

A peer-reviewed version of this preprint was published in PeerJ on 29 September 2020.

[View the peer-reviewed version](https://doi.org/10.7717/peerj.9840) (peerj.com/articles/9840), which is the preferred citable publication unless you specifically need to cite this preprint.

Limaverde S, Pêgas RV, Damasceno R, Villa C, Oliveira GR, Bonde N, Leal MEC. 2020. Interpreting character variation in turtles: *Araripemys barreto* (Pleurodira: Pelomedusoides) from the Araripe Basin, Early Cretaceous of Northeastern Brazil. PeerJ 8:e9840
<https://doi.org/10.7717/peerj.9840>

Interpreting character variation in turtles: *Araripemys barreto* (Pleurodira: Pelomedusoides) from the Araripe Basin, Early Cretaceous of Northeastern Brazil

Saulo Limaverde¹, Rodrigo Vargas Pêgas², Rafael Damasceno³, Chiara Villa⁴, Gustavo Oliveira³, Niels Bonde^{5,6}, Maria E. C. Leal^{Corresp. 1, 5}

¹ Centro de Ciências, Departamento de Geologia, Universidade Federal do Ceará, Fortaleza, Brazil

² Department of Geology and Paleontology, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

³ Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil

⁴ Department of Forensic Medicine, Copenhagen University, Copenhagen, Denmark

⁵ Section Biosystematics, Zoological Museum (SNM, Copenhagen University), Copenhagen, Denmark

⁶ Fur Museum (Museum Saling), Fur, DK-7884, Denmark

Corresponding Author: Maria E. C. Leal
Email address: castroleal@gmail.com

The Araripe Basin (Northeastern Brazil) has yielded a rich Cretaceous fossil fauna of both vertebrates and invertebrates found mainly in the Crato and Romualdo Formations, of Aptian and Albian ages respectively. Among the vertebrates, the turtles were proved quite diverse, with several specimens retrieved and five valid species described to this date for the Romualdo Fm. There were also records of turtles from Ipubi and Crato Fms., mainly fragmentary material which precluded proper specific identification; however, *Araripemys barreto* is supposed to occur on both Crato and Romualdo Fms. Here we describe thirteen specimens of *A. barreto* - including the first description of an almost complete individual, bearing a skull, from the Crato Fm. We report a great amount of morphological variation, interpreted as being essentially of intraspecific nature, including individual, sexual and ontogenetic variation.

Interpreting character variation in turtles: *Araripemys barreto* (Pleurodira: Pelomedusoides) from the Araripe Basin, Early Cretaceous of Northeastern Brazil

Saulo Limaverde¹, Rodrigo V. Pêgas², Rafael C. Damasceno³, Chiara Villa⁴, Gustavo R. Oliveira³, Niels Bonde^{5,6}, Maria E. C. Leal^{1,5*}

¹Centro de Ciências, Departamento de Geologia, Universidade Federal do Ceará, Campus do PICI – BL. 912, CEP. 60455-760, Fortaleza, CE, Brazil;

²Laboratory of Systematics and Taphonomy of Fossil Vertebrates, Departamento de Geologia e Paleontologia, Universidade Federal do Rio de Janeiro, Museu Nacional, Quinta da Boa Vista s/n, São Cristóvão, CEP. 20940-040 Rio de Janeiro, RJ, Brazil; ³Laboratório de Paleontologia & Sistemática, Área de Ecologia, Departamento de Biologia, Universidade Federal Rural de Pernambuco, R. Dom Manuel de Medeiros s/n, Dois Irmãos, CEP. 52171-900, Recife, PE, Brazil;

⁴Laboratory of Biological Anthropology, Department of Forensic Medicine, Frederik V's Vej 11, 2100 Copenhagen Ø, Denmark;

⁵Section Biosystematics, Zoological Museum (SNM, Copenhagen University), Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark;

⁶Fur Museum (Museum Salling), DK-7884 Fur, Denmark.

* Corresponding author e-mail: castroleal@gmail.com

Abstract

The Araripe Basin (Northeastern Brazil) has yielded a rich Cretaceous fossil fauna of both vertebrates and invertebrates found mainly in the Crato and Romualdo Formations, of Aptian and Albian ages respectively. Among the vertebrates, the turtles were proved quite diverse, with several specimens retrieved and five valid species described to this date for the Romualdo Fm. There were also records of turtles from Ipubi and Crato Fms., mainly fragmentary material which precluded proper specific identification; however, *Araripemys barreto* is supposed to occur on both Crato and Romualdo Fms. Here we describe thirteen specimens of *A. barreto* - including the first description of an almost complete individual, bearing a skull, from the Crato Fm. We report a great amount of morphological variation, interpreted as being essentially of intraspecific nature, including individual, sexual and ontogenetic variation.

Keywords: Araripe. Cretaceous. *Araripemys*. Intraspecific variation. Sexual dimorphism. Polymorphism. Ontogeny.

Introduction

The Testudines are remarkable reptiles that possess a bony shell alongside other unique morphological characters, such as a shoulder girdle enclosed by the ribcage. The Testudines are nowadays split in two monophyletic groups: Pleurodire (side-necked) and Cryptodire (hidden-necked) turtles (Gaffney, 1975; Joyce *et al.* 2004). Among living turtles, pleurodires show less species diversity than cryptodires and, currently, are restricted only to fresh water habitats in the southern hemisphere (e.g. Gaffney *et al.* 2006; Romano & Azevedo, 2006; Sereno & ElShafie, 2013). The diversity of species and habitats, and the geographic range of pleurodires were considerably larger in the past and seem to have reached its peak between the beginning of the Late Cretaceous (circa 100 m.y.a.) and the final Paleocene (circa 55 m.y.a.; Gaffney *et al.* 2006; Danilov & Parham 2008). The earliest record of an unambiguous pleurodire turtle – *Caribemys oxfordiensis*, a marine form – comes from the Upper Jurassic (Oxfordian) of the Jagua Fm. in Cuba (de la Fuente & Iturralde-Vinent 2001). The pleurodire crown-group potentially appears for the first time in the fossil record at the Early Cretaceous (Valanginian) with the remains of the potentially oldest podocnemidoid turtle: a left costal and a peripheral bone from the Rosablanca Fm. in Colombia (Cadena, 2011; but see Romano *et al.*, 2014). From the Barremian comes the earliest confirmed crown pleurodiran species, *Atolchelys lepida* (Pelomedusoides, Bothremydidae) from the Morro do Chaves Fm., Sergipe-Alagoas Basin (Romano *et al.*, 2014). Also from Early Cretaceous age (Aptian-Albian) are *Araripemys barretoii* from the Crato and Romualdo Formations of the Araripe Basin, Brazil (Price 1973; Oliveira *et al.* 2011; Oliveira & Kellner, 2017), and *Laganemys tenerensis*, from the Elharz Fm. of the Illumedden Basin in Niger (Sereno & ElShafie, 2013).

The Pleurodira are split in two clades: Cheloides and Pelomedusoides (Sereno & ElShafie, 2013). The Cheloides comprise a single family, Chelidae, ranging from Cretaceous to present day (de la Fuente *et al.*, 2001; Lapparent de Broin & de la Fuente, 2001; de la Fuente, 2003; Bona & de la Fuente, 2005), while the Pelomedusoides comprise five families, the extant Pelomedusidae and Podocnemididae, and the extinct Bothremydidae, Euraxemydidae and Araripemydidae (Gaffney *et al.*, 2006). Araripemydidae was first erected by Price (1973) to accommodate *Araripemys barretoii* from the Romualdo Fm. of the Araripe Basin. Later on, de Broin (1980) described *Taquetochelys decorata*, from the Elharz Fm., based on shell fragments. This taxon was assigned to the Araripemydidae based mainly on shell texture, which was deemed similar to the distinctive pitted ornamentation pattern of *Araripemys*. However, since the material is quite fragmentary lacks key diagnostic features, the genus is, at present, considered as *incertae sedis* within Pelomedusoides (de la Fuente & Lapparent de Broin, 1997; Gaffney *et al.* 2006) and has been regarded as a *nomen dubium* by Sereno & ElShafie (2013). Fielding *et al.* (2005) described a new species for the genus *Araripemys* (*A. "arturi"*) based on fragmentary material from the Crato Fm. (Araripe Basin), but the taxon was deemed poorly established and ended synonymized with *A. barretoii* in subsequent reviews (Gaffney *et al.* 2006; Oliveira & Kellner, 2007a). The Araripemydidae was thus a redundant taxon until the description of *Laganemys tenerensis* Sereno & ElShafie 2013, based on an almost complete skeleton from the Elharz Fm. of Niger, which was allocated within this family.

The genus *Araripemys* is represented by the single species *A. barretoii*, known from the Early Cretaceous of Brazil. The holotype and most of the specimens known come from the Romualdo Fm. (Early Albian) of the Araripe basin (Price 1973; Kischlat & Campos, 1990; Schleich, 1990; Meylan 1996; Gaffney *et al.* 2006), but there are records also for the Crato Fm. (Late Aptian) of the same basin (e.g. Fielding *et al.* 2005; Oliveira & Kellner, 2005; 2017; Romano

et al. 2013) and for the Itapecuru Fm. (Albian) of the Parnaíba Basin (Batista & Carvalho 2007). There is a large number of specimens retrieved from the Romualdo Fm. nodules displaying the characteristic 3D preservation of this formation, with several of them exhibiting both cranial and post-cranial elements. However, for the Crato Fm. the only known specimens are, so far, a fragment of a shell along with a hindlimb which was the holotype of *Araripemys* “*arturi*” (Fielding et al. 2005); an isolated plastron (Oliveira & Kellner 2005); two partially complete juvenile specimens displaying incomplete skulls assigned to *Araripemys* cf. *A. barreto* (Oliveira & Kellner, 2017); and an almost complete post-cranial skeleton (SMNK, no collection number provided) which was figured by Naish (2007), but remains undescribed. In this way, no complete specimen has ever been described for the Crato Fm. so far.

The abundance of fossil material assigned to *Araripemys* available in scientific collections (mostly specimens from Romualdo Fm., as mentioned above), including several acid-prepared specimens, allowed for detailed descriptions of its skeletal anatomy, which is quite well known (e.g. Schleich, 1990; Meylan & Gaffney 1991; Meylan 1996; Gaffney et al., 2006), though far from exhaustively explored to its full potential. Additionally, it brought up the interesting question of intra-specific variation, one that is highly relevant for phylogeny (e.g. polymorphic characters) but still underestimated for a number of reasons (e.g. Grande, 2004; Leal & Brito 2007).

The turtle shell presents a limited number of characters and shows a great deal of individual variation, the most usual variation occurring on the neural bones of the carapace (Romano et al., 2013). The supposed ancestral condition of eight predominantly hexagonal neurals can be modified either by proliferation or reduction of elements in the series; however, it was suggested that neomorphic elements occur rarely, with elimination and subsequent reduction in neural numbers being far more frequent (Pritchard, 1988). Changes occur usually at the end of the series, by loss of exposed neurals, by obliteration (when the neurals are present but covered by the surrounding bones), and by changes in shape (Pritchard 2008). Intra-specific variation of neural bones is widespread among living taxa, but very unevenly documented (see Pritchard, 1988, 2008, and references therein). It was first reported for *Araripemys* by Meylan (1996) concerning the contacts of the last neural. The plastron shows less variation in its number of components than the carapace, but displays as much or even more variation in shape (Pritchard, 2008).

Another important source of intra-specific variation, this one well established in living forms but sometimes not so easy to determine in the fossil record, is sexual dimorphism. It can be observed in turtles usually relative to shell and plastron features. Among the range of variation observed one can highlight: the size differences between males and females; the shape of the carapace which tends to be more rounded and domed for females, while elongated and flattened for males; the shape of plastron, which is concave in males of terrestrial species; a de-ossification of the middle plastral concavity occurring in males of some species (considered to be a 'frictional assist' for mating); the shape of the xiphiplastrs, which are rounded with a "V" shaped anal notch in females (a configuration believed to facilitate egg-layering) and slender and pointed with a "U" shaped anal notch in males (believed to facilitate extension and downcurving of the tail during copulation); shape and size of plastral fontanelles. On sexual dimorphism in recent and fossil taxa see e.g. Lagarde et al. (2001); Lapparent de Broin et al. (2007); Pritchard (2008); Cadena et al. (2013); Cadena (2015), among others.

The goal of this work is to describe 14 new specimens of *Araripemys barreto* – three from the Crato Fm. and ten from the Romualdo Fm. – and revisit other six, and to report all morphological variation, establishing patterns of intra-specific variation for this species. Such approach has never been done before for *A. barreto*, despite the many known specimens. This

new data will add to the current knowledge on the morphology of *A. barreto* and will allow a refinement of the characters used in systematic analyses. In this way, we offer here a revised diagnosis for *Araripemys barreto* and provide interpretations for the nature of the herein reported variations.

Geological Setting

The Araripe Basin is a sedimentary basin whose origin is related to the breakage of Gondwana and the opening of the South Atlantic Ocean during the Early Cretaceous. This intracratonic basin is located on the borders of the states of Ceará, Pernambuco and Piauí in Northeastern Brazil. It has an area of approximately 9000 km² encompassing not only the Araripe Plateau but also the Cariri Valley (Valença et al., 2003).

The Santana Group is the most fossiliferous unit, and includes the Crato and Romualdo Formations. These are two *konservat lagerstätten* famous for their taxonomic diversity and extraordinary preservation of organic structures, including remarkable soft tissues (e.g. Martill, 1988; Martill et al., 2007; Campos and Kellner, 1997; Kellner, 1996a; 1996b, Pinheiro et al., 2012; Maldanis et al., 2016). However, there is not much agreement concerning its stratigraphy or age, which is usually estimated as Aptian-Albian; the reader is referred to Martill (2007) for a review. In this work we use the stratigraphic framework of Valença et al. (2003), with the Santana Group being constituted, from the bottom to the top, by the Rio Batateira, Crato, Ipubi, Romualdo and Arajara Fms. The different paleoenvironments led to distinct taphonomic and diagenetic processes, resulting in different types of fossil preservation – fossils are somewhat flattened, but retaining many tridimensional structures, in the limestones from Crato Fm.; flattened in the Ipubi and Romualdo Fms. shales; and fully tridimensional inside nodules (calcareous concretions) in Romualdo Fm. (Maisey, 1991; Martill, 1998, 2007).

