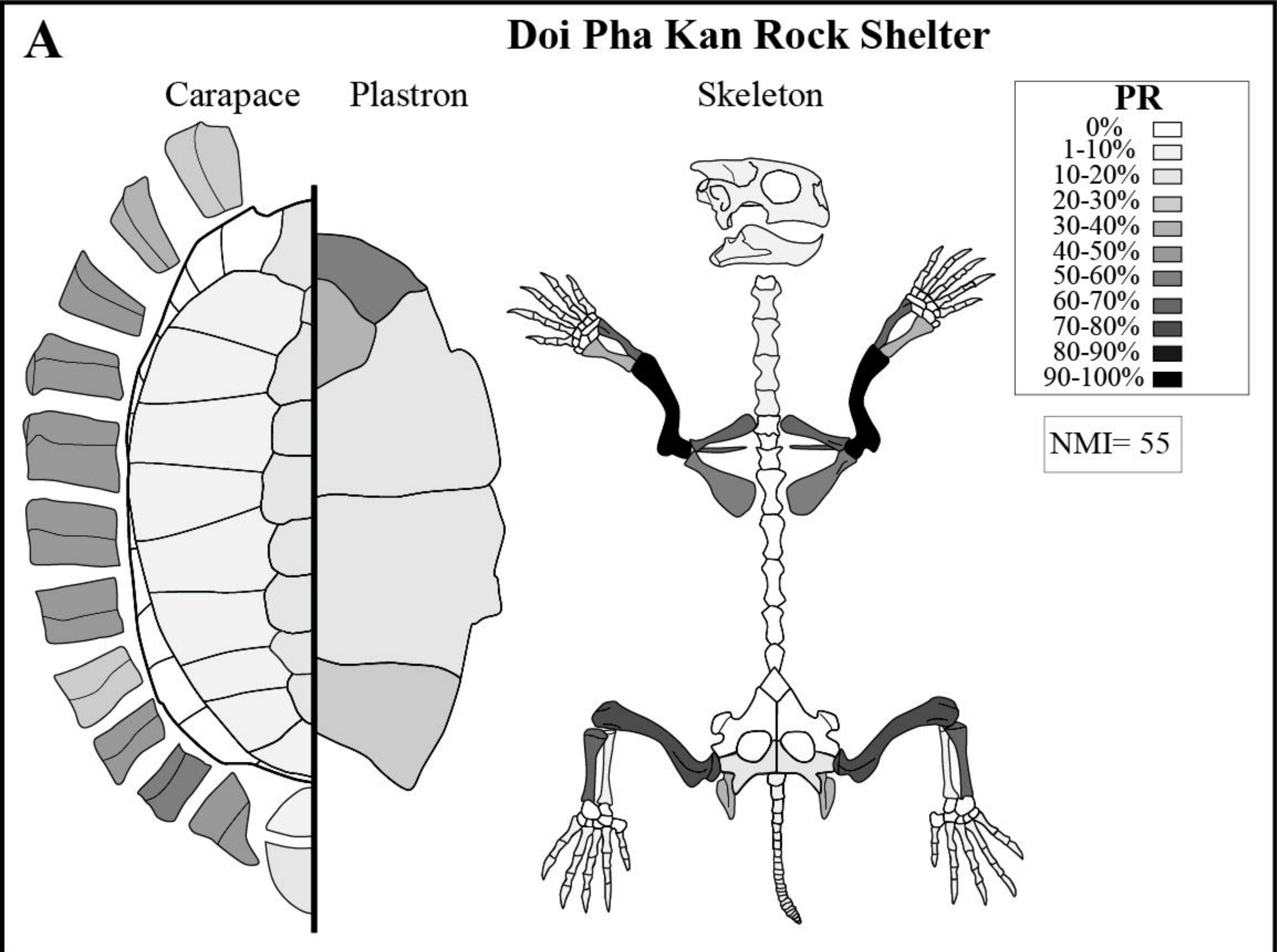


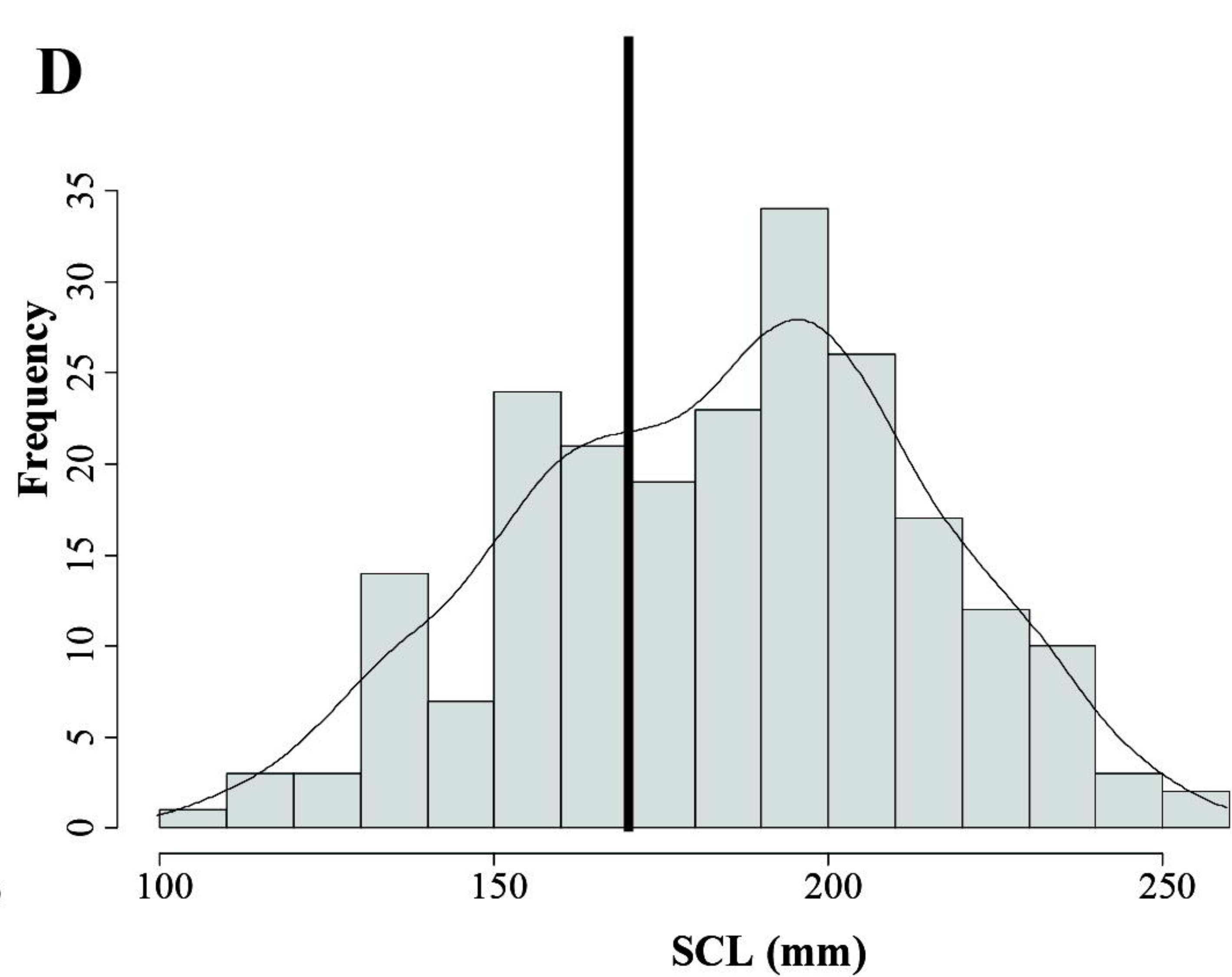
