Reinterpretation of the Spanish Late Jurassic "*Hispaniachelys prebetica*" as an indeterminate plesiochelyid turtle

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A partial postcranial skeleton (carapace, plastron, and other poorly preserved elements) of a turtle, from the late Oxfordian of the Betic Range of Spain, has recently been assigned to a new taxon, *Hispaniachelys prebetica*. This is one of the few European turtle taxa reported from pre-Kimmeridgian levels, and the oldest turtle so far known from southern Europe. The character combination identified in that taxon (including the presence of cleithra, and single cervical scale) did not allow its assignment to Plesiochelyidae, a group of turtles very abundant and diverse in the Late Jurassic of Europe. The revision of the single specimen assigned to this taxon led to the reinterpretation of some of its elements, being reassigned to Plesiochelyidae. This study confirms the presence of Plesiochelyidae in the Oxfordian. However, because the Spanish taxon does not present a unique combination of characters, it is proposed as a nomen dubium.

Key words: Testudines, Plesiochelyidae, *Hispaniachelys prebetica*, Oxfordian, Jurassic, Spain.

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Introduction

The discovery of postcranial elements of a turtle from the Upper Oxfordian of the Prebetic area of the Betic Range (Southern Spain) has been recently reported (Slater et al. 2009, 2011). This finding is of particular interest since the European pre-Kimmeridgian material of turtles is scarce (Lapparent de Broin 2001; Anquetin and Claude 2008; Anquetin et al. 2008). In addition, that specimen (RGCHSP-62-52) is the oldest turtle so far known from southern Europe (Slater et al. 2011). A new genus and species, *Hispaniachelys prebetica* Slater, Reolid, Schouten, and Benton, 2011 was erected on the basis of this material, diagnosed by a unique combination of characters. Its phylogenetic position was considered hard to resolve, being interpreted as either a paracryptodire or a basal testudine, a priori excluding its assignment to Plesiochelyidae, a family very abundant in the Late Jurassic of Europe. The study of some elements that had not been previously analysed (e.g., the right epiplastron); the reinterpretation of some characters, and new insights into the morphology of some elements hitherto poorly described in the traditional basal members of Eucryptodira from the European record allows to reconsider the taxonomy and phylogenetic position of "*Hispaniachelys prebetica*". It is proposed that it is a nomen dubium, the holotype being reassigned to Plesiochelyidae.

Review of the anatomy and diagnosis of "*Hispaniachelys prebetica*"

The new study of RGCHSP-62-52 (Fig. 1), holotype and only specimen assigned to "*Hispaniachelys prebetica*", allows reinterpretation of some of the characters used to diagnose this taxon. This specimen preserves an epiplastron, on the right (Fig. 1C–E). This plate has not been described so far. The rear edge of this plate is subperpendicular to the axial plane. This morphology contrasts with the interpretation proposed by Slater et al. (2011: fig. 3B), corresponding to the reconstruction of the ventral view of the plastron. The visceral view of this element (Fig. 1D, E) shows that, contrary to the previous interpretation, this taxon lacked dorsal epiplastral processes (cleithra) and instead the structure in

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question is probably a result of the aberrant morphology of the lateral margin of the right hyoplastron. The presence of this element motivated Slater et al. (2011) to exclude assignment of RGCHSP-62-52 to Plesiochelyidae, a family that traditionally includes several genera from the Late Jurassic of Europe: *Craspedochelys* Rütimeyer, 1873, *Plesiochelys* Rütimeyer, 1873, *Portlandemys* Gaffney, 1975a, *Tholemys* Andrews, 1921, and *Tropidemys* Rütimeyer, 1873 (Lapparent de Broin 2001; Lapparent de Broin et al. 1996).

As indicated by Slater et al. (2011), the nuchal plate is almost complete but poorly preserved as its dorsal surface is heavily weathered and obscured by erosional pits, especially in its anterior half (Fig. 1B). Therefore, the hypothesis proposed by Slater et al. (2011) about the presence of a single cervical scale cannot be confirmed. It cannot be excluded that this specimen shares with the members of Plesiochelyidae the presence of three cervicals.

The review of the plastral elements of RGCHSP-62-52 reveals new information regarding the morphology of several scales (Fig. 1C$_2$). Although the presence of short pectoral scales was considered in the diagnosis of "*Hispaniachelys prebetica*", the preserved elements of the plastron show that medially, this pair of scales was probably longer than the pair of abdominals (Fig. 1C). The presence of a partially sinusoidal humero-pectoral sulcus is refuted; it is subperpendicular to the axial plane, slightly convex medially.