Turtles are recorded in three formations of the Santana Group: Crato, Ipubi and Romualdo. At least two taxa – *Araripemys barreto* and an indeterminate Podocnemidera – were found in the Crato Fm. (Meylan 1996, Gaffney et al. 2006; Romano et al. 2013); additionally, a complete juvenile specimen of an undetermined pelomedusoid turtle from Crato Fm. has been figured by Fielding et al. (2005) and Naish (2007), but no descriptions were provided. Two similar juvenile specimens from the Crato Fm., referred to *Araripemys* cf. *A. barreto*, were described by Oliveira & Kellner (2017). From Ipubi Fm. there is a single specimen of an indeterminate pelomedusoid (Oliveira et al. 2011), and an ichnofossil consisting of an isolated footprint with scratch marks, attributed to a turtle (Dentzien-dias et al., 2010). Five turtle species were retrieved from the Romualdo Fm.: *Araripemys barreto*, *Santanachelys gaffneyi*, *Brasilemys josai*, *Cearachelys placidoi* and *Euraxemys essweini* (Price 1973; Hirayama 1998; Lapparent de Broin 2000; Gaffney et al. 2001; Gaffney et al. 2006; Oliveira & Kellner, 2007b).

Material and Methods

Institutional Abbreviations

AMNH – American Museum of Natural History (New York, United States); **BSP** – Bayerischen Staatssammlung für Paläontologie und Geologie (Munich, Germany); **DGM/DNPM**– Divisão de Geologia e Mineralogia, Museu de Ciências da Terra, Departamento Nacional da Produção Mineral (Rio de Janeiro, Brazil); **LP-UFC** – Laboratório de Paleontologia, Universidade Federal do Ceará (Fortaleza, Brazil); **MN** – Museu Nacional, Universidade Federal do Rio de Janeiro

(Rio de Janeiro, Brazil); **MPSC** – Museu de Paleontologia de Santana do Cariri (Santana do Cariri, Brazil); **UFRPE** (Universidade Federal Rural de Pernambuco (Recife, Brazil); **SMN** – Statens Naturhistoriske Museum (Copenhagen, Denmark); **SMNK** – Staatliches Museum für Naturkunde, Karlsruhe (Karlsruhe, Germany); **THUg** – Teikyo Heisey University (Chiba, Japan).

Material

Newly described material: LP-UFC 722; MPSC 134 (part and counterpart); MPSC R 137; MPSC R 874; MPSC V-010 (part and counterpart); MPSC R 2107; MPSC R 2308; MN 6743-V; MN 6744-V; MN 6949-V*; DGM 346; DGM 1449-R; UFRPE 5302.

Revisited material: DGM 765-R (holotype of *Araripemys barretoii*), SMNK PAL 3979 (holotype of *Araripemys arturi*), MN 6637-V (first described by Kischlat & Campos, 1990), BSP 1981 I 38 and BSP 1977 I 1 (first reported by Schleich, 1990)

Comparative material: *Chelonia mydas*: UFRPE 5382, 5383 and 5384; *Pelomedusa galeata*: KU SNM-CN 195; *Pelomedusa subrufa*: KU SNM-CNR2821; *Pelusios derbianus*: KU SNM-CN192; *Hydromedusa maximiliani*: KU SNM-CN211; *Phrynosoma hilarii*: KU SNM-CN 214; KU SNM-CN 266; *Araripemys barretoii*: MPSC R 135; MPSC R 136; MPSC R 778; MPSC R 873; MPSC R 1305; MPSC R 2309; MN 6745-V; MN 4893-V; MN 7191-V; AMNH 24452; AMNH 24453; AMNH 24454; AMNH 24456; AMNH 30651, THUg 1357; THUg 1907.

From the literature: MB.R.3448; SMNK no number (Naish, 2007).

All specimens used in this study are housed in public scientific collections.

*The specimen MN 6949-V was unfortunately lost during the fire who destroyed the Brazilian National Museum in the night of September 2nd. The illustrations we present here are all that was left from it.

Preparation

Mechanical and chemical preparation were conducted by us only in the following specimens: LP-UFC 722; MPSC V-010 (counterpart); MPSC R 2107 and UFRPE 5302. The protocol modified from Toombs & Rixon (1959) was adapted to particularities of each specimen following Leal & Brito (2004) and Silva & Kellner (2006). After chemical preparation, the specimen LP-UFC 722 underwent also a consolidating protocol following Cnudde et al. (2007).

Image acquisition, processing and analysis

The specimen UFC-722 was scanned using a Siemens Somatom Definition CT scanner, at the Department of Forensic Medicine, University of Copenhagen. After chemical / mechanical preparation, the entire specimen was scanned with the following settings: 140 kV, 550 mAs, 0.6 mm slice thickness, 0.4 pitch, 0.3 slice increment and a sharp reconstruction algorithm (H70h). A field of view of 182 mm was used resulting in images with a pixel size of 0.35 mm.

A detailed scanning of the skull was also performed using the same settings, but reducing the field of view to 93 mm. The resulted pixel size of the CT images was 0.18 mm. The CT scanning data processed using the image software Mimics (Materialise) version 12. A 3D model of the skull was created by using data segmentation methods described by Lynnerup and Villa (Lynnerup, 2007; Villa & Lynnerup, 2012).

Results

227

228 **Systematic Palaeontology**

229 Testudines Batsch 1788

230 Pleurodira Cope 1864

231 Pelomedusoides Cope 1868

232 Araripemydidae Price 1973

233 *Araripemys* Price 1973

234 *Araripemys barreto* Price 1973

235 **Synonymy.** *Araripemys arturi* Fielding, Martill & Naish 2005

236 **Holotype.** DGM 756-R, incomplete shell (cast MN 6945-V).

237 **Locality and Horizon.** Outcrops of the Crato (Aptian-Albian) and Romualdo Formations
238 (Albian), in the Santana Group of Araripe Basin, Northeastern Brazil.

239 **Revised diagnosis.** Pelomedusoid with flattened shell; fine ornamentation consisting variably of
240 pits and/or ridge-and-sulcus configurations; first costals separating nuchal from first peripherals;
241 small, subtriangular peripheral 1; reduced cruciform plastron with well-developed axillary and
242 inguinal buttresses; absent mesoplastra; absent gular scutes; neural series including 8-10 neurals;
243 persistence of costal fontanelles in mature forms; postatlantal cervical vertebrae with completely
244 fused postzygapophyses; processus paraoccipitalis of the opisthotic surpassing by far the
245 supraoccipital crest.

246

247 **Description**

248

249 The full, detailed and individual descriptions of all newly reported and redescribed
250 specimens can be found in the Supplemental Material. In this section we combine and compile
251 data on all specimens (mentioning them wherever appropriate) focusing on new morphological
252 data and on observed variations. These data comprise features of the skull, shell, and unguals.
253 Variations are also compiled in Table 1.

254 We present here data on 14 new specimens, as well as revisit 5 previously reported specimens.
255 The new specimens are, from the Crato Formation: UFC-722 (almost complete specimen
256 exposed in ventral view, with a skull in dorsal view; Fig. 1; Fig. 2), MPSC R 2107 (almost
257 complete plastron in ventral view; Fig. 3), UFRPE 5302 (posterior half of carapace in dorsal
258 view; Fig. 3); and from the Romualdo Formation: MN 6949-V (almost complete shell and skull,
259 plus hyoids, two cervical vertebrae, and a complete manus; Fig. 4), MN 6743-V (partial shell),
260 MN 6744-V (almost complete shell, two cervical vertebrae), DGM 346-LE (almost complete
261 shell), DGM 1449-R (carapace), MPSC V-010 (entire shell), MPSC R 2308 (entire shell), MPSC
262 R 874 (almost complete carapace), MPSC R 134 (carapace), MPSC R 137 (carapace), SMNK
263 PAL (no number) (carapace, cervicals and skull) (Fig. 5 – 6). We further revisit specimens DGM
264 756-R (partial shell and femora, holotype; Fig. 3), MN 6637-V (carapace impression, plastron,
265 several post-cranial elements including an ungual; Fig. 3), SMNK PAL 3979 (partial shell and
266 hindlimb, holotype of *A. “arturi”*; Fig. 7), BSP 1977 I 1 (almost complete shell with a few
267 posterianal elements, including an undescribed ungual; Fig. 3) and BSP 1981 I 38 (almost
268 complete shell; Fig. 3).

269

Skull.

The skull of *Araripemys barretoii* has already been described in detail by Meylan (1996) and Gaffney *et al.* (2006). We present here two new well-preserved skulls, providing further data on its morphology and character variation.

The skull of UFC-722, from the Crato Formation, is almost complete and exposed in dorsal view, but some details from the ventral view can be assessed from the CT scan-generated 3-D model (Fig. 2). Overall, the pattern of bone elements and contacts is similar to what has already been described for *Araripemys barretoii*. This skull exhibits an “extra foramen” in the opisthotic-exoccipital suture (Fig. 2D), similar to AMNH 24454 (Gaffney *et al.*, 2006) and unlike the other known skulls. The foramen jugulare posterius is clearly open as seen in the CT scan-generated 3-D model (Fig. 2D). Both hyoids are preserved, the right one being exposed and the left one hidden ventral to the skull. It can be seen in the CT scan-generated 3-D model.

MN 6949-V includes a three-dimensional, well-preserved skull from the Romualdo Formation (Fig. 4). Its general morphology is also consistent with that previously described (Meylan, 1996; Gaffney *et al.*, 2009). Differently from UFC-722, its foramen jugulare posterius is completely enclosed by a bony bridge and the “extra foramen” is absent. This specimen further exhibits the stapes preserved in natural position (Fig. 4), conforming with the previous identification of the incisura collumela auris by Gaffney *et al.* (2006). A case of asymmetry can be seen regarding this bone. In MN 6949-V, the right coronoid is quite small and forms the posterior half of the coronoid process. The anterior half is formed almost entirely by the dentary, with only a slender dorsal projection of the coronoid, similarly to what is seen in AMNH 24454 and THUg 1907 (Gaffney *et al.*, 2006). The left coronoid, on the other hand, extends onto and occupies entirely the anterior half of the process. Again, the same morphology is seen in AMNH 24454, and in THUg 1907 the coronoid occupies most of the anterior half of the coronoid process (Gaffney *et al.*, 2006).

These two skulls are the most complete up to now, especially MN 6949-V. This specimen shows quite clearly the presence of a considerable premaxillary prognathism in *Araripemys barretoii* (Figs. 2; 4). They both further reveal the presence of an extensive foraminization in the surfaces of the premaxillae, maxillae and dentaries, presumably neurovascular and related to the horny beak.

Carapace.

Elements and contacts. The composition of the carapace in *Araripemys barretoii* varied in the observed specimens only in respect of the number of neurals, varying from 8 to 10 (see Table 1; Fig. 8). Aside from that, all observed specimens exhibit a nuchal, 8 pairs of costals, 11 pairs of peripherals, a pygal and a suprapygal. In all specimens where the region could be observed, the nuchal was separated from the first pair of peripherals by the first pair of costals. Concerning also the contacts between the neurals and surrounding elements, the neural series shows great variation (see Neural Series in Table 1). In specimens MN 6744-V, UFRPE 5302 and probably DGM 1449-R there was no contact between the last neural and the suprapygal, with the last pair of costals briefly meeting medially. Finally, the pygal series also showed some variation. In specimen UFRPE 5302 there was no contact between the pygal and suprapygal, with the last pair of peripherals meeting dorsally to the pygal.

Costal fontanelles. The specimens showed variation concerning the relative sizes of the costal fontanelles. The smallest of all specimens herein described (MPSC 137) shows quite large fontanelles (Fig. 6C). Larger individuals tend to exhibit relatively larger costals and smaller fontanelles. The two largest specimens only show diminutive fontanelles (Fig. 6A-B).

Shape. The shape of the carapace in *Araripemys barretoii* is known to vary from the squared morphology described by Price (1975) and Meylan (1996) to the oval morphology seen in SMNK PAL 3979 (Fielding *et al.*, 2009). The new specimens herein presented exhibit a variety of shapes, including the oval shape and distinct forms of squared carapaces (Figs. 5 – 6). Oval-shaped carapaces can be seen in specimens UFC-722, DGM 346, MN 6744-V, and MPSC 134, while specimens MN 6949-V, DGM 1449-R, MPSC 878, MPSC 874, MPSC 135 and UFRPE 5302 exhibit all squared-carapaces. In the holotype, the marked angulature that gives the carapace a squared outline is formed between peripherals 8 and 9, as in specimens MN 6949-V and MPSC R 134. In specimen DGM 1449-R, this angulature is formed between peripherals 9 and 10, and in UFRPE 5302, MPSC 137 and MSPC V-010, between peripherals 7 and 8.

Ornamentation. The ornamentation of nuchals, neurals and costals view did not vary between the observed specimens. In the carapace, only peripherals exhibited variation in, with specimens DGM 1449-R and UFC-722 exhibiting a combination of pits and ridge-and-sulcus pattern in such elements.

334 **Plastron.**

Anal notch. Schleich (1990) described two specimens attributed to *Araripemys barretoii* which display distinct anal notch morphologies (Fig. 10), one which is U-shaped (BSP 1977 I 1) and another V-shaped (BSP 1981 I 38). The V-shaped anal notch can be further seen in specimens DGM 756-R, MN 6637-V, MN 6949-V, MPSC 874, and the U-shape in UFC 722, MPSC 878, MPSC 2107 and MPSC 2308.

Ornamentation. All observed epi- and entoplastra exhibited a pitted ornamentation. On the other hand, there was variation in the pattern seen in hyo-, hypo- and xiphiplastra (Fig. 9). Specimens DGM 756-R, SMNK-PAL 3979, MN 6949-V, DGM 364 LE, MPSC 878 and MPSC 2308 exhibited a pitted ornamentation in these elements, while the same elements showed a combination of pits and ridge-and-sulcus ornamentation in specimens UFC-722 and MN 6743-V. Specimen MPSC 2107 exhibited exclusively ridge-and-sulcus ornamentation in these elements, with no signs of pits.

Unguals. Variation in the unguals of specimens attributed to *Araripemys barretoii* has already been reported, varying from arrow-head shaped in AMNH numbers 24453, 24454 and 24456 (Meylan, 1996) to simple unguals in SMNK PAL 3979 (Fielding *et al.*, 2005) and MN 6949-V (Oliveira & Kellner, 2007). Here, we report on the unguals of MN 6637-V and UFC 722 (see Supplemental Material), which are arrow-head shaped, and of MPSC 878 and BSP 1977 I 1 (see Supplemental Material), which are simple.