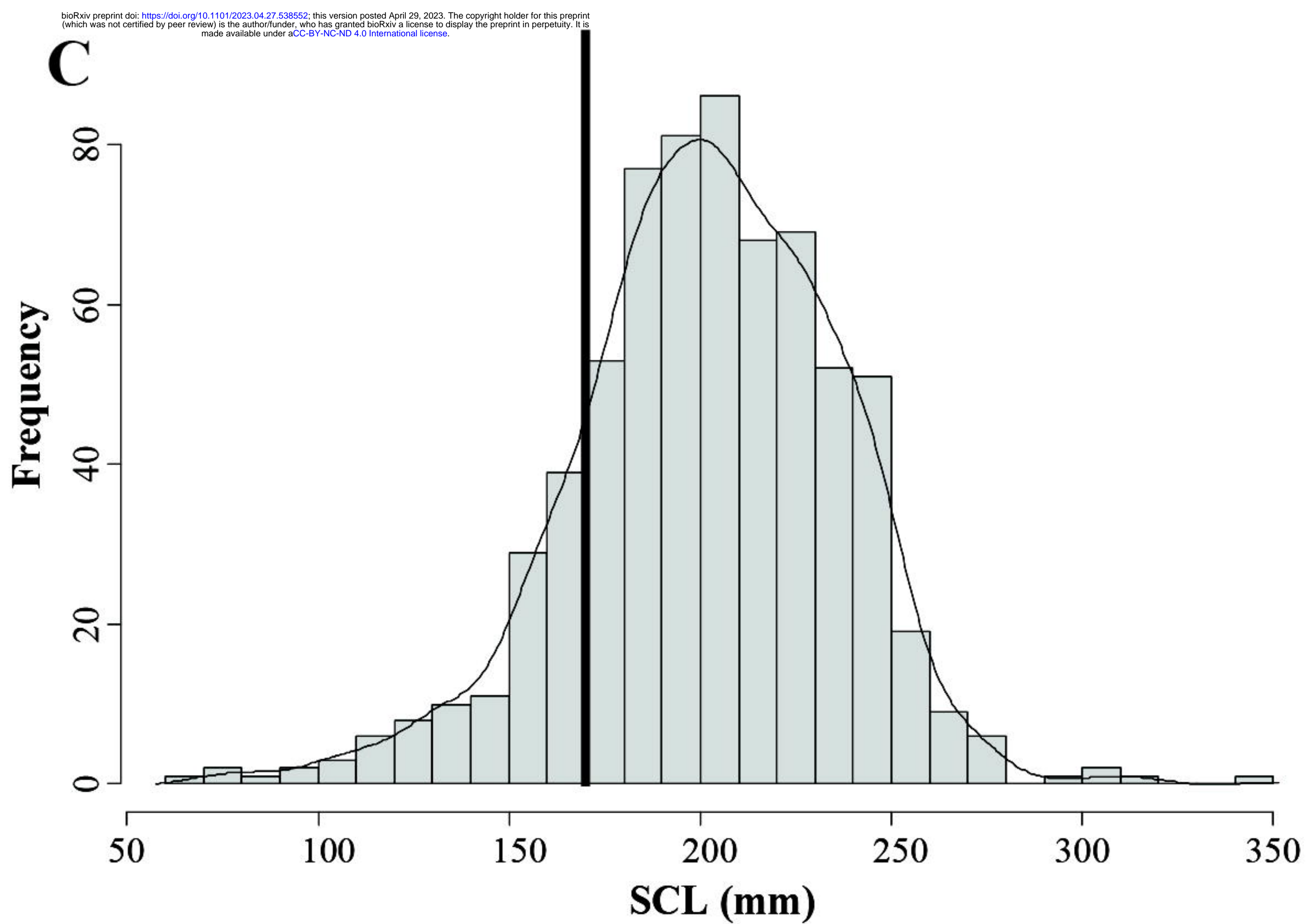
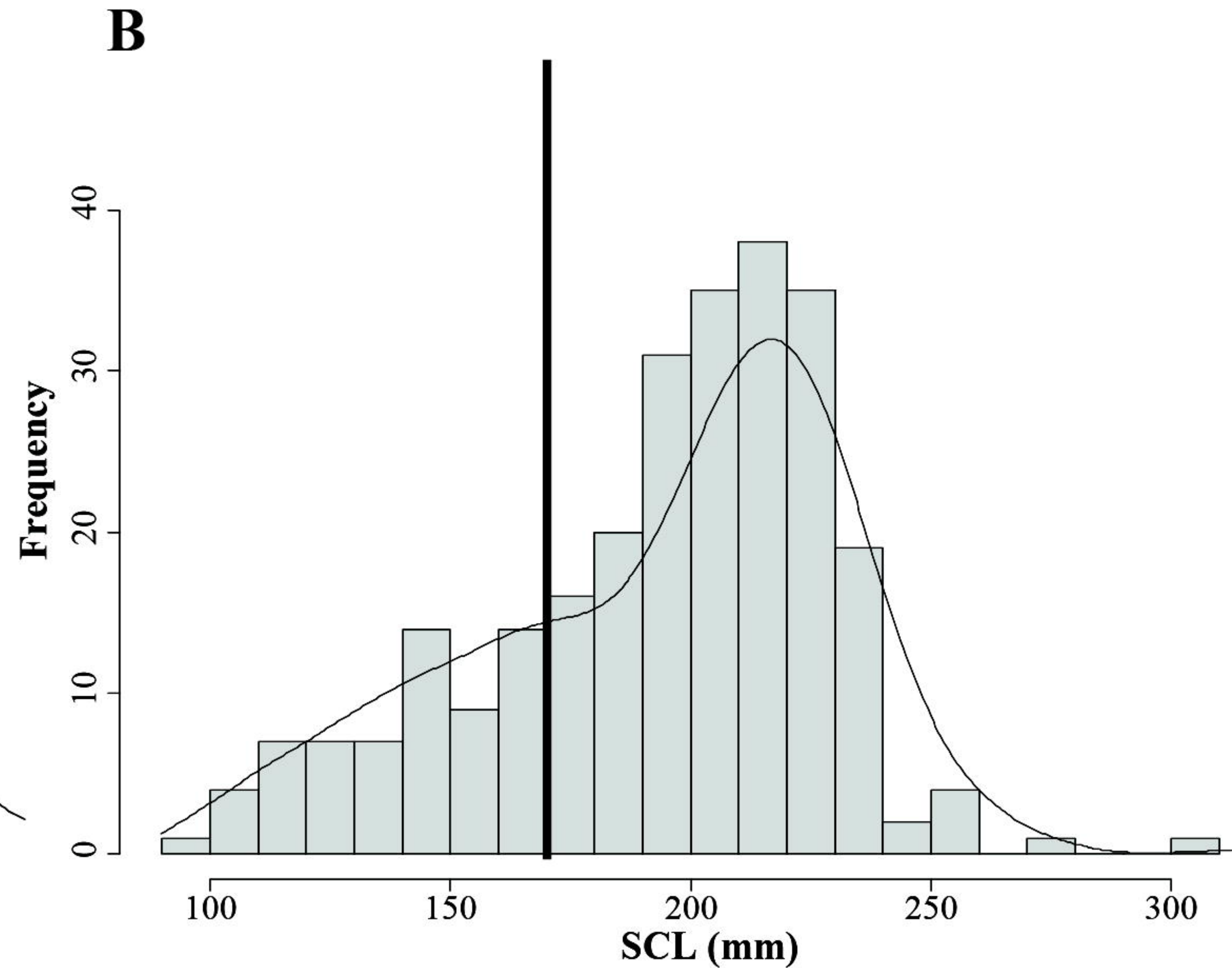