Other characters present in RGCHSP-62-52, which were not part of the diagnosis of "*Hispaniachelys prebetica*", but which had been described and incorporated in the reconstruction of that taxon (Slater et al. 2011: fig. 3), are also reinterpreted here. As indicated by Slater et al. (2011), the internal morphology of the bridge peripherals is often not described and figured in extinct turtles. This lack of information generated an erroneous interpretation of the arrangement of the disarticulated bridge peripherals of RGCHSP-62-52. Thus, the groove on the contact of the peripherals and the distal region of the dorsal ribs was provisionally interpreted as the sutural surface of the carapace and plastron. Therefore the dorsal region of these peripheral plates was interpreted as the ventral region (Slater et al. 2011: fig. 4). This also led to an erroneous interpretation of the position of these elements in the peripheral ring: the plate identified as the sixth right peripheral (Slater et al. 2011: fig. 4F, H, L) is interpreted here as the seventh right peripheral (Fig. 1I–M) and has a fully consistent morphology with the corresponding element on the left side (Fig. 1F–H). Similarly, the fifth or sixth right peripheral (Fig. 1N–P) was identified as the fourth right peripheral (Slater et al. 2011: fig. 4E, G, K). Slater et al. (2011) interpreted a unique morphology of the inframarginal scales due to the problems in the orientation of these plates (Slater et al. 2011: figs. 3B, 4K, L). However, the limited information available on these scales (Fig. 1C, G, H, J, K, N) is compatible with that of members of Plesiochelyidae, which possess a complete series of inframarginal scales, all of them with a similar width, situated from the axillary to the inguinal notch, and therefore completely blocking any contact between the carapacial and plastral scales (Joyce 2007).

Phylogenetic position of "*Hispaniachelys prebetica*"

Slater et al. (2011) explored the systematic position of RGCHSP-62-52 using a modified version of the data matrix of Joyce (2007) as proposed by Anquetin et al. (2008). The revision of the specimen RGCHSP-62-52 performed here allows emendation of some of the character coding (see Appendix 1). Because RGCHSP-62-52 corresponds to a partial postcranial skeleton, it is coded for only 43 of the 139 characters of this matrix. This new phylogenetic analysis has been conducted using TNT v. 1.0 (Goloboff et al. 2008), the hypothetical ancestor being the outgroup, and the three "rogue" taxa indicated by Joyce (2007) being excluded: *Portlandemys mcdowelli* Gaffney, 1975a, *Sandownia harrisi* Meylan, Moody, Walther, and Chapman, 2000, and *Mongolemys elegans* Khozatsky and Młynarski, 1971. This analysis has been performed using a traditional search, in which, as Slater et al. (2011) did, a tree-bisection algorithm, with 5000 replicates, was applied. All characters were considered unordered.

The phylogenetic analysis resulted in 37,501 most parsimonious trees of 370 steps (consistency index = 0.466; retention index = 0.811; rescaled consistency index = 0.378) (Fig. 2). The resulting strict consensus topology basically coincides with that proposed by Slater et al. (2011), RGCHSP-62-52 being obtained in a polytomy composed of 30 branches, corresponding to some taxa identified in other papers as members of the stem group of Testudines and the representatives of the crown group (see Joyce 2007; Anquetin 2008, 2012; Sterli and de la Fuente 2011; Pérez-García et al. 2014). However, although the majority-rule tree obtained by Slater et al. (2011) placed RGCHSP-62-52 as a member of Paracryptodira, associated with the baenid clade, the majority-rule tree obtained here does not include RGCHSP-62-52 between the representatives of Paracryptodira, from which it differs, among other characters, by the absence of mesoplastra (this character being one of the characters that diagnosed the node Paracryptodira in the majority-rule tree, and also the nodes Baenidae and Pleurosternidae in the strict consensus tree). In this tree, RGCHSP-62-52 is located in a basal polytomy of Testudines, where the other members of Plesiochelyidae included in this analysis are also situated ("*Thalassemys*" *moseri* Bräm, 1965 and *Plesiochelys solodurensis* Rütimeyer, 1873).

RGCHSP-62-52 does not have autapomorphies in this analysis. In fact, the 43 characters coded for this taxon are compatible with those coded for the two members of Plesiochelyidae included in this analysis (both taxa including not only information on the postcranial skeleton, but also on the skull).

