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General palaeontology and evolution (Vertebrate palaeontology)

A new species of the turtle *Hylaeochelys* (Eucryptodira) outside its known geographic and stratigraphic ranges of distribution



Une nouvelle espèce de la tortue Hylaeochelys (Eucryptodira) en dehors de ses champs de distribution géographique et stratigraphique connus

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ARTICLE INFO

Article history:

Received 20 August 2013
Accepted after revision 28 October 2013
Available online 17 December 2013

Handled by Philippe Taquet

Keywords:

Eucryptodira
Hylaeochelys
New species
Late Jurassic
Portugal

Mots clés :

Eucryptodira
Hylaeochelys
Nouvelle espèce
Jurassique supérieur
Portugal

ABSTRACT

A relatively complete shell of a turtle, recently found in the Tithonian (Freixial Formation) of the Lusitanian Basin (Portugal), is presented and described here. Its taxonomic adscription and systematic position are discussed in this paper. This turtle is identified as a basal member of Eucryptodira. Other basal representatives of this group, all of them attributed to Plesiochelyidae, had previously been recognized in this Formation. The new specimen cannot be assigned to that family. It is recognized as a member of the genus *Hylaeochelys*. The presence of *Hylaeochelys* had been, so far, only confirmed in Early Cretaceous levels of England. Therefore, this finding expands both the range of geographic distribution of the genus and its stratigraphic distribution. The new specimen is attributed to a new species of this so far monospecific taxon: *Hylaeochelys kappa* sp. nov.

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R É S U M É

Une carapace de tortue relativement complète, trouvée récemment dans le Tithonien (formation Freixial) du Bassin lusitanien (Portugal) est présentée et décrite ici. Elle fait l'objet d'une discussion dans ce travail. Cette tortue est identifiée comme un membre basal d'Eucryptodira. D'autres représentants basaux d'Eucryptodira, tous attribués aux Plesiochelyidae, avaient été auparavant reconnus dans cette formation. Le nouveau spécimen ne peut appartenir à cette famille. Il est reconnu comme un membre du genre *Hylaeochelys*. À ce jour, la présence d'*Hylaeochelys* n'avait été confirmée que dans le Crétacé inférieur d'Angleterre. De ce fait, cette découverte élargit la répartition géographique du genre, tout comme elle étend sa distribution stratigraphique. Le nouveau spécimen est attribué à une nouvelle espèce de ce genre, jusqu'ici monospécifique : *Hylaeochelys kappa* sp. nov.

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1. Introduction

The taxon *Hylaeochelys* Lydekker, 1889a is a European member of Eucryptodira, so far only identified in Early Cretaceous levels of the Purbeck and Weald of England, where it is relatively abundant (Milner, 2004; Pérez-García, 2012). It is known by shell elements and scarce appendicular bones. A review of all known specimens, and the study of abundant unpublished material, have recently allowed *Hylaeochelys belli* (Mantell, 1844) to be recognized as the only valid species of this genus (Pérez-García, 2012). *Hylaeochelys* is interpreted as a taxon closely related to Plesiochelyidae, but characters such as the absence of three cervical scutes, places it out of this clade (de Lapparent de Broin et al., 1996; Pérez-García, 2012).

Plesiochelyidae are a diverse group of European Late Jurassic turtles, identified in several European countries (de Lapparent de Broin, 2001; de Lapparent de Broin et al., 1996; Pérez-García, in press). In the Iberian Peninsula this clade is represented by several taxa, attributed to the genera *Craspedochelys* Rüttimeyer, 1873, *Plesiochelys* Rüttimeyer, 1873 and *Tropidemys* Rüttimeyer, 1873 (Antunes et al., 1988; de Lapparent de Broin, 2001; Pérez-García et al., 2008, 2013). A fragment of the anterior region of a carapace, lacking three cervical scutes, has recently been recognized in the Tithonian of Galve (Teruel, Spain). This finding demonstrates the presence of an indeterminate taxon related to Plesiochelyidae but not assignable to this group in the Iberian record (Pérez-García et al., 2013).

