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A new turtle species of *Brodiechelys* from the Early Cretaceous of Spain: Systematic and palaeobiogeographic implications

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Brodiechelys brodiei is an Early Cretaceous turtle from Great Britain, the only species of the genus. This taxon has been shown in recent phylogenies to be closely related to Xinjiangchelyidae and therefore could be the only representative of this group in Europe. Here, we present several specimens from the Early Cretaceous Maestrazgo Basin, in the Iberian Range of Spain attributed to the British genus, and to a new species, *Brodiechelys royoi*. This discovery shows that, as previously observed with terrestrial turtles, some freshwater turtle taxa had a wide European distribution during the Early Cretaceous, being present in both Britain and the Iberian Peninsula. This study sheds new light on the phylogenetic position of this enigmatic genus, supporting its attribution to Xinjiangchelyidae, a clade whose presence has been previously confirmed exclusively from the Middle Jurassic to Early Cretaceous of Asia. We propose that another recently identified taxon from the Iberian Peninsula (i.e., *Larachelus morla*) is also a member of this clade. Recent studies have identified several continental taxa of the clade that included the members of “Macrobaenidae” and “Sinemydidae” in Europe. This study provides new evidence of close relationships between the Early Cretaceous turtle faunas from Europe and Asia.

Key words: Testudines, Pan-Cryptodira, Xinjiangchelyidae, *Brodiechelys*, Cretaceous, Europe, Spain.

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Introduction

Brodiechelys brodiei (Lydekker, 1889) is a eucryptodiran turtle currently known only from the Wealden of the United Kingdom. Available information on this taxon was, until now, very limited. However, ten shells from the type locality of Brighstone Bay (Isle of Wight, Wessex Sub-basin) were recently attributed to it (Pérez-García 2012a). *Brodiechelys* is also present in the area of Hastings (Sussex, Weald Sub-basin), where fragmentary and poorly preserved shells, corresponding to an indeterminate species, have also been identified. Study of these specimens of *Brodiechelys brodiei* indicated its intraspecific variability, and the identification of *Plesiochelys valdensis* Lydekker, 1889 and *Plesiochelys vectensis* Hooley, 1900 as junior synonyms of *Brodiechelys brodiei*. The comparison of these shells has led a new diag-

nosis for this taxon and evidence that it is a member of the stem group of Cryptodira (Pérez-García 2012a).

The Spanish Iberian Range records the highest European diversity of Early Cretaceous continental turtles, particularly in the Hauterivian–Aptian interval (Pérez-García and Murelaga 2012a). Members of Pan-Pleurodira (Dortokidae), stem Testudines (at least two solemydid taxa), Paracryptodira (Pleurosternidae), several lineages of crown cryptodires, but also unnamed stem cryptodires, have been identified there (Pérez-García et al. 2011). Stem cryptodires from Igea (La Rioja, eastern Cameros Basin) and Morella (Castellón, Morella Sub-basin, Maestrazgo Basin) cannot be assigned to any of the taxa so far identified on the Iberian Peninsula (Pérez-García et al. 2010). Some of these specimens have been identified as one or more taxa related to the British taxon *Brodiechelys brodiei*, but the assignment was preliminary

because of limited knowledge of the variability of this taxon (Pérez-García et al. 2011).

The recent review of *Brodiechelys brodiei* (Pérez-García 2012a) allows us to study the related Spanish material. We analyze here the specimens from the Morella Sub-basin (Fig. 1), and these are identified as belonging to a new species closely related to *Brodiechelys brodiei* and are therefore assigned to the genus *Brodiechelys*. Several characters that cannot be scored for the British material help to improve knowledge of this clade of turtles. The proposal of a new species of *Brodiechelys* means the diagnosis for this until now monospecific genus, as well as its two species, are revised. This new material provides valuable information on the palaeobiogeographic relationships of the Early Cretaceous European turtles.

Institutional abbreviations.—CMP, Collection of the Mas de la Parreta Quarry, housed in the Valltorta Museum, Tírig, Castellón, Spain; IWCMS, Isle of Wight County Museum, Sandown, UK; NHMUK, Natural History Museum, London, UK.

Systematic palaeontology

Testudines Batsch, 1788 sensu Joyce, Parham, and Gauthier, 2004

Pan-Cryptodira Joyce, Parham, and Gauthier, 2004

Xinjiangchelyidae Nessov in Kaznyshkin et al., 1990

Genus *Brodiechelys* Nopcsa, 1928

Type species: *Plesiochelys brodiei* Lydekker, 1889; Brighstone Bay, south-west coast of the Isle of Wight, UK; Vectis Formation (Barremian–early Aptian), Wealden Group, Wessex Sub-basin.