Discussion

We have presented above a plethora of morphological variation within specimens of *Araripemys*. Some of these variations are easily recognizable as intraspecific (e.g. ontogenetic changes, or individual variations, like polymorphisms and sexual dimorphism), while others pose challenges over their interpretations. Accurate discrimination of intra- and interspecific variations in the fossil record can be difficult, especially when control provided by extant analogues is inexistent or insufficient. Here we will explore each of the variations recognized and argue in favor of a given interpretation for each.

Morphological variation remains the keystone over which most of the natural sciences are built, and its distinct categories are at play in our sample; we proceed thus to define them. Following the very didactic paper by Grande (2004), there are three main categories of morphological variation: taxonomic, ontogenetic and individual. **Taxonomic variation** consists of the morphological differences between taxa. Characters are the morphological variants allowing the differential diagnosis of discrete taxa (either specific or higher taxa). Taxonomic variation thus includes **interspecific** variation. The two other categories fall under the umbrella of **intraspecific** variation. **Ontogenetic variation** describes the morphological changes in a growth series, and can be approached either by analyzing the onset of a specific structure (at which stage it develops), or by examining how a structure changes shape and size during development (included here allometric and isometric changes). **Individual variation** may be present as **intraindividual** or **interindividual** variation. Intraindividual variation occurs within a single individual (e.g. assymetries concerning presence/absence of bones), while interindividual variation occurs between individuals of a same species, often sharing similar ages and sizes. There are three main categories under interindividual variation: sexual dimorphism, polymorphisms, and anomalies.

The proper identification of ontogenetic and individual variation (intraspecific) is fundamental to the recognition of taxonomic variation (interspecific).

Pritchard (1988) has already drawn attention to how uneven are the studies on intraspecific variation in turtles, with a “frustratingly incomplete” literature concerning extant species. Adding to the problem, palaeontologists usually have to study shell-only material, as it is the most common form of preservation: complete specimens retaining the skull are a rare find. Using *Araripemys* as an example, for which dozens of shell-only specimens are known (the holotype, for instance, is a shell-only material), there are only 4 nearly complete skulls described (AMNH 24453, AMNH 24454, THUg 1357 and THUg 1907; see Gaffney et al., 2006); this work adds now two more to this count (UFC 722 and MN 6949-V).

The identification of morphological variations in fossil turtles has important implications for phylogenetic analysis. As an example, the diagnostic features presented by Fielding *et al.* (2005) to erect a new *Araripemys* species were invalidated, those being: 1) ovoid-shaped carapace, whereas *A. barretoii* would display a posterolateral angulation at the carapace lateral margin (Price, 1975; Meylan, 1996); 2) peripherals IX and X equally long as wide; and 3) lack of arrow-shaped pedal unguals, supposedly characteristic of *A. barretoii* after Meylan (1996). The first has been proposed to be taphonomical or dubious due to the material incompleteness; while the second could represent ontogenetic, sexual or individual variation; and the third, in turn, has been proposed to represent individual variation (Gaffney et al., 2006; Oliveira and Kellner, 2007a).

Although the new species were synonymized with *A. barretoii*, the very nature of the features claimed were never elucidated. The knowledge of morphological variation due to sexual

dimorphism as well as individual and ontogenetic variation will allow a refinement of the characters used for phylogenetic or systematic purposes, at least at the species taxonomic level.

Other illustrative examples can be taken from some extant species, which demonstrate the importance of dealing with polymorphisms and their implications for phylogenetic analyses. Furthermore, understanding of variation seen in extant species should serve as a control for interpreting variation in the fossil record. Sometimes, osteological variation in extant turtles can be extensive, as what is seen in the orbital margin of *Chelonia mydas* (Cryptodira: Cheloniidae). Two specimens of *Chelonia mydas*, a female and a male (respectively UFRPE 5383 and 5384) are here illustrated, and topographic variation can be observed on some of the skull bones (see Supplementary Material). On the female skull, the frontal composes a significant part of the orbital margin, standing between the pre-frontal and the post-orbital. However, on the skull of the male specimen, the frontal does not take part on the orbital margin; instead, the contact between the pre-frontal and post-orbital precludes the frontal from reaching the orbit.

In this section, we discuss the diversity and plausible explanation for all variations reported. One must bear in mind that not always the condition found/described in a holotype or figured specimen turns out to be the typical condition observed in a larger sample; see, for instance, the case of *Amia calva* and the single vs paired parietals (Grande, 2004).

Sexual dimorphism: anal notch

Sexual dimorphism in turtles manifests in several ways: the size difference between males and females, the shape of the carapace which tends to be more rounded and domed for females while elongated and flattened for males, or the shape of the plastron which is concave in males of terrestrial species (Pritchard, 2008).

It has been addressed several times in the literature the common sexual variation in turtles concerning the anal notch width measurements (e.g. Willemsen & Hailey, 2003; Kaddour *et al.*, 2008; Djordjević *et al.*, 2011; Ceballos *et al.*, 2014). Translating such morphometric character into morphological terms, one can say that under this variation, female anal notches can be recognized as V-shaped, while those of males are U-shaped, with a slender terminus of the xiphiplastra.

Sexual dimorphism expressed in the xiphiplastra was already reported for *Araripemys* (Schleich, 1990) and other fossil pleurodires, for instance, on the Jurassic platychelyids *Notoemys zapatoacaensis*, *Notoemys laticentralis* and *Platychelys oberndorferi* (see e.g. Pritchard, 2008; Cadena *et al.*, 2013; Cadena, 2015; Sullivan & Joyce, 2017).

The specimens of *Araripemys barretoii* LP UFC 722, BSP 1981 I 38, MPSC R 010, MPSC R 2107, MPSC R 2308 share the V-shaped anal notch (Fig. 10) indicative of females. By contrast, MPSC R 874, DGM 756-R, MN 6637-V, MN 6949-V and BSP 1977 I 1 have xiphiplastra with U-shaped anal notch (Fig. 10) indicating that these specimens represent males for the species.

Individual variation: polymorphisms

Skull: Though the majority of the variation we report here is concentrated on the shell, there are some skull variations worth noticing. As previously reported by Gaffney *et al.* (2006), there exists in the specimens referred to *Araripemys barretoii* variation in the condition of the *foramen jugulare posterius*, which varies from completely open to completely closed (see Gaffney *et al.*, 2006). The following conditions are known: completely open for the juvenile specimen

THUg 1357 and the subadult specimens AMNH 24453, AMNH 24454 (Gaffney *et al.*, 2006) and UFC 722 (this work), and completely closed for the subadult specimens THUg 1907 (Gaffney *et al.*, 2006) and MN 6949-V (this work). Taphonomic alteration is not a possible explanation for this diversity since different conditions can be seen in beautifully, three-dimensionally preserved skulls from the Romualdo Fm. that exhibit undamaged surfaces of the exoccipital (Gaffney *et al.*, 2006). Indeed, Gaffney *et al.* (2006) considered this variation to be real and coded *Araripemys barretoii* as polymorphic for this character in their analysis. This feature cannot be regarded as sexually dimorphic because the same condition (open) can be seen in AMNH 24453 (a female) and in UFC 722 (a male). Finally, as Gaffney *et al.* (2006) had already pointed out, it could not be explained by ontogeny because different conditions can be seen in AMNH 24454 (open) and THUg 1907 (closed), which are both of similar size and close to osteological maturity (Gaffney *et al.*, 2006). Because THUg 1357 is a juvenile and exhibits an open foramen jugulare posterius, it remains unclear if this specimen would exhibit an open or closed configuration if it had achieved a subadult stage with more ossification (Gaffney *et al.*, 2006).

Another variation can be found in the shape of the paraoccipital process of the opisthotic, which has a convex posteromedial margin in THUg 1357 and THUg 1907, and a concave one in AMNH 24453 and AMNH 24454 (see Supplemental Material). Unfortunately, the condition is unclear for MN 6949-V and UFC-722, in which the tips of the paraoccipital processes have been lost.

The mandible of specimens attributed to *Araripemys barretoii* further provide a curious case of a repeated intra-individual variation, specifically in the coronoid. In three specimens (MN 6949-V, AMNH 24454 and THUg 1907), the left coronoid is considerably more developed than the right coronoid. In all three specimens, the right coronoid is relatively small, mostly restricted to the posterior half of the coronoid process. The anterior half is occupied mainly by the dentary, with the participation of the coronoid restricted to a slender dorsal projection on the anterodorsal margin. On the left hemimandible, however, the coronoid is relatively more extended anteriorly, occupying the anterior half of the coronoid process in AMNH 24454 and MN 6949-V and most of it in THUg 1907.

Neural bones: there is an astonishing amount of variation on neural bones throughout Testudines (Pritchard, 1988). The presumed ancestral condition of about 8 predominantly hexagonal neurals can be modified by proliferation, reduction and changes in shape of neurals (Pritchard, 2008). Variation on neural bones occur both between species and between individuals of the same species (Pritchard, 1988). *Araripemys barretoii* has typically nine neural bones with the following neural formula $6 > 6 > 4 < 6 < 6 < 6 < 6 > 3$. By contrast, MPSC V-010 has 10 neural bones instead of nine and the following neural formula $6 < 6 > 4 < 5 > 6 > 6 > 6 > 6 > 4 < 4$. It deviates from the typical pattern of *Araripemys* for having a first neural smaller than the second, the fourth neural reaches left costal three and, besides an additional element at the end of series, the last neural has four contacts instead of three. In UFRPE 5302, most of the neural bones were lost given the specimen is only a fragment of a shell. Nevertheless, this specimen shows two deviations from the typical shell morphology of *Araripemys barretoii*: the neural series is interrupted at the end by the eighth pair of costals, which meet at midline, thus precluding the contact between neural 9 and the suprapygal (Fig. 3). This condition has already been reported for *Araripemys barretoii* specimens from Romualdo Fm. by Meylan (1996; specimens AMNH 22556 and AMNH 24453), and by Schleich (1990; specimen BSP 1981 I 38). The second deviation is the pygal bone, which has a triangular shape instead of the usual square shape, and do not contact the suprapygal, with

peripherals 11 from both sides meeting at the midline precluding the contact between the pygal and suprapygal (Fig. 3). The specimen MN 6744-V also exhibits contact between the eight pair of costals, and is further variable in exhibiting a rounded last neural, like BSP 1981 I 38.

In this way, there are, among our specimens with complete neural series, 7 specimens with 10 neurals (DGM 756-R, MPSC 134-R, MPSC R 874, MPSC 2308, MPSC V-010, MN 6949-V, MN 7191-V), 5 specimens with 9 neurals (MN 6744-V, AMNH 24453, AMNH 22550, AMNH 22556, BSP 1981 I 38) and 2 specimens with 8 neurals (UFC-722 and MN 6743-V), other than an incomplete specimen with, most likely, 8 neurals as well (UFRPE 5302). There are several specimens with an incomplete neural series and it is thus unclear what configuration is more common, and could be considered “typical” for *Araripemys*. Nonetheless, the condition of 8 neurals, similar to *Laganemys tenerensis*, seems to be the least common.

The last neural contacts the suprapygal in at least 5 specimens (UFC-722, AMNH 22550, MPSC V-010, MPSC R 874, MN 6949-V) and does not in 5 specimens (UFRPE 5302, MN 6744-V, AMNH 22556, AMNH 24453 and BSP 1981 I 38).

A rounded last neural can be found in three specimens (DGM 756-R, MN 6744-V, BSP 1981 I 38), and a triangular pygal that does not contact the suprapygal is so far reported exclusively for UFRPE 5302. In this way, we consider these two features to most likely represent variations from the typical pattern: a polygonal last neural and the presence of a pygal-suprapygal contact.

Shape of the carapace: Another variation identified herein concerns the shape of the carapace in dorsal view. The holotype (Price, 1973), as well as the carapaces described by Meylan (1996), all exhibit a “squared” morphology, that is, they exhibit a posterior extension as opposed to terminating in a gentle rounded curve. This characteristic has been considered as diagnostic for *Araripemys barretoii* in the revised diagnosis of Sereno & ElShafie (2009) and has been used to distinguish that species from the purported species *Araripemys “arturi”* by Fielding *et al.* (2005), whose holotype (SMNK PAL 3979) exhibits an oval-shaped carapace. We found the oval-shaped morphology in the specimens UFC-722, DGM 346, MN 6744-V, and MPSC 134, other than the previously described specimen BSP 1981 I 38 (Schleich, 1990). The square-shaped morphology can be seen in MN 6949-V, DGM 1449-R, MPSC 878, MPSC 874, MPSC 135 and UFRPE 5302, other than the previously reported specimens AMNH 24453, AMNH 22550, AMNH 22556 (Meylan, 1996) and the SMNK’s postcranial skeleton (Naish, 2007). It is thus likely that the typical configuration is the square-shaped morphology, with the oval morphology as a variation. This individual variation is interpreted here as a polymorphism, and not related to sexual dimorphism, because UFC 722 and MN 6949-V are both inferred males, notwithstanding exhibiting distinct carapace shapes. In the same way, AMNH 24453 is an inferred female specimen that exhibits a carapace shape similar to MN 6949-V.

Furthermore, there also exists variation in the region of carapacial expansion within the square-shaped carapaces. In the holotype, MN 6949-V, MPSC R 134 and BSP 1981 I 38, the most acute angulation in the carapace, which indicates the lateral expansion, is present between peripherals 8 and 9. In specimens DGM 1449-R, AMNH 22550 and AMNH 22553, however, the lateral expansion is more prominent between peripherals 9 and 10. In specimens UFRPE 5302, MPSC 137 and MSPC V-010, the most acute angle in formed between peripherals 7 and 8, similar to the holotype of *Laganemys tenerensis* (see Sereno & ElShafie, 2013).

Shell texture: Shell ornamentation has been for long used as a character in turtle identification and phylogeny (e.g. de la Fuente & de Lapparent de Broin, 1997; Gaffney *et al.*, 2006; Sereno &

ElShafie, 2013). Characters related to shell surface texture grow in importance in paleontology when describing fragmentary material (a common occurrence in the fossil record). Groups known by a constant and distinct ornamentation pattern are, for instance, the Trionychidae, whose members possess on their shells a unique surface ornamentation and subsurface structure (Scheyer et al., 2007) allowing “even the smallest fossil fragment” to be recognized in the fossil record (Joyce & Lyson, 2010). Also for pleurodires, many authors have resorted to ornamentation patterns in order to identify their specimens, or when diagnosing species or constructing phylogenetic hypothesis (see a review in Gaffney et al., 2006). A “pelomedusoid” ornamentation (“a pattern of reticulate and anastomosing furrows and/or long striations that do not radiate from growth centers”; Gaffney et al., 2006) was recognized and described by de Broin (1977; “décoration pélomédusidienne”). Araripemydidae (*sensu* Sereno and ElShafie, 2013) is supposed to be characterized by a distinctive ornamentation pitted pattern, as can be seen from the character 175 by Gaffney et al. (2006), “shell texture”, with state 5 being “pits (*Araripemys*)”.

