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General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

## Largest shell of a basal eucryptodiran turtle reveals Late Jurassic *Thalassemys hugii* in the British record



*Identification de la tortue du Jurassique Supérieur Thalassemys hugii dans le registre britannique grâce à la découverte de la plus grande carapace connue d'une eucryptodira basale*

Adán Pérez-García <sup>a,\*,b</sup><sup>a</sup> Centro de Geología, Faculdade de Ciências da Universidade de Lisboa (FCUL), Edifício C6, Campo Grande, 1749-016 Lisbon, Portugal<sup>b</sup> Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Paseo de la Senda del Rey 9, 28040 Madrid, Spain

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## ABSTRACT

A British turtle specimen with the largest shell of a basal eucryptodiran turtle recognized globally is presented and analyzed. It belongs to *Thalassemys hugii*, the type species of both *Thalassemys* and *Thalassemydidae*, a poorly-known European Late Jurassic clade. *T. hugii* is recognized outside Central Europe for the first time. Therefore, this finding offers new data on its geographical distribution and on its intraspecific variability.

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## R É S U M É

Un spécimen de tortue britannique, dont la carapace correspond à la plus grande reconnue chez une tortue Eucryptodira basale, est présenté et analysé dans cet article. Il est identifié comme appartenant à *Thalassemys hugii*, l'espèce type à la fois de *Thalassemys* et des *Thalassemydidae*, clade mal connu du Jurassique supérieur européen. *T. hugii* est reconnu, pour la première fois, en dehors de l'Europe centrale. Par conséquent, cette découverte apporte de nouvelles données sur sa répartition géographique, mais aussi sur sa variabilité intraspécifique.

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## 1. Introduction

The Late Jurassic was a very successful period for the diversification of several European taxa of basal

\* Correspondence.

E-mail address: [paleontologo@gmail.com](mailto:paleontologo@gmail.com)

Eucryptodira (i.e. members of Eucryptodira outside Cryptodira). The best-known members are the traditional Eurysternidae and Plesiochelyidae, very abundant and diverse clades, defined in the nineteenth century (see Baur, 1888; Dollo, 1886). Thalassemydidae were also described in that century (see Zittel, 1889). Due to limited information available on *Thalassemys*, the validity of the clade Thalassemydidae (exclusively represented by *Thalassemys Rüttimeyer, 1873*) has been questioned in recent papers, where the genus was identified as a member of Plesiochelyidae (see Milner, 2004; Tong et al., 2009). However, several more recent studies have provided important data on the diversity of the basal eucryptodirans in the European Late Jurassic record. On one hand, the attribution of *Thalassemys* to a clade other than Eurysternidae and Plesiochelyidae (i.e. Thalassemydidae) has been confirmed by a review of previously known material of this genus and by the discovery of new specimens (see Pérez-García, 2015a). Furthermore, the known diversity of Eucryptodira in the European Late Jurassic has significantly increased due to the identification of three taxa recognized as not belonging to the classic Eurysternidae, Plesiochelyidae, or Thalassemydidae:

- a new species of *Hylaeochelys Lydekker, 1889* (*Hylaeochelys kappa Pérez-García and Ortega, 2014*), a genus so far only known in the Cretaceous, has been recognized in the Portuguese Jurassic record (Pérez-García and Ortega, 2014);
- the validity of *Enaliochelys chelonia Seeley, 1869*, a British taxon ignored since the late nineteenth century because of its putative synonymy with *Thalassemys hugii Rüttimeyer, 1873*, has been confirmed (Pérez-García, 2015a);
- a new genus and species (i.e. *Jurassichelon oleronensis Pérez-García, 2015a*) has been defined from the Oléron Island (France) Tithonian specimen, previously attributed by Rieppel (1980) to “*Thalassemys*” *moseri Bräm, 1965*, but which differs from that taxon, defined in the Kimmeridgian of Solothurn (Switzerland) (Pérez-García, 2015a).