Emended diagnosis (modified after Pérez-García 2012a).—Pancryptodiran turtle sharing the following character combination: oval, longer than wide, and relatively low shell; dorsal surface of the vertebral and pleural scutes sculptured by grooves radiating forwards; nuchal trapezoidal, wider than long, with lateral margins convergent forward; 7–9 neural plates; first neural or first pair of neurals rectangular, the following plates hexagonal, and the last neural or pair of neurals subpentagonal to subcircular; medial contact of the seventh or seventh and eighth pairs of costals; two suprapyrgals, the length of both plates being similar; 11 pairs of peripherals; mediolaterally expanded posterior peripherals; short first dorsal rib; single cervical scute; first vertebral wider than long, trapezoidal, with lateral margins divergent forward; second to fifth vertebrae slightly wider than long; first vertebral slightly narrower than the second one, and decreasing in width from second to fifth vertebrae; first pleural scute overlapping the anterior peripheral plates; fifth marginals overlap the lateral margin of the second pair of costals; absence of costal-peripheral and plastral fontanelles; osseous connection between carapace and plastron; contact of both the axillary and inguinal buttresses exclusively with the peripheral

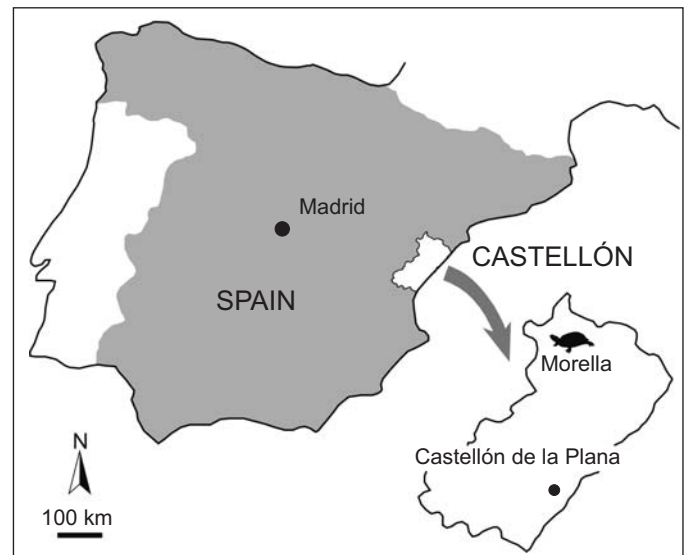


Fig. 1. Geographical location of Morella (Castellón, Spain), the type locality of *Brodiechelys royoi*.

series; posterior plastral lobe longer than the anterior one; distal region of the posterior lobe sub-perpendicular to the axial axis, lacking anal notch; entoplastron small, of similar length and width; contact between epiplastra and hyoplastra sub-perpendicular to the axial plane; hyoplastra longer than hypoplastra; absence of mesoplastra; postero-lateral expansion of the hypoplastra; undeveloped sinuosity in the medial sulcus of the plastron; presence of one pair of gular scutes, longer than the extragulars; gulars superimposed on the antero-medial region of the entoplastron; humeral-pectoral sulcus situated far behind the posterior margin on the entoplastron; four inframarginals; anal scutes medially overlapping the hypoplastra or near the posterior region of this pair of plates.

Geographic and stratigraphic range.—Early Cretaceous of Western Europe.

Brodiechelys brodiei (Lydekker, 1889)

1889 *Plesiochelys valdensis* Lydekker, 1889; Lydekker 1889: 239.

1900 *Plesiochelys vectensis* Hooley, 1900; Hooley 1900: 264–265.

1928 *Brodiechelys brodiei* (Lydekker, 1889); Nopcsa 1928: 50.

Holotype: NHMUK R2643, a partial shell.

Type locality: Brighstone Bay, south-west coast of the Isle of Wight, UK.

Type horizon: Vectis Formation (Barremian–early Aptian), Wealden Group, Wessex Sub-basin (Naish and Martill 2001).

Referred material.—Several shells from the type locality and horizon: NHMUK R6683 (holotype of *Plesiochelys vectensis* Hooley, 1900), NHMUK R11146, NHMUK R11147, NHMUK R11173–75, NHMUK 28967 (holotype of *Plesiochelys valdensis* Lydekker, 1889); IWCMS 2005.14, IWCMS 3868. IWCMS 1816 from a costal plate also from the Vectis Formation of the Isle of Wight, but found in Yaverland.

Emended diagnosis (modified after Pérez-García 2012a).—Species of *Brodiechelys* differing from *B. royoi* by the following autapomorphies: anterior margin of the carapace straight