To this date, two fragmentary turtles were referred as related to Araripemydidae based on the ornamentation pattern. Lapparent de Broin (1980) described a new genus and species, *Taquetochelys decorata*, from the Elrhaz Fm. (Niger); later, de la Fuente & Lapparent de Broin (1997) tentatively referred a specimen from the Paleocene of Argentina as an *Araripemys*-like taxon. Both descriptions relied heavily on the distinctive pitted ornamentation displayed by the specimens, considered typical of *Araripemys*. It is worth mentioning that the holotype specimen of *Laganemis tenerensis* was originally referred to the genus *Araripemys*, when first presented to the scientific community (Sereno & ElShafie, 2009).

MPSC V-010 exhibits the pitted ornamentation on several costals and neurals of the carapace, and on every bone of the plastron, but it shows no signs of the ridge-and-sulcus ornamentation. UFRPE 5302 has the typical pitted ornamentation covering densely the suprapygal, all the costals and neurals, while the peripherals exhibit the ridge-and-sulcus ornamentation instead. The carapace surface texture of UFC 722 is mostly unknown due to the dorsal decubitus of the specimen. However, both the pitted and ridge-and-sulcus ornamentation can be seen on the peripherals, contrasting with MPSC V-010, which has no ornamentation whatsoever on the peripherals (similar to BSP 1981 I 38 and AMNH 22550), and with UFRPE 5302, which has the ridge-and-sulcus ornamentation on the peripherals instead of the pitted one. The plastron of UFC 722 exhibit both types of ornamentation: the pitted ornamentation on heavily on the epiplastra and entoplastron, and slightly on all other bones, while the hyo- and hypoplastra display the ridge-and-sulcus ornamentation – similarly to AMNH 24453. MN 6949-V includes all the shell elements preserved, and all of them exhibit exclusively the pitted pattern. The same is true for DGM 346 (despite the incomplete surface of the carapace; pits can be seen in costals and peripherals), MN 6744-V (with only the carapace visible, costals and peripherals) and DGM 1449-R (only a few carapace elements with preserved surfaces; neurals, peripherals and costals).

In this way, we consider as variations of the extensive pitted pattern the following configurations: smooth peripherals (MPSC V-010, MPSC 137, AMNH 22550 and BSP 1981 I 38), ridge-and-sulcus pattern on peripherals (UFRPE 5302), combined pitted and ridge-and-sulcus ornamentation on peripherals (UFC 722 and DGM 1449-R) and ridge-and-sulcus pattern on the hyo-, hypo- and xiphiplastra, but not on entoplastron and epiplastra (UFC 722, AMNH 24453, MPSC 2107 and MN 6743-V).

Unguals:

The unguals of *A. barretoii* were described for the first time by Meylan (1996), based on the specimens AMNH 24453, 24454, 24455 and 22550. In the combined reconstruction, the unguals are figured as arrowhead-shaped, to the exception of manual digit V, which is simple; the ungual of pedal digit V was unknown. Subsequently, Fielding *et al.* (2005) described the specimen SMNK-PAL 3979 (holotype of *A. "arturi"*), which exhibits simple unguals instead of arrowhead-shaped ones, and interpreted the shape differences as a taxonomic feature distinguishing *A. "arturi"* from *A. barretoii*. Later on, Oliveira & Kellner (2007a) figured the manual unguals of MN 6949-V, which are also simple, considering thus *A. "arturi"* as a junior synonym of *A. barretoii*. It is worth mentioning that Sereno & ElShafie (2013) considered arrow-shaped unguals as diagnostic for *Araripemys barretoii*, despite accepting the synonymy between *A. barretoii* and *A. "arturi"*, which does not exhibit this feature. More recently, Oliveira & Kellner (2017) reported two Crato Fm. hatchling specimens, MN 4893-V and AMNH 30651, both exhibiting arrowhead-shaped unguals. These specimens were attributed to *Araripemys* cf. *A. barretoii* because of, among other characters, the arrowhead-shaped unguals.

Our comparative sample comprises 11 specimens for which the unguals are known, including some of the illustrated described here (UFC 722, MN 6949-V, MN 6637-V) as well as some of the comparative specimens (AMNH numbers: 24453, 24454, 24455, 22550, 30651; SMNK-PAL 3979, MN 4893-V). This variation seems not to be correlated to sex or ontogenetic stage.

Ontogeny: intercostal fontanelles:

Intercostals fontanelles could be, potentially, morphological features associated with sexual dimorphism, in this case with fontanelle-bearing specimens representing males. The presence of intercostal fontanelles in adults is characteristic for males of some extant species e.g. *Macrochelys temminckii*, and for females of some other species e.g. *Graptemys barbouri* (Pritchard, 2008). However, in our sample, MPSC V-010, a female, also displays intercostal fontanelles. As intercostal fontanelles were found in all *Araripemys* specimens herein and previously described, comprising the putative two sexes among the specimens of this study, this feature is rendered inconclusive for sexual determination in *Araripemys barretoii*.

Costal fontanelles are, on the other hand, often present as juvenile features in many extant taxa, especially among chelids. In other instances, the persistence of large carapacial fontanelles could be related to cases of paedomorphosis (Li *et al.*, 2008; Reisz & Head, 2008). All described specimens of *Araripemys barretoii* exhibit costal fontanelles (contrasting with *Laganemys tenerensis*, whose holotype lacks costal fontanelles); notwithstanding, variation concerning their relative sizes were observed.

The hatchling specimen AMNH 30651 exhibits thin, slender, completely unfused costals, and peripherals were not even ossified yet (Oliveira & Kellner, 2017). In the small, early juvenile specimen MPSC R 137 (150 cm in length x 140 cm in width), the costals contact each other only in the medial half, with large fontanelles enclosed between them and the peripherals. In the larger, presumably subadult specimens MN 6949-V, MPSC R 878 and UFRPE 5302, contact between costals extends further laterally and the fontanelles become relatively smaller. Finally, the large specimens MPSC 134 and DGM 1449-R exhibit comparatively diminutive costal fontanelles. This variation is thus here regarded as ontogenetic and presumably related to the ossification of the costal bones, increasing with age and diminishing the relative size of the intercostal fontanelles.

630

631 **Problematic, Co-occurring Features: Potential Interspecific Variations?**

632 Some of the variations here reported are difficult to regard with much certainty as, indeed,
633 intraspecific variations of any sort – either polymorphism, anomalies or sexual dimorphism – or
634 ontogenetic changes. For instance, the condition of the foramen jugulare posterius which varies
635 from completely open to completely closed in *Araripemys* (see Gaffney *et al.*, 2006). As described
636 above, the following conditions are known: open for the juvenile specimen THUg 1357 and the
637 subadult specimens AMNH 24453, AMNH 24454 (Gaffney *et al.*, 2006) and UFC-722 (this work),
638 and completely closed for the subadult specimens THUg 1907 (Gaffney *et al.*, 2006) and MN
639 6949-V (this work). Its interpretation as a polymorphism is severely hampered by the fact that such
640 variation is unseen in any pleurodire species (Gaffney *et al.*, 2006 p. 142, first column, lines 45-
641 48). We thus propose here the existence of two morphotypes of *Araripemys* in the Araripe Basin.
642 For practical reasons, we shall now refer as morphotype 1 the one that exhibits an open condition
643 and morphotype 2 the one with the closed condition. Because THUg 1357 is a juvenile and exhibits
644 an open foramen jugulare posterius, it remains unclear if this specimen would exhibit an open or
645 closed configuration if it had achieved a subadult stage with more ossification (Gaffney *et al.*,
646 2006). The condition in this specimen is not as widely open as it is in AMNH 24453 or AMNH
647 24454, existing a subtle ventral and lateral expansion of the opisthotic above it, so that it is possible
648 that, had it grown further, it would have developed an enclosed foramen (Gaffney *et al.*, 2006).

649 Secondly, the shape of the unguis is also problematic. Arrow-head shaped unguals have
650 been regarded as diagnostic of *Araripemys barretoii* (Serenio & ElShafie, 2013; Oliveira & Kellner,
651 2017) subsequently to the description of AMNH 24453 and AMNH 24454 by Meylan (1996). The
652 holotype of *Araripemys "arturi"* displays simple unguals, what led Fielding *et al.* (2005) to regard
653 this feature as diagnostic of the proposed new species, differentiating it from *A. barretoii*, among
654 other features. As mentioned before, these two species have been synonymized under *Araripemys*
655 *barretoii* and their differences regarded as intraspecific (Gaffney *et al.*, 2006; Oliveira *et al.*, 2007).
656 However, together with the condition of the foramen jugulare posterius, we completely ignore the
657 existence of any turtle species displaying such a degree of intraspecific variation in the shape of
658 the unguals. In addition, regarding our sample as currently known (though acknowledgedly limited
659 as it may be), this variation coincides with the variation in the foramen jugulare posterius. Arrow-
660 head shaped unguals are present in specimens AMNH 24453, AMNH 24454, and UFC-722, which
661 exhibit an open foramen jugulare posterius; while the unguals are simple in specimen MN 6949-
662 V, which displays a closed foramen jugulare posterius. In this way, morphotype 1 would be
663 characterized by an open foramen jugulare posterius and arrow-head shaped unguals, and
664 morphotype 2 by a closed foramen jugulare posterius and simple unguals.

665 Thirdly, these conditions further coincide with the plastral ornamentation pattern (Table 1).
666 The ornamentation is pitted in the costals, neurals, nuchal and pygal series, as well as on the
667 epiplastra and entoplastra, in every specimen where these elements are visible. However, the
668 ornamentation can consist of a sulcus-and-ridge pattern in the hyo-, hypo- and xiphiplastra in some
669 specimens, while pitted in others. Specimens UFC-722 and AMNH 24453 exhibit an open foramen
670 jugulare posterius, arrow-head shaped unguals and ridge-and-sulcus ornamentation on the hyo-,
671 hypo- and xiphiplastra. On the other hand, specimen MN 6949-V exhibits a closed foramen
672 jugulare posterius, simple unguals and pitted ornamentation on all shell elements. Specimens
673 SMNK PAL 3979 exhibits a pitted ornamentation on the hyo- and hypoplastra also, as well as
674 simple unguals (skull unknown). Specimen BSP 1977 I 1 exhibits a pitted ornamentation on all
675 plastral elements and simple unguals as well (skull unknown).

There also seems to be a co-occurring variation involving the shape of the paraoccipital process of the opisthotic. As pointed out, the juvenile specimen THUg 1357 and the subadult specimen THUg 1907 exhibit a convex medial margin of this process, while AMNH 24453 and AMNH 24454 clearly exhibit a concave margin. This difference could also be related to the morphotypic pattern, with the concave margin coinciding with the morphotype 1, while the convex margin coincides with morphotype 2. However, we refrain from affirming this with certainty before more well-preserved skulls are described, since the tips of the paraoccipital processes of MN 6949-V and UFC-722 are broken off, precluding confirmation of their shapes.

Lastly, AMNH 24454 and UFC-722 share a unique feature, which is the “extra foramen” described by Gaffney *et al.* (2006) for the former specimen. It is located in the suture between the exoccipitals and opisthotics, at the base of the paraoccipital processes. This foramen is lacking completely in MN 6949-V, THUg 1357 and THUg 1907 (undescribed for AMNH 24453).

These comparisons suggest that morphotype 1 could likely be characterized by 1) an open foramen jugulare posterius, 2) arrow-head shaped unguals, 3) the presence of ridge-and-sulcus ornamentation in the hyo-, hypo- and xiphiplastra, and possibly 4) presence of an extra foramen on the suture between exoccipitals and opisthotics. Morphotype 2, in turn, would be characterized by 1) a closed foramen jugulare posterius, 2) simple unguals, and 3) pitted ornamentation on all plastral elements. As a comparison, the holotype of *Laganemys tenerensis* exhibits a third, distinct combination: 1) an open foramen jugulare posterius, 2) simple unguals, and 3) ridge-and-sulcus ornamentation on all carapacial and plastral elements (Serenio & ElShafie, 2013).

The consistency of these morphotypes is to be confirmed, or not, by the detailed description of more specimens in the future, particularly of those housed in AMNH and THUg collections. If these specimens are to confirm the consistency of such morphotypes, the possibility that their differences correspond to inter-specific variation ought to be seriously considered, especially as heterobatmy would be present. We await new data to better assess such possibility.

Conclusions and future perspectives

Araripemys is a remarkable fossil taxon in bearing so many individuals. Including the specimens described herein, there have been a total of 45 specimens referred to *Araripemys barretoii* in the literature, to our knowledge (Price, 1975; Kischlat & Campos, 1990; Schleich, 1990; Meylan, 1996; Fielding *et al.*, 2005; Oliveira & Kellner, 2005; Gaffney *et al.*, 2006; Batista & Carvalho, 2007; Carvalho & Barreto, 2015; Oliveira & Kellner, 2017; this work). This has allowed us to compile a particularly detailed account of the morphological variation seen in a fossil turtle.

Among the specimens presented here, of particular interest is LP UFC 722 for being the first almost complete, articulated skeleton from the Crato Fm. including a remarkably well-preserved skull.

Our identification of two morphotypes characterized by variations unreported as intraspecific variations within any known species provides evidence for the possibility that what is currently known as *Araripemys barretoii* is actually composed of two distinct species. Accordingly, we advent the hypothesis that these morphotypes could correspond to two putative species. In such a scenario, morphotype 1 would represent a new species, while morphotype 2 would correspond to the type species *Araripemys barretoii* and *A. “arturi”* as well as a junior synonym.

However, given our relatively low skull sample (which is still rather high for a fossil species), we refrain from affirming with confidence the existence of two species of *Araripemys* before more material can corroborate this hypothesis. A geometric morphometric analysis of the skull is also planned in the future development of this investigation, as a mean of further testing this hypothesis.

We finish by quoting Gaffney *et al.* (2006) who, in a memorable line in their paper, when trying to explain the meaning of the complex variation exhibited by the foramen jugulare posterius of *Araripemys*, put plainly (but apparently not without some exasperation): “It all goes to show that some of this crap makes no sense at all.” (Gaffney *et al.*, 2006; p. 148, line 53). We hope we have helped to disentangle this issue a bit.