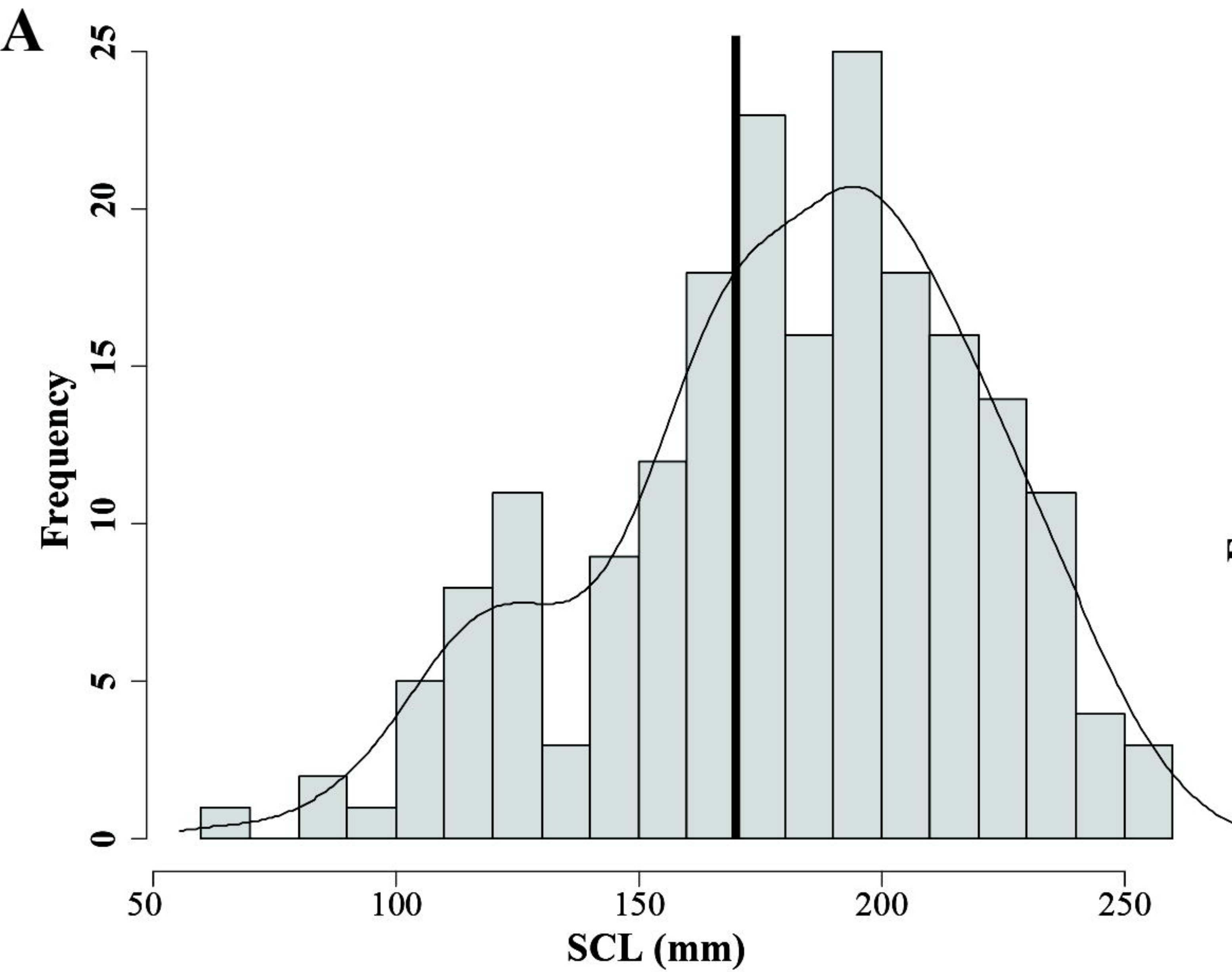
Fibula
(Posterior view)