The type species of *Thalassemys*, *T. hugii*, has only been recognized in the Kimmeridgian of Solothurn. A second valid species of this genus, *Thalassemys marina Fraas, 1903*, is exclusively represented by its type specimen, from the Tithonian of Schnaithaim (Germany). The only known specimen of the genus *Thalassemys* outside central Europe was recently identified in Dorset (England) in Kimmeridgian levels of the Kimmeridge Clay Formation (Pérez-García, 2015a) (Fig. 1g). A relatively high diversity of basal eucryptodirans is recognized in the British Late Jurassic record, where several taxa are defined (*Plesiochelys planiceps* (Owen, 1842), *Portlandemys mcdowellii Gaffney, 1975a*, *Tropidemys blakii* (Seeley, 1875), *Tholemys passmorei Andrews, 1921*, and *Enaliochelys chelonia*; Fig. 1a–e). The British specimen of *Thalassemys* was a relatively small individual (Fig. 2a) recognized as *Thalassemys* sp., but not attributed to a specific species for several reasons: it was probably not an adult individual, scarce information could be gathered from its shell (the partial carapace was

preserved, but not the plastron), it was the only specimen of this genus recognized in the British record, and, as indicated, information on known species of *Thalassemys* was limited (Pérez-García, 2015a). *Thalassemys* is the largest taxon known from its type locality, where several basal members of Eucryptodira are recorded (Anquetin et al., 2014; Bräm, 1965; Lapparent de Broin et al., 1996; Rüttimeyer, 1873). A new British specimen, whose shell is larger than those hitherto recognized for *Thalassemys*, is presented here (Figs. 2c–d, 3). This specimen also comes from the Kimmeridge Clay Formation, but from the town of Abingdon (Oxfordshire) (Fig. 1f). The new specimen, an adult individual, preserves elements unknown on the British specimen previously assigned to *Thalassemys*. The study of the Abingdon specimen provides relevant data on the variability and range of distribution of this poorly-known coastal eucryptodiran member. In this regard, its attribution to the type species of *Thalassemys*, to *Thalassemys marina*, or to a new species is evaluated.

**Institutional abbreviations:** CAMSM, Sedgwick Museum, Department of Geology, University of Cambridge, UK; NHMUK, Natural History Museum, London, UK; NMS, Naturmuseum Solothurn, Switzerland; OUMNH, Oxford University Museum of Natural History, UK.

