

The oldest turtle from Portugal corresponding to the only pre-Kimmeridgian plesiochelyid (basal Eucryptodira) recognized at the generic level

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A shell coming from an upper Oxfordian section of the Lusitanian Basin located in Alqueidão da Serra (Municipality of Porto de Mós, West Central Portugal), is here presented. It corresponds to the oldest remain of a turtle identified in Portugal. In fact, the record of Jurassic turtles identified in pre-Kimmeridgian levels of Europe is very scarce. The new specimen represents the second worldwide identification of a Plesiochelyid turtle (basal Eucryptodira) performed in pre-Kimmeridgian levels, being the only one recognized at generic level. Therefore, this specimen corresponds to the oldest identification of *Craspedochelys*, a genus well-represented in Kimmeridgian and Tithonian levels of several European countries. This finding contributes the first evidence on the synchronous coexistence of more than a member of Plesiochelyidae in pre-Kimmeridgian levels, which provides arguments to justify the relatively wide diversity known for this exclusively Jurassic clade during the Kimmeridgian and the Tithonian.

Keywords: Plesiochelyidae; *Craspedochelys*; Late Jurassic; Oxfordian; Lusitanian Basin; Porto de Mós.

Introduction

Eucryptodira is a very successful lineage of turtles whose crown group (i.e. Cryptodira) is very abundant and diverse today (Rhodin et al. 2008). The record of Eucryptodira is known from the Late Jurassic. This clade is well-represented in the uppermost Jurassic levels of Europe, being known by several Kimmeridgian and Tithonian basal forms. Those best represented are Plesiochelyidae, Eurysternidae and Thalassemydidae (Lapparent de Broin et al. 1996; Lapparent de Broin 2001; Anquetin et al. 2014; Bardet et al. 2014). However, other taxa are also known. The validity of the British Kimmeridgian *Enaliochelys chelonia* Seeley 1869 has recently been confirmed, corresponding to a eucryptodiran member not assignable to any of those three clades (Pérez-García 2015a). A new species of *Hylaeochelys* Lydekker 1889a, *Hylaeochelys kappa* Pérez-García and Ortega 2014, a genus previously only known in Lower Cretaceous levels, has recently been described in the Portuguese Tithonian record (Pérez-García and Ortega 2014). In addition, a third basal eucryptodiran form currently not assignable to any of these three clades has recently been defined: the French Tithonian

Jurassichelon oleronensis Pérez-García 2015a. Therefore, the recent findings have allowed identifying a significantly larger diversity of Upper Jurassic European eucryptodires than previously thought, exclusively represented by taxa endemic to this continent (Pérez-García and Ortega 2014; Pérez-García 2015a, 2015b).

A putative new taxon, '*Hispaniachelys prebetica*' Slater, Reolid, Schouten and Benton 2011, was defined by a shell from the upper Oxfordian of the Prebetic area of the Betic Range (Southern Spain). Its phylogenetic position was considered hard to resolve, being interpreted as either a paracryptodire or a basal testudine, but its assignment to Plesiochelyidae having being excluded (Slater et al. 2011). However, the revision of this specimen allowed its identification as an indeterminate member of Plesiochelyidae, corresponding to the only reference of both that lineage, and of a basal member of Eucryptodira, until now performed in the European pre-Kimmeridgian levels (Pérez-García 2014).

Plesiochelyidae corresponds to a diverse group of Upper Jurassic coastal turtles, identified in several European countries (Lapparent de Broin 2001; Lapparent de Broin et al. 1996). The recent refutation of the identification of '*Plesiochelys valdensis*' Lydekker 1889b and '*Plesiochelys vectensis*' Hooley 1900 as members of Plesiochelyidae, and the identification of *Hylaeochelys* as a taxon outside that clade, allowed to restrict the known distribution of Plesiochelyidae to the Jurassic (Bardet 1994; Pérez-García 2012; Pérez-García et al. 2013).