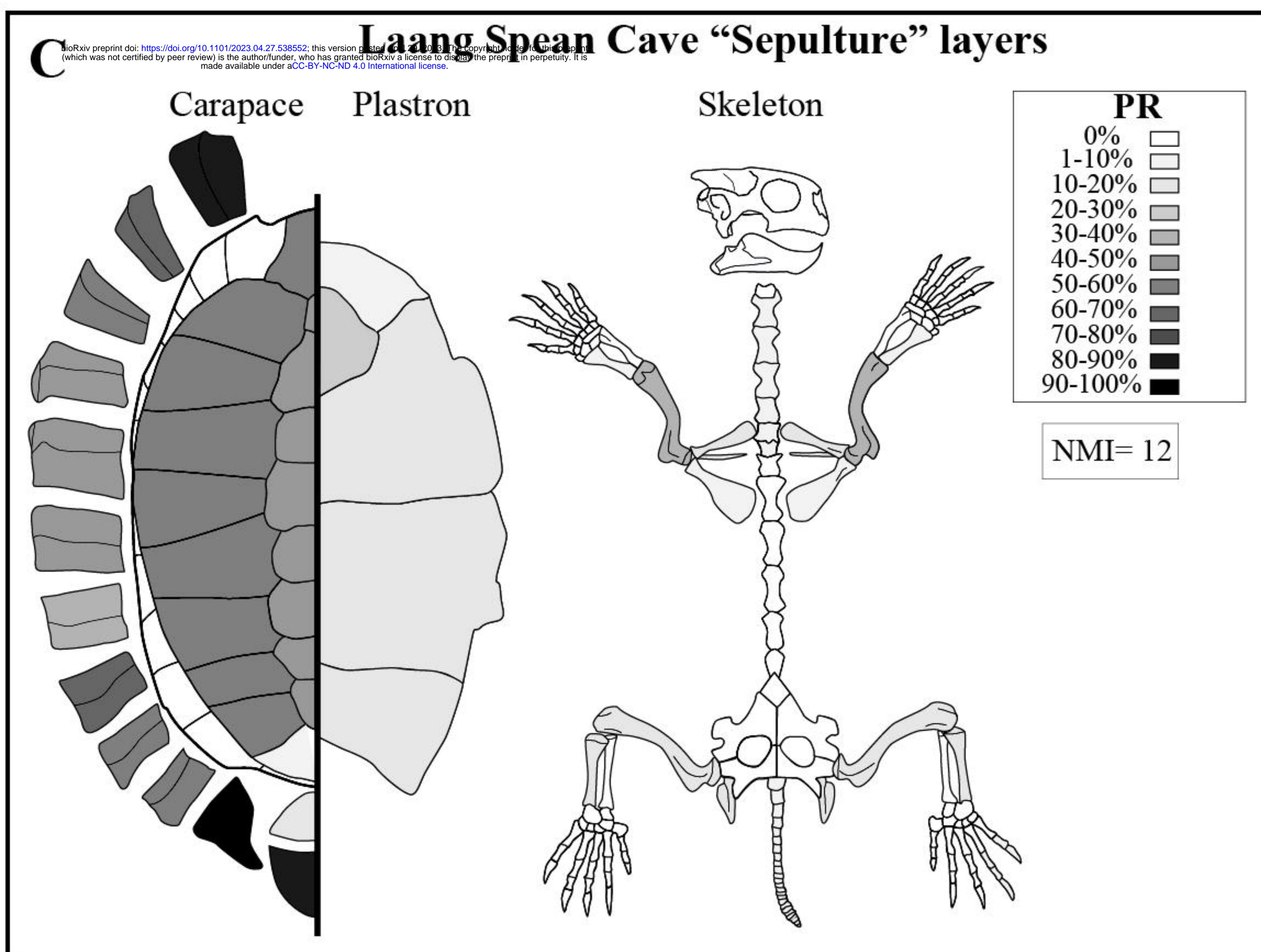
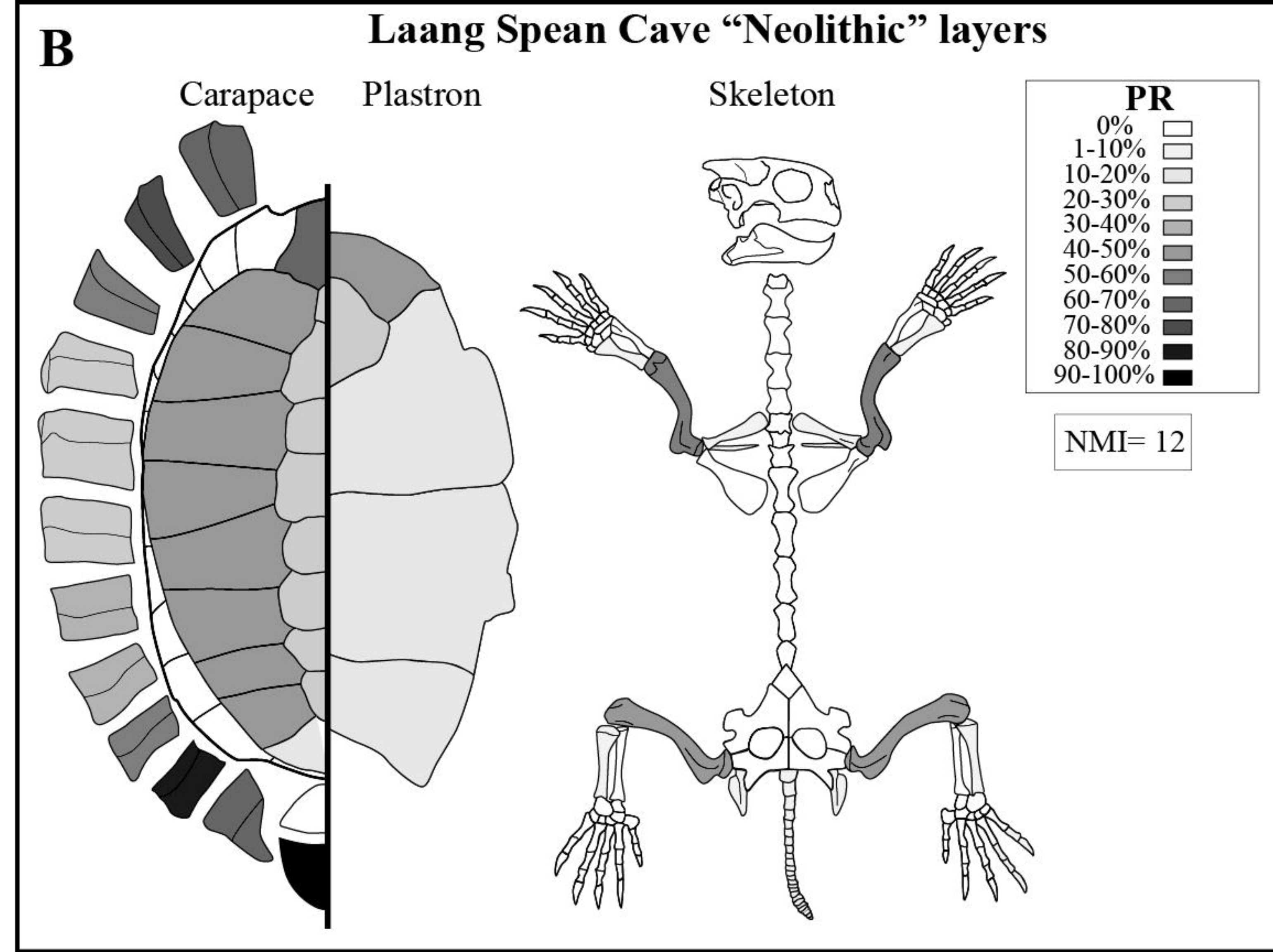