Acknowledgements

For access to specimens under their care, we thank: Márcio Mendes (Departamento de Geologia, Universidade Federal do Ceará); Luciana B. Carvalho, Uiara G. Cabral, Alexander W. A. Kellner and Sergio A.K. Azevedo (Museu Nacional, Universidade Federal do Rio de Janeiro – MN/UFRJ); Peter Rask Møller (Statens Naturhistoriske Museum, University of Copenhagen); Paula Nuvens, Renan Bantim, Álamo Saraiva, Carlos Eduardo de Sousa and Sérgio Vilaça (Museu de Paleontologia de Santana do Cariri, Universidade Regional do Cariri – MPSC/URCA), Rodrigo Machado (Museu de Ciências da Terra – DGM/DNPM), Eberhard (Dino) Frey, Dieter Schreiber, Christiane Birnbaum and Wolfgang Munk (Staatliches Museum für Naturkunde Karlsruhe – SMNK) and Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie – BSPG). We also thank Thomas Pape (Statens Naturhistoriske Museum, University of Copenhagen), Sten Lennart Jakobsen (Geologisk Museum, University of Copenhagen), Jørn Bredal-Jørgensen (School of Conservation, The Royal Danish Academy of Arts, Copenhagen), Frank Osbeck (Bevaringscenter Skive), Marcus Krag (Statens Naturhistoriske Museum, University of Copenhagen), Thales Nascimento (Laboratório de Paleontologia e Sistemática, Universidade Federal Rural de Pernambuco), and Niels Lynnerup (Laboratory of Biological Anthropology, University of Copenhagen). SL thanks Irineudo Bezerra (Departamento de Geologia, Universidade Federal do Ceará) for all help and support and Capes for his grant. RVP thanks Rafael G. Souza and Thiago Mariani (Museu Nacional, Universidade Federal do Rio de Janeiro) for fruitful discussions and CNPq for his grant (#131186/2017-5). NB thanks the University of Copenhagen for his emeritus workspace and also for his connection as Senior Scientist to Fur Museum. MECL thanks Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) and CNPq for her grant (CNPq/FUNCAP-DCR/305426/2014-1 and DCR-0024-01186.01.00/14).

References

Batista, D. L. and Carvalho, I. S. 2007. O gênero *Araripemys* (Chelonii, Pleurodira) no Cretáceo brasileiro. *Paleontologia: Cenários de Vida*. Rio de Janeiro, Editora Interciência. 1: 291-297.

- 763 Bona, P. and De la Fuente, M. S. 2005. Phylogenetic and paleobiogeographic implications of
764 *Yaminuechelys major* (Staeche, 1929) new comb., a large long-necked chelid turtle from the Early
765 Paleocene of Patagonia, Argentina. *Journal of Vertebrate Paleontology*. 25(3): 569-582.
766
- 767 Brinkman, D. B. and Wu, X. C. 1999. The skull of *Ordosemys*, an early cretaceous turtle from
768 Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia,
769 Cryptodira). *Paludicola*. 2 (2): 134-147.
770
- 771 Cadena, E. A. 2011. Potential earliest record of panpodocnemidid turtles, from the Early
772 Cretaceous (Valanginian) of Colombia. *Journal of Paleontology* 85:877-881
773
- 774 Cadena, E. A. 2015. A global phylogeny of Pelomedusoides turtles with new material of *Neochelys*
775 *franzeni* Schleich, 1993 (Testudines, Podocnemididae) from the middle Eocene, Messel Pit, of
776 Germany. *PeerJ*, 3, e1221.
777
- 778 Cadena, E. A., Jaramillo, C. A., Bloch, J. I. 2013. New Material of the Platyhelid Turtle *Notoemys*
779 *zapatocaensis* from the Early Cretaceous of Colombia; Implications for Understanding Pleurodira
780 Evolution. *Morphology and Evolution of Turtles*. Springer. 105-120.
781
- 782 Campos, D. A. and Kellner, A. W. A. 1997. Short note on the first occurrence of Tapejaridae in the
783 Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. *Anais da Academia*
784 *brasileira de Ciências*, Rio de Janeiro, 66 (2): 253.
785
- 786 Catto, B., Jahnert, R. J., Warren, L. V., Varejão, F. G., Assine, M. L. 2016. The microbial nature
787 of laminated limestones: Lessons from the Upper Aptian, Araripe Basin, Brazil. *Sedimentary*
788 *Geology*. 341: 304–315.
789
- 790 Cnudde, V., Dierick, M., Vlassenbroeck, J., Masschaele, B., Lehmann, E., Jacobs, P., Van
791 Hoorebeke, L. 2007. Determination of the impregnation depth of siloxanes and ethylsilicates in
792 porous material by neutron radiography. *Journal of Cultural Heritage*. 8 (4): 331-338.
793
- 794 Danilov, I, and J. Parham. 2008. A reassessment of some poorly known turtles from the middle
795 Jurassic of China, with comments on the antiquity of extant turtles. *Journal of Vertebrate*
796 *Paleontology*. 28:306–318.
797
- 798 De Broin, F. 1977. Contribution à l'étude des chéloniens: chéloniens continentaux du crétacé et du
799 tertiaire de France. Ed. du Muséum National d'Histoire Naturelle.
800
- 801 De Broin, F. D. L. 1980. Les tortues de Gadoufaoua (Aptien du Niger); aperçu sur la
802 paléobiogéographie des Pelomedusidae (Pleurodira). *Mémoires de la Société géologique de*
803 *France*. 139: 39-46.
804
- 805 De Broin, F. D. L. 2000. The oldest pre-Podocnemidid turtle (Chelonii, Pleurodira), from the early
806 Cretaceous, Ceará state, Brasil, and its environment. *Treballs del Museu de Geologia de*
807 *Barcelona*. 9: 43-95.
808

- De Broin, F. D. L., and De la Fuente, M. S. 2001. Oldest world Chelidae (Chelonii, Pleurodira) from the Cretaceous of Patagonia. *Comptes Rendues de l'Académie des Sciences de Paris, Sciences de la Terre et des Planetes*. Paris. 333: 463-470.
- De Broin, F. L., De La Fuente, M. S. and Fernandez, M. S. 2007. *Notoemys laticentralis* (Chelonii, Pleurodira), Late Jurassic of Argentina: new examination of the anatomical structures and comparisons. *Revue de Paléobiologie*. 26 (1): 99-136.
- De la Fuente, M. S., and De Broin, F. D. L.,. 1997. An *Araripemys*-like decorated turtle in the Paleocene of Northwestern Argentina. *Geobios*. 30(2): 235-242.
- De la Fuente, M. S., and Iturralde-Vinent, M. 2001. A new pleurodiran turtle from the Jagua Formation (Oxfordian) of western Cuba. *Journal Information*. 75 (4): 860-869.
- De la Fuente, M.S. 2003. Two new pleurodiran turtles from the Portezuelo Formation (Upper Cretaceous) of Northern Patagonia, Argentina. *Journal of Paleontology*. 77(3): 559-575.
- Dentzien-Dias, P. C., De Figueiredo, A. E. Q., Pinheiro, F. L., Schultz, C. L. 2010. Primeira Evidência Icnológica de um Tetrápode Natante no Membro Crato (Cretáceo Inferior), Formação Santana (Bacia do Araripe, Nordeste do Brasil). *Revista Brasileira de Paleontologia*. 13 (3): 257-260
- Fielding, S., Martill, D. M., Naish, D. 2005. Solnhofen-style soft-tissue preservation in a new species of turtle from Crato Formation (Early Cretaceous, Aptian) of northeast Brazil. *Paleontology*. 48(6): 1301-1310.
- Gaffney, E. S. 1975. A Phylogeny and Classification of the Higher Categories of Turtles. *Bulletin of the American Museum of Natural History*, New York. 155 (5): 391-436.
- Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, New York. 194:1-263.
- Gaffney, E. S., de Almeida Campos, D. and Hirayama, R. 2001. *Cearachelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil. *American Museum Novitates*. 1-20.
- Gaffney, E.S., Tong, H., Meylan, P.A. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, New York. 300: 1-700.
- Grande, L. 2004. Categorizing various classes of morphological variation, and the importance of this to vertebrate paleontology. *Mesozoic Fishes*. 3: 123-136.
- Goloboff, P. A., Farris, J. S. and Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*. 24 (5): 774-786.

- Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S. P., Martill, D. M., Rios-Netto, A. 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-eastern Brazil). *Sedimentology*. 57 (2): 677-694.
- Hirayama, R. 1995. Phylogenetic systematics of chelonoid sea turtles. *The Island Arc*. 3: 270-284.
- Hirayama, R. 1998. Oldest known sea turtle. *Nature*. 392 (6677): 705.
- Hirayama, R., Brinkman, D. B. and Danilov, I. G. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology*. 7 (3): 181-198.
- Joyce, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*. 48 (1): 3-102.
- Joyce, W. G. and Lyson, T. R. 2010. A neglected lineage of North American turtles fills a major gap in the fossil record. *Palaeontology*. 53 (2): 241-248.
- Kellner, A. W. A. 1996. Reinterpretation of a remarkably well preserved pterosaur soft tissue from the Early Cretaceous of Brazil. *Journal of vertebrate Paleontology*. 16 (4): 718-722.
- Kellner, A. W. A. 1996. Fossilized theropod soft tissue. *Nature*. 379 (6560): 32.
- Kellner, A. W. A. 1998. Panorama e Perspectiva do Estudo de Répteis Fósseis no Brasil. *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, 70(3): 647–676.
- Kellner, A. W. A. and Campos, D. A. 1998. Archosaur soft tissue from the Cretaceous of the Araripe Basin, Northeastern Brazil. *Boletim do Museu Nacional, nova série, Geologia*, Rio de Janeiro. 42: 1 – 22.
- Kellner, A. W. A. and Campos, D. A. 2000. Brief review of dinosaur studies and perspectives in Brazil. *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, 72(4): 509 – 564.
- Lagarde, F., Bonnet, X., Henen, B. T., Corbin, J., Nagy, K. A., and Naulleau, G. (2001). Sexual size dimorphism in steppe tortoises (*Testudo horsfieldi*): growth, maturity, and individual variation. *Canadian Journal of Zoology*. 79 (8): 1433-1441.
- Leal, M. E. C., and Brito, P. M. 2004. The ichthyodectiform *Cladocycclus gardneri* (Actinopterygii: Teleostei) from the Crato and Santana Formations, Lower Cretaceous of Araripe Basin, North-Eastern Brazil. *Annales de paléontologie*. 90 (2): 103-113.
- Leal, M. E. C. and Brito, P. M. 2007. Intraspecific variation of the caudal fin skeleton in *Osteoglossum bicirrhosum* Cuvier 1829 (Teleostei: Osteoglossomorpha: Osteoglossidae). *Zootaxa*. 1434 (1): 1-26.

- Li, C., Wu, X. C., Rieppel, O., Wang, L. T., Zhao, L. J. 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature*. 456:497-501.
- Lynnerup, N. 2007. Computed Tomography Scanning and Three-Dimensional Visualization of Mummies and Bog Bodies. *Advances in Human Palaeopathology*, eds Pinhasi R, Mays S (Wiley, Chichester, UK).
- Maldanis, L., Carvalho, M., Almeida, M. R., Freitas, F. I., de Andrade, J. A. F. G., Nunes, R. S., Rochitte, C. E., Poppi, R. J., Freitas, R. O., Rodrigues, F. and Siljeström, S. 2016. Heart fossilization is possible and informs the evolution of cardiac outflow tract in vertebrates. *Elife*, 5, p.e14698.
- Mariani, T. F. and Romano, P. S. 2017. Intra-specific variation and allometry of the skull of Late Cretaceous side-necked turtle *Bauruemys elegans* (Pleurodira, Podocnemididae) and how to deal with morphometric data in fossil vertebrates. *PeerJ*, 5, e2890.
- Matos, R.M.D., 1999. History of the northeastern Brazilian rift system: kinematic implications for the break-up between Brazil and West Africa. In: *The Oil and Gas Habitats of the South Atlantic*, Cameron, N.R., Bate, R.H., Clure, V.S., (Eds.), Geological Society of London. London. 153: 55-73.
- Martill, D. M. 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology*. 31(1): 1-18.
- Martill, D. M., Bechly, G., Loveridge, R. F. 2007. *The Crato Fossil Beds of Brazil – Window Into an Ancient World*. Cambridge University Press. New York. 625 pg.
- Meylan, P. 1996. Skeletal Morphology and Relationships of the Early Cretaceous Side-Necked Turtle, *Araripemys barretoii* (Testudines: Pelomedusoides: Araripemydidae) from the Santana Formation of Brazil. *Journal of Vertebrate Paleontology*. 16 (1): 20-33.
- Meylan, P. A. and Gaffney, E. S. 1989. The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. *American Museum novitates*. no. 2941.
- Naish, D. 2007. Turtles of the Crato Formation. In: *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press London. 452-457.
- Oliveira, G. R. 2007. Aspectos tafonômicos de Testudines da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. *Anuário do Instituto de Geociências*. 30 (1): 83-93.
- Oliveira, G. R., and Kellner, A. W. A. 2005. Note On A Plastron (Testudines, Pleurodira) From The Lower Cretaceous Crato Member, Santana Formation, Brazil. *Arquivos do Museu Nacional*. Rio de Janeiro. 63: 523-528.