Plesiochelyidae are very abundant in the Kimmeridgian and Tithonian levels of the Lusitanian Basin (central Portugal) (Antunes et al., 1988; Ortega et al., 2009; Pérez-García et al., 2008, 2010; Sauvage, 1898). New findings demonstrate that the diversity of Eucryptodira in the Jurassic levels of this basin is greater than previously recognized. A new specimen, from the Tithonian of Barril (Mafra) (Fig. 1), which is described here, adds to this diversity. The new specimen is a shell, which cannot be assigned to Plesiochelyidae. It is recognized as a form closely related to that clade and, more specifically, to the British Early Cretaceous taxon *Hylaeochelys belli*. The analysis of this new species provides additional data on the diversity of the basal eucryptodirans in the Late Jurassic of Europe, as well as on the geographic and stratigraphic distribution of the genus *Hylaeochelys*.

Institutional Abbreviations: NHMUK: Natural History Museum, London, UK; NHMW: Naturhistorisches Museum Wien, Austria; MPG: Museo Paleontológico de Galve, Galve, Teruel, Spain; OUM: Oxford University Museum, UK; SHN.LPP: Laboratório de Paleontologia e Paleocologia da Sociedade de História Natural, Torres Vedras, Portugal.

2. Systematic palaeontology

CHELONII Latreille, 1800

PANCRYPTODIRA Joyce et al., 2004

EUCRYPTODIRA Gaffney, 1975

Hylaeochelys Lydekker, 1889a

Type species: *Hylaeochelys belli* (Mantell, 1844)

Distribution: Late Jurassic (Late Tithonian) to Early Cretaceous (Valanginian) of Europe

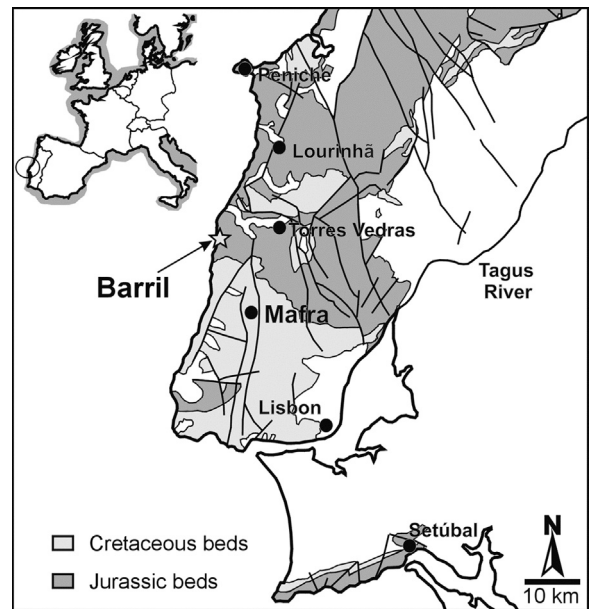


Fig. 1. Map of the central-west region of Portugal showing the location of the Late Jurassic locality of Barril (Mafra), where the holotype of *Hylaeochelys kappa* sp. nov. was found.

Fig. 1. Carte de la région centre-ouest du Portugal montrant l'emplacement de la localité jurassique de Barril (Mafra), où a été trouvé l'holotype de *Hylaeochelys kappa* sp. nov.

Modified from Oliveira et al. (1992) and Pérez-García and Ortega (2011).