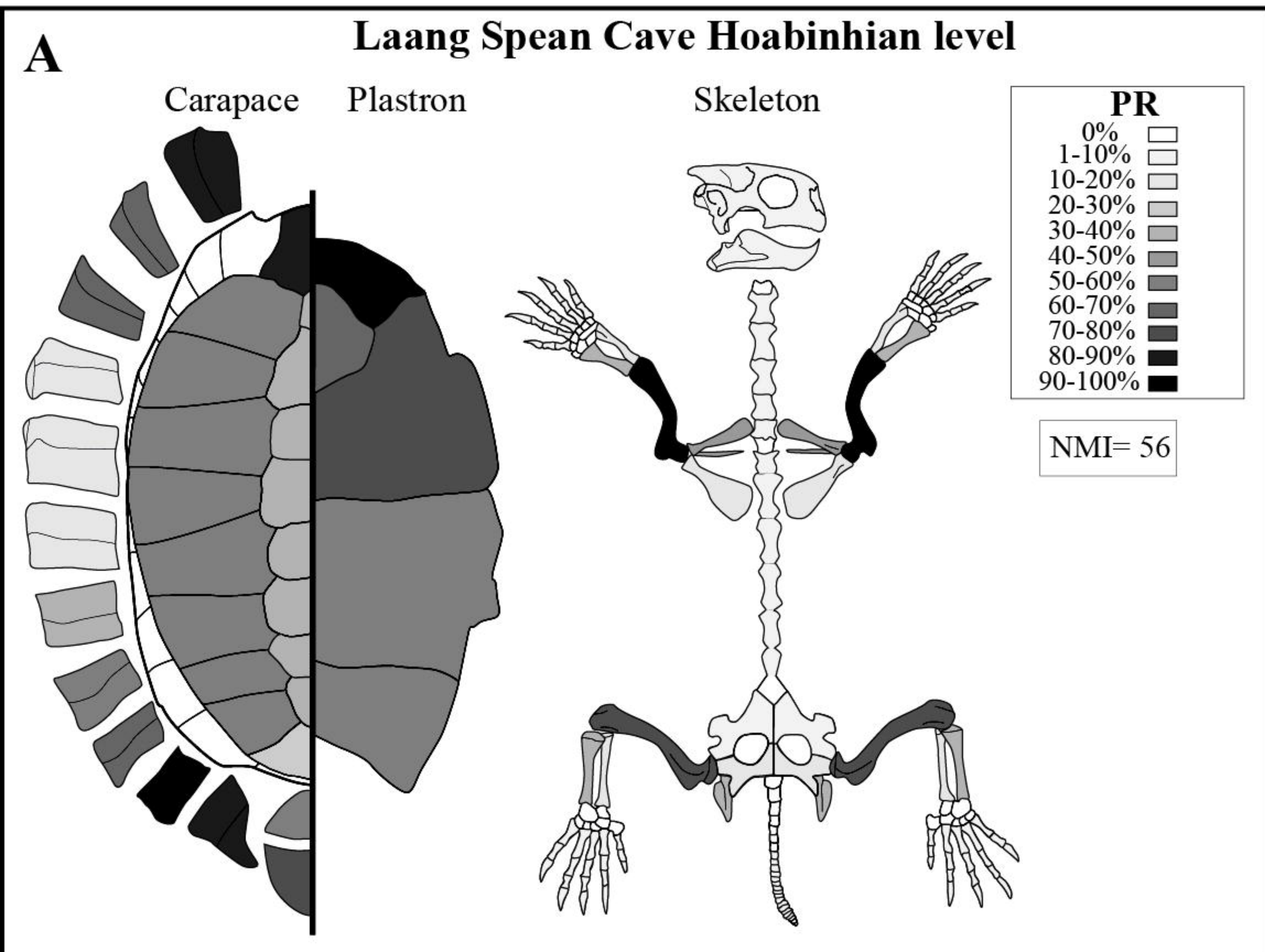
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