The holotype of '*Hispaniachelys prebetica*' is not the only specimen of Plesiochelyidae found in the Iberian record. It also includes the identification of *Craspedochelys* Rüttimeyer 1873 in Portuguese upper Kimmeridgian and Tithonian levels, *Plesiochelys* Rüttimeyer 1873 in Spanish and Portuguese Tithonian sites, and *Tropidemys* Rüttimeyer 1873 in Spanish and Portuguese upper Kimmeridgian and Tithonian deposits (Antunes et al. 1988; Lapparent de Broin et al. 1996; Lapparent de Broin 2001; Pérez-García et al. 2008, 2013; Pérez-García 2015c).

All Portuguese references on the clade Plesiochelyidae come from the Lusitanian Basin series of West Central Portugal (Sauvage 1898; Antunes et al. 1988; Pérez-García et al. 2008, 2010; Ortega et al. 2009) where, as indicated, it was represented by both Kimmeridgian and Tithonian remains. A new specimen, corresponding to a relatively complete and articulated shell, is here presented. It also comes from the onshore of the Lusitanian Basin, but from a region where, so far, no fossil turtles were known: Alqueidão da Serra, belonging to the Municipality of Porto de Mós (Figure 1). It represents the oldest plesiochelyid of the Portuguese record, coming from an upper Oxfordian succession. In fact, it corresponds to the

oldest evidence of a turtle in that country. Its systematic study is here carried out, providing information on the early diversity of the clade Plesiochelyidae.

Institutional Abbreviations

MMPM, Museu Municipal de Porto de Mós, Porto de Mós, Portugal.

Geographical and geological context

The turtle shell studied here was collected from upper Oxfordian beds exploited in a small limestone quarry opened near the summit of Cabeço da Vaca, a calcareous hill adjacent to the locality of Alqueidão da Serra (Municipality of Porto de Mós, West Central Portugal). The coordinates of this finding are 39°36.767' N; 008°47.474'S (Figure 1A-B). In this area, several artisanal quarries have been exploiting, for a long time, a variety of Jurassic light grey limestone and the famous 'black limestone', a dark mudstone with quite uniform colour, mainly for the production of ubiquitous Portuguese cobblestone designs ('calçada portuguesa'). These carbonate layers are quite rather fossiliferous and yielded many invertebrate specimens, mostly of shallow, fresh to brackish environments (Manuppella et al. 1985, 2000; Costa et al. 1988).

[Figure 1 near here]

The reliefs of Cabeço da Vaca are part of the calcareous massifs of Estremadura, a large mountainous range placed on the northwest border of the Lower Tagus Cenozoic basin, with a geological substrate dominated by thick successions of Lower to Upper Jurassic carbonated and siliciclastic-carbonated mixed strata uplifted and faulted by Alpine tectonics, during Upper Cretaceous and Cenozoic episodes of compression that deformed the West Portuguese continental margin of the Iberian microplate (Rasmussen et al. 1998; Alves et al. 2003; Rey et al. 2006; Dinis et al. 2008; Pais et al. 2010; Kullberg et al. 2013) (Figure 1C-D).

The studied area is characterized by a karstic landscape with a profusion of limestone cornices and lapies masked by a vegetation cover of *Quercus*, *Olea* and calcicolous shrubs, well-adapted to dryness conditions during summer (Martins 1949). Besides the microclimate environment and the carbonated substrate, the evolution of this natural low-mountain landscape, yet barely anthropized in the slopes of Alqueidão da Serra, was controlled by local tectonics, showing several escarpments and local drainage systems developed on the dependence of faulted blocks (Manuppella et al. 2000).

The overall Jurassic units record the main episodes of the tectonosedimentary evolution and infill of the Mesozoic Lusitanian Basin, during the first rifting phases and post-rift

detumescence intervals that occurred in the proto-Atlantic in front of Iberia (Wilson 1979, 1988; Leinfelder 1986; Wilson et al. 1989; Hiscott et al. 1990; Pinheiro et al. 1996, Alves et al. 2009). Regarding the Cabeço da Vaca area, the local succession is late Oxfordian in age (Manuppella et al. 2000), being correlative of the beginning of a rifting phase marked by a transgressive context on sedimentation with gradual installation of fully marine conditions (Montejunto Formation) over freshwater, brackish and restricted lagoon carbonated parasequences (Cabaços Formation) (Ruget-Perrot 1961; Mouterde et al. 1979; Reis et al. 1996; Azerêdo and Wright 2002; Azerêdo et al. 2003).