## 2. Systematic paleontology

TESTUDINES Batsch, 1788

PAN-CRYPTODIRA Joyce et al., 2004

EUCRYPTODIRA Gaffney, 1975b sensu Joyce, 2007

THALASSEMYDIDAE Zittel, 1889

THALASSEMYS Rüttimeyer, 1873

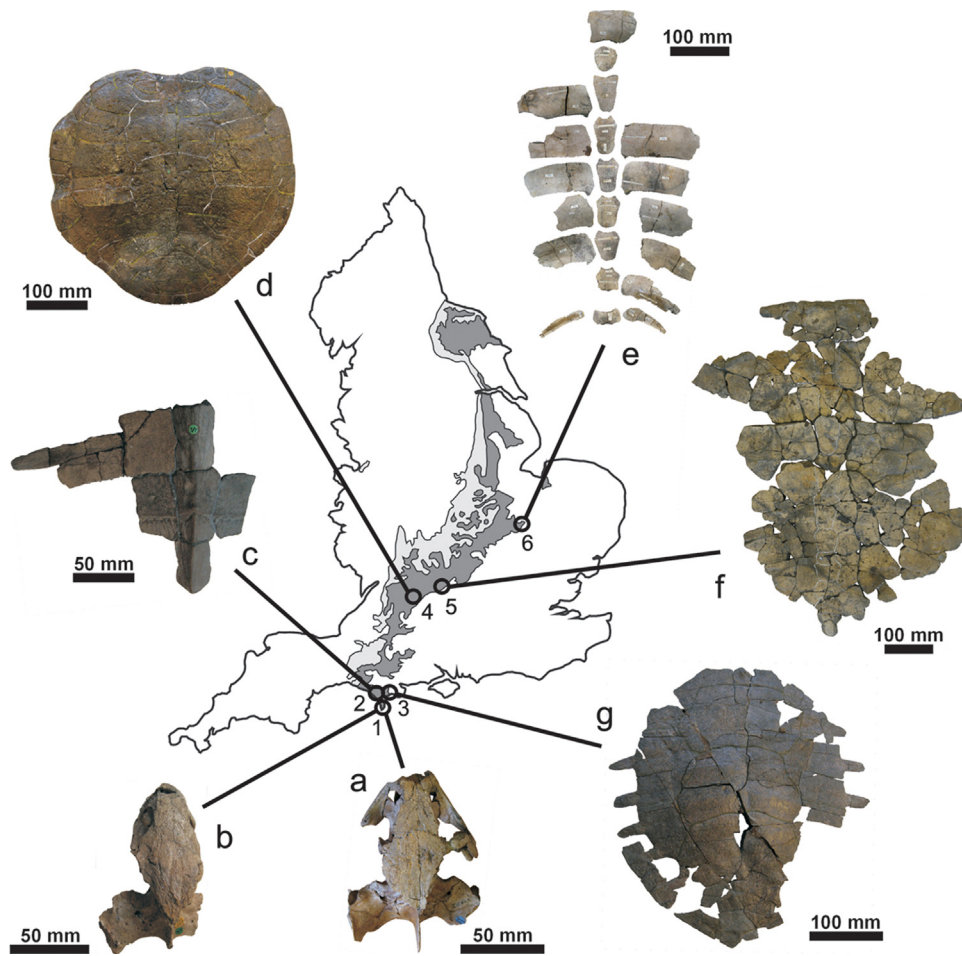
*Thalassemys hugii Rüttimeyer, 1873*

Figs. 1f, 2c–d, 3

**Material:** OUMNH J.66966, a relatively complete shell and other postcranial elements, corresponding to a single individual.

**Locality and horizon:** OUMNH J.66966 comes from a gravel pit near Thrupp Lane, in Abingdon, Oxfordshire, England (Fig. 1f). Kimmeridgian, Kimmeridge Clay Formation.

**Description of the shell of OUMNH J.66966:** Although very flattened due to postmortem deformation, the shell of OUMNH J.66966 can be seen to have been low (Fig. 3a). Despite the relatively poor preservation of the outer shell surface, linear striations perpendicular to some of the sutures are noted. The maximum length of the preserved region (from the anterior edge of the carapace to the posterior half of the second suprapygal) is about 79 cm. Comparing it with other known shells of *Thalassemys*, the estimated length for its complete shell is therefore about 95 cm. This taxon lacks a sagittal keel and a nuchal notch. The nuchal plate is twice as wide as long. The anteriormost areas of the lateral margins of this plate are subparallel. It has a continuous neural series, consisting of 10 elements: the second and sixth neurals are divided into two elements. The first neural is subrectangular (with convex lateral margins), with its maximum width in the anterior half. The other neurals are hexagonal. The latero-anterior margins of all these plates, except those of the last neural, are shorter