The poor resolution of phylogenetic relationships among the members of the stem group of Cryptodira, and between Pancryptodira and Panpleurodira, offers an incomplete resolution of several of the major clades (see Joyce 2007; Anquetin 2008, 2012; Sterli and de la Fuente 2011). In this sense, the phylogenetic relationships among the representatives of

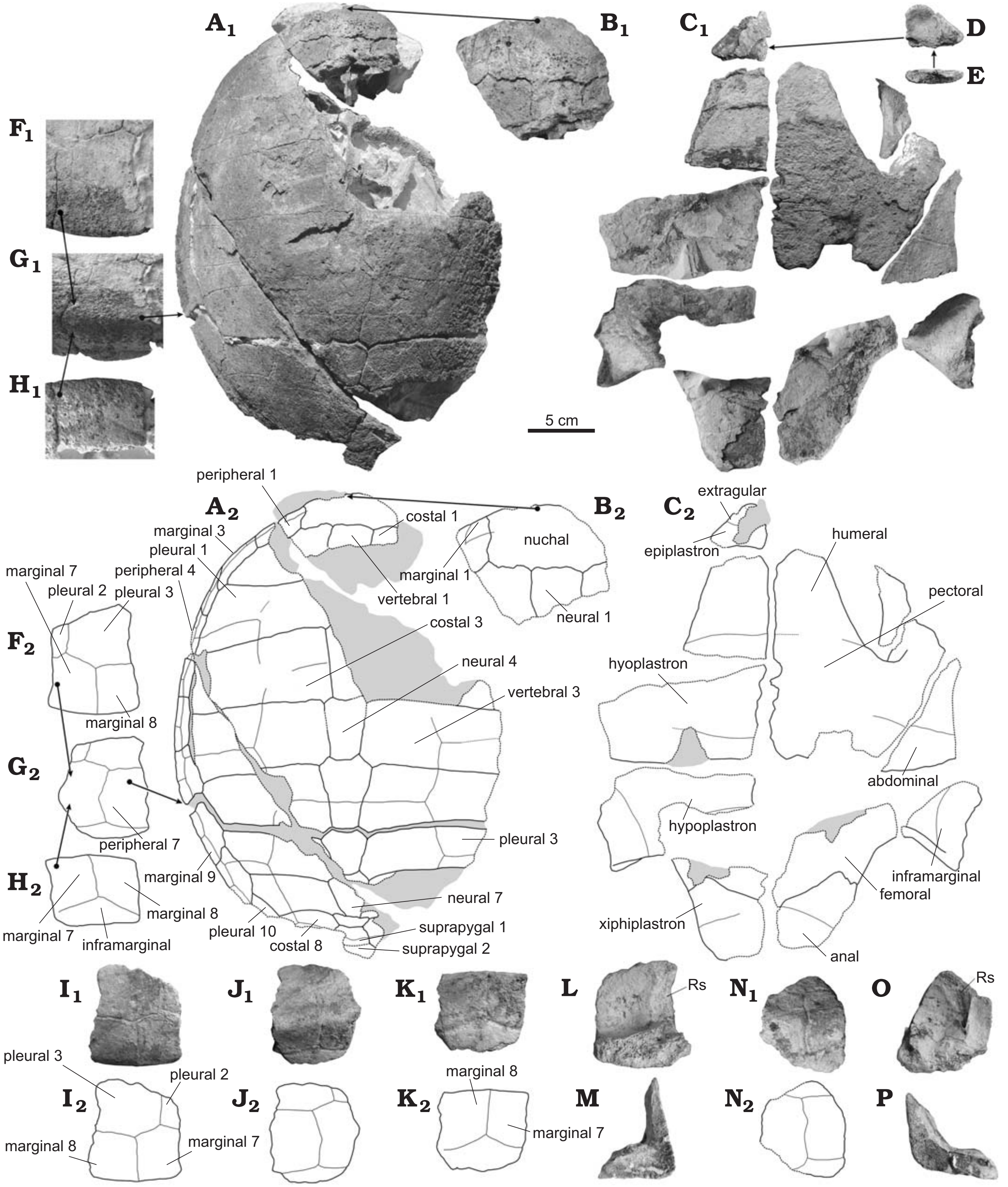

Fig. 1. RGCHSP-62-52, shell of the holotype of "*Hispaniachelys prebetica*" from late Oxfordian of the Betic Range of Spain, interpreted as plesiochelyid turtle herein. Carapace in dorsal view (**A**); most-anterior region of the carapace in dorsal view (**B**); plastron in ventral view (**C**); right epiplastron in dorsal (**D**) and posterior (**E**) views; seventh left peripheral in dorso-lateral (**F**), latero-ventral (**G**), and ventral (**H**) views; seventh right peripheral in dorso-lateral (**I**), latero-ventral (**J**), ventral (**K**), medial (**L**), and posterior (**M**) views; fifth or sixth right peripheral in latero-ventral (**N**), medial (**O**), and anterior (**P**) views. Photographs (A_1–C_1, F_1–K_1, N_1) and explanatory drawings (A_2–C_2, F_2–K_2, N_2). Rs, groove generated by the distal region of the dorsal ribs on the visceral surface of the peripherals.

