



New data on the shell anatomy of *Selenemys lusitanica*, the oldest known pleurosternid turtle in Europe

Adán Pérez-García^{1,2}  · Bruno Camilo^{2,3} · Francisco Ortega^{1,2} 

Received: 15 March 2023 / Accepted: 12 January 2024 / Published online: 23 January 2024
© The Author(s) 2024

Abstract

One of the most diverse turtle lineages in the Upper Jurassic and Lower Cretaceous record of Europe is that of the stem turtles Pleurosternidae (Paracryptodira), also distributed in North America. The oldest European representative of this lineage is the Portuguese *Selenemys lusitanica*, known from upper Kimmeridgian to lower Tithonian levels (Late Jurassic). The information on the shell of this taxon is so far very limited, being exclusively restricted to that provided in the publication in which the taxon was defined. New specimens from several upper Kimmeridgian to Tithonian localities in the Consolação Sub-basin of the Portuguese Lusitanian Basin, both from the Leiria District and the Lisbon District, are studied here. They include the most complete shell of the species found so far, as well as several isolated plates that allow us to improve knowledge about it. Thus, new information about the shell anatomy of *Selenemys lusitanica* is provided, but also about its intraspecific variability.

Keywords Paracryptodira · Pleurosternidae · Late Jurassic · Lusitanian Basin · Shell anatomy · Intraspecific variability

Resumen

Uno de los linajes de tortugas más diversos en los registros tanto del Jurásico Superior como del Cretácico Inferior de Europa es el de las tortugas basales Pleurosternidae (Paracryptodira), estando también presente en Norteamérica. El representante europeo más antiguo de este linaje es la especie portuguesa *Selenemys lusitanica*, conocida desde el Kimmeridgiense superior hasta el Titoniense inferior (Jurásico Superior). La información sobre el caparazón de este taxón era hasta el momento muy limitada, estando restringida a aquella aportada en la publicación en la que la especie fue definida. Nuevos ejemplares de varias localidades del Kimmeridgiense superior al Titoniano en la Subcuenca de Consolación, en la Cuenca Lusitánica (Portugal) son aquí estudiados. Proceden de los distritos de Leiria y de Lisboa. Entre estos restos se incluye el caparazón más completo de la especie encontrado hasta el momento, así como varias placas aisladas que permiten mejorar el conocimiento sobre la misma. De esta forma, nueva información sobre la anatomía del caparazón de *Selenemys lusitanica* es aportada, así como sobre su variabilidad intraespecífica.

Palabras clave Paracryptodira · Pleurosternidae · Jurásico Superior · Cuenca Lusitánica · Anatomía del caparazón · Variabilidad intraespecífica

✉ Adán Pérez-García
a.perez.garcia@ccia.uned.es

¹ Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Avda. Esparta s/n, 28232 Las Rozas, Madrid, Spain

² Laboratório de Paleontologia e Paleoecologia da Sociedade de História Natural, Polígono Industrial do Alto do Ameal, Pav.H02 e H06, Torres Vedras 2565-641, Portugal

³ Faculdade de Ciências e Tecnologia, GeoBioTec, Universidade Nova de Lisboa, Campus da Caparica, Caparica 2829-516, Portugal

1 Introduction

Pleurosternidae is a lineage of Paracryptodira (stem turtles; i.e., Testudinata not attributable to the crown Testudines) exclusive to the Upper Jurassic to Lower Cretaceous record of Europe and North America (Gaffney, 1979; Lapparent de Broin, 2001; Pérez-García, 2017). Several representatives are known in Europe, the greatest diversity being recognized in the Iberian Peninsula (see Pérez-García, 2017;

and references therein). Thus, in addition to forms such as the Spanish *Riodevemyss inumbragigas* Pérez-García et al., 2015a and *Pleurosternon moncayensis* Pérez-García et al., 2022, which have been found in outcrops close to the Jurassic-Cretaceous boundary, the Iberian record includes both the oldest pleurosternid of the continent (i.e., the Portuguese *Selenemys lusitanica* Pérez-García & Ortega, 2011, whose holotype comes from an upper Kimmeridgian to basal Tithonian outcrop) as the youngest globally known representative (i.e., the Spanish Albian *Toremys cassiopeia* Pérez-García et al., 2015b).

The only fossils so far documented for *Selenemys lusitanica* are those published in the paper where this taxon was described: its holotype (i.e., a partial shell preserving the almost complete and articulated plastron, and several disarticulated elements of the carapace), and four additional specimens included in the hypodigm of the taxon (i.e., a partial and articulated shell, an isolated second costal, an isolated first peripheral, and an isolated xiphiplastron) (Pérez-García & Ortega, 2011). All of them were found in the Consolação Sub-basin of the central Lusitanian Basin, in West-Central Portugal. The holotype come from the upper Kimmeridgian to basal Tithonian Praia da Amoreira-Porto Novo Formation *sensu* Manuppella et al. (1999) [equivalent to the Porto Novo Member of the Lourinhã Formation *sensu* Hill (1988); see Mocho et al., 2017; and references therein], and was found north of the Santa Rita Beach (Torres Vedras Municipality, Lisbon District; Fig. 1). The other specimens come from outcrops located south of the Peralta Beach (Atalaia Civil Parish, Lourinhã Municipality, Lisbon District; Fig. 1), having been found in upper Kimmeridgian to lower Tithonian levels of the Sobral Formation *sensu* Manuppella et al. (1999) [equivalent to the Praia Azul Member of the Lourinhã Formation *sensu* Hill (1988); see Mocho et al., 2017; and references therein]. This scarce availability of specimens, corresponding to two partial shells and some isolated plates, barely provided data on the variability of the taxon. The intraspecific variability has been documented as relatively high for some European pleurosternids represented by several specimens, such as *Dorsetochelys typocardium* (Seeley, 1869) and, especially, *Pleurosternon bullockii* (Owen, 1842) (see Pérez-García, 2014; Guerrero & Pérez-García, 2021a, b). Furthermore, relevant features for the characterization of the Portuguese taxon (e.g., the carapace shape) are so far unknown or could not be adequately described from the documented remains.