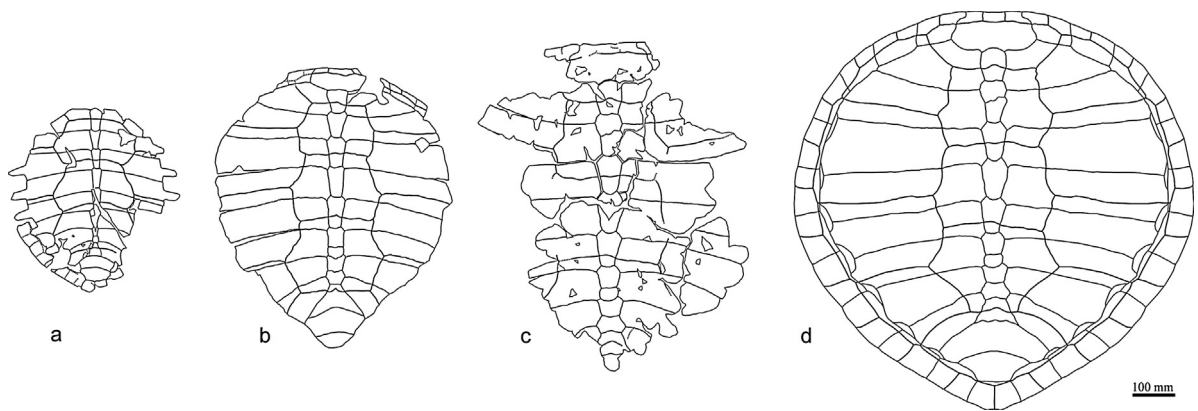


**Fig. 1.** (Color online.) Geographical and geological position of the findings of the basal eucryptodiran taxa defined in the British record and currently considered valid (a–e), and also of the two shells of *Thalassemys* found in that country (f–g): a–e: type specimens of: a, *Plasiochelys planiceps*, OUMNH J.1582, probably from the Tithonian of the Island of Portland, in Dorset (1); b, *Portlandemys mcdowellii*, NHMUK R2914, from the Tithonian of the Island of Portland (1); c, *Tropidemys blakii*, NHMUK R2a, from the Kimmeridgian of Weymouth, in Dorset (2); d, *Tholemys passmorei*, NHMUK R5871, from the Kimmeridgian or Tithonian of Swindon, in Wiltshire (4); e, *Enaliochelys chelonia*, CAMSM J29898 to CAMSM J29955, from the Kimmeridgian of Ely, in Cambridgeshire (6); f, OUMNH J.66966, specimen of *Thalassemys hugii* Rüttimeyer, 1873 from the Kimmeridgian of Abingdon, in Oxfordshire (5); g, NHMUK R8699, specimen of *Thalassemys* sp. from the Kimmeridgian of the Isle of Purbeck, in Dorset (3). The light-grey area represents the Lower Jurassic levels of England. The dark-grey area corresponds to the Middle and Upper Jurassic levels.

**Fig. 1.** (Couleur en ligne.) Situation géographique et géologique des découvertes d'Eucryptodira basales, définies dans le registre britannique et actuellement considérées comme valides (a–e), et aussi de ceux des deux carapaces de *Thalassemys* trouvées dans ce pays (f–g) : a–e : spécimens type de : a, *Plasiochelys planiceps*, OUMNH J.1582, probablement du Tithonien de l'île de Portland, dans le Dorset (1) ; b, *Portlandemys mcdowellii*, NHMUK R2914, du Tithonien de l'île de Portland (1) ; c, *Tropidemys blakii*, NHMUK R2a, du Kimméridgien de Weymouth, dans le Dorset (2) ; d, *Tholemys passmorei*, NHMUK R5871, du Kimméridgien ou Tithonien de Swindon, dans le Wiltshire (4) ; e, *Enaliochelys chelonia*, CAMSM J29898 à CAMSM J29955, du Kimméridgien de Ely, dans le Cambridgeshire (6) ; f, OUMNH J.66966, *Thalassemys hugii* Rüttimeyer, 1873 du Kimméridgien de Abingdon, dans l'Oxfordshire (5) ; g, NHMUK R8699, spécimen de *Thalassemys* sp. du Kimméridgien de l'île de Purbeck, dans le Dorset (3). Les zones en gris clair correspondent aux niveaux du Jurassique inférieur de l'Angleterre et celles en gris foncé aux niveaux du Jurassique moyen et supérieur.

than the posterior ones. All the elements of the neural series, except the last two plates, are significantly longer than wide. OUMNH J.66966 had at least two suprapyrgals. The first is trapezoidal, posteriorly wider than in the anterior region. The morphology of the second one is not known. The first pair of costals is relatively short, its maximum length similar to that of the second pair. The unsutured contact between the costals and the peripherals reveals that relatively narrow fontanelles connected these plates. A single cervical scute is recognized, wider than long. The vertebral scutes are relatively narrow.