Emended diagnosis (since Pérez-García, 2012): pancryptodiran turtle sharing the following character combination: roughly circular, low shell; reduced thickness of the carapace and plastron plates; wide, shallow notch restricted to the anterior margin of the nuchal plate; shell surface slightly fluted; anteriormost area of the lateral margins of the nuchal subparallel or slightly divergent; continuous or discontinuous neural series consisting of 7–9 plates, the anterior ones very elongated; first neural rectangular, the following plates hexagonal, and the last neural or pair of neurals subpentagonal to subcircular; two suprapyrgals, the anterior being longer and the posterior wider; first costal more than twice as wide as long; 11 pairs of peripherals; sinuous medial margin of the peripherals; posterior peripherals longer than those of the anterior region; absence of dorsal thickening of the lateral edges in the anterior peripherals; medio-laterally expanded posterior peripherals; single, very short and wide cervical scute; vertebral scutes at least twice as wide as they are long and over half the width of the carapace; first vertebral rectangular, considerably wider than the nuchal, similar in width to that of the fifth vertebral, and considerably wider than the second suprapygal; second to fourth vertebrae similar in width, considerably wider than the first and last vertebrae; narrow pleural scutes, extending over one-third of the width of the peripheral plates; sulcus between the first and second marginals posteriorly contacting the first pair of pleurals; contact of the last pair of marginals and the second suprapygal absent; absence of costal-peripheral and bridge fontanelles, but presence of a central plastral fontanelle in

some adult specimens, of variable size; partially osseous connection between plastron and peripherals; broad plastral lobes, with the anterior rounded, and the distal region of the posterior one subperpendicular to the axial axis, lacking anal notch; hyoplastra longer than hypoplastra; absence of mesoplastra; straight to markedly sinuous medial sulcus of the plastron; presence of one pair of intergular scutes, similar in size to the gulars; five inframarginals; anal scutes not contacting the hypoplastra.

Hylaeochelys belli

Synonyms: *Chelone belli* Mantell, 1844; *Pleurosternum emarginatum* Owen, 1853; *Pleurosternum laticutatum* Owen, 1853; *Chelone costata* Owen, 1853; *Platemys mantelli* Owen, 1853; *Platemys dixonii* Owen, 1853; *Hylaeochelys sollasi* Nopcsa, 1928.

Holotype: NHMUK 36529, a distal fragment of costal plate (see Mantell, 1827, pl. 6, fig. 2; 1844, fig. 240; 1851, fig. 33).

Type locality and type horizon: Tilgate forest, Cuckfield, Sussex, England; Hastings Group, (Berriasian–Valanginian), Weald Sub-basin of the Wessex–Weald Basin (Pérez-García, 2012).

Etymology: Not specified.

Diagnosis: Species of *Hylaeochelys* differing from the new *Hylaeochelys kappa*, the other representative of this genus, in the presence of: slightly convex sulcus corresponding to the limit between the third and fourth vertebral scutes, being exclusively located on the fifth pair of costals and on the fifth neural; relatively large entoplastron, significantly longer than wide; distance between the rear margin of the entoplastron and the humero-pectoral sulcus less than half of the length of the entoplastron; intergulars not overlapping onto the anterior region of the entoplastron.

Hylaeochelys kappa sp. nov.

Fig. 2

Holotype: SHN.LPP 172, a shell preserving the nuchal plate, the first to seventh neurals, the anterior region of the eighth neural, the first pair of costals, the complete second to fourth right costals, the medial region of the fifth to seventh right and second to eighth left costals, the first to fourth pairs of peripherals, the fifth to eighth right peripherals, the complete left epiplastron, the medial margin of the right epiplastron, the entoplastron, the pair of hyoplastra lacking their postero-medial region, and the lateral margin of right hypoplastron. Some of the plates are disjointed, but have a very low dispersion.

Type locality and type horizon: Porto do Barril beach, Barril, Mafra municipality, Lusitanian Basin, Portugal (Fig. 1). The site is located in channel facies with sands laterally replaced by clays. Freixial Formation. Middle to Late Tithonian (Kullberg et al., 2011; Pereda Suberbiola et al., 2005).

Etymology: The specific name corresponds to that of an aquatic creature from the Japanese mythology that has a partially baldhead and a turtle shell attached to the back. The word “*kappa*” is considered as a Japanese

transliteration of the Portuguese “*capa*”, the term for the robe worn by Portuguese monks, with a shaved pate, who arrived in Japan in the sixteenth century. This garment hung down their back was viewed as similar to the kappa’s shells.

