



A new European Albian turtle that extends the known stratigraphic range of the Pleurosternidae (Paracryptodira)

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ABSTRACT

Postcranial material corresponding to three specimens of freshwater turtles, from the lower Albian (upper Lower Cretaceous) of Ariño (Teruel Province, Spain), is analysed in this paper. This study allows us to identify the presence of Pleurosternidae (Paracryptodira) outside its known stratigraphic range, from Kimmeridgian to Barremian, and extends its distribution to the Albian. The species from Ariño represents a new taxon, *Toremys cassiopeia* gen. et sp. nov., which is the only pleurosternid described so far in post-Berriasian levels. *Toremys cassiopeia* is closely related to other taxa from Europe, to which the Cretaceous pleurosternids are restricted. Knowledge about the European freshwater turtle faunas distributed between the Barremian and the uppermost Cretaceous is very limited. The new finding provides relevant data on these poorly understood faunas.

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1. Introduction

Pleurosternidae (Paracryptodira) is the only group of freshwater turtles recognized in the Upper Jurassic of North America and Europe. This clade is identified as the sister group of the North American Baenidae (Pérez-García et al., in press). Pleurosternidae are restricted in North America to the Upper Jurassic, whereas they occur in Europe in the Upper Jurassic and in the Lower Cretaceous. The type species, *Pleurosternon bullockii* (Owen, 1842), was described from the Lower Cretaceous (Berriasian) of the Purbeck Limestone Group of United Kingdom. This genus is also known in the Upper Jurassic. The new combination *Dorsetochelys typocardium* (Seeley, 1869) has recently been proposed for other pleurosternid species, also described in the same British levels (Purbeck Limestone Group) (Pérez-García, 2014). Recent findings of two new Iberian Late Jurassic pleurosternid taxa improved the knowledge about the diversity of Pleurosternidae in Europe (Portuguese *Selemys lusitanica* Pérez-García and Ortega, 2011; Spanish *Riodevemyms inumbragigas* Pérez-García, Royo-Torres and Cobos, in press). Therefore, the so far described members of Pleurosternidae from

Europe come from Upper Jurassic levels (Kimmeridgian and Tithonian), and from the oldest stage of the Lower Cretaceous (Berriasian). The presence of fragmentary plates of indeterminate pleurosternids has recently been recognized in several European Lower Cretaceous locations, including some findings in post-Berriasian levels such as in the French locality of Angeac (Charente; Hauterivian–Barremian) and the Spanish locality of Galve (Teruel; Hauterivian and Barremian levels) (Neraudeau et al., 2012; Pérez-García et al., 2013). Considering these new findings, Pérez-García et al. (in press) postulated that the known stratigraphic distribution of Pleurosternidae must be extended and reaches now from the Kimmeridgian (Upper Jurassic) to the Barremian (Lower Cretaceous).

The finding of a new bonebed, in the lower Albian of the Spanish town of Ariño (Teruel Province), has recently been reported (Alcalá et al., 2012) (Fig. 1). This bonebed has yielded thousands of fossils, including abundant material of several groups of vertebrates. This discovery immensely expanded the knowledge on the vertebrate faunas from the Albian of Europe, and especially, from the Iberian Peninsula, which was so far very limited. Several new taxa of crocodylians (the most recent European goniopholidids: *Hulkepholis plotos* Buscalioni, Alcalá, Espílez and Mampel, 2013, and *Anteophthalmosuchus escuchae* Buscalioni, Alcalá, Espílez and Mampel, 2013) and dinosaurs (basal nodosaurid ankylosaur *Europelta carbonensis* Kirkland, Alcalá, Loewen, Espílez, Mampel and Wiersma, 2013; basal iguanodont ornithopod *Proa valdearinnoensis*

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Fig. 1. Geographical location of Ariño (Teruel Province, Spain), the type locality of *Toremys cassiopeia*, gen. et sp. nov.

McDonald, Espílez, Mampel, Kirkland and Alcalá, 2012) have currently been described (McDonald et al., 2012; Buscalioni et al., 2013; Kirkland et al., 2013).

The remains of turtles, hitherto unpublished, are very abundant in Ariño. Most of them can be attributed to Solemydidae, a group of primitive turtles (stem Testudines) recently recognized as terrestrial forms (Scheyer et al., in press). However, three of the turtle specimens found in Ariño do not correspond to Solemydidae. These specimens are studied here. They are assigned to a new taxon of Pleurosternidae, representing the worldwide most recent record of this clade.

Collection abbreviations. AR, Ariño collection, deposited in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis), Teruel, Spain.