The stratigraphic section of the quarry consists of 18 massive beds of micritic, gray to dark gray limestones, mostly mudstone to wackstone, with a rather scarce and low diversity macrofossil content (Figure 2). The invertebrate remains are mostly isolated moulds of small corbulids (*Jurassicorbula* sp.) and larger valves of mytilids (*Arcomytilus* sp.), sometimes yet articulated. This assemblage is comparable to fossil associations already described by Fürsich (1981) and Fürsich and Werner (1984, 1985, 1986) for the Oxfordian of West Portugal, corresponding to a successful colonization of inner shelf, littoral plain and lagoonal, slightly restricted environments of carbonate platform.

[Figure 2 near here]

Besides the turtle shell, two hemispheric teeth of pycnodontid fish were collected on the adjacent strata. The absence of fully marine benthic elements like scleractinian corals, brachiopods or echinoids suggests that the studied section belongs to the upper part of the Cabaços Formation, above levels of freshwater limestone with unionid bivalves and charophyta oogonia also recognized not far away from the quarry.

The sampled facies of micritic limestone with brackish to restricted marine faunal elements suggest that the Cabeço da Vaca turtle lived in a low energy, probably lagoonal environment, located near a large tidal flat with fine-grained micritic sedimentation connected with inner sectors of a carbonate shelf. This local environment was rather restricted and shows low to moderate diversity, but allowed colonization by eurytopic, non-specialized benthic elements, together with vertebrate species tolerant to salinity, oxygen and temperature changes.

Systematic paleontology

Testudines Batsch 1788

Panryptodira Joyce, Parham and Gauthier 2004

Eucryptodira Gaffney 1975

Plesiochelyidae Baur 1888

Craspedochelys Rüttimeyer 1873

Craspedochelys sp.

(Figures 3, 4)

Material: MMPM37, a partial shell preserved in two blocks of rock. Most of the carapace plates are preserved, with the exception of some peripherals. The plastron lacks its posterior lobe, its left margin, and the anterior region of the anterior lobe. The outer surface of many of the plates is not preserved, so the morphology of most of the scutes is not known.

Locality and horizon: Cabeço da Vaca area (Alqueidão da Serra, Municipality of Porto de Mós). Lusitanian Basin (West Central Portugal). Upper part of the Cabaços Formation, upper Oxfordian.

Description: MMPM37 corresponds to a domed shell. It lacks a sagittal keel on the carapace. This shell has a subpentagonal morphology (Figures 3A, 4A). The length of this shell is estimated to be about 45 cm. The plates of both the carapace and the plastron are relatively thick. The outer surface is smooth.

MMPM37 has a shallow nuchal notch (Figures 3A, 3D, 4A, 4D). It is exclusively located on the nuchal plate. This plate is wider than long. The lateral sides of the anterior region of this plate are divergent. Due to its preservation, the total number of neural plates present in this specimen is not known. Six neurals are identified. All of them are longer than wide. The first one is subrectangular. The others are hexagonal, with latero-anterior margins longer than the latero-posterior. The neural series anteriorly contacts the nuchal plate. However, it does not contact the suprapyrgals because of the medial contact of, at least, the last pair of costals. Three suprapyrgals are recognized (Figures 3A, 3C, 4A, 4C). The second is the widest. It contacts the eleventh pair of peripherals. The last suprapygal contacts both that pair of peripherals and the pygal plate. Eight pairs of costals are identified. The first pair is relatively short, its length being similar to that of the second. The contact between the costal and the peripheral series is osseous, lacking fontanelles. The anterior pairs of peripherals are wider than long. The posterior peripherals and the pygal are also short relative to their lengths.