The preserved elements do not reveal whether OUMNH J.66966 had lateral plastral fontanelles. If present, though, they were narrow. A large central plastral fontanelle and a (probably) small xiphiplastral fontanelle are recognized (Fig. 3c). This specimen lacks a sutural connection of the epiplastra and entoplastron with the hyoplastra. An interdigitating medial contact of the hyoplastra is observed. The hyoplastra are longer than the hypoplastra. The contact line between the hyoplastra and the xiphiplastra zigzags slightly due to the latero-posterior prolongation of the hyoplastra. The lateral margins of the posterior plastral



**Fig. 2.** Interpretative drawings of the dorsal view of three carapaces of *Thalassemys* from the Kimmeridgian of England and Switzerland: a, NHMUK R8699, *Thalassemys* sp. from the Isle of Purbeck (England); b, NMS 1, lectotype of *Thalassemys hugii*, from Solothurn (Switzerland); c, OUMNH J.66966, *T. hugii* from Abingdon (England); d, hypothetical reconstruction of the complete carapace of OUMNH J.66966. The narrow black lines represent plate margins, and the wide grey lines correspond to the scute sulci. The grey areas are the matrix.

**Fig. 2.** Dessins de trois carapaces en vue dorsale de *Thalassemys* du Kimméridgien d'Angleterre et de Suisse : a, NHMUK R8699, *Thalassemys* sp. de l'île de Purbeck (Angleterre) ; b, NMS 1, lectotype de *Thalassemys hugii*, de Soleure (Suisse) ; c, OUMNH J.66966, *T. hugii* de Abingdon (Angleterre) ; d, reconstruction hypothétique de la carapace complète de OUMNH J.66966. Les lignes noires fines représentent les limites de plaques, et les lignes grises larges les sillons des écailles. Les zones grises correspondent à la matrice.

lobe are markedly convergent towards the posterior region. OUMNH J.66966 lacks an anal notch.

### 3. Discussion

The shell of the Abingdon specimen is compared with those of basal eucryptodirans in the European Late Jurassic record: the two described species of *Thalassemys*, *Plesiochelyidae*, *Eurysternidae*, *Hylaeochelys*, *Jurassichelon oleronensis*, and *Enaliochelys chelonia*. Information on the characters discussed here is based on personal observations and on several papers, including those of Anquetin and Joyce, 2014; Anquetin et al., 2014; Joyce, 2007; Lapparent de Broin et al., 1996; Pérez-García, 2014; Pérez-García and Ortega, 2014; Pérez-García, 2015a,b.

A low shell distinguishes it from members of *Plesiochelyidae* and *Jurassichelon oleronensis*. A shell length of over 60 cm was only recognized in *T. hugii*; Anquetin et al., 2014 and *Enaliochelys chelonia*. The plates of the carapace and plastron of OUMNH J.66966 are thinner relative to the length of the shell than those in *Plesiochelyidae*, but thicker than those of *Hylaeochelys*.

The specimen studied here shares with *Thalassemys* and *Enaliochelys chelonia* the absence of a nuchal notch. It also lacks the sagittal keel found on the carapace of representatives of the plesiochelyid *Tropidemys* Rüttimeyer, 1873. The presence of a continuous neural series contrasts with the condition in some members of *Eurysternidae* (e.g. *Idiochelys fitzingeri* Meyer, 1839b) and in some individuals of *Hylaeochelys* and *Plesiochelyidae*. The significantly longer than wide first neural of OUMNH J.66966 differs from the neural morphology usually observed in *Eurysternidae*, and from that of *Enaliochelys chelonia*. OUMNH J.66966 lacks anterior and middle neurals as wide as those of *Tropidemys langii* Rüttimeyer, 1873 and *Tropidemys seebachi* Portis, 1878. The absence of a sutured contact between the costal and the peripheral plates is not shared