Diagnosis: Species of *Hylaeochelys* differing from *Hylaeochelys belli*, the only previously known representative of this genus, in the presence of: omega-shaped sulcus corresponding to the limit between the third and fourth vertebral scutes, laterally located on the sixth pair of costals and medially on the fifth pair of costals and on the fifth neural; small entoplastron, as long as wide; distance between the rear margin of the entoplastron and the humero-pectoral sulcus greater than the total length of the entoplastron; intergulars overlapping onto the anterior region of the entoplastron.

3. Description

The outer surface of the specimen SHN.LPP 172 is ornamented with shallow flutes. It is a relatively wide and low shell. A wide and shallow notch is present in the anterior margin of the shell, restricted to the nuchal plate.

The width of the nuchal exceeds twice its length. There is a caudally directed protrusion in the sagittal region of its posterior edge. The lateral margins of this plate are convergent anteriorly in the posterior half, but they are subparallel in the anteriormost area. This specimen has eight neurals. The first neural is subrectangular. The second to seventh neurals are hexagonal, markedly longer than wide. The neural series is discontinuous, due to the presence of a short medial contact of the seventh pair of costals. The first pair of costals is more than twice as wide as long. The contact between the costal and the peripheral plates is sinuous. The anterior peripherals lack a dorsal thickening in the lateral edges.

This taxon has a single cervical scute. It is very short, especially in the medial region. The vertebral scutes are very wide, its width being two or more times greater than its length. In this regard, the first vertebral scute is considerably wider than the nuchal plate. The second and third vertebrae are wider than the first one, both with a similar width. The contacts between the first and second vertebrae, and between the second and third vertebrae, are subperpendicular to the axial plane. However, the contact between the third and fourth vertebrae is markedly convex, with a sharp change of curvature on the costal plates, acquiring an omega-shaped. That contact occurs laterally on the sixth pair of costals. Due to its morphology, that sulcus medially overlaps the proximal region of the fifth pair of costals and the fifth neural. The vertebral scutes are extending over more than half of the width of the peripheral plates. The boundary between the first and second marginal scutes posteriorly contacts the first pair of pleurals.

The epiplastra are wider than long. The entoplastron, small in size, is subrounded and as wide as long. The contact between the epiplastra and the hyoplastra is subperpendicular to the axial plane. The hyoplastra and the hypoplastra contact the peripheral plates through a partially osseous connection. This specimen lacks fontanelles