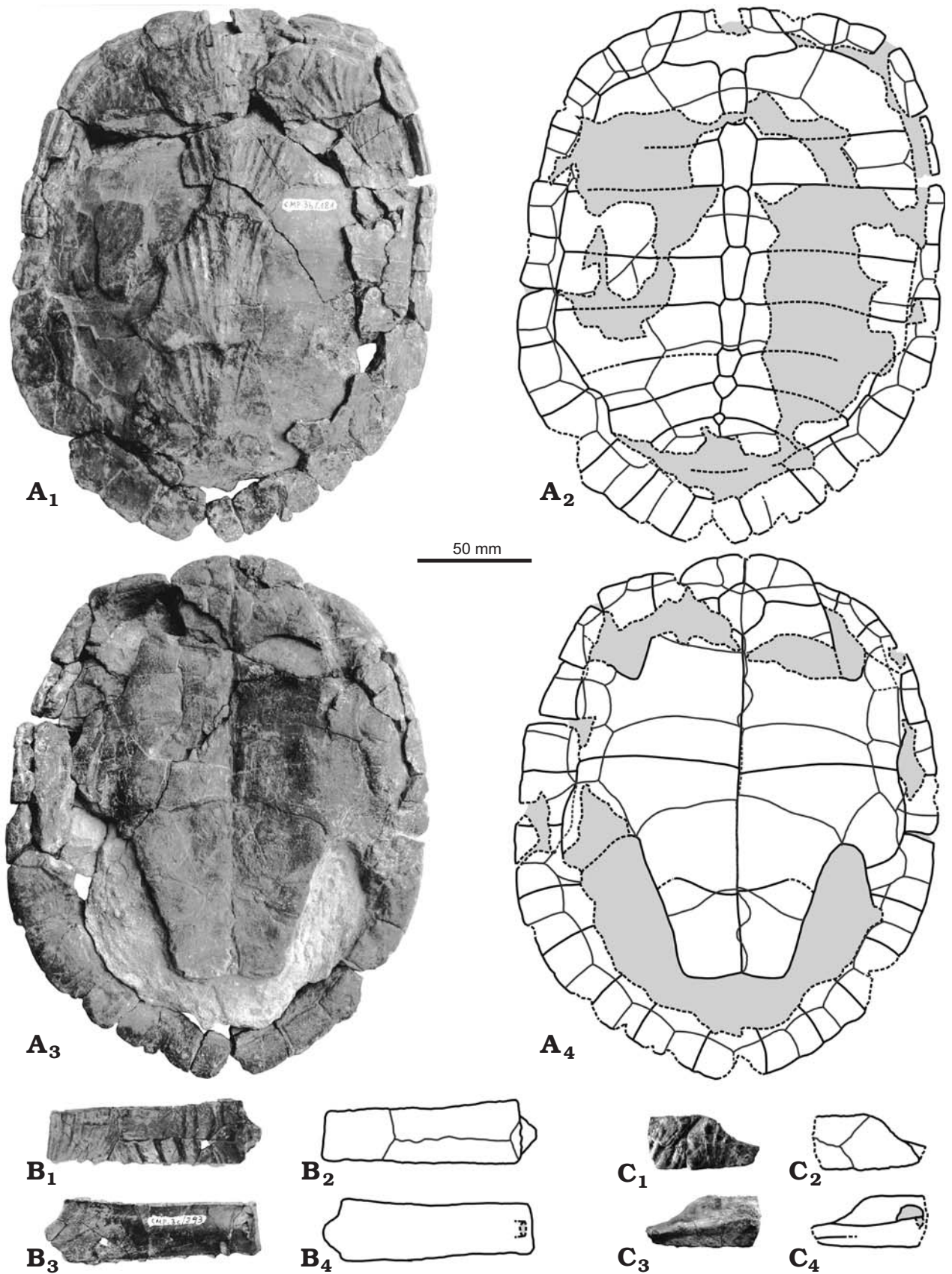


Fig. 2. Type specimens of *Brodiechelys royoi* sp. nov. from Morella (Castellón, Spain). **A.** CMP-3b/181, holotype, shell in dorsal (A₁, A₂) and ventral (A₃, A₄) views. **B.** CMP-3c/293, second right costal plate in dorsal (B₁, B₂) and ventral (B₃, B₄) views. **C.** CMP-3c/122, first right costal in dorsal (C₁, C₂) and ventral (C₃, C₄) views.

or slightly notched; slender and very numerous grooves on the vertebral and pleural scutes; length of the first pair of costal plates equal or slightly greater than that of second pair; absence of dorsal thickening on the lateral edges of the anterior peripherals; cervical scute more than four times wider than long; medially convex sulcus between third and fourth vertebrals, without a marked change of profile in the area of contact; first pleural scute overlapping the medial half of the first peripheral plates; fifth to seventh marginals slightly overlapping the lateral margins of the second to fourth costal plates; subrounded anterior plastral lobe; subrounded lateral margins of the posterior lobe.

Geographic and stratigraphic range.—Isle of Wight, UK; Vectis Formation (Barremian–early Aptian), Wealden Group, Wessex Sub-basin.

Brodiechelys royo sp. nov.

Fig. 2A–C.

Etymology: In honor of José Royo y Gómez (1895–1961), a Spanish palaeontologist closely linked to Morella, who promoted the development of Mesozoic vertebrate palaeontology in Spain, with special emphasis on the Early Cretaceous faunas, especially those from the Arcillas de Morella Formation.

Type material: Holotype: CMP-3b/181, an articulate and almost complete shell (Fig. 2A). Paratypes: CMP-3c/293, a second right costal plate (Fig. 2B); CMP-3c/122, a partial first right costal plate (Fig. 2C).

Type locality: Mas de la Parreta Quarry, Morella, Castellón, Morella Sub-basin, Maestrazgo Basin, Iberian Range, Spain (Fig. 1).

Type horizon: Arcillas de Morella Formation, Early Aptian (Gámez et al. 2003; Salas et al. 2003).

Material.—Type material only.

Diagnosis.—Species of *Brodiechelys* differing from *B. brodiei* by the following autapomorphies: convex anterior margin of the carapace, lacking cervical notch; broad, strong, and few in number grooves on the vertebral and pleural scutes; length of the first pair of costal plates twice that of the second pair; lateral edges of the anterior peripherals dorsally thickened, with a deep groove which runs along its dorsal surface; width of the cervical scute less than twice its length; medially concave sulcus between third and fourth vertebrals, with a marked change of profile in the area of contact; first pleural scute overlapping less than one third of the length of the second pair of peripheral plates; sixth and seventh marginals not overlapping the lateral margins of the costal plates; subtrapezoidal anterior plastral lobe; trapezoidal posterior lobe, with straight lateral margins.