The first vertebral scute is subrectangular, wider than long (Figures 3A, 4A). The second is wider than the first. However, they are relatively narrow, their maximum overlap on the costals being equivalent to no more than half the width of these plates. The marginal

scutes do not contact the costal series (Figures 3A, 3C, 4A, 4C). The last pair of marginals does not contact the last suprapygal.

The carapace-plastron attachment is osseous (Figures 3B, 4B). Thus, MMPM37 lacks bridge fontanelles. The plastral buttresses are in contact with both the peripheral and the costal series. A relatively small central plastral fontanelle is present. It is longer than wide. The plastron is relatively wide in relation to the length of the plastral bridge. In this sense, both the hyoplastra and the hypoplastra are recognized as relatively wide. MMPM37 lacks mesoplastra.

[Figures 3 and 4 near here]

Discussion

The absence of mesoplastra allows to exclude the attribution of the specimen studied here to Pleurosternidae, a lineage of Paracryptodira well represented in the Upper Jurassic record of Portugal (Pérez-García and Ortega 2011; Pérez-García et al. 2015). In fact, this character allows its attribution to its sister group Eucryptodira, which also shows an abundant record in the Upper Jurassic levels of that country, being represented by *Hylaeochelys* and by several members of Plesiochelyidae (Sauvage 1898; Antunes et al. 1988; Pérez-García et al. 2008, 2010; Ortega et al. 2009; Pérez-García and Ortega 2014; Pérez-García 2015c). Each of the characters of interest from a systematic point of view are here compared to those present in Eurysternidae, *Thalassemys* spp., *Jurassichelon oleronensis*, *Enaliochelys chelonia*, *Hylaeochelys* spp. and Plesiochelyidae (see discussion of these characters in Lapparent de Broin et al. 1996; Joyce 2000; Pérez-García et al. 2008, 2013; Pérez-García 2012, 2014; Anquetin et al. 2014; Pérez-García and Ortega 2014; Pérez-García 2015a, 2015b; Püntener et al. 2015).

The presence of a domed shell is shared with the representatives of Plesiochelyidae and with *Jurassichelon oleronensis*. The members of Eurysternidae, *Thalassemys* and *Hylaeochelys* have a low shell. The roughly circular shell of the representatives of *Hylaeochelys* is not shared with the specimen studied here. It also lacks the cordiform morphology present in *Thalassemys*. The relatively large size of this specimen is compatible with those of all taxa compared here, except with those of the representatives of Eurysternidae. The plates of both the carapace and the plastron of MMPM37 are thicker than those of Eurysternidae, *Thalassemys* and *Hylaeochelys*. This condition is shared with the members of Plesiochelyidae, as well as with *Jurassichelon oleronensis* and *Enaliochelys chelonia*. The shell of MMPM37 lacks the slightly fluted surface that characterizes