The first-hand study of collections deposited in several scientific institutions, as well as the analysis of new finds of Jurassic turtles in the Lusitanian Basin, allow us to recognize the presence of *Selenemys lusitanica* as relatively abundant there. In this sense, a selection of several specimens, both recently found (an articulated and well-preserved shell),

and others hitherto unpublished but found decades ago and deposited at the Museu Geológico of Lisbon, allow us to improve knowledge about the shell anatomy of this taxon. These specimens are here presented, so that new data on the intraspecific variability of the oldest European pleurosternid are provided.

Institutional abbreviations

MG Museu Geológico, Lisboa, Portugal
SHN Sociedade de História Natural, Torres Vedras, Portugal

Anatomical abbreviations

Ab abdominal scute
An anal scute
c costal
Fe femoral scute
hp hypoplastron
Hu humeral scute
hy hyoplastron
If inframarginal scute
M marginal scute
ms mesoplastron
n neural
nu nuchal
p peripheral
Pc pectoral scute
Pl pleural scute
V vertebral scute
xi xiphiplastron

2 Systematic paleontology

Testudinata Klein, 1760.

Paracryptodira Gaffney, 1975.

Baenoidea Williams, 1950.

Pleurosternidae Cope, 1868.

Pleurosternidae Cope, 1868.

Selenemys Pérez-García & Ortega, 2011.

Selenemys lusitanica Pérez-García & Ortega, 2011.
(Figs. 2–3)

New referred material An articulated and relatively complete shell (SHN.003, Fig. 2), and six isolated shell plates: the distal half of a second right costal (MG 8733a, Fig. 3A–B), a complete neural (MG 8743, Fig. 3C–D), an almost complete first right peripheral (MG 8750a, Fig. 3E–F), the distal half of a first right peripheral (MG 8733b, Fig. 3G–H), the distal half of a first left peripheral (MG 8733c, Fig. 3I–J),

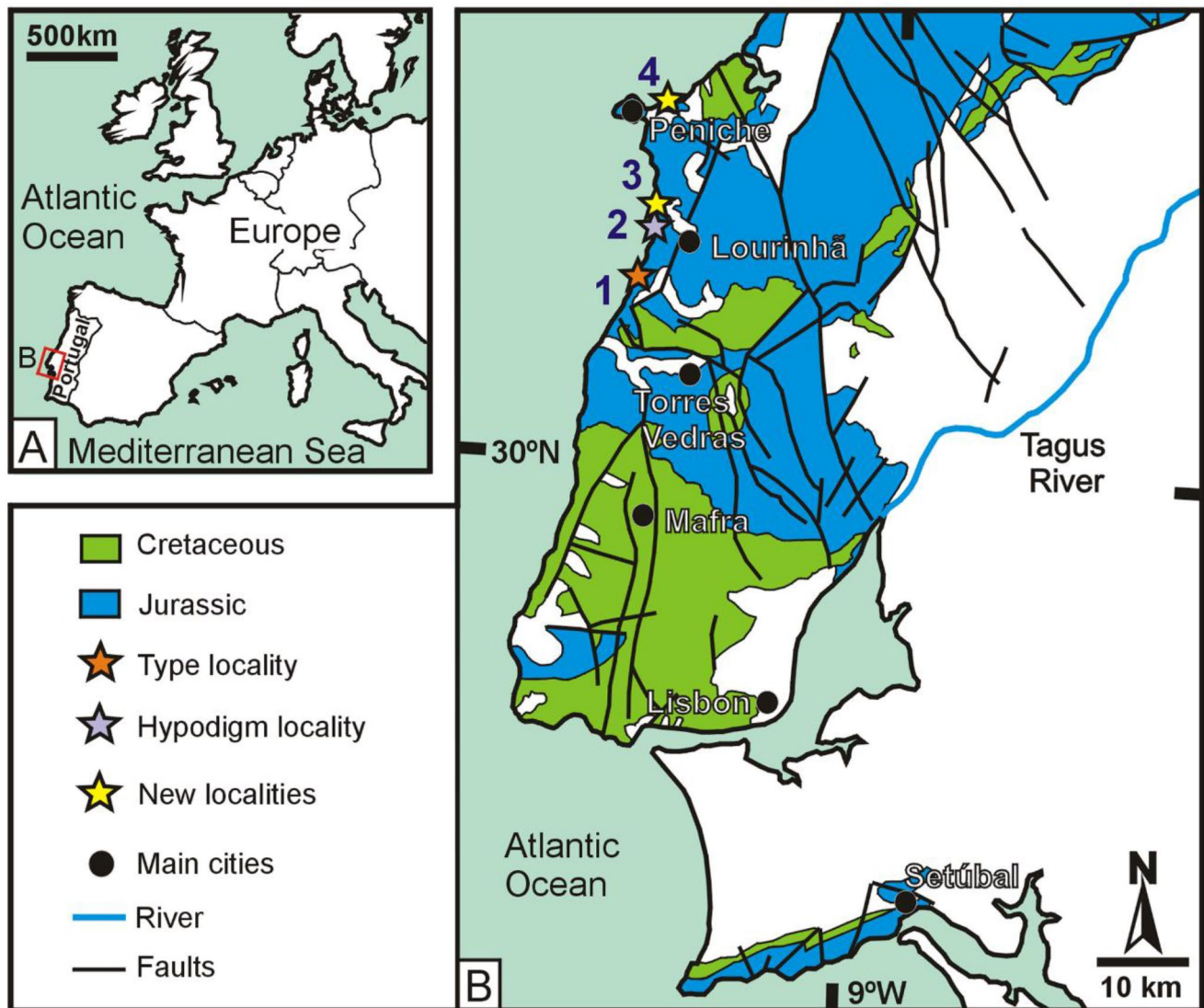


Fig. 1 Location of the finds of the pleurosternid turtle *Selenemys lusitanica* currently documented, all of them from the Consolação Sub-basin, in the Lusitanian Basin (West-Central Portugal). **A**, location of the southern half of the Lusitanian Basin (red rectangle) in a geographic map of Europe. **B**, map of the southern half of the Lusitanian Basin showing the main Jurassic and Cretaceous areas, and the position of the outcrops in which remains attributable to *Selenemys lusitanica* have been found: 1, type locality of the species [north of the Santa Rita Beach (Torres Vedras Municipality, Lisbon District); upper Kimmeridgian or basal Tithonian]; 2, locality where the other