Description.—The holotype of *Brodiechelys royo*, CMP-3b/181, has an oval and relatively low shell (Fig. 2A). The maximum length of its shell is 205 mm, its maximum width is 160 mm, and the maximum length of its plastron is 157 mm. This taxon lacks fontanelles, both in the carapace and in the plastron. Its anterior margin is not notched, but it is convex. The dorsal surface of the vertebral and pleural scutes is sculptured by strong grooves radiating forwards. Its nuchal plate is trapezoidal and wider than long and presents a rear

protrusion which contacts the first neural. This shell has eight neural plates. However, the last plate does not contact the seventh neural or the suprapyrgals due to a midline contact of the seventh costals. The longest neural is the second one. From this plate, the length of the neurals decreases backward. The first and third neurals are subrectangular. The second one is sub-octagonal. The fourth to the sixth are hexagonal. The first to sixth neurals are longer than wide. The seventh is pentagonal and as long as wide. The eighth is very small and rhombic. This specimen had two suprapyrgal plates, being identified at the boundary between them on the internal mould of it. The width of the first costal plate is less than twice its antero-posterior length. However, the length of this plate is twice that of the second costal. The first pair of peripherals is wider than long, the width of its anterior margin being twice that of the rear. The lateral edges of the anterior peripherals are dorsally thickened, and a deep groove runs along the dorsal surface of the first five pairs of peripherals. The rear peripherals are transversely expanded. The width of the cervical scute is less than twice its length. The first vertebral scute is trapezoidal, with the lateral margins markedly diverging forward. The second vertebral is the widest. The fourth and fifth vertebrals are narrower than the first. The second to fourth vertebral scutes are less than twice as wide as long. Although the sulcus that delimits the vertebral scutes I/II and II/III are convex, the sulcus located between the IV and V vertebrals is oriented perpendicular to the axial plane, and that which is situated between scutes III and IV is concave medially. This sulcus is located on the posterior region of the fifth neural plate. The first pleural scute overlaps less than one third of the length of the anterior pairs of peripherals. Only the medial end of the fifth pair of marginal slightly overlaps the costal series. The plastron-carapace connection is osseous. The plastral buttresses exclusively contact the peripheral series. The posterior lobe is slightly longer than the anterior. The anterior lobe is subtrapezoidal. Its curvature drastically changes on the epiplastra, in the region covered by the extragular scutes. The posterior lobe is trapezoidal, with straight margins. This taxon lacks mesoplastra and an anal notch. The entoplastron is small, diamond-shaped, and almost as wide as long. This plate is longer than the epiplastral symphysis. The hyoplastra are longer than the hypoplastra. The medial sulcus of the plastron is slightly sinuous between the pair of pectoral scutes and also between the pair of anals. The pair of gular scutes is superimposed on the antero-medial region of the entoplastron. The humeropectoral sulcus is situated far behind the posterior margin on the entoplastron. Medially, the pectorals and abdominal scutes have a similar length. Four pairs of inframarginals are present. The pectoroabdominal sulcus contacts the antero-medial region of the third pair. Medially, the anal scutes overlap minutely onto hypoplastra.

The isolated costal plates CMP-3c/293 and CMP-3c/122 are decorated by a strong ornamental pattern characterizing the holotype (Fig. 2B, C). In CMP-3c/293, identified as a second costal plate, the fifth marginal scute also overlaps onto

the middle of its lateral margin (Fig. 2B). In CMP-3c/122, identified as a first costal plate, the lateral margins of the first vertebral scute also diverge markedly forward (Fig. 2C). Although the most medial area of this plate is broken, it is observed that the first dorsal rib is short.

Discussion

Phylogenetic analyses.—To establish the phylogenetic position of the new Spanish taxon, two cladistic analyses were conducted. For the first, we used the modified version of the data matrix of Sterli and de la Fuente (2011) proposed by Pérez-García and Murelaga (2012b), in which all representatives of Pan-Pleurodira are excluded and several Asian and European eucryptodires are included (*Chengyuchelys baenoides* Young and Chow, 1953, *Tholemys passmorei* Andrews, 1921, *Plesiochelys planiceps* [Owen, 1842], *Brodiechelys brodiei*, *Hylaeochelys belli* [Mantell, 1844], *Chitracephalus dumonii* Dollo, 1885, and the Spanish *Larachelus morla* Pérez-García and Murelaga, 2012b; see Appendix 1). Moreover, another two taxa currently proposed as members of Xinjiangchelyidae (sensu Tong et al. 2012), are also included (using the character encoding proposed by Tong et al. 2011): *Protoxinjiangchelys salis* Tong, Danilov, Ye, Ouyang, and Peng, 2011 and *Xinjiangchelys tianshanensis* Nessov, 1995. The modifications in the processing of certain characters in *Pleurosternon bullockii* (Owen, 1842), *Dinochelys whitei* Gaffney, 1979, and *Glyptops plicatulus* Marsh, 1890 proposed by Pérez-García and Ortega (2011), and in *Peltochelys duchastelii* Dollo, 1885 proposed by Pérez-García (2011) have been included. The modification in the coding of character 82 (costal B) in *Xinjiangchelys latimarginalis* (Young and Chow, 1953) sensu Peng and Brinkman (1993) proposed by Tong et al. (2012) has been included.