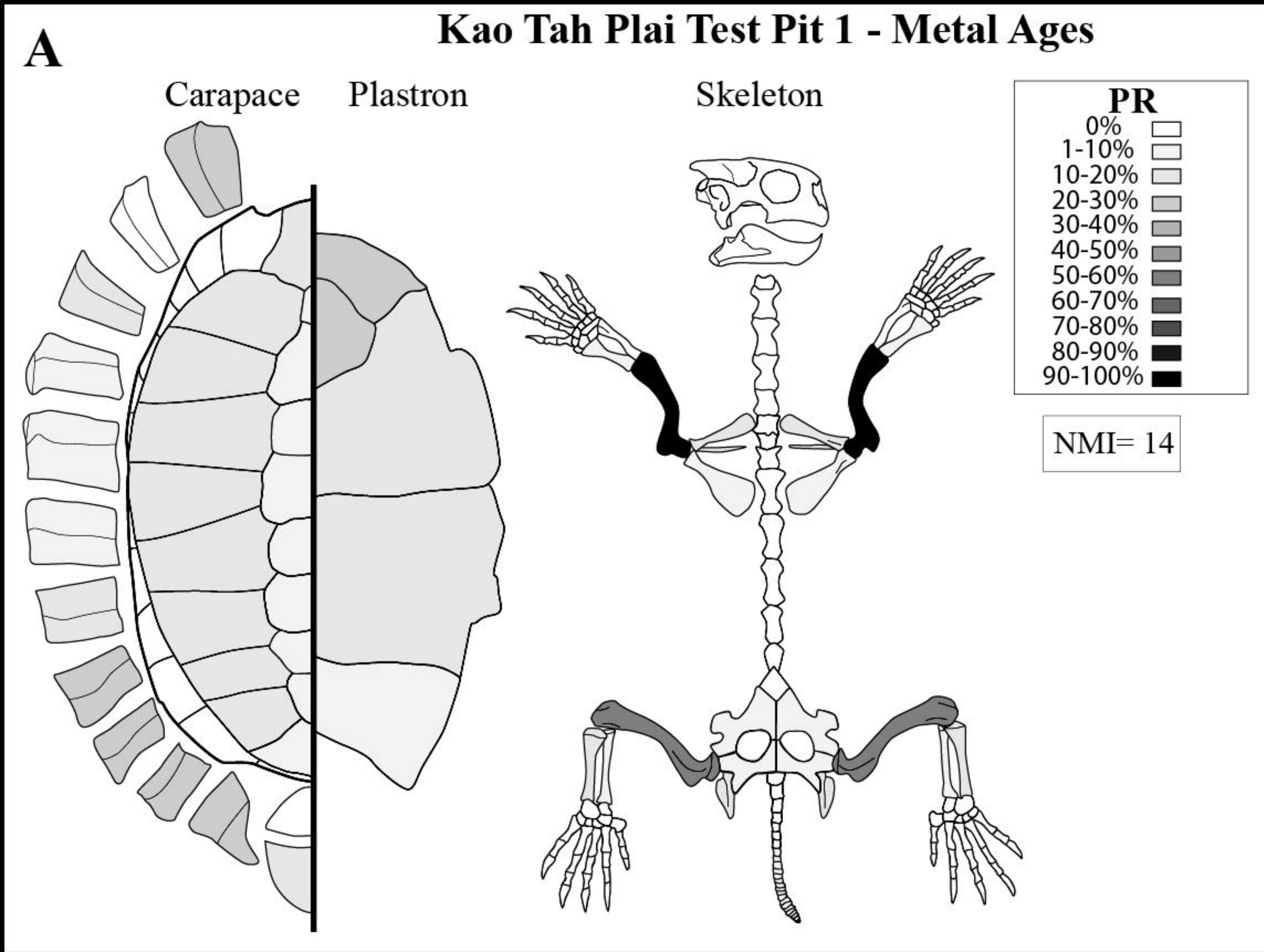