remains composing the hypodigm and new specimen MG 8743 where found [south of the Peralta Beach (Lourinhã Municipality, Lisbon District); upper Kimmeridgian or lower Tithonian]; 3, Areia Branca Beach (Lourinhã Municipality, Lisbon District), late Kimmeridgian or probably Tithonian, where MG 8733a, MG 8750a, MG 8733b, MG 8733c and MG 8750b were discovered; 4, North of the Baleal Beach (Peniche Municipality, Leiria District), upper Kimmeridgian or lower Tithonian, from where SHN.003 comes from. Modified from Pérez-García et al. (2023)

and the posterior half of a right xiphiplastron (MG 8750b, Fig. 3K-L).

Localities and horizon The outcrops from which all these referred materials come are located in the Consolação Sub-basin of the central Lusitanian Basin, in West-Central Portugal (Fig. 1). SHN.003 comes from the north of the Baleal Beach (Pedras Muitas, Atouguia da Baleia Civil Parish, Peniche Municipality, Leiria District), found at the lower

part of the Bombarral Formation sequence cropping out in this area which is Tithonian in age (Manuppella et al., 1999) [equivalent to the Santa Rita Member of the Lourinhã Formation *sensu* Hill (1988)] (for the stratigraphical and sedimentological context see Mocho et al., 2017; and references therein). The specimen was collected by one of us (BC) in a silt layer with inclusions of clasts, and with a high amount of plant remains. MG 8743 comes from the south of the Peralta Beach (Atalaia Civil Parish, Lourinhã Municipality,

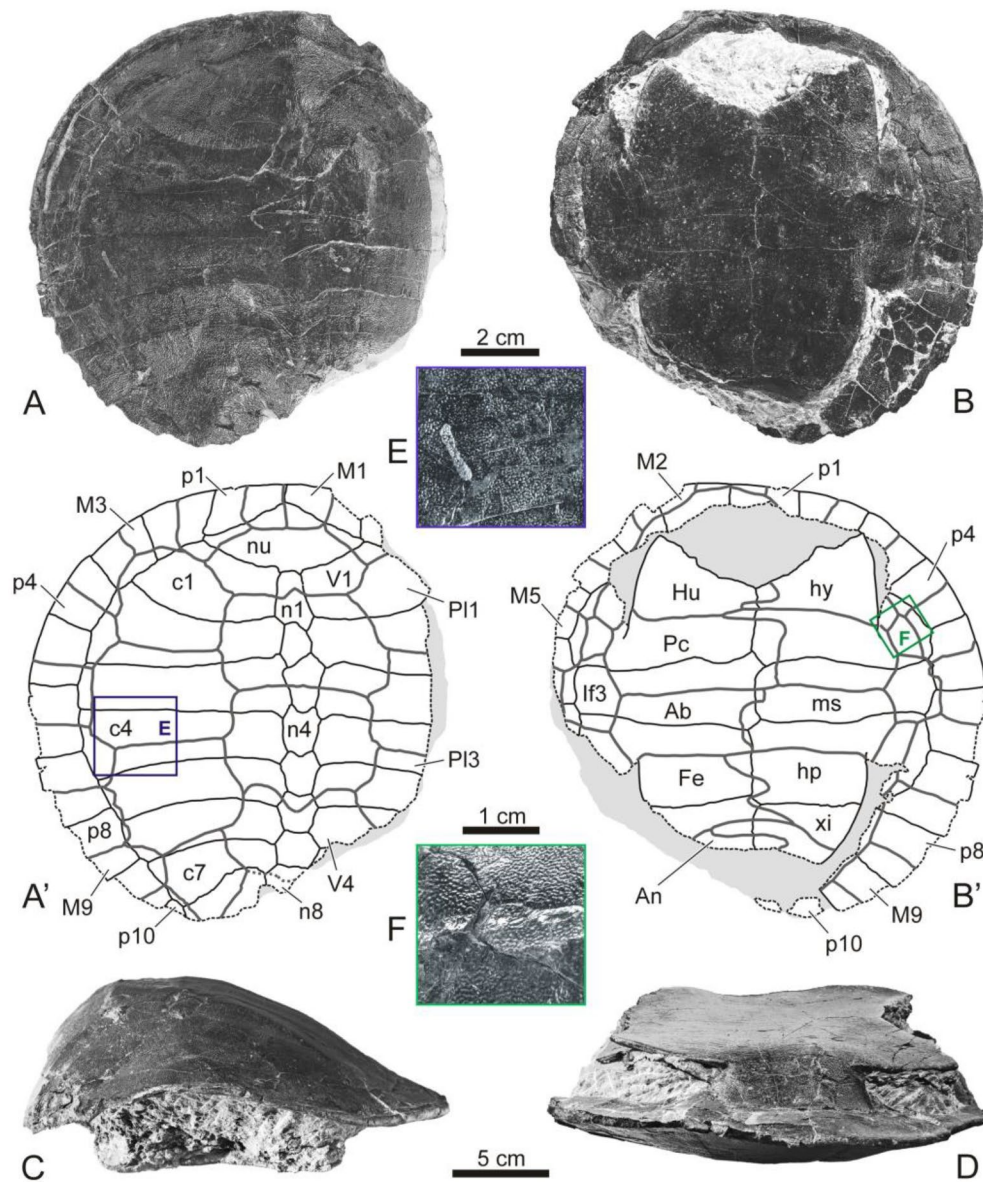


Fig. 2 SHN.003, articulated shell of *Selenemys lusitanica*, from the north of the Baleal Beach (Pedras Muitas, Peniche Municipality, Leiria District, West-Central Portugal), found at upper Kimmeridgian-lower Tithonian levels, in dorsal **A**, ventral **B**, anterior **C** and left lateral **D** views. **A'** and **B'** represent schematic drawings of the specimen, in

which the dotted lines indicate broken edges; the continuous black lines correspond to the margins of the plates; the borders of the scutes are represented by thicker gray lines; and the gray surfaces correspond to sediment. **E** and **F** show details of the carapacial and plastral outer surfaces (its location is indicated in **A'** and **B'**)