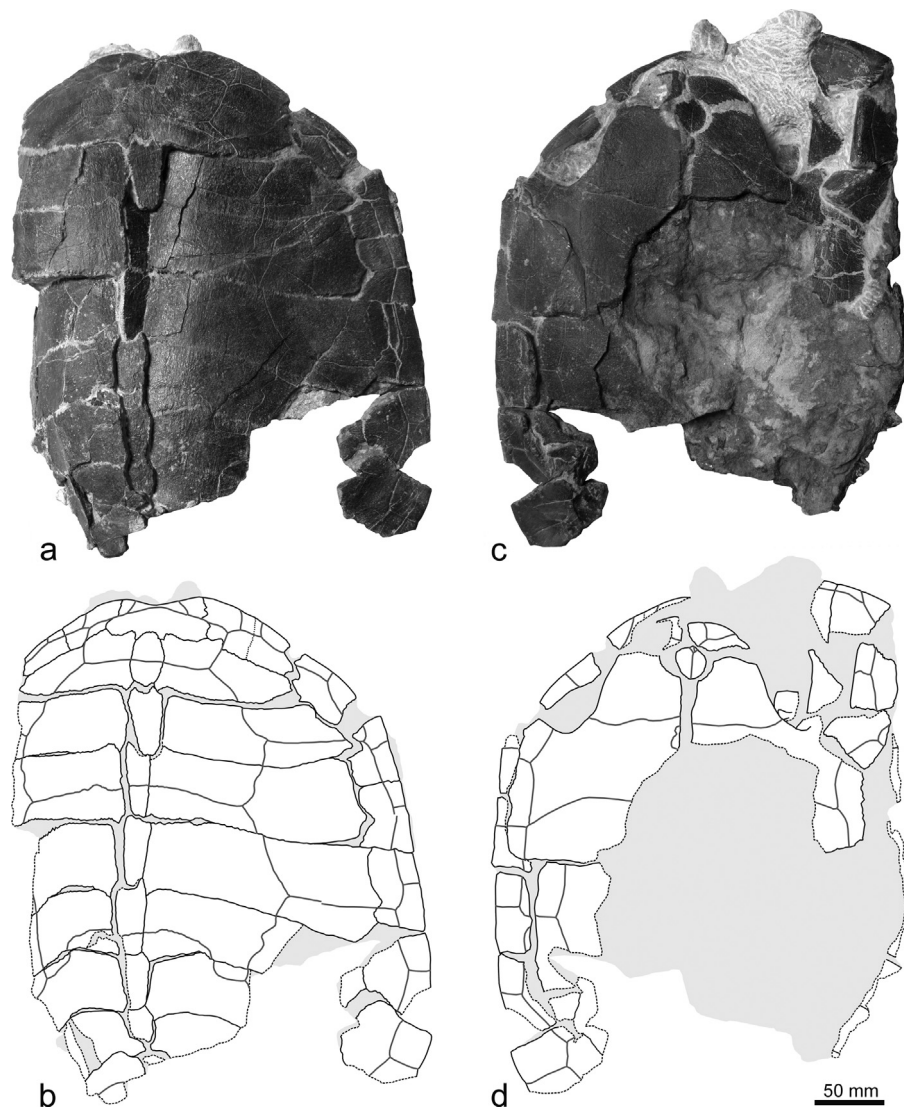


Fig. 2. Shell of the holotype of *Hylaeochelys kappa* sp. nov., SHN.LPP 172, from the Late Jurassic of Barril (Mafra), in dorsal (a, b) and ventral (c, d) views.
Fig. 2. Carapace de l'holotype de *Hylaeochelys kappa* sp. nov., SHN.LPP 172, du Jurassique supérieur de Barril (Mafra), en vues dorsale (a, b) et ventrale (c, d).

in the area of the bridge. Its preservation does not reveal whether it possessed a central plastral fontanelle. It lacks mesoplastra.

The medial sulcus of the plastron, preserved on the medial region of the hyoplastra, is sinuous. A pair of intergular scutes is present. Their size is similar to that of the gulars. The intergulars overlap the anterior end of the entoplastron. The distance between the rear margin of the entoplastron and the humero-pectoral sulcus exceeds the length of the entoplastron. The humero-pectoral sulcus is subperpendicular to the axial plane. Five pairs of inframarginal scutes are present. They are superimposed on the medial region of the bridge peripherals. The pectoro-abdominal sulcus contacts the posterior region of the second pair of inframarginals laterally.

4. Discussion and conclusions

SHN.LPP 172 shares with the previously known specimens of *Hylaeochelys* (sensu Pérez-García, 2012) an exclusive combination of characters (see these characters in the emended diagnosis proposed above).

A single valid species of this genus, *Hylaeochelys belli*, has been identified (Pérez-García, 2012). Therefore, the generic diagnosis did not differ from the specific one. However, the identification of the new species allows some characters used in the diagnosed of *Hylaeochelys* to be reinterpreted as unique to *Hylaeochelys belli*. For example, *Hylaeochelys belli* differs from *Hylaeochelys kappa* sp. nov. in the presence of a relatively large entoplastron, significantly longer than wide. In *Hylaeochelys kappa* sp. nov. the entoplastron is small and as wide as long.