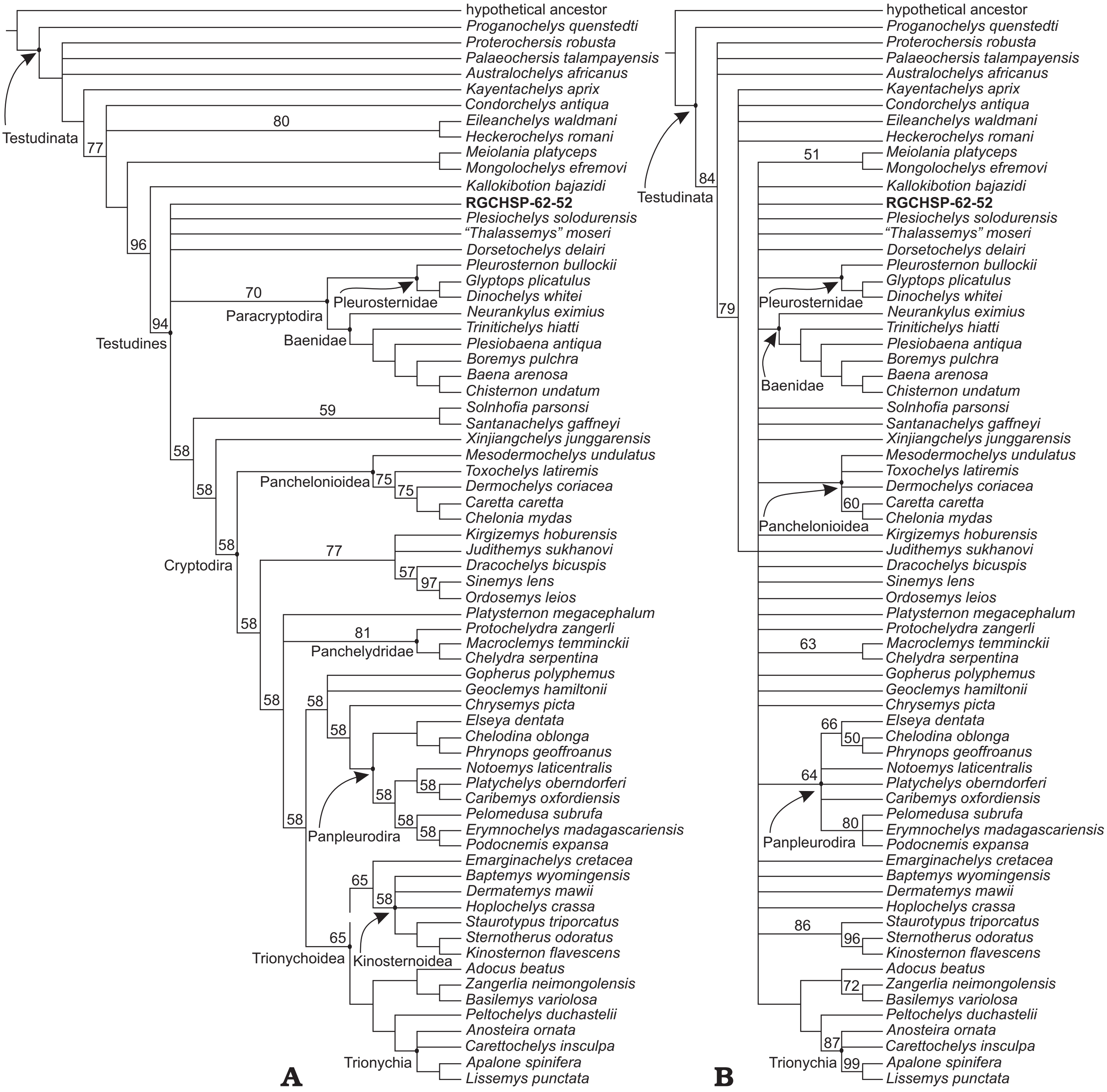

Fig. 2. Hypothesized phylogenetic position of the specimen RGCHSP-62-52, holotype of "*Hispaniachelys prebetica*" from late Oxfordian of the Betic Range of Spain, based on the modified data set of Joyce (2007) as proposed by Anquetin et al. (2008). **A**. Majority rule tree. Values are percentages under 100% obtained in this analysis. **B**. Strict consensus tree with bootstrap values (1000 replicates, only values over 50% shown).

Plesiochelyidae, and between them and other nodes, are currently poorly understood. This was, in part, due to the limited information about the members of Plesiochelyidae so far considered in global phylogenetic analyses.