Lisbon District), where all hypodigm remains of the taxon, except its holotype, were found at the upper Kimmeridgian to lower Tithonian Sobral Formation *sensu* Manuppella et al. (1999) [equivalent to the Praia Azul Member of the Lourinhã Formation *sensu* Hill (1988)]. MG 8733a, MG 8750a, MG 8733b, MG 8733c, and MG 8750b were found in the Areia Branca Beach (Areia Branca Civil Parish,

Lourinhã Municipality, Lisbon District), coming from the Tithonian Bombarral Formation.

Description The maximum preserved length for the articulated shell SHN.003 is about 26 cm, and its maximum width is about 25 cm (Fig. 2). It is slightly deformed, as result of lateral compression (Fig. 2C). It is recognized as a sub-rounded carapace (Fig. 2A-B). It lacks a nuchal notch. The carapace lacks several elements, due to the erosion it suffered between the exposure and its discovery, which especially affected its right half (having lost the almost complete

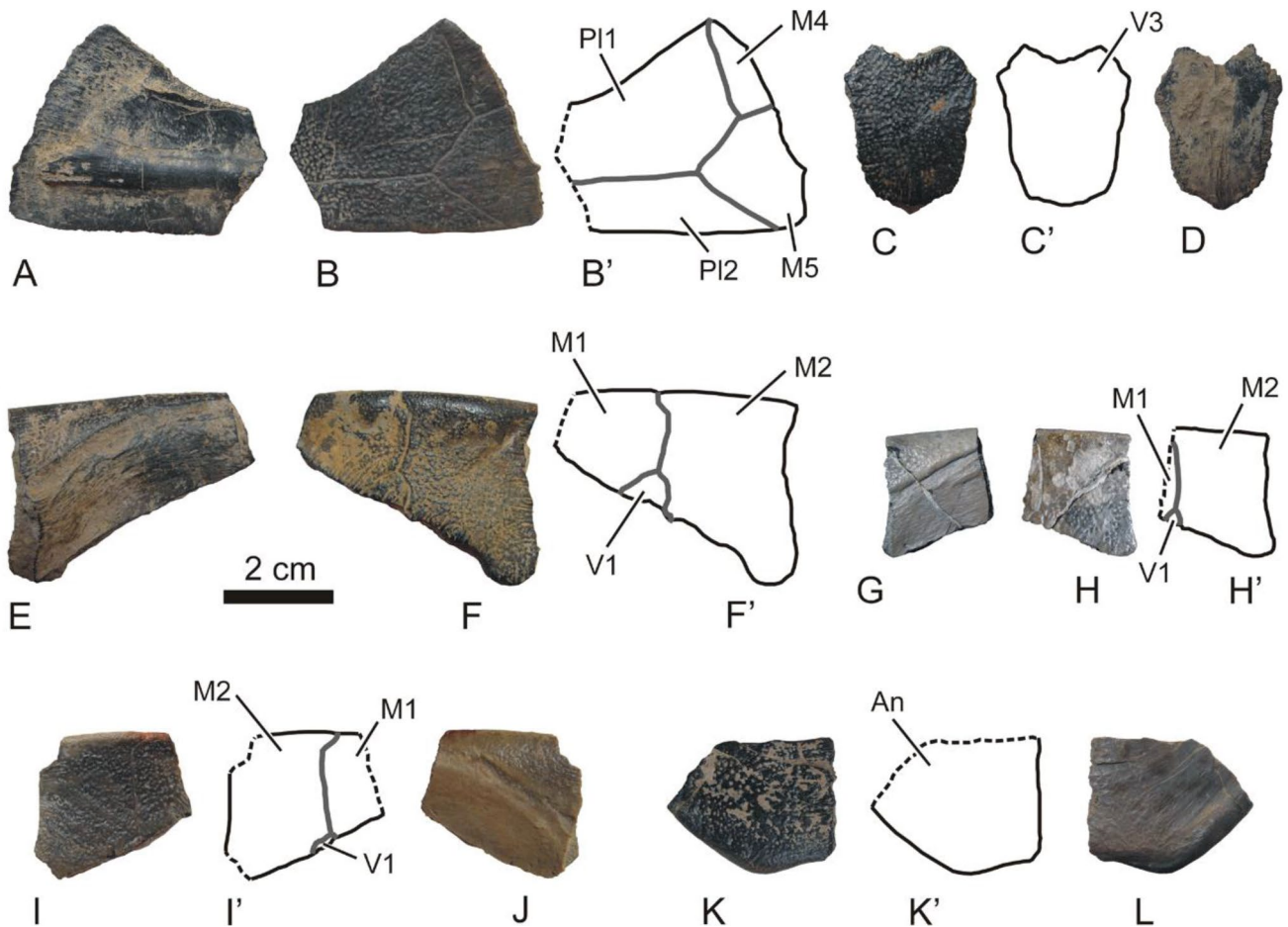


Fig. 3 Isolated shell plates of *Selenemys lusitanica*, from the Lourinhã Municipality (Lisbon District, West-Central Portugal). **A–B**, MG 8733a, distal half of a second right costal. **C–D**, MG 8743, neural. **E–F**, MG 8750a, almost complete first right peripheral. **G–H**, MG 8733b, distal half of a first right peripheral. **I–J**, MG 8733c, distal half of a first left peripheral. **K–L**, MG 8750b, posterior half of a right xiphiplastron. All of them in dorsal **B, C, F, H, I, and L** and ventral **A, D, E, G, J, and K** views. These specimens come from late Kimmeridgian or probably