The second phylogenetic analysis was conducted using the data matrix proposed by Tong et al. (2012). In addition to the inclusion of the new taxon, *Brodiechelys brodiei* and *Larachelus morla* are also incorporated (see Appendix 1).

The phylogenetic analyses were conducted using TNT v. 1.0 (Goloboff et al. 2008), with *Sphenodon punctatus* (Gray, 1842) as the outgroup for the first, and *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987 for the second. All characters were considered unordered and equally weighted.

Results and systematic implications.—The first phylogenetic analysis resulted in 94 most parsimonious trees of 420 steps (CI = 0.469, RI = 0.841) (Fig. 3A). The resulting majority rule tree topology basically coincides with that proposed by Pérez-García and Murelaga (2012b). *Santanachelys gaffneyi* Hirayama, 1998 and *Solnhofia parsonsi* Gaffney, 1975 are obtained as the two most basal taxa of Pan-Cryptodira. All other members of Pan-Cryptodira are grouped into two lineages in all trees obtained. The Asian *Siamochelys peninsularis* Tong, Buffetaut, and Suteethorn, 2002, *Chengyuchelys baenoides*,

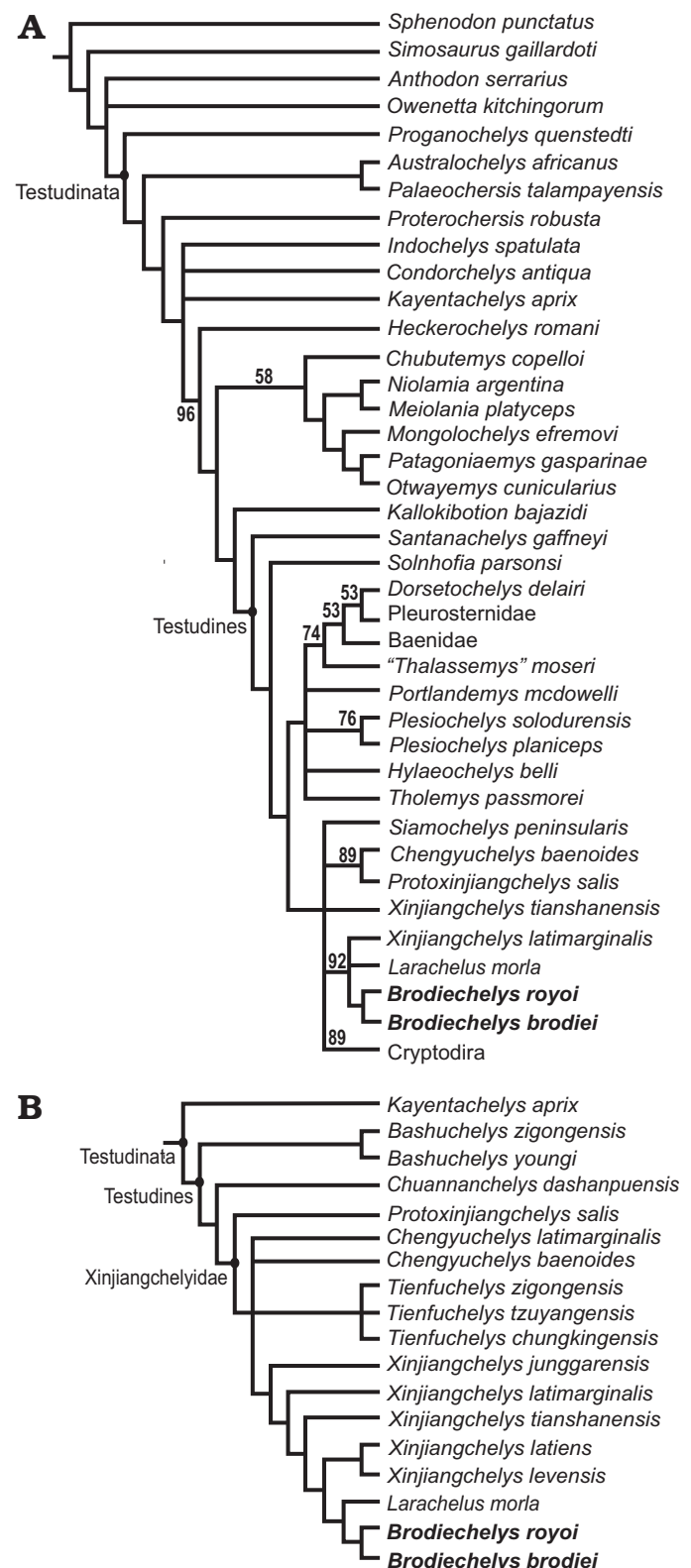


Fig. 3. Phylogenetic hypotheses of the new taxon *Brodiechelys royoi* based on the modified data set of Sterli and de la Fuente (2011) proposed here (A), and on the data matrix proposed by Tong et al. (2012) (B). Values refer percentages under 100% obtained in the majority rule analyses.