There are other global analyses of turtle relationships where information about Plesiochelyidae is combined into a single terminal taxon, called Plesiochelyidae. RGCHSP-62-52 is included here in two of them, those proposed by Hirayama et al. (2000) and by Gaffney et al. (2007) (see Appendix 1). These two analyses were also processed with TNT v. 1.0, using a traditional search in which a tree-bisection algorithm, with 5.000 replicates, is applied. All characters are considered unordered and equally weighted. Some previously not processed characters are coded for the taxon *Hylaeochelys* Lydekker, 1889 in the first of these two analyses: character 67 (inframarginals) as 0 (four or three pairs present), character 70 (epiplastron) as 0 (moderately broad), character 71 (epiplastra subdivided by entoplastron) as 1 (no). In addition, the character 68 (femoral-anal sulcus reaching hypoplastron) of Plesiochelyidae is recoded as 0 and 1 (no and yes). Character

109 (pectoral scale) of Plesiochelyidae is coded as 0 (not on epiplastron), and character 110 (femoral-anal sulcus) of the same taxon is recoded as 0 and 1 (not reaching hypoplastron and reaching hypoplastron) in the second analysis. Both the coding of the 16 characters of RGCHSP-62-52 processed in the analysis of Hirayama et al. (2000) (data matrix consisting of 76 characters), and the 21 characters processed in the analysis of Gaffney et al. (2007) (data matrix consisting of 111 characters) coincide with the states of those characters present in Plesiochelyidae, differing from the coding of the members of other nodes. The strict consensus tree obtained from the first of these analyses generates a polytomy in which RGCHSP-62-52, Plesiochelyidae, *Hylaeochelys*, and a node which includes the remaining members of Eucryptodira (sensu Joyce et al. 2004) are located (Fig. 3A). These taxa are grouped by several apomorphies, one of them observed in the preserved material of RGCHSP-62-52: the absence of mesoplastra (character 74). The coding of the characters of RGCHSP-62-52 differs from that of *Hylaeochelys* due to the absence of vertebral scales much broader than costal scales (character 59) and the presence of a femoro-anal sulcus reaching the hypoplastron (character 68). The node that groups the other representatives of Eucryptodira is diagnosed by several character states, only one of them corresponding to the elements preserved in RGCHSP-62-52: plastral buttresses reaching only peripherals (character 66). In the second analysis, RGCHSP-62-52, Plesiochelyidae and *Solnhofia* Gaffney, 1975b (a member of Eurysternidae, another group of basal eucryptodires, also exclusive of the European Upper Jurassic record) are grouped in a node diagnosed by several characters corresponding to elements not preserved in the specimen analysed here (Fig. 3A). The node grouping RGCHSP-62-52 and Plesiochelyidae is diagnosed by the presence of sutured carapace-plastron attachment (character 96) and plastral buttresses reaching the costals (character 97).

Therefore, all the relatively limited character states of RGCHSP-62-52 codified in all the analyses are the same as those encoded to both Plesiochelyidae (in the analyses in which Plesiochelyidae is encoded as a single taxon) and all the coded representatives of Plesiochelyidae: *Plesiochelys solodurensis* and "*Thalassemys*" *moseri*. In fact, the characters available in RGCHSP-62-52 (both those considered in the cladistic studies and those not included in these global analyses but incorporated in other more traditional systematic analyses) indicate several character states that constitute a unique combination of the eucryptodire group Plesiochelyidae (sensu Lapparent de Broin et al. 1996): nuchal notch very small or absent; sub-trapezoidal morphology of the nuchal, in which the most-anterior region of their lateral margins generally changes its curvature, resulting in diverging margins; anterior peripherals shorter and wider than that of the members of Eurysternidae, with its anterior margin being more delayed than that of the nuchal; presence of at least two suprapygal plates; hexagonal vertebrals, no much broader than pleural scales; absence of overlapping of the marginal scales onto the costal plates; absence of fontanelles in the car-