Hylaeochelys. This specimen differs from *Thalassemys* and *Enaliochelys chelonia* due to the presence of a nuchal notch. Its nuchal notch is not as deep as that developed in the members of *Hylaeochelys* and in *Jurassichelon oleronensis*. The observed condition is shared with some members of Eurysternidae and Plesiochelyidae. The presence of the most-anterior region of the lateral areas of the nuchal plate presenting a well-developed change of curvature, resulting in diverging margins, is shared with some representatives of Eurysternidae, *Hylaeochelys* and Plesiochelyidae. The presence of a discontinuous neural series is shared with some members of Eurysternidae, *Hylaeochelys* and Plesiochelyidae, contrasting with the known condition for *Enaliochelys chelonia* and *Thalassemys*. MMPM37 does not share with *Jurassichelon oleronensis* the presence of the first pair of costal less than twice as wide as long. The relatively long anterior costals of this taxon have substraight lateral margin, which are not present in the specimen studied here. The presence of the first pair of peripherals markedly wider than long contrasts with the condition in Eurysternidae. The presence of short posterior peripherals is shared with *Thalassemys* and Plesiochelyidae, but not with Eurysternidae and *Hylaeochelys*. The sinuous medial margin of the peripherals observed in *Hylaeochelys* is not present in the specimen studied here. This specimen also lacks costo-peripheral fontanelles, as in the case of the plesiochelyids, *Hylaeochelys* and some eurysternids. Carapace fontanelles are developed in *Thalassemys*, *Jurassichelon oleronensis* and, especially, in *Enaliochelys chelonia*, in which the well-developed free regions of the dorsal ribs are very wide relatively to the width of these plates. MMPM37 lacks the wide vertebral scutes identified in the eurysternids, in the members of *Hylaeochelys* and, especially, in *Enaliochelys chelonia*. The presence of an osseous carapace-plastron attachment is shared with *Thalassemys* and the plesiochelyids. The members of *Hylaeochelys*, *Jurassichelon oleronensis* and the eurysternids have a partially osseous or a ligamentous connection between the plastron and peripherals. The contact between the axillary buttresses and the costal series is present in *Jurassichelon oleronensis* and the members of Plesiochelyidae. They only contact the peripheral plates in the case of *Thalassemys* and the eurysternids. The absence of bridge fontanelles is shared with *Jurassichelon oleronensis*, *Hylaeochelys* and Plesiochelyidae, but not with the members of Eurysternidae and with *Thalassemys*. A central plastral fontanelle is developed in some adult specimens of Plesiochelyidae, *Hylaeochelys* and *Eurysternidae*, and also in all known specimens of *Jurassichelon oleronensis* and *Thalassemys*. The presence of sutural connections of the epiplastra with the entoplastron and the hyoplastra is shared with *Hylaeochelys* and Plesiochelyidae, but not with the eurysternids, *Thalassemys* and *Jurassichelon oleronensis*.

Therefore, the character combination in the shell MMPM37 allows its attribution to Plesiochelyidae. The characters available are compared to those of the members of Plesiochelyidae in which the shell is known: *Tropidemys*, *Tholemys passmorei* Andrews 1921, '*Thalassemys moseri*' Bräm 1965, *Plesiochelys* and *Craspedochelys* (see the discussion of these characters in Antunes et al. 1988; Lapparent de Broin et al. 1996; Anquetin et al. 2014; Pérez-García et al. 2008, 2013; Püntener et al. 2014; Pérez-García 2015b, 2015c). It cannot be attributed to *Tropidemys* (i.e. a taxon identified, by several species, in the Kimmeridgian and Tithonian records of several European countries, including a reference in the upper Kimmeridgian-lower Tithonian levels of Portugal; see Pérez-García, 2015c) due to the absence of: a sagittal keel on the carapace; continuous neural series, from the nuchal plate to the suprapygals; and very wide neurals relative to the length, especially the posterior ones, which are wider than long, lacking short antero-lateral sides. MMPM37 differs from the holotype and only known specimen of *Tholemys passmorei* (i.e. a genus only known by that species), from the Kimmeridgian of Swindon (Wiltshire, UK). Thus, that British taxon has a continuous neural series; the lateral margins of the nuchal plate are anteriorly convergent; its shell is lower; it lacks a central plastral fontanelle; and its anterior plastral lobe is shorter in relation to its width. MMPM37 differs from '*Thalassemys moseri*', a species currently only known by scarce specimens from the Kimmeridgian of Solothurn (Switzerland), whose attribution to *Jurassichelon oleronensis*, from the Tithonian of the Oléron Island (France), cannot be currently sustained (see Pérez-García 2015a). Thus, the specimen studied here has a larger size than that of those problematic specimens, lacking both costo-peripheral fontanelles and ligamentous contact between the entoplastron and the hyoplastra. The combination of these characters, in addition to that of others such as the presence of width vertebral scutes or of a poorly ossified postero-medial region of the xiphiplastra, could indicate that '*Thalassemys moseri*' corresponds to an invalid form, as was previously proposed by Lapparent de Broin et al. 1996. Thus, the Solothurn specimens attributed to it could correspond to juvenile individuals of another plesiochelyid known in that region and, more specifically, of *Craspedochelys* or, probably, of *Plesiochelys*. All characters discussed as different between MMPM37 and the members of Plesiochelyidae *Tropidemys*, *Tholemys passmorei* and '*Thalassemys moseri*' are compatible with those of the representatives of both *Plesiochelys* and *Craspedochelys*, both genera being known in the Portuguese record, *Plesiochelys* in the Tithonian levels (Pérez-García et al. 2008) and *Craspedochelys* in upper Kimmeridgian and Tithonian sites (Sauvage 1898; Antunes et al. 1988). Both *Plesiochelys* and *Craspedochelys* are genera known through several species.