Protoxinjiangchelys salis, *Xinjiangchelys tianshanensis*, *Xinjiangchelys latimarginalis*, and the European *Brodiechelys*

brodiei, the new taxon from Morella, and the taxon from Salas de los Infantes (i.e., *Larachelus morla*) are obtained as members of the stem group of Cryptodira. This analysis could not establish the precise phylogenetic relationships among these taxa owing to limited information on several of them, in most cases including only characters of the shell. In fact, putative members of the same genus (e.g., *Xinjiangchelys tianshanensis* and *X. latimarginalis*) are not grouped in this analysis. The monophyletic group within Pan-Cryptodira comprising stem and crown-group Cryptodira is diagnosed by two synapomorphies: vertebrals II–IV as narrow as or narrower than pleurals (character 87); length of first dorsal rib intermediate to short, extends less than half-way across first costal (character 113). The European representatives of the stem group of Cryptodira and the Asian taxon *Xinjiangchelys latimarginalis* form a monophyletic group, diagnosed by the presence of a medial contact of the posterior costals (character 82). The node grouping *Brodiechelys brodiei* and *Brodiechelys royo* is diagnosed by the presence of an osseous connection between the carapace and the plastron (character 89).

The node that groups species of *Brodiechelys* with *Xinjiangchelys latimarginalis* is consistent with the hypothesis proposed by some authors that *Brodiechelys brodiei* belongs to the clade of freshwater turtles Xinjiangchelyidae, whose presence has been confirmed exclusively in the Middle Jurassic to Early Cretaceous of Asia (Hirayama et al. 2000; Tong et al. 2012). Information on many xinjiangchelyids is limited, so making it difficult to establish their relationships, and indeed the monophyly of this group has been questioned (Rabi et al. 2010). Recently, Tong et al. (2011) performed a global phylogenetic analysis, based on a modified version of the phylogenetic proposal of Joyce (2007), and this indicated a node of Testudines grouping *Bashuchelys* sp. (Tong et al. 2011) and *Chuannanchelys dashanpuensis* (Fang, 1987), taxa identified there as members of Bashuchelyidae, and this clade was identified as the sister group of *Protoxinjiangchelys salis*. The lineage grouping these three taxa was part of a polytomy with *Xinjiangchelys latimarginalis* and *X. tianshanensis*. Therefore, Xinjiangchelyidae in the traditional sense and Bashuchelyidae can therefore not be recognized as two non-overlapping monophyletic clades in that analysis. The global phylogenetic analysis performed by Anquetin (2012), also based on the matrix of Joyce (2007), generated a poorly supported clade identified as Xinjiangchelyidae, comprising *Siamochelys peninsularis*, *Xinjiangchelys qiguensis* Matzke, Maisch, Sun, Pfretzschner, and Stöhr, 2004, *X. tianshanensis*, *X. latimarginalis*, and *Annemys levensis* Sukhanov and Narmandakh, 2006 (taxon reassigned to *Xinjiangchelys levensis* by Tong et al. 2012). In order to better understand the relationships among the members of Bashuchelyidae and Xinjiangchelyidae, Tong et al. (2012) proposed a new data matrix with only 24 characters, all of them referring to the shell, and with *Kayentachelys aprix* as outgroup. They found a monophyletic Bashuchelyidae, comprising only the species *Bashuchelys youngi* Tong, Danilov, Ye, Ouyang, and Peng 2011 and *Bashuchelys zigongensis* (Ye, 1982), and this

was the sister group of the node grouping *Chuannanchelys dashanpuensis* and Xinjiangchelyidae. In addition to the members of *Protoxinjiangchelys* Tong, Danilov, Ye, Ouyang, and Peng, 2011, *Chengyuchelys* Young and Chow, 1953, *Tienfuchelys* Young and Chow, 1953, and *Xinjiangchelys* Ye, 1986. Tong et al. (2012) considered that Xinjiangchelyidae also contained another Asian taxon, *Yanduchelys* Peng, Ye, Gao, Shu, and Jiang 2005, and the European *Brodiechelys*, neither of them included in the analysis.

The new *Brodiechelys royo* allows characterization of some previously unknown characters of this genus (Pérez-García 2012a), which are shared with the Asian members of Xinjiangchelyidae: the first dorsal rib is short and both the axillary and inguinal buttresses contact exclusively with the peripheral series.

Tong et al. (2012) proposed a new diagnosis for Xinjiangchelyidae. *Brodiechelys brodiei* and *Brodiechelys royo* share with the exclusive combination of characters of Xinjiangchelyidae: shell height moderate to low domed (their character 1); first thoracic rib reduced (character 2); two or three suprapygals, being the last two suprapygals of similar width or the last one slightly wider (character 3); seventh to eleventh peripherals transversely expanded (character 5); pectoral and abdominal scutes similar in length or pectoral slightly longer (character 11); femoro-anal sulcus usually omega-shaped, reaching or extending onto the hypoplastron (character 12); three or four pairs of inframarginals (character 13). The node *Brodiechelys*, or at least one of its representatives, shows autapomorphies in other characters of the cited diagnosis. *B. royo* has anterior peripherals with prominent guttered edges (character 4). However, *B. brodiei* does not share this character state. The members of *Brodiechelys* share with the Asian representatives of Xinjiangchelyidae the overlapping of some marginals on the lateral region of the costal plates (character 6). Nevertheless, the number of marginals that overlap the costals is lower than in the Asian taxa, being the fifth to seventh marginals in *B. brodiei* but only the fifth in *B. royo*. The relationship between the size of the entoplastron and that of the epiplastra can be highly variable in the representatives of *Brodiechelys*, these two plates not always being similar in size (character 8). It is very different, for example, in the specimen of *B. brodiei* NHMUK R11173 (see Pérez-García 2012a: figs. 3F and 4F). Although in some *Brodiechelys* specimens, the entoplastron is quite large, in others it is very small (e.g., NHMUK R11173). Although this plate is longer than wide or as long as wide in some specimens, it also can be wider than long (e.g., NHMUK R6683; Pérez-García 2012a: figs. 3J and 4J) (character 9). The posterior sulcus of gulars and extragulars of *Brodiechelys* is not a straight line, and the pair of gulars is slightly (e.g., NHMUK R11146; Pérez-García 2012a: figs. 3K and 4K) or significantly (e.g., NHMUK R11174; Pérez-García 2012a: figs. 3G and 4G) overlapped onto the entoplastron (character 10). The midline sulcus of the plastron of some specimens is sinuous (character 14), but it is very little or not sinuous in others. It is slightly sinuous in some specimens of *B. brodiei* (e.g.,