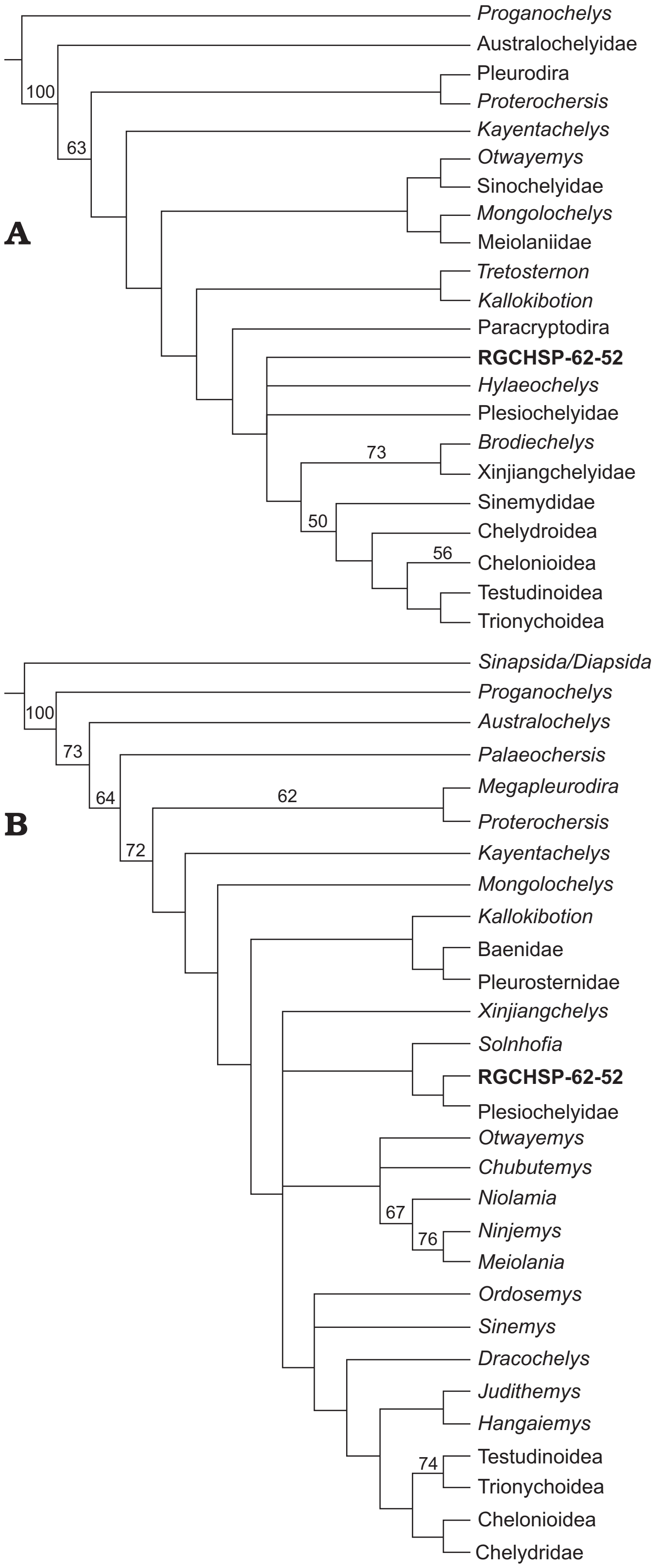

Fig. 3. Strict consensus trees showing the hypothesized phylogenetic positions of the specimen RGCHSP-62-52, holotype of "*Hispaniachelys prebetica*", based on the data set of: **A**, Hirayama et al. (2000) (trees retained: 2, tree length: 133, CI: 0.624, RI: 0.745); **B**, Gaffney et al. (2007) (trees retained: 2, tree length: 225, CI: 0.569, RI: 0.744). Bootstrap values (1000 replicates) over 50% are shown.

apace; more domed shell than in Eurysternidae and Thalassemydidae; sutured carapace-plastron attachment; buttresses of the hyoplastra and hypoplastra in contact with the costal series; absence of bridge fontanelles but presence of a central plastral fontanelle in many inferred adult individuals.

Taxonomy of "*Hispaniachelys prebetica*"

As indicated, the diagnosis of "*Hispaniachelys prebetica*" (sensu Slater et al. 2011) does not include autapomorphies. In fact, many taxa that could belong to Plesiochelyidae, determined by scarce material, and whose validity has not been assessed, have been described in the Late Jurassic of Europe (e.g., *Plesiochelys hannoverana* [Maack, 1869], "*Stylemys*" *lindenensis* Maack, 1869, "*Emys*" *dollfussi* Lennier, 1870, "*Chelonides*" *robusta* Portis, 1878, *Plesiochelys normandicus* Bergounioux, 1937). As previously indicated, the reinterpretation of some of these characters shows that RGCHSP-62-52 lacked epiplastral process, and the length of the pectoral scales and the morphology of the humero-pectoral groove were not different to those present in the members of Plesiochelyidae. Due to its preservation, the number of cervical scales is not known. The other characters present in RGCHSP-62-52 and included in the diagnosis of "*Hispaniachelys prebetica*" (see Slater et al. 2011) are shared with all the taxa traditionally attributed to Plesiochelyidae for which the shell is known (e.g., *Craspedochelys*, *Plesiochelys*, *Tholemys*, *Tropidemys*): the moderately large size of the shell, lacking fontanelles between the costal and peripheral plates; the morphology of the neural plates (not all being hexagonal, but the first one sub-rectangular and the others hexagonal, except the last one, whose morphology is irregular); the presence of eight neurals (number generally subject to intraspecific variability in basal eucryptodires, as noted, for example, by Lapparent de Broin et al. 1996 and Pérez-García 2012); the number of costals (not eight plates but eight pairs of plates); the sub-trapezoidal morphology of the nuchal (in which the most-anterior region of their lateral margins changes its curvature, resulting in diverging margins); the diamond shape of the entoplastron that does not separate the anterior portions of the epiplastra; the arrangement of the sulcus generated between the third and fourth vertebrals crossing the fifth neural; and the presence of anal scales confined to the xiphiplastra (actually in contact with the hypoplastra in RGCHSP-62-52). This last character may be subject to individual variability, in which these scales in different specimens are limited to the xiphiplastra, in contact with the most posterior region of the hypoplastra, or overlapping onto the hypoplastra (see examples of the three situations in *Craspedochelys jaccardi* (Pictet, 1860: pls. 1, 4.4, 3, respectively; Lapparent de Broin et al. 1996), and of the first and last in *Plesiochelys solodurensis* (Bräm 1965: pls. 5.2, 5.4, respectively). Since the taxonomic validity of "*Hispaniachelys prebetica*" cannot be supported by the characters described in the single specimen attributed to it, it cannot be either validated or synonymized with other plesiochelyid representatives, this taxon is here identified as a nomen dubium. Several characters observed in RGCHSP-62-52, but not taken into account in the diagnosis of "*Hispaniachelys prebetica*", are shared with several members of *Plesiochelys* (e.g., the overall shape of its shell, the absence of a sagittal keel, the width of the vertebral scales). Due to the limited information on the diagnosed characters of several genera and species of Plesiochelyidae, and to the scarce information available on RGCHSP-62-52, this specimen is considered here as an indeterminate member of Plesiochelyidae. Review of several members of this clade is needed to establish the phylogenetic position of this specimen.