Tithonian levels of the Praia da Areia Branca except MG 8743 **C–D**, from the upper Kimmeridgian or lower Tithonian of the south of the Peralta Beach, in the Atalaia Civil Parish. **B', C', F', H', I', and K'** represent schematic drawings of the specimens, in external views (i.e., in dorsal view for the carapace elements and in ventral for the plastral ones), in which the dotted lines indicate broken edges; the continuous black lines correspond to the margins of the plates; and the borders of the scutes are represented by thicker gray lines

right peripheral series and the distal end of the right costals), as well as its posterior margin (lacking the suprapygal and the pygal plates) (Fig. 2A). The plastron lacks the posterior region of the xiphiplastra, because of the erosion, but also the epiplastra and the entoplastron, due to the disarticulation of these elements before burial (Fig. 2B). The complete shell outer surface shows an ornamental pattern composed of small, regular and clearly defined pits (Fig. 2E–F).

The nuchal plate does not reach the anterior carapacial margin (Fig. 2A). This plate is more than twice as wide as long. It laterally reaches the second pair of peripherals. The plate shows a slight posterior protrusion for contact with the neural series. This series is composed of at least eight elements. An anomaly is recognized in the first to third neurals, being asymmetric. Thus, the second right costal contacts

these three plates, but the left one only the first two neurals. The first to sixth neurals are longer than wide, but the seventh is slightly wider than long. Most neurals are hexagonal, the shortest margins of the second to seventh neurals being the latero-anterior ones. The first pair of costals is twice as wide as long. Laterally, it contacts the second and third peripherals. The second pair of costals shows a marked lateral development, being the longest of the costal series, and reaching three pairs of peripherals (the third to the fifth ones). Each of the remaining pairs of costals laterally contact two pairs of peripherals. The first pair of peripherals is short, being almost twice as wide as long. It reaches the axial axis, where it is almost three times shorter than laterally. The second pair of peripherals shows a very short contact with the nuchal plate.

SHN.003 lacks a cervical scute (Fig. 2A). The vertebral scutes are subequal in width, being as wide as the nuchal plate. At least the first to fourth vertebrals are hexagonal, being wider than long. The right anterior vertex of the first vertebral reaches the posterior margin of the first right peripheral. The sulci between the vertebrals are located on the first, third, sixth, and eighth neurals. Some of them are sinuous but others are perpendicular to the axial plane. The pleural scutes do not overlap the peripheral series, except the first over the second and, especially, the third peripherals, reaching the contact with the fourth ones. The sulci between the third and fourth pleurals do not run across the middle of the sixth costals, but rather converge posteriorly with the suture between that pair of plates and the posterior one. The first marginals are almost as wide as they are long.

The anterior plastral lobe is slightly wider than the posterior (Fig. 2B). Both lobes are broad, and subrounded. The suture between the hyoplastra and the entoplastron shows that this plate was very large, probably notably wider than long. This specimen has a pair of mesoplastra, which are developed from the medial plane to the contact with the peripheral series (reaching the fifth and sixth pairs of peripherals).

The midline plastral sulcus is markedly sinuous (Fig. 2B). The sulci between the humeral and pectoral, pectoral and abdominal, and abdominal and femoral scutes are perpendicular to the axial plane, in contrast to those between the femoral and anal scutes. The specimen showed four pairs of inframarginal scutes. The smallest was the two most anterior, located on the hyoplastra. The anal scutes were restricted to the xiphiplastra.

The ornamental pattern of all the isolated plates here attributed to *Selenemys lusitanica* is the same as that described for the shell SHN.003 (Fig. 3). MG 8733a is a distal half of a second right costal whose sulci pattern is consistent with that in SHN.003, showing a slightly greater overlap of the marginal scutes on it (Fig. 3A–B). MG 8743 is a longer than wide hexagonal neural (Fig. 3C–D). Its shorter margins are the latero-anterior ones. Considering its morphology, it is recognized as attributable to the middle part of the neural series. The morphology of the peripherals MG 8750a, MG 8733b and MG 8733c (Fig. 3E–F, G–H, I–J) is compatible with that of the first pair of SHN.003. However, they show an overlap of the first vertebral scute, being longer in MG 8750a than in the other specimens. The partial xiphiplastron MG 8750b lacks an anal notch (Fig. 3K–L).

3 Discussion

The isolated plates analyzed here (see Fig. 3) are compatible with the same taxon as the articulated and relatively complete shell SHN.003 (Fig. 2) considering both their morphology, the arrangement of the scutes, and the ornamental pattern of the shell outer surface. The material studied here can be attributed to the lineage of exclusively aquatic turtles Pleurosternidae (*sensu* Pérez-García et al., 2022), within Paracryptodira, considering characters such as: contact of the sixth neural with the fifth and sixth costals; anterior plastral lobe wider than the posterior one; and poorly developed plastral buttresses, only weakly extending onto the costals. In addition to this combination of characters exclusive to Pleurosternidae, the specimens analyzed here differ from the other paracryptodiran lineage recorded in Europe, i.e., Compsemydidae (only recognized in this continent in Paleocene sites, see Pérez-García, 2012), since they do not share the synapomorphies of that clade (e.g., trapezoidal first vertebral, with the anterior margin significantly wider than the posterior; and wider than long fifth neural), nor other characters of the exclusive combination recognized for Compsemydidae (e.g., the presence of straight lateral carapace margins or the overlap of all pleural scutes on the peripheral series Pérez-García et al., 2015a). Although Joyce and Rollot (2020) recently proposed that some traditional members of Pleurosternidae could belong to Compsemydidae, this interpretation has been shown to be methodologically incorrect, as well as based on some subjective interpretations and including problems in the coding of several taxa (see Pérez-García et al., 2022). Some of those errors were reproduced by subsequent authors (Rollot et al., 2021, 2022a, b; Tong et al., 2022; Joyce et al., 2022), additional problematic issues being added in some of those new papers. Thus, Tong et al. (2022) defined a putative new compsemydid turtle, not only not considering the compatibility of its cranial characters with those of the Helochelydridae clade, but ignoring the close similarity and even probable cogenetic or even cospecific attribution with a helochelydid shell taxa also described in southwestern Europe and at synchronous or almost synchronous levels. Joyce et al. (2022) also defined an additional putative new compsemydid turtle, but based on juvenile individuals. In fact, considering the absence of cranial remains, it is currently not possible to justify European taxa as *Selenemys lusitanica*, *Riodevemys inumbragigas* or *Toremys cassiopeia* as not being part of the same clade as the members of the genus *Pleurosternon* (i.e., Pleurosternidae).