The width/length ratio of the shell is a character generally used to differentiate the members of *Plesiochelys* from those of *Craspedochelys*, *Craspedochelys* being proportionally wider (i.e. almost as wide as long). Although MMPM37 appears to be longer than width, its preservation does not allow accurately known its width/length ratio. Its subpentagonal outline is shared with the members of *Craspedochelys*, those of *Plesiochelys* generally being more elliptical. The nuchal notch is less deep than that usually known for *Plesiochelys*, as in *Craspedochelys*. In fact, this specimen lacks the lateral development of this structure up to the middle area of the anterior borders of the first pair of peripherals, generally present in *Plesiochelys*. Although the plastron of *Plesiochelys* is identified as relatively longer than that of *Craspedochelys*, presenting longer plastral lobes, the preservation of the specimen analyzed here does not allow a detailed comparison of this character. However, a morphology similar to that of the members of *Craspedochelys* can be interpreted considering the preserved evidence. Thus, it lacks the markedly longer than wide hyoplastra present in *Plesiochelys*, being proportionally wider, as in *Craspedochelys*. The absence of overlap of the last pair of marginals on the last suprapygal is shared with the members of *Craspedochelys* (e.g. *Craspedochelys jaccardi* and *Craspedochelys picteti*) but not with those of *Plesiochelys* (e.g. *Plesiochelys etalloni* and *Plesiochelys solodurensis*). The presence of relatively narrow vertebral scutes in MMPM37, whose maximum overlap on the second pair of costals is not more than half the width of those plates, is shared with *Craspedochelys* but not with *Plesiochelys*. The presence or absence of both a discontinuous neural series and a central plastral fontanelle are part of the range of intraspecific variability known for *Craspedochelys*. Therefore, MMPM37 can be attributed to this genus. However, considering both the limited information available on this specimen, and the need for the review and evaluation of the possible validity of the Portuguese Tithonian form '*Plesiochelys choffati*' Sauvage 1898, whose holotype and unique known specimen possibly corresponds to a juvenile individual of *Craspedochelys*, a more precise determination cannot be performed.

'*Hispaniachelys prebetica*', defined by a single specimen from the late Oxfordian of the Betic Range (Southern Spain), was considered as one of the few European turtle taxa reported from pre-Kimmeridgian levels (Slater et al. 2011). It was reassigned to an indeterminate member of Plesiochelyidae, corresponding to both the oldest turtle remain so far known from southern Europe, and the oldest eucryptodiran specimen in this continent (Pérez-García 2014). Despite the limited availability of characters in that Spanish shell, it could correspond to *Plesiochelys* or to a taxon closely related to it (considering its relatively long shell, long plastron lobes, longer than wide hyoplastra, and relatively wide vertebral scutes), but not to

Craspedochelys. Therefore, two members of Plesiochelyidae are here recognized for the pre-Kimmeridgian record, both found in synchronous levels of the Iberian Peninsula, one in Spain and the other in Portugal.

Conclusions

A turtle shell from the Portuguese locality of Alqueidão da Serra (Municipality of Porto de Mós, Lusitanian Basin, West Central Portugal) is presented here. It comes from an upper Oxfordian (Late Jurassic) carbonate succession. This specimen is the oldest remain of a turtle so far identified in Portugal, the record of Jurassic turtles identified in pre-Kimmeridgian European levels being very scarce. The new specimen is identified as a member of the clade of basal Eucryptodira Plesiochelyidae.