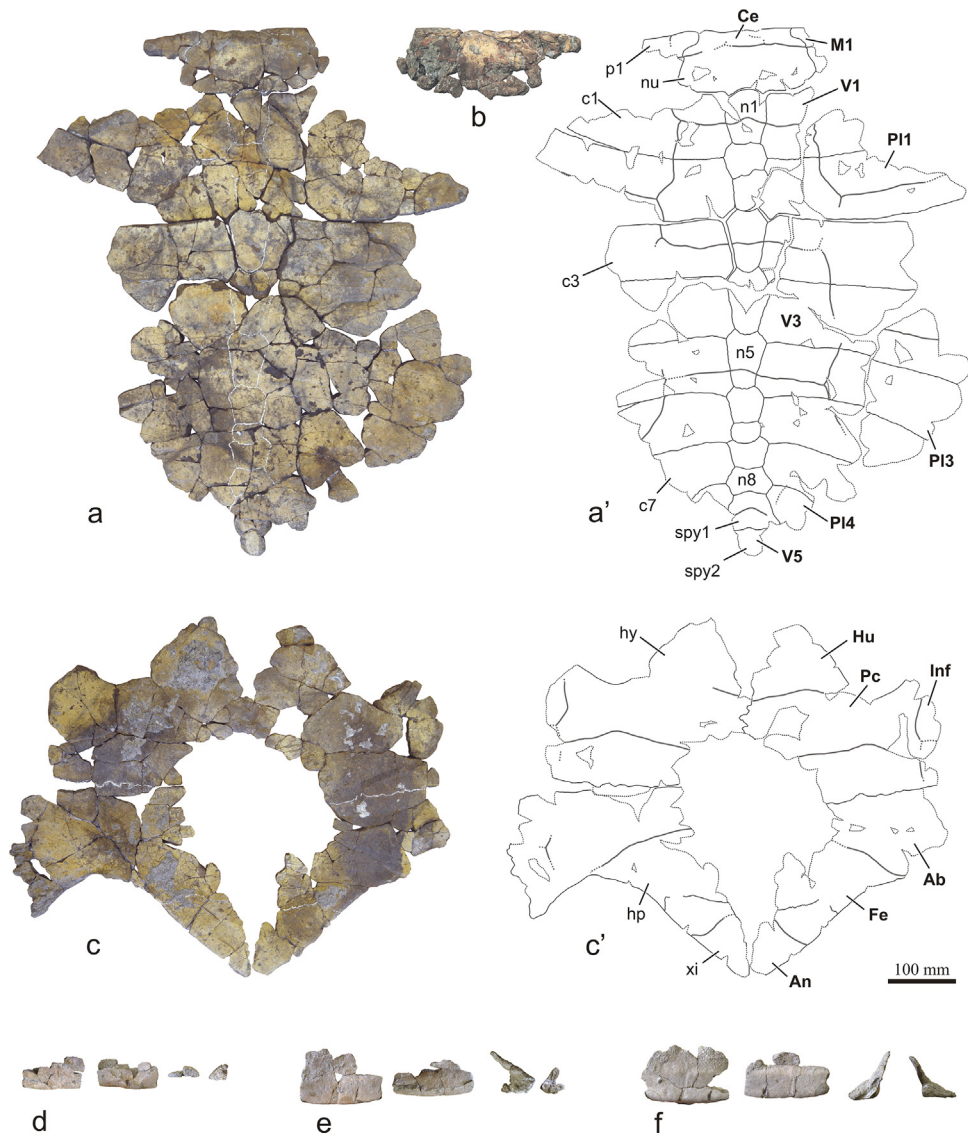
with the adult specimens of *Plesiochelyidae*, at least some representatives of *Eurysternidae*, and *Hylaeochelys*. However, the wider fontanelles of *Enaliochelys chelonia* are not present in OUMNH J.66966. In fact, well-developed free regions of the dorsal ribs, corresponding to more than three-quarters of the width of the last pair of costals, is exclusive to *Enaliochelys chelonia*.

The interpreted single cervical scute differs from the condition in *Plesiochelyidae* and in some *eurysternids* (e.g. *Eurysternum wagleri* Meyer, 1839a and *Palaeomedusa testa* Meyer, 1860), where it is divided into three scutes, and from *Jurassichelon oleronensis*, which lacks a cervical, the first vertebral scute being in contact with the anterior edge of the carapace. The vertebral scutes of OUMNH J.66966 are significantly narrower than those of some members of *Eurysternidae* (e.g. *Eurysternum wagleri*), *Hylaeochelys*, and *Enaliochelys chelonia*.