Only a single entoplastron of *Hylaeochelys belli* has so far been reported (see figs. 5F and 6F in Pérez-García, 2012, corresponding to the complete and articulate plastron NHMW 2011/0310/0001). However, many hyoplastra of *Hylaeochelys belli*, from the Early Cretaceous of England, are recognized. Their anterolateral margin is compatible with the presence of an elongated entoplastron (e.g., NHMUK 2313, figured by Pérez-García, 2012 on figs. 5G and 6G; NHMUK 21351X; NHMUK 23624; NHMUK 39457; NHMUK 45937; NHMUK R6840; NHMUK R6863; NHMUK R6882, figured by Pérez-García, 2012 on figs. 5E and 6E; NHMUK R6885). The pectoral scutes do not contact the entoplastron in this genus. The cited specimens of *Hylaeochelys belli* show that the distance between that pair of scutes and the entoplastron is less than half of the length of the entoplastron. However, this distance is greater than the total length of the entoplastron in *Hylaeochelys kappa* sp. nov. The diagnosis of *Hylaeochelys* previously included the character of the intergulars not superimposed on the entoplastron (see Pérez-García, 2012). However, this condition is not present in the Portuguese species. The omega-shaped morphology of the sulcus that delimits the third and fourth vertebrae is unique to *Hylaeochelys kappa* sp. nov. That sulcus is slightly convex in *Hylaeochelys belli*, being exclusively located on the fifth pair of costals, but not in the sixth one.

The medial contact of the seventh pair of costals, present in *Hylaeochelys kappa* sp. nov., has not been described in any of the specimens of *Hylaeochelys belli*. However, great variability has been detected in the neural series of the British species. Specimens with both continuous and discontinuous neural series, and specimens consisting of seven to nine plates, have been identified. The medial contact of the costals in the specimens with discontinuous series, which is always located between the eighth pair of costals, isolates the last neural from the more anterior neurals in some specimens, and occurs behind that plate in others. Therefore, given the large variability in the posterior region of the neural series and in the medial margin of the last pairs of peripherals, this character is not included in the differential diagnosis of these species. OUM J13796 is the only known specimen of *Hylaeochelys belli* in which the dorsal region of at least the dorsal view of one plate of each pair of the peripheral series is recognized (see figs. 5B and 6B in Pérez-García, 2012). In this specimen, the surface of the peripherals covered by the pleural scutes is over one-third of the width of these plates. The pleurals of *Hylaeochelys kappa* sp. nov. overlap over half of the width of the peripherals. However, because the width of the some scutes of the carapace varies greatly comparing several specimens of *Hylaeochelys belli* (as, for example, the vertebral scutes), this character is not included in the diagnosis. The discovery of new specimens of *Hylaeochelys kappa* sp. nov. is necessary to include more characters in the specific diagnosis and to evaluate the variability of several features.

The comparison of these two species allows some hitherto not considered characters to be included in the exclusive combination of the genus *Hylaeochelys*, whose character states are not shared with all the European basal members of Eucryptodira (the medial margin of the peripheral plates is sinuous; the sulcus between the first and second marginals posteriorly contacts the first pair

of pleurals, and not with the first vertebral scute), and a character state not shared with any of them (despite its relatively large size, the plates of the carapace and of the plastron have a very reduced thickness).

Therefore, the presence of a basal representative of Eucryptodira not assignable to Plesiochelyidae is identified in a Portuguese formation (Freixial Formation) where the plesiochelyids are abundant (Pérez-García et al., 2008). A similar situation has recently been recognized in another region of the Iberian Peninsula, also in Tithonian levels: in the Spanish town of Galve (Teruel), in the Villar del Arzobispo Formation. The presence of members of Plesiochelyidae and of a basal member of Eucryptodira not assignable to this clade, identified as aff. Plesiochelyidae, has been recognized there (Pérez-García et al., 2013). The taxon identified as aff. Plesiochelyidae, identified on the basis of a fragment of the anterior region of a carapace (MPG-731), shares with the members of *Hylaeochelys* the presence of a single cervical scute. However, it is excluded from *Hylaeochelys* because of the more elongated cervical scute relative to its width, the absence of decoration, the narrower first costal relative to its length and, especially, the high thickness of the plates (similar to that present in the members of Plesiochelyidae). Therefore, the European Late Jurassic record of basal members of Eucryptodira, and specifically that of the Iberian Peninsula, is more diverse than the hitherto described. The presence of representatives of several clades in the same Formation is recorded both in Portugal and Spain.