A single member of the Pleurosternidae (*sensu* Pérez-García et al., 2022) has so far been recognized, both generically and specifically, at the Portuguese record: *Selenemys lusitanica*. This taxon is known from the upper

Kimmeridgian to lower Tithonian (Late Jurassic) record of the Consolação Sub-basin of the central Lusitanian Basin, in West-Central Portugal (Pérez-García & Ortega, 2011). Therefore, it is compatible both geographically and stratigraphically with the material analyzed here. In fact, the new specimens are attributable to *Selenemys lusitanica* since they share a combination of characters unique to this taxon: small, regular and clearly defined pits on the outer surface of the shell; nuchal broad and short, with a convex posterior margin and two concave segments in the anterior edge; first pair of peripherals tapering toward the axial region and joining medially; absence of a cervical scute; plastral lobes broad and subrounded; absence of epiplastral processes; large entoplastron, wider than long; absence of a xiphiplastral notch; sinuous midline plastral sulcus.

Knowledge about the shell anatomy of *Selenemys lusitanica* is here improved thanks to the study of these new finds. A subrounded carapace morphology had been interpreted for *Selenemys lusitanica* from the observation of its holotype, as well as of that of the partial carapace SHN.118 (see Pérez-García & Ortega, 2011). The articulated shell analyzed here, SHN.003, allows us to confirm this hypothesis, no other pleurosternid with such a rounded carapace being currently known (Fig. 2A–B). The first complete nuchal identified for *Selenemys lusitanica* is that of SHN.003 (Fig. 2A). The posterior region of this plate was hitherto unknown. Furthermore, neither the holotype nor SHN.118 preserved the anterior region of the neural series. The only known neural for the holotype was the most posterior, the other specimen preserving the third to the last ones (see Figs. 2B and 3B in Pérez-García & Ortega, 2011). Although the second neural of SHN.003 shows an anomalous morphology (which is common in Pleurosternidae, see Guerrero & Pérez-García, 2021a), the first one is identified as hexagonal, with short latero-posterior margins, in contrast to the condition in the third hexagonal neural, in which the shorter margins are the latero-anterior ones (Fig. 2A). The two European pleurosternids in which the anterior region of the neural series is known for several individuals (i.e., *Dorsetochelys typocardium* and *Pleurosternon bullockii*) show variability in that area. Thus, specimens with a rectangular second neural, and with hexagonal first and third neurals, the shorter margins of the first plate being the latero-posterior, and the shorter margins of the third being the latero-anterior ones, are known for both taxa (e.g., see Fig. 4 in Pérez-García, 2014; and 2E and 3B in Guerrero & Pérez-García, 2021a). SHN.003 allows us to confirm that, as it had been interpreted from the holotype of *Selenemys lusitanica*, a short contact between the nuchal plate and the second pair of peripherals is present in this pleurosternid (Fig. 2A). This condition, which implies the absence of contact between the first pair of costals and the first pair of

peripherals, is here recognized as an autapomorphy of the taxon within Pleurosternidae. Thus, although the contact of the first pair of costals with the second, third and the anterior region of the fourth pairs of peripherals was interpreted for this species (see Pérez-García & Ortega, 2011), the find of the articulated shell SHN.003 (see Fig. 2A) allows us to refute the presence of a contact with the fourth peripherals. The overlap of the sulci between the first and second vertebrae on the neural series, as well as that of the third and fourth ones on these plates, is observed for the first time for the taxon (Fig. 2A). In contrast to those sinuous sulci, the substraight contact between the second and third vertebrae observed in SHN.003 is compatible with that previously interpreted for the only specimen of the taxon for which the middle region of the neural series had been recognized (see Fig. 3 in Pérez-García & Ortega, 2011). However, the degree of sinuosity in these sulci has been identified as intraspecifically variable in pleurosternids known from several individuals (see Guerrero & Pérez-García, 2021a). The absence of an anal notch is confirmed for *Selenemys lusitanica* (Fig. 3K–L), contrasting with the European representatives *Pleurosternon bullockii*, *Dorsetochelys typocardium* and *Toremys cassiopeia*.