NHMUK R6683, NHMUK R11146, and NHMUK R11147), but not in others (e.g., NHMUK R11173, NHMUK R11174). The presence of dorsal processes of the epiplastra (character 7) and musk ducts (character 15) has not been, until now, reported in this taxon.

The known material of *Larachelus morla* (see Pérez-García and Murelaga 2012b) also supports its assignment to Xinjiangchelyidae. However, it differs from the other members of this group in the presence of a single suprapygial plate, and in that, as in the case of the representatives of *Brodiechelys*, the pair of gular scutes is superimposed on the antero-medial region of the entoplastron.

We obtain three most parsimonious trees of 49 steps (CI = 0.531, RI = 0.803) as result of the inclusion of *Larachelus morla*, *Brodiechelys brodiei*, and *Brodiechelys royo* in the data matrix of Tong et al. (2012) (Fig. 3B). The resulting majority rule tree basically coincides with that proposed by Tong et al. 2012. The clade that groups *Chuannanchelys dashanpuensis* and the members of Xinjiangchelyidae is characterized by the following synapomorphies: epiplastra with long midline contact (character 12 of the data matrix proposed by Tong et al. 2012); posterolateral process of epiplastron (character 13); weak or absent overlapping of entoplastron by intergulars (character 16); diamond shape of the entoplastron (character 23). The Xinjiangchelyidae share the absence of mesoplastra (character 15). The node grouping the *Xinjiangchelys* species and the three European taxa is diagnosed by: absence of overlapping of the tenth peripheral by the fifth vertebral (character 10); ligamentous plastron/carapace connection (character 11); oval shape of the entoplastron (character 23). The three European taxa are grouped by the presence of: strong overlapping of entoplastron by intergulars (character 16); middle part of the humeropectoral sulcus anterior to the base of the anterior lobe (character 17); diamond shape of the entoplastron (character 23). *Brodiechelys brodiei* and *Brodiechelys royo* share a sutural plastron/carapace connection (character 11). *Brodiechelys brodiei* presents an autapomorphy in this analysis: straight sulcus between the third and fourth vertebrae (character 7).

Palaeobiogeographic implications.—The recent studies of *Brodiechelys brodiei* (Pérez-García 2012a) and some Spanish material (Pérez-García and Murelaga 2012b) support the presence of Xinjiangchelyidae outside Asia (Hirayama et al. 2000; Tong et al. 2012), and this is confirmed here with the new Spanish taxon.

Studies of Iberian Early Cretaceous sites, especially in the Arcillas de Morella Formation (Maestrazgo Basin), have revealed numerous terrestrial and freshwater reptile taxa with clear similarities with Hauterivian to Aptian Wealden facies from northwest Europe (Canudo et al. 1996; Escaso et al. 2005; Torcida Fernández-Baldor 2006; Pereda-Suberbiola et al. 2007; Sánchez-Hernández et al. 2007; Buscalioni et al. 2008; Gasulla et al. 2009, 2011; Mateus et al. 2011). Holtz et al. (2004) proposed that the Greater Wealden, comprising localities of the Lower Cretaceous of England and continental

Europe, as well as comparable faunas of southern and central Europe, western North America, and Africa, share a common composition of dinosaur faunas. In general, the Iberian Wealden faunas share most of their members with localities of the Wealden Supergroup and its equivalents in Belgium, England, France and Germany (Naish and Martill 2001; Weishampel et al. 2004). Some areas in southern England (Wessex Sub-basin of the Isle of Wight and Dorset, Weald Clay of West Sussex and Surrey) and Belgium (Bernissart, in the Mons Basin) seem to have the greatest similarity with the Arcillas de Morella Formation, especially in its dinosaur and crocodile faunas (Gasulla et al. 2009, 2011).

Several freshwater and terrestrial turtles from the Iberian Hauterivian–Aptian interval are shared or are closely related to taxa from the European Wealden areas.

The two aquatic turtles from Bernissart include one, *Peltochelys duchastelii*, that is unique to that locality, and *Chitrasephalus dumonii*, which has recently been identified in Spain (Pérez-García 2012b). This taxon is present in both the eastern Cameros Basin (Hauterivian–Barremian of Tenadas del Jabalí, Pinilla de los Moros Formation, Urbion Group) and in the western Cameros Basin (Barremian–Aptian of Torremuña, Enciso Group).