The plesiochelyids were coastal forms, exclusively known in the European record. They were very abundant and diverse in Kimmeridgian and Tithonian levels of several countries. Despite this abundance and diversity, the information about this group from pre-Kimmeridgian levels is extremely limited. Only one specimen, from the upper Oxfordian of Spain, had hitherto been identified as corresponding to Plesiochelyidae. It was an indeterminate form, probably corresponding to *Plesiochelys* or to a closely related taxon. The new specimen studied here is the second plesiochelyid identified in pre-Kimmeridgian levels, being the only one recognized at generic level. It is identified as a member of *Craspedochelys*, a relatively abundant genus so far known in the Portuguese upper Kimmeridgian and Tithonian records, being also present in Kimmeridgian and Tithonian sites of other European countries, such as Switzerland, Germany and France.

The new finding not only allows us identifying the oldest presence of *Craspedochelys*, but it also provides the first evidence of the existence of more than one synchronous member of this lineage at pre-Kimmeridgian levels. Therefore, the diversity recognized for this lineage during the Kimmeridgian and the Tithonian could already be present in pre-Kimmeridgian levels, not having been recognized until now due to the poor record of turtles at these littoral levels.

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Figure 1. Geographic location and geological context of Porto de Mós (West Central Portugal), where the studied turtle shell was found. The asterisk marks the location of the studied area. A, Location in the western margin of Iberia. B, Detailed geographical location of Porto de Mós, Alqueidão da Serra and Cabeço da Vaca, in the calcareous mountain ranges of Portuguese Estremadura (adapted from the topographic map 1:25000 of Porto de Mós - Geographical Institute of the Army). C, Geological setting of the mountain ranges of Portuguese Estremadura showing the main Mesozoic units of the onshore of the West Iberian Margin. D, Geological map of the studied area, showing the Upper Jurassic units of the Lusitanian Basin. Legend: 1, Hettangian evaporites (Dagorda Fm.); 2–3, Oxfordian shallow marine carbonates (Cabaços Fm. and Montejunto Fm.); 4, Kimmeridgian shallow marine carbonates and clays (Alcobaça Fm.); 5, Tithonian fluvio-deltaic sandstones and clays (Bombarral Fm.); 6, Aptian-Cenomanian alluvial sandstones; 7, Miocene non-marine sandstones; 8, Pleistocene alluvial deposits; 9, Holocene alluvial deposits; 10, doleritic intrusive rocks.

Figure 2. Stratigraphic setting of the Cabeço da Vaca quarry (Alqueidão da Serra, Porto de Mós, West Central Portugal), where the studied turtle shell was found. A, Stratigraphic section of the quarry showing part of the Cabaços Fm. local carbonate succession. Legend: 1, Mainly greyish or whitish grey mudstone or packstone; 2, marly limestone; 3, greyish marl whose identified faunal elements are mainly bivalves; 4, mytiloids (*Brachiodontes* and *Arcomytilus*); 5, *Isognomon*; 6, gryphaeids; 7, corbulids (*Jurassicorbula*); 8, lucinids and crassatellids; 9, pycnodontid teeth; 10, turtle shell studied here; 11, biostratonomic concentrations of shell debris. B, Panoramic view of Cabeço da Vaca. C, Upper part of the studied section, with numbered beds.

Figure 3. Photographs of the specimen MMPM37, a shell of *Craspedochelys* sp. from the late Oxfordian (upper part of the Cabaços Formation) of Cabeço da Vaca are (Alqueidão da Serra, Municipality of Porto de Mós, West Central Portugal). A, Dorsal view. B, Ventral view. C, Left postero-lateral view. D, Right antero-lateral view.

Figure 4. Schematic drawings of the specimen MMPM37, a shell of *Craspedochelys* sp. from the late Oxfordian (upper part of the Cabaços Formation) of Cabeço da Vaca are (Alqueidão da Serra, Municipality of Porto de Mós, West Central Portugal). A, Dorsal view. B, Ventral view. C, Left postero-lateral view. D, Right antero-lateral view. Abbreviations: C, costal; Ep, epiplastron; Fo, fontanelle; Hp, hypoplastron; Hy, hyoplastron; M, marginal scute; N, neural; Nu, nuchal; P, peripheral; Pl, pleural scute; Py, pygal; Spy, suprapygal; V, vertebral scute.