- 944 Oliveira, G. R., Kellner, A. W. A. 2007a. Taxonomic status of *Araripemys* “*arturi*” Fielding,
945 Martill & Naish, 2005 (Testudines, Pleurodira, Araripemydidae). In: Paleontologia: Cenários de
946 Vida. Rio de Janeiro. Interciência. 393-399.
- 947
- 948 Oliveira, G.R. & Kellner, A.W.A. 2007b. A new side-necked turtle (Pleurodira, Pelomedusoides)
949 from the Santana Formation (Early Cretaceous), Araripe Basin, northeastern Brazil. Zootaxa,
950 1425:53-61.
- 951
- 952 Oliveira, G. R., Saraiva, A. A. F., Silva, H. D. P., De Andrade, J. A. F. G., Kellner, A. W. A. 2011.
953 First Turtle from Ipubi Formation (Early Cretaceous), Santana Group, Araripe Basin, Brazil.
954 Revista Brasileira de Paleontologia. 14(1): 61-66.
- 955
- 956 Oliveira, G. R., Kellner, A. W. A. 2017. Rare hatchling specimens of *Araripemys* Price, 1973
957 (Testudines, Pelomedusoides, Araripemydidae) from the Crato Formation, Araripe Basin. Journal
958 of South American Earth Sciences, 79:137-142. <https://doi.org/10.1016/j.jsames.2017.07.014>
- 959
- 960 Pinheiro F.L., Horn B.L.D., Schultz C.L., Andrade J.A.F.G., Sucerquia P.A. 2012. Fossilized
961 bacteria in a Cretaceous pterosaur headcrest. Lethaia, 45:495-499.
- 962
- 963 Price, L. 1973. Quelonio amphichelydia no Cretaceo inferior do nordeste do Brasil. Revista
964 Brasileira de Geociencias. 3: 84-96.
- 965
- 966 Pritchard, P. C. 1988. A survey of neural bone variation among recent chelonian species, with
967 functional interpretations. Acta Zoologica Cracoviensia. 31 (26): 625-686.
- 968
- 969 Pritchard, P. C. 2008. Evolution and structure of the turtle shell. Biology of Turtles: From
970 Structures to Strategies of Life. 45-84.
- 971
- 972 Romano, P. S. R., and Azevedo, S. A. K. 2006. Are extant podocnemidid turtles relicts of a
973 widespread Cretaceous ancestor? South American Journal of Herpetology. 1(3): 175-184.
- 974
- 975 Romano, P. S. R., Oliveira, G. R., Azevedo, S. A. K, Kellner, A. W. A., Campos, D. A. 2013. New
976 Information about Pelomedusoides (Testudines: Pleurodira) from the Cretaceous of Brazil.
977 Morphology and evolution of turtles. Springer Netherlands. 261-275.
- 978
- 979 Romano, P.S.R., Gallo, V., Ramos, R.R.C., Antonioli, L. 2014. *Atolchelys lepida*, a new side-
980 necked turtle from the Early Cretaceous of Brazil and the age of crown Pleurodira. Biology Letters.
981 10 (7)
- 982
- 983 Rougier, G.W., de la Fuente, M.S., Arcucci, A.B. 1995. Late Triassic turtles from South America.
984 Science.268: 855–858.
- 985
- 986 Scheyer, T. M., Sander, P. M., Joyce, W. G., Böhme, W. and Witzel, U. 2007. A plywood structure
987 in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary
988 implications. Organisms Diversity & Evolution. 7 (2): 136-144.
- 989

Schleich, H. H. 1990. Neues material zu *Araripemys barreto* Price 1973 (Testudines: Pleurodira). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, 30: 39-49.

Shaffer, H. B., Meylan, P. and McKnight, M. L. 1997. Tests of turtle phylogeny: molecular, morphological, and paleontological approaches. Systematic Biology. 46 (2): 235-268.

Sereno, P. C. and ElShafie, S.J. 2013. A new long-necked turtle, *Laganemys tenerensis* (Pleurodira: Araripemydidae), from the Elrhaz Formation (Aptian–Albian) of Niger. Morphology and evolution of turtles. Springer Netherlands. 215-250.

Silva, H. P. and Kellner, A. W. A. 2006. A combinação de técnicas na preparação de vertebrados fósseis: o exemplo de *Thalassodromeus sethi* (Pterosauria, Tapejaridae). Paleontologia de Vertebrados Grandes Temas e Contribuições Científicas. Rio de Janeiro: Interciência. 293-301.

Sullivan, P. M., & Joyce, W. G. (2017). The shell and pelvic anatomy of the Late Jurassic turtle *Platycheilus oberndorferi* based on material from Solothurn, Switzerland. *Swiss Journal of Palaeontology*, 1-21.

Toombs, H. A. and Rixon, A. E. 1959. The use of acids in the preparation of vertebrate fossils. Curator: The Museum Journal. 2 (4): 304-312.

Valença, L. M. M., Neumann, V. H., Mabessone, J. M. 2003. An overview on Callovian-Cenomanian intracratonic basins of Northeast Brazil: Onshore stratigraphic record of the opening of the southern Atlantic. Acta Geologica. 1 (3): 261-275.

Villa, C. and Lynnerup, N. 2012. Hounsfield Units ranges in CT scanings of bog bodies and mummies. Anthropol Anz. 69 (2):127–145.

Legends of Figures

Fig. 1. UFC-722; whole specimen, photograph to the left and schematic drawing to the right. Photo by Marcus Krag. Drawing by Thales Nascimento.

Fig. 2. UFC-722; A) skull; B) schematic drawing; C) 3D-model in dorsal and D) ventral view. A) by Marcus Krag and drawing B) by Thales Nascimento.

Fig. 3. A) MPSC-2107, plastron in ventral view and B) schematic drawing. Photo and drawing by Thales Nascimento. C) UFRPE-5302, carapace in dorsal view and B) schematic drawing. Photo and drawing by Thales Nascimento.

Fig. 4. MN 6949-V. Skull in A) dorsal, B) ventral, C) right and D) left views. E), F), G) and H), respective schematic drawings. I) Plastron in ventral view and J) carapace in dorsal view. Manus in K) dorsal and L) ventral views. Photos by RVP and Thiago Mariani. Drawings by MECL and RVP.

Fig. 5. Holotype, A) carapace, dorsal view and B) plastron, ventral view. Photo by RVP. MPSC 2308, C) carapace in dorsal view and D) plastron in ventral view. Photo by Renan Bantim. DGM 346-LE. E) Carapace in dorsal view and F) plastron in ventral view. Photo by RVP and Thiago Mariani. MN 6744-V, G) part with carapace in dorsal view and H) counterpart with carapace remains in internal view. Photo by RVP and Thiago Mariani. BSP 1977 I 1, I) carapace in dorsal view and J) plastron in ventral view. Photo by RVP. BSP 1981 I 38, K) carapace in dorsal view and L) plastron in ventral view. Photo by RVP. MN 6637-V. MN 6743-V, M) carapace in dorsal view, encased in resin and N) plastron in ventral view. Photo by RVP and Thiago Mariani. O) Impression of the carapace in internal view and P) plastron in visceral view. Photo by RVP and Thiago Mariani.

Fig. 6. A) DGM 1449-R, carapace in dorsal view. Photo by RVP. B) MPSC 134, carapace in dorsal view. Photo by Renan Bantim. C) MPSC 137. Carapace in dorsal view. Photos by Renan Bantim. D) SMNK no number, carapace in dorsal view. Photo by RVP.

Fig. 7. SMNK PAL 3979. A) Whole specimen, ventral view. B) Plastral elements showing pitted ornamentation on the preserved ventral surface. C) Pes showing simple unguals.

Fig. 8. Comparative neurals. A) BSP 1981 I 38, B) MPSC R 010, C) UFC-722, D) MN 6949-V, E) UFRPE 5302, F) MN 6744-V. Drawings by MECL.

Fig. 9. Ornamentation variation in the ventral surface of the hyo- and hypoplastra. Pitted pattern, as seen in A) MN 6949-V, left side and B) DGM 346 R, left side. Combined pitted + ridge-and-sulcus patterns, as seen in C) UFC 722, right side, and D) MN 6637-V, left side.

Fig. 10. Anal notch variation. A) V-shaped morphology of the inferred females, as seen in BSP 1981 I 38. B) U-shaped morphology of the inferred males, as seen in UFC-722. Drawing by SL and RVP.

Figure 1

Specimen UFC-722; whole specimen.

Photograph to the left and schematic drawing to the right. Photo by Marcus Krag. Drawing by Thales Nascimento.

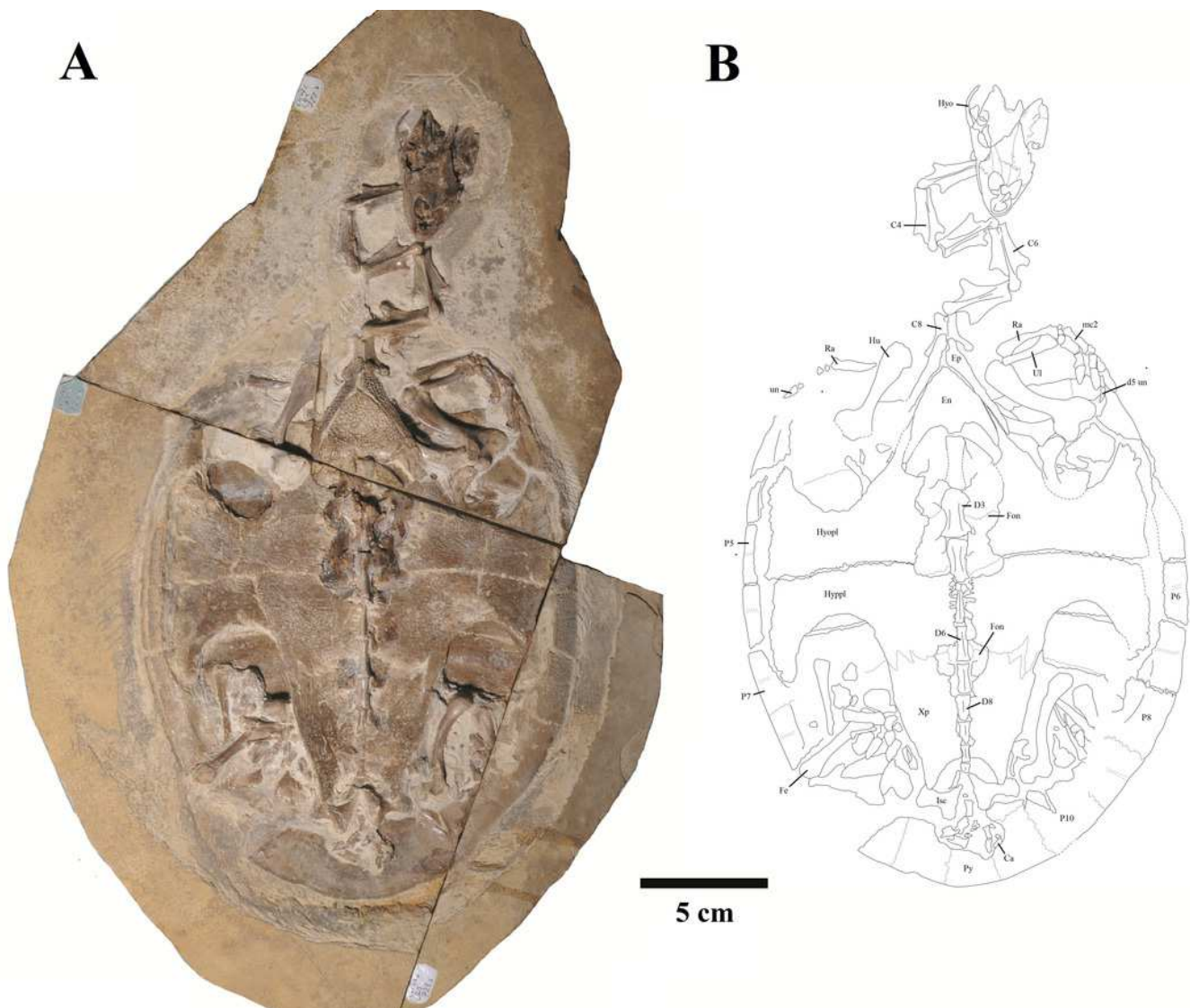


Figure 2

Specimen UFC-722.

A) skull; B) schematic drawing; C) 3D-model in dorsal and D) ventral view. A) by Marcus Krag and drawing B) by Thales Nascimento.

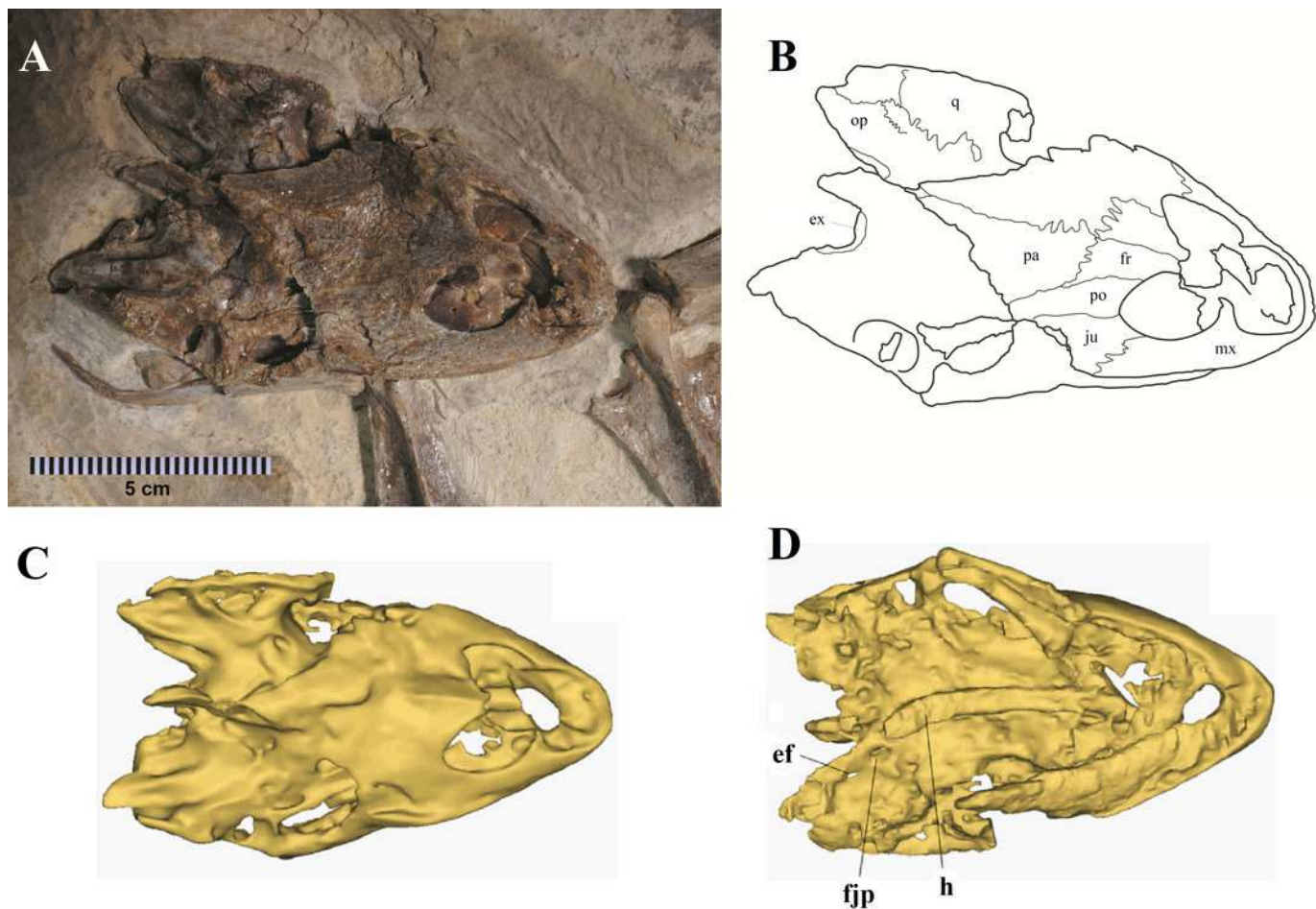


Figure 3

Specimens MPSC-2107 and UFRPE-5302.