The English and Spanish records of turtles share members of Solemydidae (stem Testudines). A form closely related to the British taxon *Helochelydra nopcsai*, from the Wessex Formation of the Isle of Wight, is identified in Morella and in two locations of the Cameros Basin (Barbadillo del Mercado and Cabezón de la Sierra, Pantano de la Cuerda del Pozo Formation/Castrillo de la Reina Formation, Urbión Group) (Pérez-García et al. 2011). A second member of Solemydidae is identified in the Early Cretaceous (Aptian and Albian) of Gargallo and Cabezo de las Eras (Teruel, Maestrazgo Basin). It could be closely related to the British *Plastremys*, from the Upper Greensand of the Isle of Wight (Albian–?earliest Cenomanian) and in the Cambridge Greensand (Albian) of Cambridge (Joyce et al. 2011; Pérez-García et al. 2011). Solemydidae is interpreted as a terrestrial group of turtles (Laparent de Broin and Murelaga 1999; Scheyer et al. 2012).

No Early Cretaceous freshwater turtle genus shared between United Kingdom and the Iberian Peninsula had been so far identified. However, the freshwater *Brodiechelys*, from the Vectis Formation of the Isle of Wight (Barremian–early Aptian, Wealden Group, Wessex Sub-basin, Wessex-Weald Basin), and recognized in the Hasting Group of Hastings (Sussex) (Berriasian–Valanginian of the Weald Sub-basin, Wessex-Weald Basin), is identified herein for the Iberian record (Early Aptian of the Morella Sub-basin).

The monophyly of Xinjiangchelyidae (Anquetin 2012; Tong et al. 2012) is supported, and the presence of Xinjiangchelyidae outside Asia is confirmed here. The European taxa *Brodiechelys brodiei*, *B. royo*, and *Larachelus morla* are attributed to this clade. In addition, some poorly known European Early Cretaceous taxa, as well as new forms, have recently identified another freshwater clade also present in the synchronous Asian record. So, *Chitrasephalus dumonii* and

the recently described *Hoyasemys jimenezi* (Upper Barremian of Las Hoyas, Cuenca, Spain) and *Galvechelone lopezmartinezae* (Lower Barremian of Galve, Teruel, Spain), have been attributed to the clade comprising members of “Macrobaenidae” and “Sinemydidae” (Pérez-García et al. 2012; Pérez-García 2012b; Pérez-García and Murelaga 2012a).

Conclusions

Brodiechelys was a hitherto poorly known European taxon based on scarce material. New materials from the Early Cretaceous of the Iberian Range (Spain) indicate the presence of *Brodiechelys* outside the United Kingdom. We propose here that, as previously shown by terrestrial (e.g., dinosaurs) and freshwater reptiles (e.g., crocodiles), some groups of turtles also had a wide European distribution during the Early Cretaceous, including both terrestrial and freshwater representatives.

Brodiechelys royoii, *B. brodiei*, and *Larachelus morla* are here attributed to Xinjiangchelyidae, a group of freshwater turtles whose presence had been confirmed exclusively from the Middle Jurassic to the Early Cretaceous of Asia. Recent studies have shown that Pan-Cryptodira was a very diverse lineage of turtles in the Early Cretaceous of Europe. The identification of Early Cretaceous European Xinjiangchelyidae and members of the clade that groups “Macrobaenidae” and “Sinemydidae” indicates a close biogeographical relationship in the Early Cretaceous between freshwater turtles of Eastern and Western Eurasia.

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Appendix 1

Scored characters for the taxa included in the data matrix of Tong et al. (2012)

Brodiechelys brodiei: 1, 1; 2, 1; 3, 0; 4, 1; 5, 0; 6, 1; 7, 1; 8, 0; 9, 0; 10, 1; 11, 0; 12, 1; 14, 2; 15, 1; 16, [01]; 17, 0; 18, 1; 19, 1; 20, 1; 21, 0; 22, 1; 23, [12]; 24, [01].

Brodiechelys royo: 1, 1; 2, 1; 3, 0; 4, 1; 5, 0; 6, 1; 7, 0; 8, 0; 9, 0; 11, 0; 12, 1; 14, 2; 15, 1; 16, 0; 17, 0; 18, 1; 19, 1; 20, 1; 21, 0; 22, 1; 23, 1; 24, 1.

Larachelus morla: 2, 1; 4, 1; 6, 0; 7, 0; 8, 0; 10, 1; 11, 1; 12, 1; 14, 2; 15, 1; 16, 0; 17, 0; 18, 1; 19, 1; 20, 1; 21, 0; 22, 1; 23, 1.

Scored characters for the taxon included in the data matrix of Sterli and de la Fuente (2011)

Brodiechelys royo: 73, 0; 74, 0; 75, 1; 76, 1; 77, 0; 78, 0; 79, 1; 81, 0; 82, 1; 83, 0; 84, 0; 85, 2; 86, 1; 87, 1; 88, 1; 89, 0; 90, 0; 91, 0; 92, 1; 93, 1; 94, 1; 95, 0; 96, 0; 97, 0; 98, 0; 99, 2; 100, 0; 101, 0; 102, 0; 103, 0; 104, 0; 105, 0; 106, 0; 107, 0; 108, 1; 109, 0; 110, 0; 111, 0; 112, 0; 113, 1; 114, 0; 127, 2.