The discovery of new specimens of *Selenemys lusitanica* allows us to confirm the presence of several variable characters for the taxon, as well as increase the knowledge about its intraspecific variability evidenced by other characters. The presence of at least eight neurals in the specimen SHN.003 (Fig. 2A) is not shared with the condition in the holotype of the species (which has been described as having seven neurals; see Fig. 2A–B in Pérez-García & Ortega, 2011), but with the specimen SHN.118 (see Fig. 3A–B in Pérez-García & Ortega, 2011), the elements of the middle region of the neural series being longer in relation to their width in the new specimen. Specimens with seven neurals and others with eight are also recognized for *Pleurosternon bullockii* (see Guerrero & Pérez-García, 2021a; and references therein). Although the medial margin of the first pair of peripherals was approximately five times shorter than the lateral one in the *Selenemys lusitanica* holotype (Fig. 2A–B in Pérez-García & Ortega, 2011), this proportion may be lower in the taxon, being less than three times shorter than lateral margin, as seen in SHN.003 (Fig. 2A). This last condition is compatible with that of the isolated first peripheral presented in the type description (see Fig. 3E in Pérez-García & Ortega, 2011). The presence of the first vertebral scute of SHN.003 (Fig. 2A) as wide as the nuchal plate is shared with the holotype of the taxon (see Fig. 2A–B in Pérez-García & Ortega, 2011), that of SHN.118 being narrower (see Fig. 3A–B in Pérez-García & Ortega, 2011). Although the contact between the fourth and fifth vertebrae was located on the first suprapygal in both the *Selenemys lusitanica*

holotype (see Fig. 2A–B in Pérez-García & Ortega, 2011) and in SHN.118 (see Fig. 3A–B in Pérez-García & Ortega, 2011), it is located on the eighth neural in SHN.003 (Fig. 2A). This character is also recognized as variable in *Pleurosternon bullockii* (see both situations by comparing Figs. 2D and 3A in Guerrero & Pérez-García, 2021a). The overlap of the first and second pairs of marginal scutes on the nuchal is shorter in SHN.003 (Fig. 2A) than in the holotype of the taxon (see Fig. 2A–B in Pérez-García & Ortega, 2011). In fact, some of the isolated specimens show a greater range of variability for this character. Thus, although the first vertebral scute does not contact the first pair of peripherals in the holotype (see Fig. 2A–B in Pérez-García & Ortega, 2011), and only with the posterior margin of the right peripheral in SHN.003 (Fig. 2A) (none of these conditions being shared with other pleurosternids), different degrees of overlap on these plates were present in other individuals (see Fig. 3F, H and I). The relatively long overlap of the third pair of marginals on the first pair of costals in the two previously known articulated specimens of *Selenemys lusitanica* contrasts with the condition in SHN.003 (Fig. 2A). The plastral medial sulcus of the taxon was recognized as markedly sinuous throughout most of its trajectory except between the anal scutes, where the sinuosity was very slight in the case of the holotype (see Fig. 2C–D in Pérez-García & Ortega, 2011). By contrast, at least the anterior region of the sulcus between the anals of SHN.003 is recognized as markedly sinuous (Fig. 2B). The presence of four inframarginal scutes is confirmed for this taxon. However, although the fourth pair of inframarginals overlapped the postero-lateral area of the mesoplastra in the holotype (see Fig. 2C–D in Pérez-García & Ortega, 2011), it did not reach this pair of plates in SHN.003 (Fig. 2B), this last condition being shared with SHN.118 (see Fig. 3C–D in Pérez-García & Ortega, 2011). A similar intraspecific variability for this character is also identified for *Pleurosternon bullockii* (Guerrero & Pérez-García, 2021a).

4 Conclusions

New remains of the oldest pleurosternid turtle (Paracryptodira) in Europe are presented here. It corresponds to *Selenemys lusitanica*, a taxon exclusively known from upper Kimmeridgian to lower Tithonian (Late Jurassic) outcrops of the Consolação Sub-basin of the central Lusitanian Basin, in West-Central Portugal. All the material documented up to now for this species was restricted to that analyzed in the publication in which it was defined, corresponding to five specimens (two partial shells and three isolated plates), which had barely provided data on the variability of the taxon, nor had they allowed to recognize all the anatomical characters of its shell. One of the new specimens described

here corresponds to the most complete shell of this species so far found. It does not come from the Lisbon District, where all previously documented material was found, but from the Leiria District, also in the Consolação Sub-basin. Specifically, it comes from a Tithonian outcrop at the Peniche Municipality. The isolated plates documented here were found in several upper Kimmeridgian to lower Tithonian and also Tithonian localities of the Lourinhã Municipality (Lisbon District).

Among the anatomical characters of the shell of *Selenemys lusitanica* so far poorly known or documented here for the first time are those related to the morphology of its carapace, the relationship between the nuchal and the peripheral series, that between the first pair of costals and the peripheral series, the characterization its complete neural series, as well as that of the vertebral series. All this new information, which includes the identification of several exclusive characters for the species, allows us to improve knowledge about the taxon in relation to the other members of Pleurosternidae. Given the limited number of specimens known for most representatives of this lineage, knowledge about the intraspecific variability of many of them is very limited or even non-existent. The analysis of the new material of *Selenemys lusitanica* has allowed us to characterize its intraspecific variability considering several characters of both of its carapace and its plastron.

Acknowledgements The authors thank Pedro Mocho (Universidade de Lisboa/SHN) for information on the stratigraphy of the Lusitanian Basin; the recently deceased Miguel Ramalho (Museu Geológico, Lisboa) for the access to some of the specimens studied here; Verena Fuchs for the photographs of SHN.003; and the editors and the reviewers Walter Joyce and Yann Rollot for their comments and suggestions.