A) MPSC-2107, plastron in ventral view and B) schematic drawing. Photo and drawing by Thales Nascimento. C) UFRPE-5302, carapace in dorsal view and B) schematic drawing. Photo and drawing by Thales Nascimento.

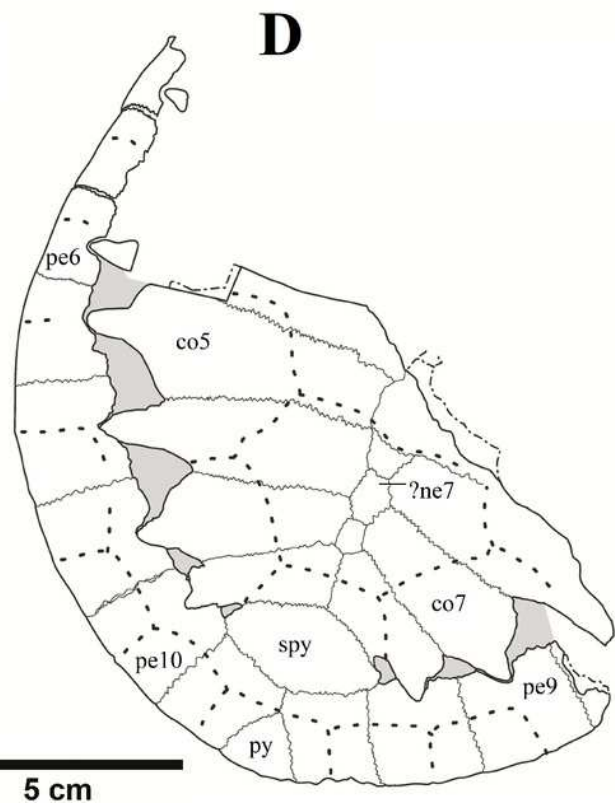
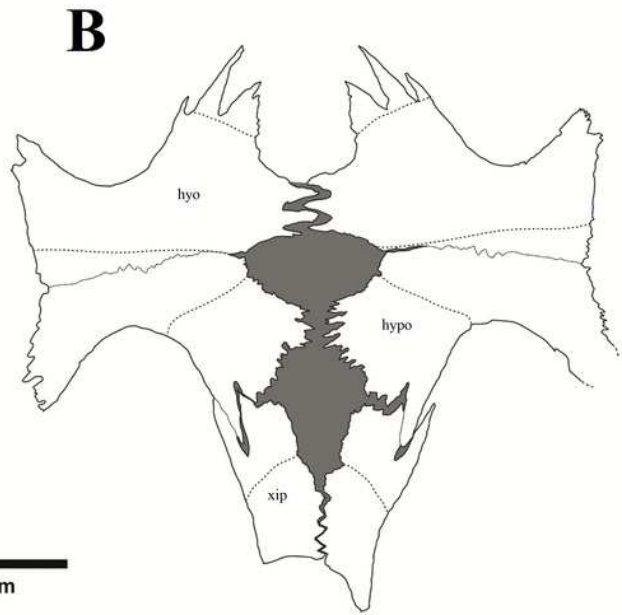
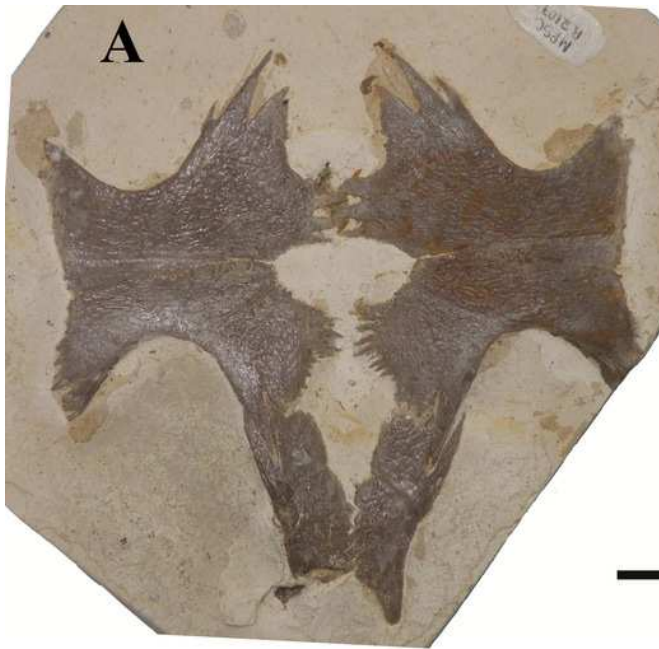


Figure 4

Specimen MN 6949-V.

Skull in A) dorsal, B) ventral, C) right and D) left views. E), F), G) and H), respective schematic drawings. I) Plastron in ventral view and J) carapace in dorsal view. Manus in K) dorsal and L) ventral views. Photos by RVP and Thiago Mariani. Drawings by MECL and RVP.

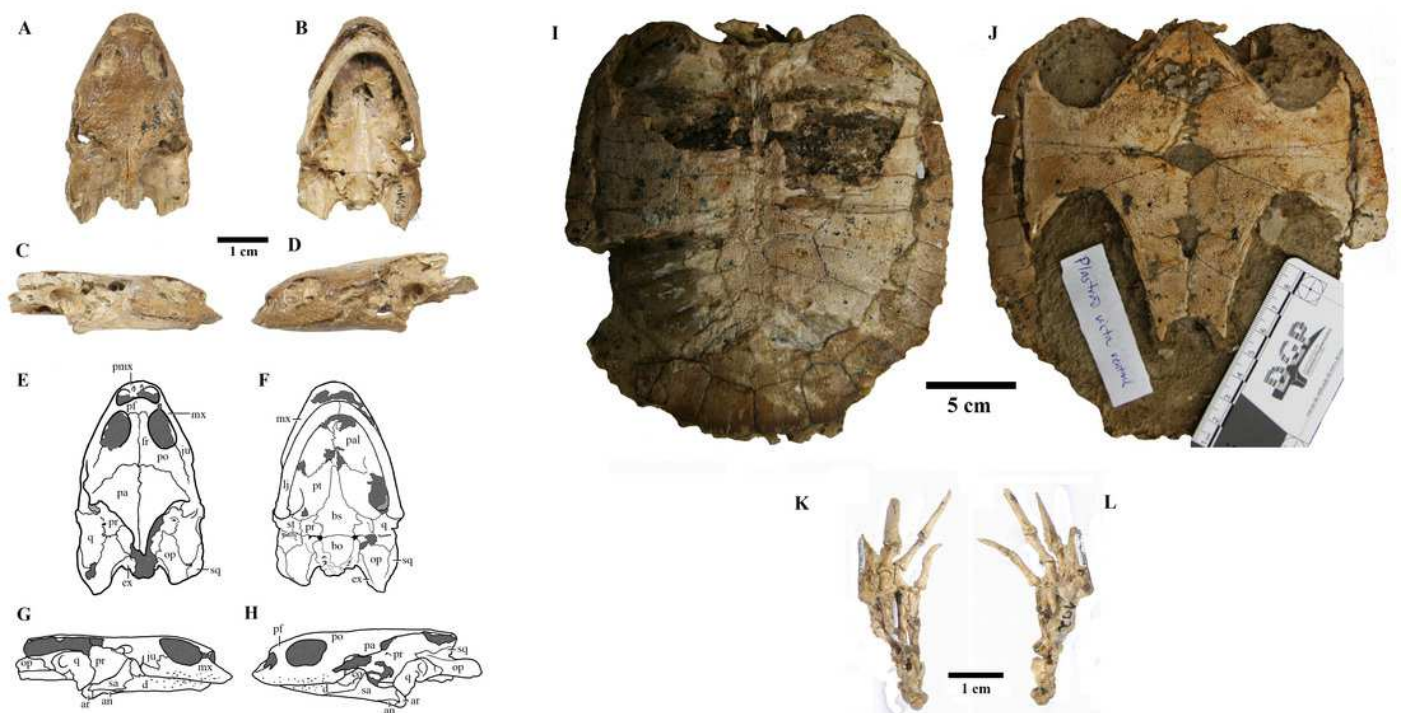


Figure 5

Shells of several specimens.

Holotype, A) carapace, dorsal view and B) plastron, ventral view. Photo by RVP. MPSC 2308, C) carapace in dorsal view and D) plastron in ventral view. Photo by Renan Bantim. DGM 346-LE. E) Carapace in dorsal view and F) plastron in ventral view. Photo by RVP and Thiago Mariani. MN 6744-V, G) part with carapace in dorsal view and H) counterpart with carapace remains in internal view. Photo by RVP and Thiago Mariani. BSP 1977 I 1, I) carapace in dorsal view and J) plastron in ventral view. Photo by RVP. BSP 1981 I 38, K) carapace in dorsal view and L) plastron in ventral view. Photo by RVP. MN 6637-V. MN 6743-V, M) carapace in dorsal view, encased in resin and N) plastron in ventral view. Photo by RVP and Thiago Mariani. O) Impression of the carapace in internal view and P) plastron in visceral view. Photo by RVP and Thiago Mariani.

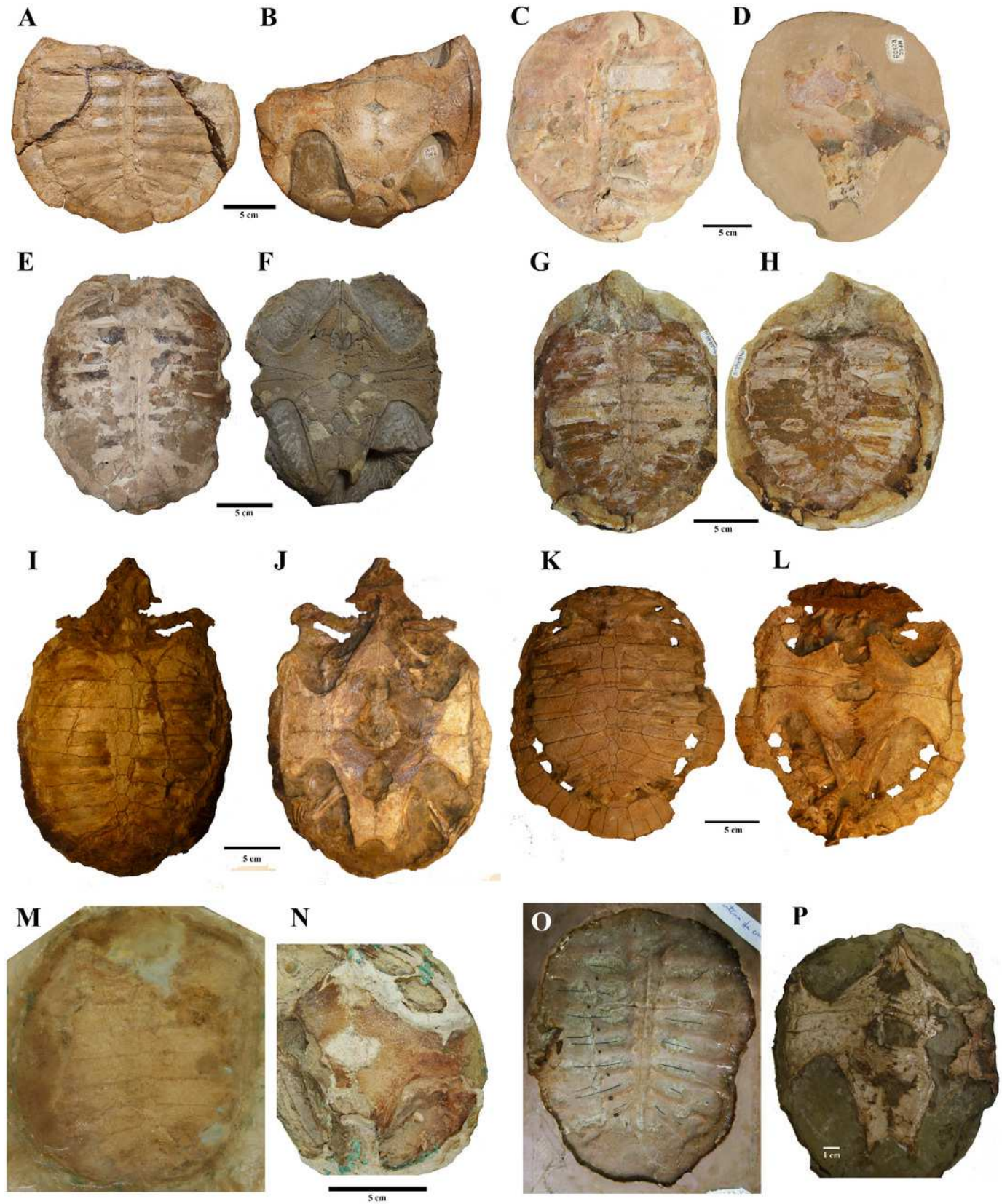
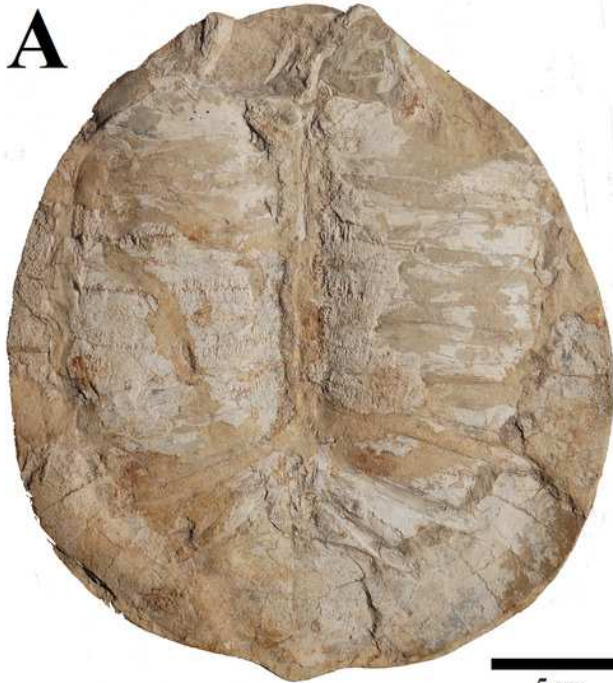


Figure 6

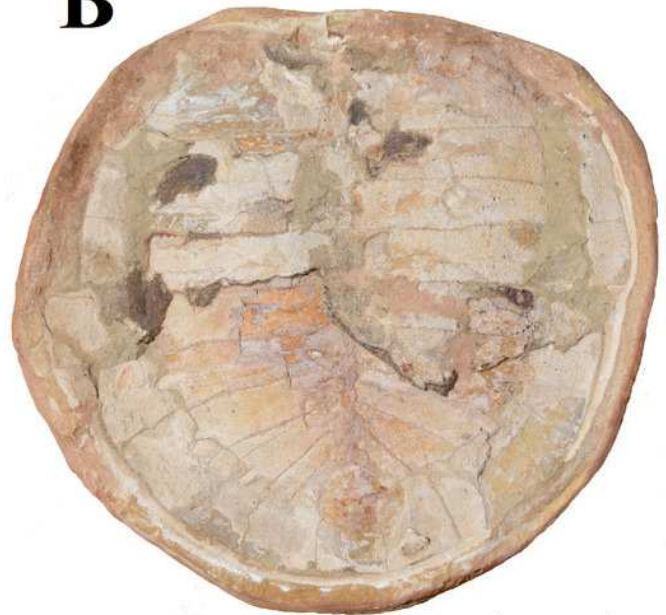
Dorsal view of carapace from the following specimens:

A) DGM 1449-R, carapace in dorsal view. Photo by RVP. B) MPSC 134, carapace in dorsal view. Photo by Renan Bantim. C) MPSC 137. Carapace in dorsal view. Photos by Renan Bantim. D) SMNK no number, carapace in dorsal view. Photo by RVP.