Lateral plastral fontanelles are identified in *Thalassemys* and in *Eurysternidae*. The adult specimens of all the compared taxa, except some specimens of *Plesiochelyidae*, some *eurysternids* (e.g. *Idiochelys fitzingeri*), and some specimens of *Hylaeochelys* have a central plastral fontanelle. A xiphiplastral fontanelle has been exclusively identified in *Thalassemys*, but this structure may also be present in the *eurysternid* *Eurysternum wagleri* (see Anquetin and Joyce, 2014). The absence of sutural connections of the epiplastra and entoplastron with the hyoplastra is shared with *Thalassemys*, the *eurysternids*, "*Thalassemys*" *moseri*, and *Jurassichelon oleronensis*.

Therefore, all the characters discussed are shared exclusively with *Thalassemys*, allowing the assignment of specimen OUMNH J.66966 to this genus. In addition, linear striations perpendicular to sutures between the shell elements have recently been identified as exclusive to the genus *Thalassemys* (Anquetin et al., 2014). Anquetin et al. (2014) also indicated that *Thalassemys* differs from some European Late Jurassic basal eucryptodirans (e.g. *Plesiochelys* Rüttimeyer, 1873, *Craspedochelys* Rüttimeyer, 1873,





**Fig. 3.** (Color online.) Most of the preserved elements of shell OUMNH J.66966, a specimen of *Thalassemys hugii* from the Kimmeridge Clay Formation of Abingdon (Oxfordshire, England): a, carapace, in dorsal view; b, nuchal, in ventral view; c, plastron, in ventral view; d–f, three disjunct peripheral plates, in dorsal, ventral, and lateral views. The narrow black lines represent plate margins, and the wide grey lines correspond to the scute sulci. Abbreviations: c, costal plate; hy, hyoplastron; hp, hypoplastron; n, neural plate; nu, nuchal plate; spy, suprapylal plate; xi, xiphiplastron; Ab, abdominal scute; An, anal scute; Ce, cervical scute; Fe, femoral scute; Hu, humeral scute; Inf, inframarginal scute; M, marginal scute; Pc, pectoral scute; Pl, pleural scute; V, vertebral scute.

**Fig. 3.** (Couleur en ligne.) La plupart des éléments conservés de la carapace de OUMNH J.66966, un spécimen de *Thalassemys hugii* de la formation Kimmeridge Clay d'Abingdon (Oxfordshire, Angleterre) : a, carapace, en vue dorsale ; b, nucal, en vue ventrale ; c, plastron, en vue ventrale ; d–f, trois plaques périphériques disjointes, en vues dorsale, ventrale et latérale. Les lignes noires fines représentent les limites de plaques, et les lignes grises larges les sillons des écailles. Abréviations : c, plaque costale ; hy, hyoplastron ; hp, hypoplastron ; n, plaque neurale ; nu, plaque nuchale ; spy, plaque suprapylale ; xi, xiphiplastron ; Ab, écaïlle abdominale ; An, écaïlle anale ; Ce, écaïlle cervicale ; Fe, écaïlle fémorale ; Hu, écaïlle humérale ; Inf, écaïlle inframarginale ; M, écaïlle marginale ; Pc, écaïlle pectorale ; Pl, écaïlle pleurale ; V, écaïlle vertébrale.

and *Tropidemys*) in the significant anterior widening of the first neural. The finding of new specimens sheds fresh light on this taxon's variability, revealing that the ratio between the width of the anterior and the posterior halves of that plate is subject to intraspecific variability. This ratio is significantly lower in *T. hugii* NMS 12 (see fig. 6 I–J in Anquetin et al., 2014), from the type locality and horizon, than in the lectotype (Fig. 2b). In fact, this ratio is consistent with that

observed in some specimens of the three aforementioned genera of Plesiochelyidae. In comparison, the Dorset *Thalassemys* specimen (NHMUK R8699) has a narrower first neural relative to its length (see Fig. 2a). Similar variations in the morphology of the first neural have also been reported in other European basal eucryptodirans (compare the four specimens of *Hylaeochelys belli* in Pérez-García, 2012, fig. 6A–D).