Funding No funding was received for conducting this study. Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose. They declare that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Cope, E. D. (1868). On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20, 242–300.
- Gaffney, E. S. (1975). A phylogeny and classification of higher categories of turtles. *Bulletin of the American Museum of Natural History*, 155, 387–436.
- Gaffney, E. S. (1979). The Jurassic turtles of North America. *Bulletin of the American Museum of Natural History*, 162, 93–135.
- Guerrero, A., & Pérez-García, A. (2021a). Morphological variability and shell characterization of the European uppermost Jurassic to lowermost Cretaceous stem turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). *Cretaceous Research*, 125, 104872. <https://doi.org/10.1016/j.cretres.2021.104872>
- Guerrero, A., & Pérez-García, A. (2021b). Ontogenetic development of the European basal aquatic turtle *Pleurosternon bullockii* (Paracryptodira, Pleurosternidae). *Fossil Record*, 24, 357–377. <https://doi.org/10.5194/fr-24-357-2021>.
- Hill, G. (1988). *The sedimentology and lithostratigraphy of the Upper Jurassic Lourinhã formation, Lusitanian Basin, Portugal*. Open University.
- Joyce, W. G., Bourque, J. R., Fernandez, V., & Rollot, Y. (2022). An alternative interpretation of small-bodied turtles from the Middle Purbeck of England as a new species of compsemydid turtle. *Fossil Record*, 25, 263–274. <https://doi.org/10.3897/fr.25.85334>.
- Joyce, W. G., & Rollot, Y. (2020). An alternative interpretation of *Peltochelys duchastelii* as a paracryptodire. *Fossil Record*, 23, 83–93. <https://doi.org/10.5194/fr-23-83-2020>.
- Klein, I. T. (1760). *Klassifikation und kurze Geschichte Der vierfüßigen Thiere*. Jonas Schmidt.
- Lapparent de Broin, F. (2001). The European turtle fauna from the Triassic to the Present. *Dumerilia*, 4, 155–216.
- Manuppella, G., Antunes, M. T., Pais, J., Ramalho, M. M., & Rey, J. (1999). *Notícia Explicativa Da Folha 30-A (Lourinhã)*. Departamento de Geologia do Instituto Geológico e Mineiro.
- Mocho, P., Royo-Torres, R., Escaso, F., Malafaia, E., de Miguel Chaves, C., Narváez, I., Pérez-García, A., Pimentel, N., & Ortega, F. (2017). Upper Jurassic sauropod record in the Lusitanian Basin (Portugal): Geographical and lithostratigraphical distribution. *Palaeontologia Electronica*, 20(2.27A), 1–50. <https://doi.org/10.26879/662>.
- Owen, R. (1842). Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science*, 11, 60–204.
- Pérez-García, A. (2012). *Berruchelus Russellii* gen. et sp. nov., a paracryptodiran turtle from the Cenozoic of Europe. *Journal of Vertebrate Paleontology*, 32, 545–556. <https://doi.org/10.1080/02724634.2012.658933>.
- Pérez-García, A. (2014). Revision of the poorly known *Dorsetochelys typocardium*, a relatively abundant pleurosternid turtle (paracryptodira) in the early Cretaceous of Europe. *Cretaceous Research*, 49, 152–162. <https://doi.org/10.1016/j.cretres.2014.02.015>.
- Pérez-García, A. (2017). The Iberian fossil record of turtles: An update. *Journal of Iberian Geology*, 43, 155–191. <https://doi.org/10.1007/s41513-017-0016-4>.
- Pérez-García, A., Camilo, B., & Ortega, F. (2023). New data on the poorly known Jurassic record of the turtle *hylaechelys* (Thalasocheilydia), based on new finds from Portugal. *Diversity*, 15, 167. <https://doi.org/10.3390/d15020167>
- Pérez-García, A., Espílez, E., Mampel, L., & Alcalá, L. (2015b). A new European albian turtle that extends the known stratigraphic range of Pleurosternidae (Paracryptodira). *Cretaceous Research*, 55, 74–83. <https://doi.org/10.1016/j.cretres.2015.02.007>
- Pérez-García, A., Martín-Jiménez, M., Aurell, M., Canudo, J. I., & Castanera, D. (2022). A new Iberian pleurosternid (Jurassic-Cretaceous transition, Spain) and first neuroanatomical study of this clade of stem turtles. *Historical Biology*, 34, 298–311. <https://doi.org/10.1080/08912963.2021.1910818>.
- Pérez-García, A., & Ortega, F. (2011). *Selenemys Lusitanica*, gen. et sp. nov., a new pleurosternid turtle (Testudines: Paracryptodira) from the Upper Jurassic of Portugal. *Journal of Vertebrate Paleontology*, 31, 60–69. <https://doi.org/10.1080/02724634.2011.540054>
- Pérez-García, A., Royo-Torres, R., & Cobos, A. (2015a). A new European late Jurassic pleurosternid (Testudines, Paracryptodira) and a new hypothesis of paracryptodiran phylogeny. *Journal of Systematic Palaeontology*, 13, 351–369. <https://doi.org/10.1080/14772019.2014.911212>.
- Rollot, Y., Evers, S. W., Cifelli, R. L., & Joyce, W. G. (2022a). New insights into the cranial osteology of the early Cretaceous paracryptodiran turtle *Lakotemys australodakotensis*. *PeerJ*, 10, e13230. <https://doi.org/10.7717/peerj.13230>
- Rollot, Y., Evers, S. W., & Joyce, W. G. (2021). A redescription of the late Jurassic (tithonian) turtle *Uluops uluops* and a new phylogenetic hypothesis of Paracryptodira. *Swiss Journal of Palaeontology*, 140, 1–30. <https://doi.org/10.1186/s13358-021-00234-y>.
- Rollot, Y., Evers, S. W., Pierce, S. E., & Joyce, W. G. (2022b). Cranial osteology, taxonomic reassessment, and phylogenetic relationships of the early Cretaceous (Aptian-Albian) turtle *trinitichelys hiatti* (Paracryptodira). *PeerJ*, 10, e14138. <https://doi.org/10.7717/peerj.14138>.
- Seeley, H. G. (1869). *Index to the fossil remains of Aves, Ornithosauria and Reptilia, from the secondary system of strata arranged in the Woodwardian Museum of the University of Cambridge*. Deighton Bell.
- Tong, H., Tortosa, T., Buffetaut, E., Dutour, Y., Turini, E., & Claude, J. (2022). A compsemydid turtle from the Upper Cretaceous of Var, southern France. *Annales De Paléontologie*, 108, 102536. <https://doi.org/10.1016/j.annpal.2022.102536>.
- Williams, E. E. (1950). Variation and selection in the cervical central articulations of living turtles. *Bulletin of the American Museum of Natural History*, 94, 511–561.