Anatomical abbreviations. Plates: c, costal; en, entoplastron; ep, epiplastron; hp, hypoplastron; hy, hyoplastron; ms, mesoplastron; n, neural; nu, nuchal; p, peripheral; py, pygal; spy, suprapygal; xi, xiphoplastron. Scutes: Ab, abdominal; An, anal; Fe, femoral; Gu, gular; Hu, humeral; Ig, intergular; Inf, inframarginal; M, marginal; Pc, pectoral; Pl, pleural; V, vertebral.

2. Systematic paleontology

Testudines Batsch, 1788

Paracryptodira Gaffney, 1975

Baenoidea Williams, 1950

Pleurosternidae Cope, 1868

Toremys cassiopeia, gen. et sp. nov.

Figs. 2–5

Holotype. AR-1-4893, a nearly complete and articulated shell, and some appendicular elements (Fig. 2).

Paratypes. AR-1-4863, a relatively complete and partially articulated shell, and several appendicular elements (Fig. 3). AR-1-3923, a partial and disarticulated shell (Fig. 4).

Locality and horizon. Site AR-1, Santa María Quarry, Ariño, Teruel Province, Northeastern Spain. Oliete Geological Sub-basin, South

Iberian Range. Lower Escucha Formation, lower Albian (Alcalá et al., 2012; Tibert et al., 2013).

Etymology. The generic name is composed by Tor-, from the Spanish word toro (bull in English), an animal closely linked in several legends and traditions to Teruel Province; and -emys (Greek), meaning turtle. The specific name refers to Cassiopeia, the turtle of the fantasy novel Momo (Ende, 1973), which could see the future and knew the way to travel to the place where the administrator of the time worked, alluding to the fact that the new pleurosternid lived outside the stratigraphical range known for the other representatives of this clade. In addition, Cassiopeia is a star constellation and a bull and a star are integrated in the emblem of Teruel Province.

Diagnosis. Pleurosternid with the following autapomorphies: maximum width of the anterior edge of the nuchal plate (constituting the anterior margin of the carapace) being less than four times the maximum width of this plate; maximum width of the vertebral 1 greater than twice the width of its posterior edge. It is distinguished from other pleurosternids by an exclusive character combination: shallow emargination of the anterior carapace region (shared with *Dinochelys whitei*, *Glyptops plicatulus*, *Riodevemys inumbragigas* and some specimens of *Pleurosternon bullockii*); absence of notched posterior carapace rim (shared with *Di. whitei*, *G. plicatulus*, *Dorsetochelys typocardium*, *P. bullockii*, and *Selenemys lusitanica*); absence of carapace sagittal keel (shared with *Di. whitei*, *G. plicatulus*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*); width of the nuchal less than twice its maximum length (shared with *G. plicatulus*, *R. inumbragigas*, and *P. bullockii*); straight latero-anterior nuchal margins (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, and *P. bullockii*); neural 1 rectangular, neurals 2–8 hexagonal (shared with *G. plicatulus*, *R. inumbragigas*, and some specimens of *Do. typocardium* and *P. bullockii*); suprapygal 1 much narrower than suprapygal 2 (shared with *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*); slight dorsal curvature of the lateral part of the anterior and bridge peripherals (shared with *G. plicatulus*, *Do. typocardium*, and *R. inumbragigas*); peripherals 11 longer than wide (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*); absence of cervical scute (shared with *P. bullockii* and *S. lusitanica*); vertebrals relatively narrow, pleurals wider than long (shared with *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*); straight anterior margin of the vertebral 1 (shared with *Di. whitei*, *G. plicatulus*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*); vertebral 1 wider than the nuchal (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, and *P. bullockii*); suprapygal 1 carrying the sulcus between vertebrals 4 and 5 (shared with *Di. whitei* and *S. lusitanica*); vertebral 1 overlapping on the peripheral series (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, and *P. bullockii*); pleuro-marginal sulci near the costo-peripheral sutures (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*); marginals 1 wider than long (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, and *P. bullockii*); marginals 2 exclusively located at the peripheral series (shared with *Di. whitei*, *G. plicatulus*, and *Do. typocardium*); marginals 11 not overlapping on the suprapygal 2 (shared with *Di. whitei*, *R. inumbragigas*, and *P. bullockii*); marginals 12 overlapping on the suprapygal 2 (shared with *Do. typocardium*, *P. bullockii*, and *S. lusitanica*); subrounded lateral and anterior margins of the anterior plastral lobe (shared with *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*); absence of well-developed gular protrusions (shared with *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*); entoplastron rhomboidal and wider than long (shared with *Do. typocardium*,