Anquetin et al. (2014) considered that *T. hugii* differs from *Thalassemys marina* in having narrower vertebral scutes, with anterolateral and posterolateral margins of equal length, and in smaller lateral plastral fontanelles. Great variability is identified here when the ratio between the length of the latero-anterior and the latero-posterior margins of the second pair of vertebral scutes is compared in the lectotype of *T. hugii* (about 1), the Dorset *Thalassemys* (about 1.5), the new British specimen of *Thalassemys* (about 2.1), and the holotype of *Thalassemys marina* (about 1.54). Therefore, this character is not considered here as valid to characterize different species of *Thalassemys*. Relatively narrow vertebral scutes are observed in all known specimens of *T. hugii* from its type locality, including juvenile and adult individuals. The vertebral scutes of OUMNH J.66966 are also narrow. However, those of NHMUK R8699 are wide, as in *Thalassemys marina*. As indicated, the plastron of NHMUK R8699 is not known. The only identified specimen with large lateral plastral fontanelles is the holotype and sole known specimen of *Thalassemys marina*. In fact, these fontanelles are narrow in both juvenile and adult specimens of *T. hugii*. Considering all the discussed characters, OUMNH J.66966 is attributed to *T. hugii*, representing the only member of this species known outside its type locality. NHMUK R8699 differs from adult specimens of *T. hugii* (including both the type specimen of this taxon and OUMNH J.66966) in the wider carapace fontanelles. As indicated, some differences between NHMUK R8699 and OUMNH J.66966 can be justified by individual variability (i.e. those corresponding to the ratio between the length of the latero-anterior and the latero-posterior margins of the vertebrals, the morphology of these scutes, the morphology of the first neural, and the ratio between the width and length of the neurals). The presence of wider vertebrals excludes NHMUK R8699 from *T. hugii*. This character is shared with *Thalassemys marina*. The angle between the scapular and acromion processes is about 101° in the Dorset specimen but about 118° in the *T. hugii* lectotype. This character is not known in *Thalassemys marina*. Therefore, NHMUK R8699 is identified here as belonging to an indeterminate representative of *Thalassemys*, which differs from the Kimmeridgian *T. hugii*. The coexistence of two species of *Thalassemys* in the same formation (i.e. the Kimmeridge Clay Formation) is proposed here.

#### 4. Conclusions

A turtle specimen from the Kimmeridgian of Abingdon (Oxfordshire, England) is studied here. Specimen OUMNH J.66966 is assigned to the European Late Jurassic basal member of Eucryptodira *Thalassemys*. The new specimen has been compared with all known specimens of the genus *Thalassemys*, recognizing several characters subject to intraspecific variability. OUMNH J.66966 is identified as a member of *T. hugii*, a species so far only recognized in its type locality (the Kimmeridgian of Solothurn, Switzerland). However, a second species of *Thalassemys* is also recognized in the British record. Both species are identified from specimens from the Kimmeridge Clay Formation. Therefore, the coexistence of two species of *Thalassemys* in the same formation, and in the same country, is recognized

here for the first time. In fact, as this paper clarifies, only one species of *Thalassemys* had hitherto been recognized in the Kimmeridgian record.

The identification of *T. hugii* outside its type locality, and also outside Central Europe, shows that this coastal turtle had a relatively large paleobiogeographical distribution. *Thalassemys* was recognized as the largest basal eucryptodiran turtle (sensu Joyce, 2007) recorded in its type locality (Solothurn). The new British specimen demonstrates that this species can be larger than so far identified. In fact, OUMNH J.66966 is not only identified as the largest known basal eucryptodiran shell in the Late Jurassic of Europe, but is also recognized as the largest known member of this clade worldwide.

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