The record of Plesiochelyidae, a group of coastal marine turtles, is abundant in the Kimmeridgian–Tithonian levels, having being recognized in several European countries (Lapparent de Broin 2001; Lapparent de Broin et al. 1996). In the Iberian Peninsula this clade has been identified both in the Kimmeridgian of Spain and Portugal (Antunes et al. 1988; Pérez-García et al. 2010), and in the Tithonian of both countries (Pérez-García et al. 2008; Pérez-García et al. 2013). The currently known Iberian record includes representatives of *Craspedochelys*, *Plesiochelys*, and *Tropidemys* (Antunes et al. 1988; Lapparent de Broin 2001; Pérez-García et al. 2008; Pérez-García et al. 2013). The abundance, diversity and relative wide distribution of this European clade during the Kimmeridgian and Tithonian (Britain, France, Switzerland, Germany, Portugal, Spain) means that the discovery of Plesiochelyidae in the upper Oxfordian of the Iberian Peninsula was expected.

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References

Andrews, C.A. 1921. On a new chelonian from the Kimmeridge Clay of Swindon. *Annals and Magazine of Natural History* 7: 145–153.

Anquetin, J. 2011. Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). *Journal of Systematic Palaeontology* 10: 3–45.

Anquetin, J. and Claude, J. 2008. Reassessment of the oldest British turtle:

Protochelys from the Middle Jurassic Stonesfield Slate of Stonesfield, Oxfordshire, UK. *Geodiversitas* 30: 331–344.

Anquetin, J., Barrett, P.M., Jones, M.E.H., Moore-Fay, S., and Evans, S.E. 2008. A new stem turtle from the Middle Jurassic of Scotland: new insights into the evolution and palaeoecology of basal turtles. *Proceedings of the Royal Society of London*, *Series B* 278: 879–886.

Antunes, M.T., Becquart, D., and Broin, F. de 1988. Découverte de "*Plesiochelys*", Chélonien marin-littoral, dans le Kimméridgien d'Alcobaça, Portugal. *Ciências da Terra* 3: 179–195.

Bergounioux, F.M. 1937. Chéloniens fossiles du Kimméridgien du Cap de la Hève. *Bulletin de la Société d'Histoire Naturelle de Toulouse* 71: 180–191.

Bräm, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Paläontologische Abhandlungen* 83: 1–190.

Gaffney, E.S. 1975a. A taxonomic revision of the Jurassic turtles *Portlandemys* and *Plesiochelys*. *American Museum Novitates* 2574: 1–19.

Gaffney, E.S. 1975b. *Solnhofia parsonsi*, a new cryptodiran turtle from the Late Jurassic of Europe. *American Museum Novitates* 2576: 1–25.

Gaffney, E.S., Rich, T.H., Vickers-Rich, P., Constantine, A., Vacca, R., and Kool, L. 2007. *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *American Museum Novitates* 3599: 1–35.

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Hirayama, R., Brinkman, D.B., and Danilov, I.G. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology* 7: 181–198.

Joyce, W.G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48: 3–102.

Joyce, W.G., Parham, J.F., and Gauthier, J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* 78: 989–1013.

Khosatzky, L.I. and Młynarski, M. 1971. Chelonians from the Upper Cretaceous of the Gobi Desert, Mongolia. *Paleontologica Polonica* 25: 131–144.

Lapparent de Broin, F. de 2001. The European turtle fauna from the Triassic to the present. *Dumerilia* 4 : 155–216.