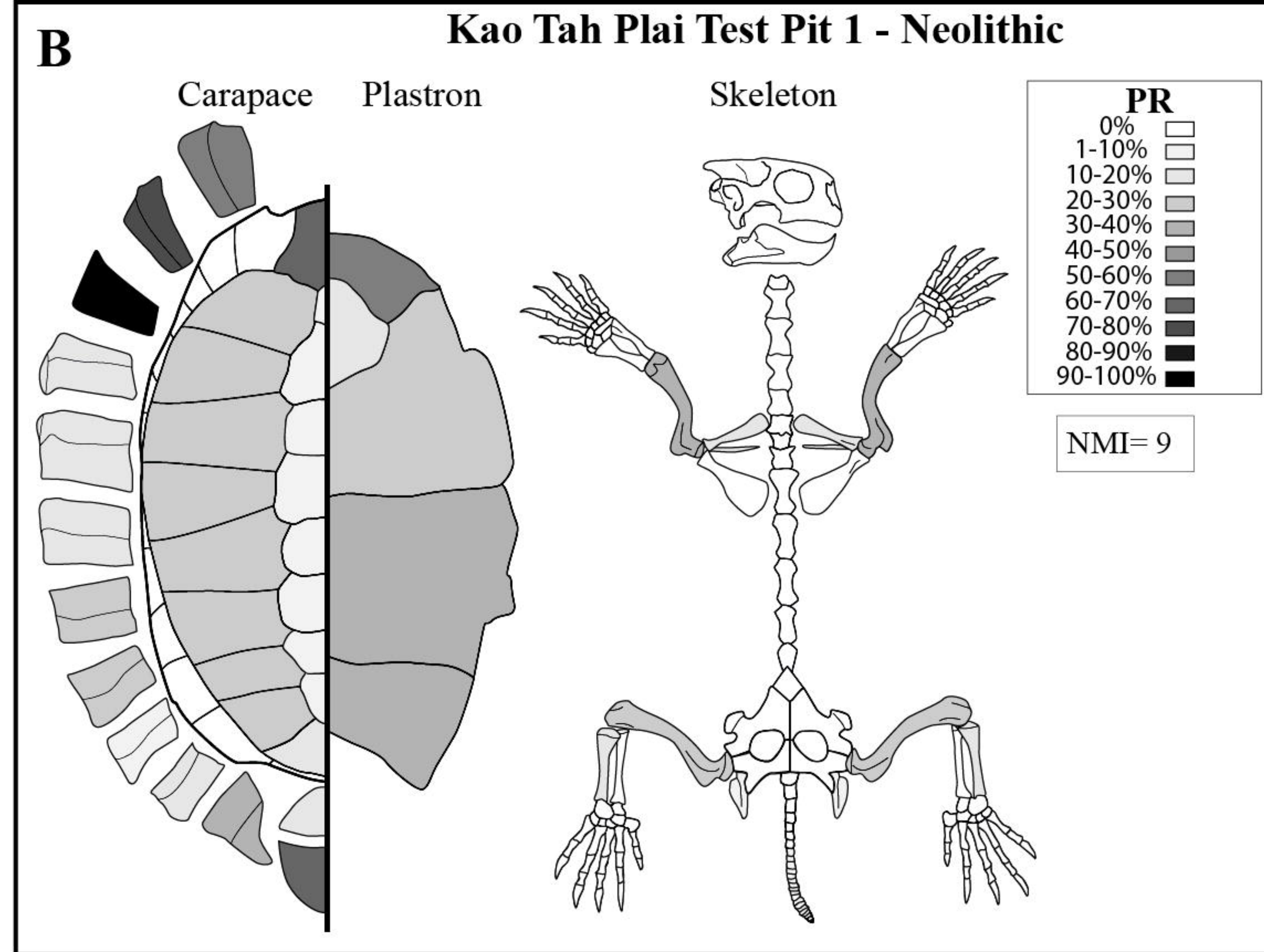




Kao Tah Plai Test Pit 1 - Metal Ages



Kao Tah Plai Test Pit1 - Neolithic



Kao Tah Plai Test Pit 2 - Neolithic