A



B



C



D



Figure 7

Specimen SMNK PAL 3979.

A) Whole specimen, ventral view. B) Plastral elements showing pitted ornamentation on the preserved ventral surface. C) Pes showing simple unguals.

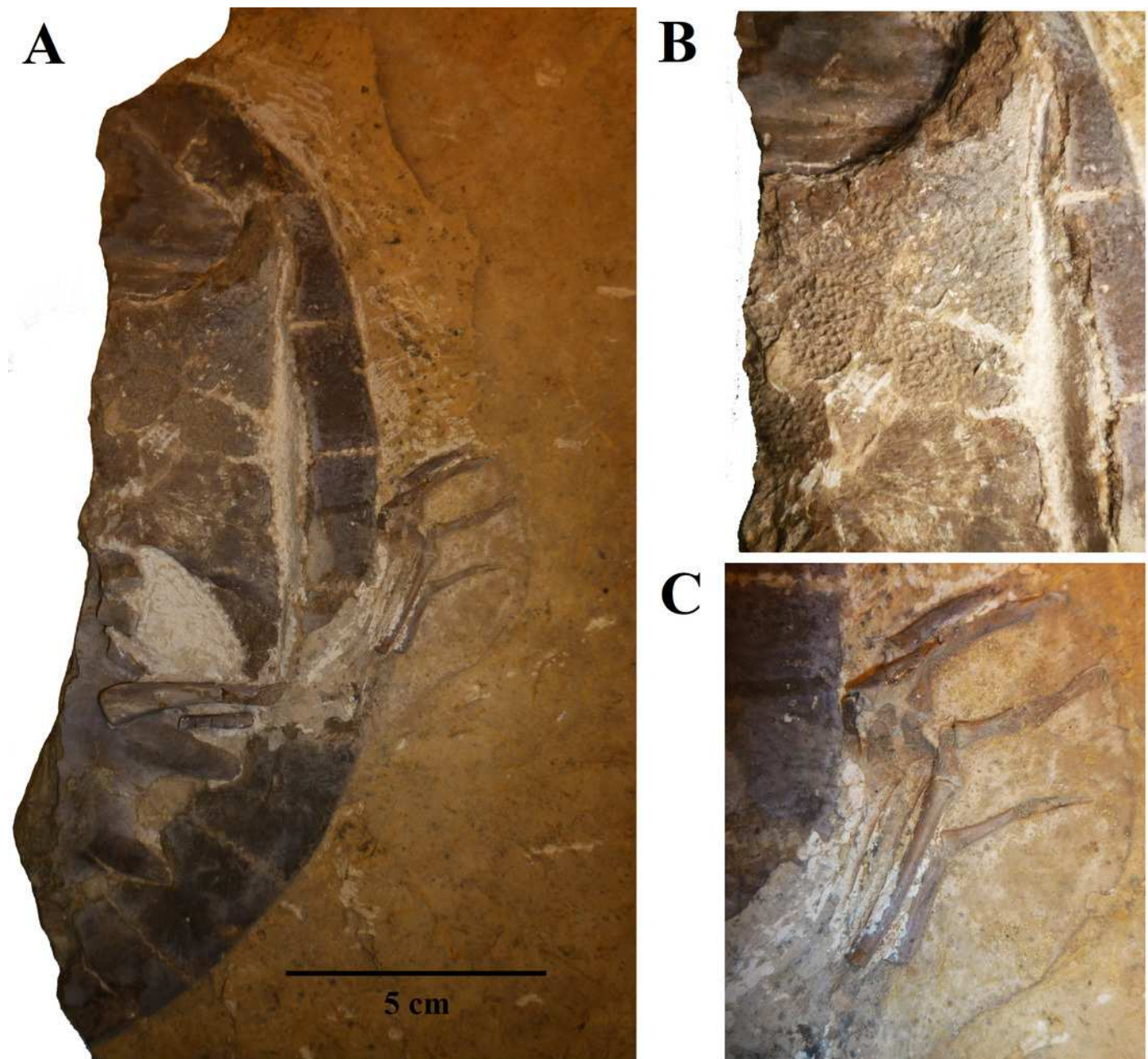


Figure 8

Comparative drawing of neural series from different specimens.

A) BSP 1981 I 38, B) MPSC R 010, C) UFC-722, D) MN 6949-V, E) UFRPE 5302, F) MN 6744-V.

Drawings by MECL.

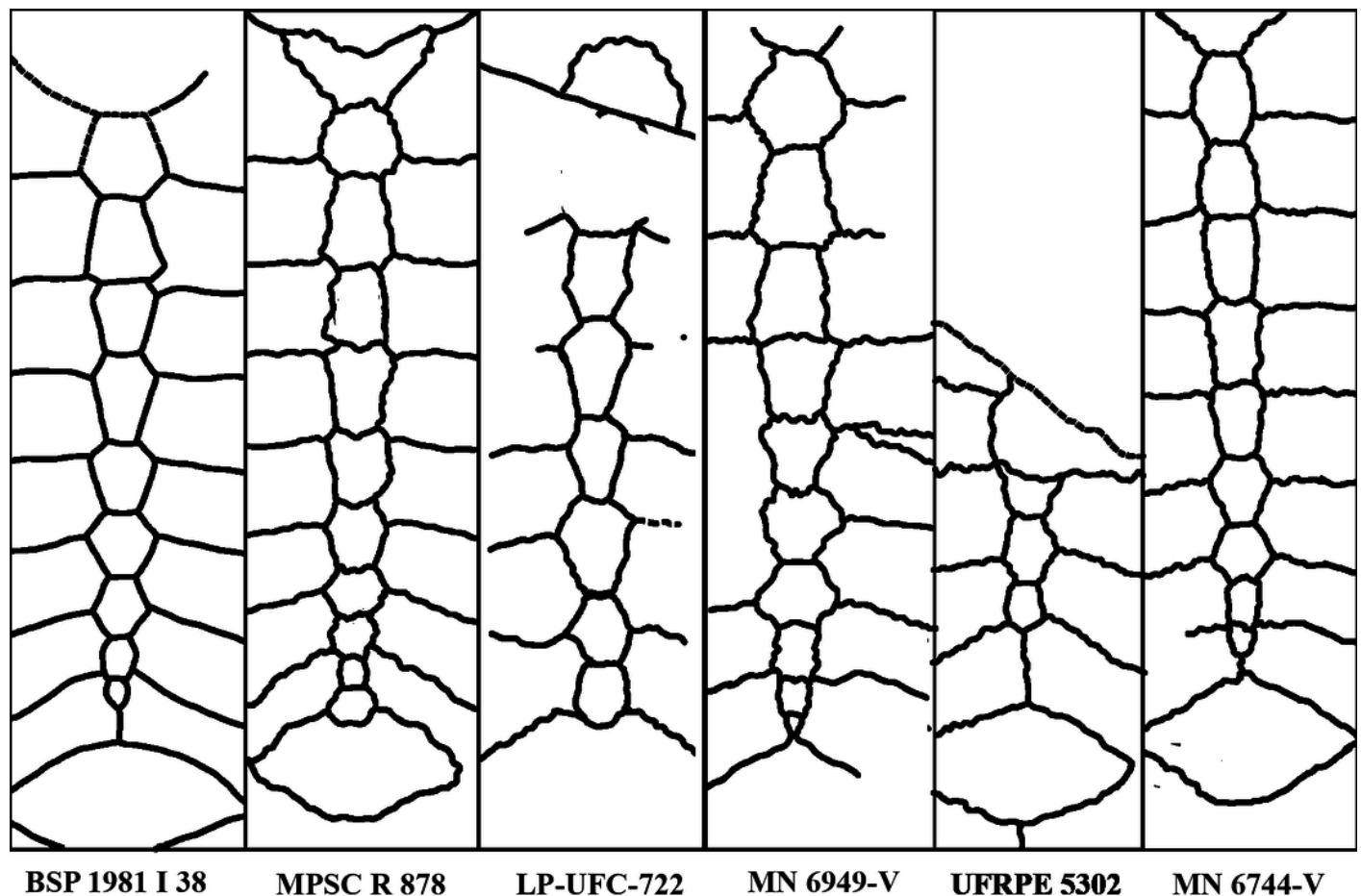


Figure 9

Ornamentation variation in the ventral surface of the hyo- and hypoplastra.

Pitted pattern, as seen in A) MN 6949-V, left side and B) DGM 346 R, left side. Combined pitted + ridge-and-sulcus patterns, as seen in C) UFC 722, right side, and D) MN 6637-V, left side.

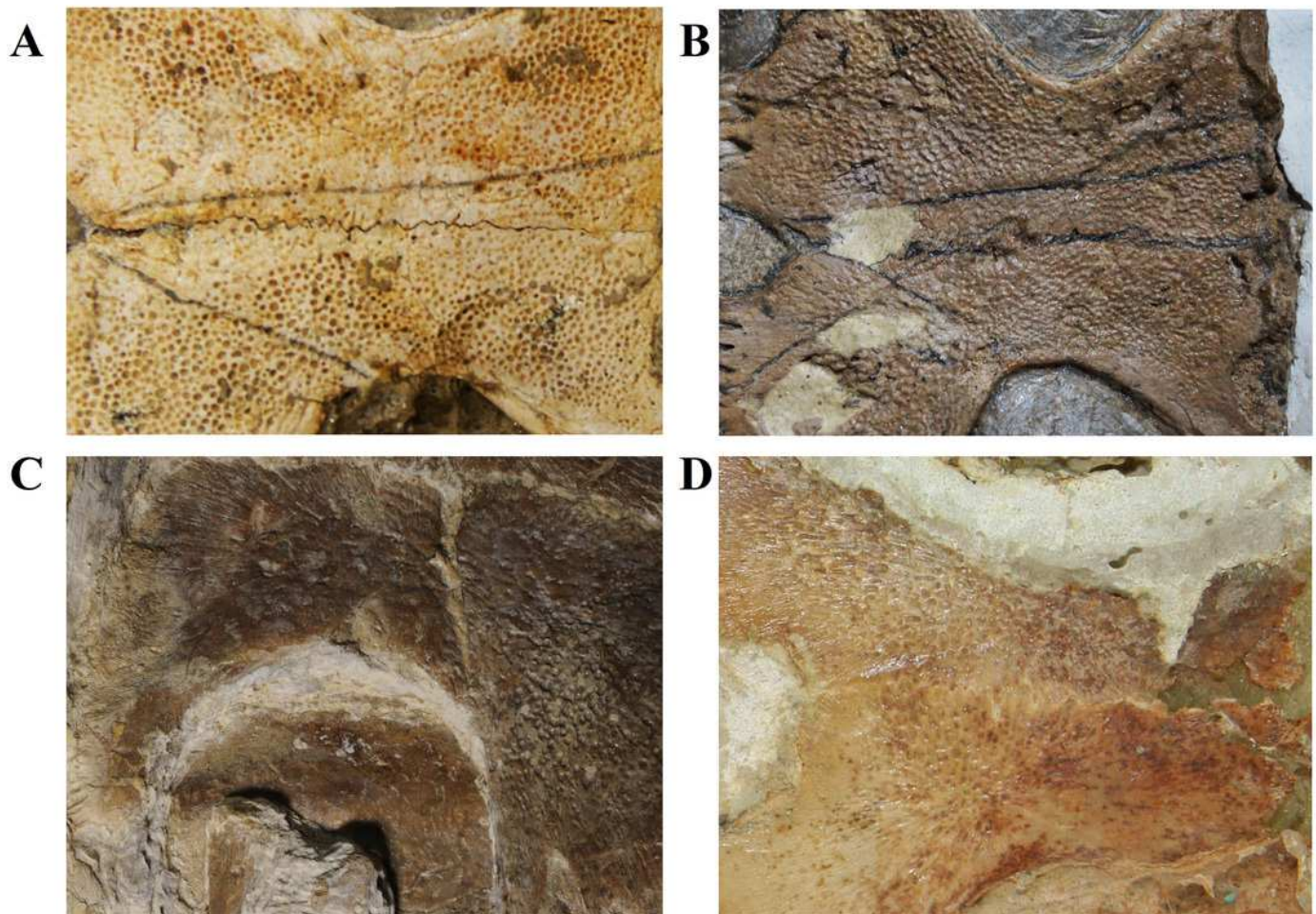


Figure 10

Anal notch variation.

A) V-shaped morphology of the inferred females, as seen in BSP 1981 I 38. B) U-shaped morphology of the inferred males, as seen in UFC-722. Drawing by SL and RVP.