The basal members of Eucryptodira so far identified in the European Jurassic record (Plesiochelyidae, Thalassemydidae and Eurysternidae) are considered to be clades that are endemic to this continent (de Lapparent de Broin, 2001; de Lapparent de Broin et al., 1996; Pérez-García et al., 2013). The new specimen, SHN.LPP 172, demonstrates the presence of the genus *Hylaeochelys* in the Jurassic. Therefore, *Hylaeochelys* is the only of these taxa recorded in both the Late Jurassic and the Early Cretaceous. In fact, this turtle is interpreted as a freshwater taxon, unlike the members of Plesiochelyidae, Thalassemydidae and Eurysternidae, all of which are recognized as inhabitants of coastal environments, living in both saltwater (Plesiochelyidae, Thalassemydidae) or generally brackish waters (Eurysternidae) (Billon-Bruyat et al., 2005; de Lapparent de Broin, 2001; de Lapparent de Broin et al., 1996; Pérez-García, 2012; Pérez-García et al., 2013). In this sense, it has been proposed that these groups of coastal turtles, and other reptiles that lived in the same environments, disappeared during the Jurassic-Cretaceous transition as a result of a regression of the shallow shelf seas of Europe, which drastically reduced their habitat (Bardet, 1994). Other members of Eucryptodira are recognized in Europe during the Early Cretaceous, and especially in the Iberian Peninsula. However, they correspond to lineages that are non-European in origin. Specifically, they are representatives of Xinjiangchelyidae, a group of freshwater turtles coming from Asia (Pérez-García et al., in press). The British taxon *Brodiechelys brodiei* (Lydekker, 1889b), and the Spanish forms *Brodiechelys royoi* Pérez-García et al., in press, *Larachelus morla* Pérez-García and Murelaga, 2012 and *Camerochelys vilanovai* Pérez-García and Murelaga,

2013 belong to this clade. Thus, this and other recent studies show that the basal members of Eucryptodira were abundant and diverse in both the Iberian Late Jurassic (represented by members of *Craspedochelys*, *Plesiochelys*, *Tropidemys*, *Hylaeochelys* and several still undefined forms), and in the Early Cretaceous (represented by members of *Brodiechelys*, *Larachelus*, *Camerochelys* and forms undefined yet).

Although the presence of *Hylaeochelys* had not yet been confirmed outside England, unpublished material from the Early Cretaceous of Germany that has been observed suggests the likely presence of the this taxon there, probably being represented by the same species recorded in the British synchronous levels (e.g., lacking of the omega-shaped sulcus generated in the contact area of the third and fourth vertebral scutes). Future studies should confirm the generic and specific attribution of those specimens.

In summary, the first specimen of *Hylaeochelys* recognized outside the British record that can be attributed, in a robust way, to this genus is figured, described and discussed here. It is a new species of this genus so far recognized by a single representative, *Hylaeochelys belli*. The Portuguese *Hylaeochelys kappa* sp. nov. increases the known range of temporal distribution for the genus, being the only representative of *Hylaeochelys* identified in the Jurassic record.

Acknowledgements

The authors thank Sandra Chapman (NHMUK), Ursula Göhlich (NHMW), the Herrero family (MPG), Paul Jeffery (OUM), and, especially, Bruno Silva (SHN.LPP) for access to material; Pedro Mocho (Universidad Autónoma de Madrid/SHN.LPP) for information on the geology; Jose Joaquin dos Santos for location of the holotype of the new species; France de Lapparent de Broin (Muséum national d'histoire naturelle, Paris) for the correct writing of the abstract in French; and Walter Joyce (University of Fribourg), an anonymous reviewer and the editorial secretary Judith Goldschmidt for comments and suggestions. The comparative studies have been supported by the SYNTHESIS Project <http://www.synthesys.info/>, financed by the European Community Research Infrastructure Action under the FP7 Integrating Activities Programme.

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