Lapparent de Broin, F. de, Lange-Badré, B., and Dutrieux, M. 1996. Nouvelles découvertes de tortues dans le Jurassique Supérieur du Lot (France) et examen du taxon Plesiochelyidae. *Revue de Paléobiologie* 15: 533–570.

Lennier, G. 1870. *Etudes géologiques et paléontologiques sur l'embouchure de la Seine et les falaises de la Haute Normandie*. 245 pp. Eugene Costey, Le Havre.

Lydekker, R.A. 1889. On remains of Eocene and Mesozoic Chelonia and a tooth of (?) *Ornithopsis*. *Quarterly Journal of the Geological Society of London* 45: 227–246.

Maack, G.A. 1869. Die bis jetz bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. *Palaontographica* 18: 193–336.

Meylan, P.A., Moody, R.T.J., Walther, C.A., and Chapman, S.D. 2000. *Sandownia harrisi*, a highly derived trionychoid turtle (Testudines: Cryptodira) from the Early Cretaceous of the Isle of Wight, England. *Journal of Vertebrate Paleontology* 20: 522–532.

Pérez-García, A. 2012. High diversity of pancryptodiran turtles in the Lower Cretaceous of Europe. *Cretaceous Research* 36: 67–82.

Pérez-García, A., Gasulla, J.M., and Ortega, F. 2014. A new turtle species of *Brodiechelys* from the Early Cretaceous of Spain: Systematic and palaeobiogeographic implications. *Acta Palaeontologica Polonica* 59: 333–342.

Pérez-García, A., Murelaga, X., García-Ramos, J.C., Piñuela, L., and Ruiz-Omeñaca, J.I. 2010. Las tortugas del Kimmeridgiense (Jurásico Superior) de Asturias (España). *In*: J.I. Ruiz-Omeñaca, L. Piñuela, and J.C. García-Ramos (eds.), *Comunicaciones del V Congreso del Jurásico de España*, 192. Museo del Jurásico de Asturias, Asturias.

Pérez-García, A., Ortega, F., Murelaga, X., and Dantas, P. 2008. *Plesiochelys* sp. (Testudines; Eucryptodira) de la Fm. Freixial (Jurásico Superior) en Ulsa (Torres Vedras, Portugal. *Publicaciones del Seminario de Paleontología de Zaragoza* 8: 331–344.

Pérez-García, A., Scheyer, T.M., and Murelaga, X. 2013. The turtles from the uppermost Jurassic and Early Cretaceous of Galve (Iberian Range, Spain): anatomical, systematic, biostratigraphic and palaeobiogeographical implications. *Cretaceous Research* 44: 64–82.

Pictet, F.J. 1860. Description des fossiles. *In*: F.J. Pictet (ed.), *Matériaux pour la Paléontologie suisse, 3*, 15–88. Kessmann, J. and Georg, H., Geneva.

Portis, A. 1878. Ueber Fossile Schildkröten aus dem Kimmeridge von Hannover. *Palaeontographica* 25: 125–142.

Rütimeyer, L. 1873. Die fossilen Schildkröten von Solothurn. *Neue Denkschrift der Allgemeinen Schweizerischen Naturforschenden Gesellschaft* 25: 1–185.

Slater, B.J., Reolid, M., and Benton, M.J. 2009. Description, taphonomy and phylogenetic implications of a new Upper Jurassic Turtle (External Prebetic, southern Spain). *In*: P. Palmqvist and J.A. Pérez-Claros (eds.), *Comunicaciones de las XXV Jornadas de la Sociedad Española de Paleontología*, 329–332. Universidad de Málaga, Malaga.

Slater, B.J., Reolid, M., Schouten, R., and Benton, M.J. 2011. A new Late Jurassic turtle from Spain: Phylogenetic implications, taphonomy and palaeoecology. *Palaeontology* 54: 1393–1414.

Sterli, J. and de la Fuente, M.S. 2011. A new turtle from the La Colonia Formation (Campanian–Maastrichtian), Patagonia, Argentina, with remarks on the evolution of the vertebral column in turtles. *Palaeontology* 54: 63–78.

Appendix 1

Scored characters for the specimen RGCHSP-62-52 in the data matrices used here.

Data matrix of Joyce (2007) as proposed by Anquetin et al. (2008):

?????????? ?????????? ?????????? ?????????? ?????????? ?????????0 010010000? 2101010111 0001210000 0001000000 ?????????? ?????0???2 ?????????? ?????????0

Data matrix of Hirayama et al. (2000):

?????????? ?????????? ?????????? ?????????? ?????????? ??????1010 ?01?010110 1?110?

Data matrix of Gaffney et al. (2007):

?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???00??0?? ?????????? ???????00? ?1?2101120 0010??0001?