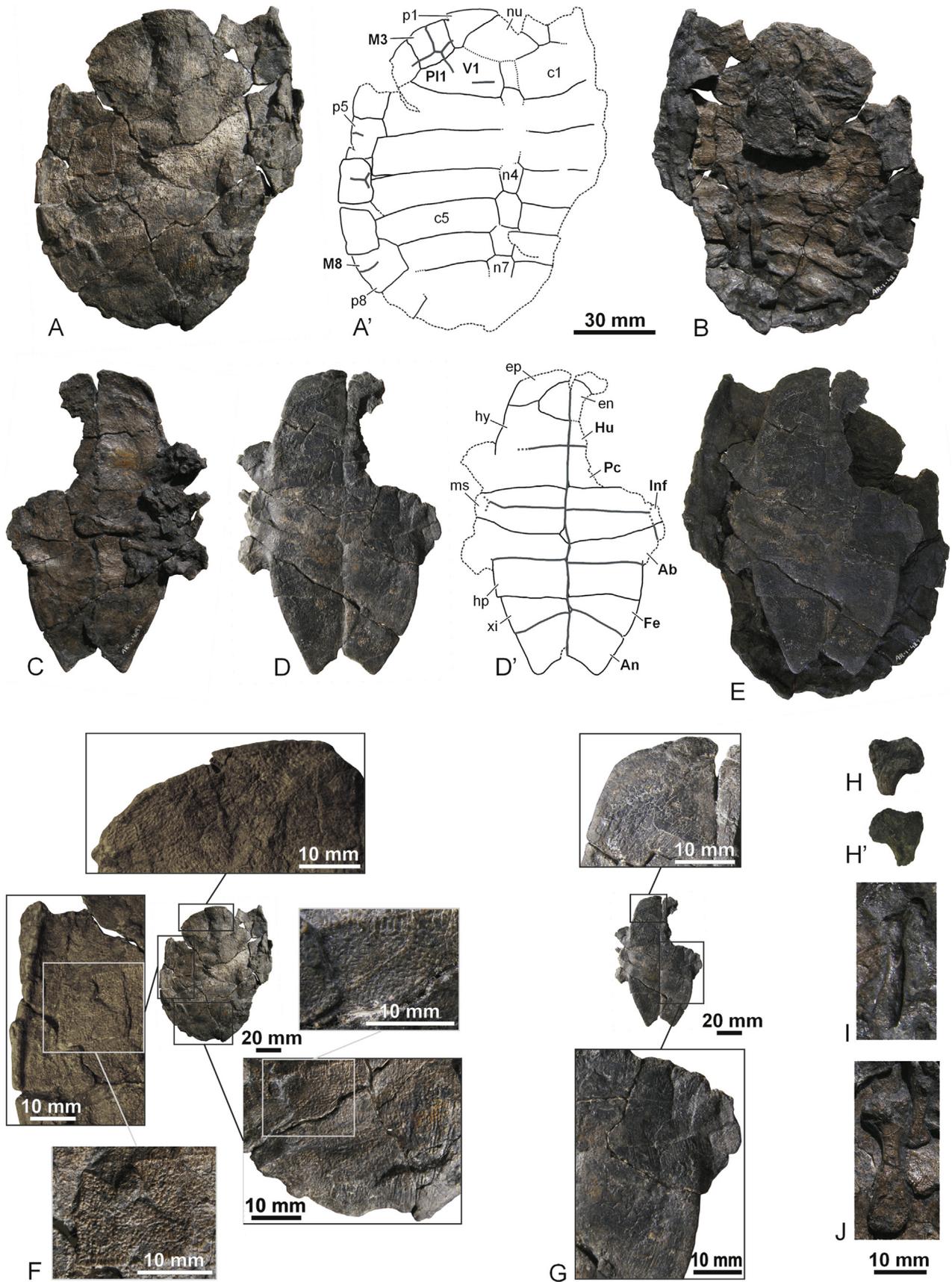


Fig. 2. AR-1-4893, holotype of *Toremys cassiopeia*, gen. et sp. nov., from the lower Albian of Ariño (Teruel Province, Spain). A–B, carapace, in dorsal (A) and ventral (B) views. C–D, plastron, in dorsal (C) and ventral (D) views. E, carapace, in ventral view. F, details of the ornamental pattern of several regions of the dorsal view of the carapace. G, details of the ornamental pattern of several regions of the ventral view of the plastron. H, proximal region of the right femur, in posterior (H), and anterior (H') views. I, left femur, in anterior view. J, left humerus, in dorsal view.

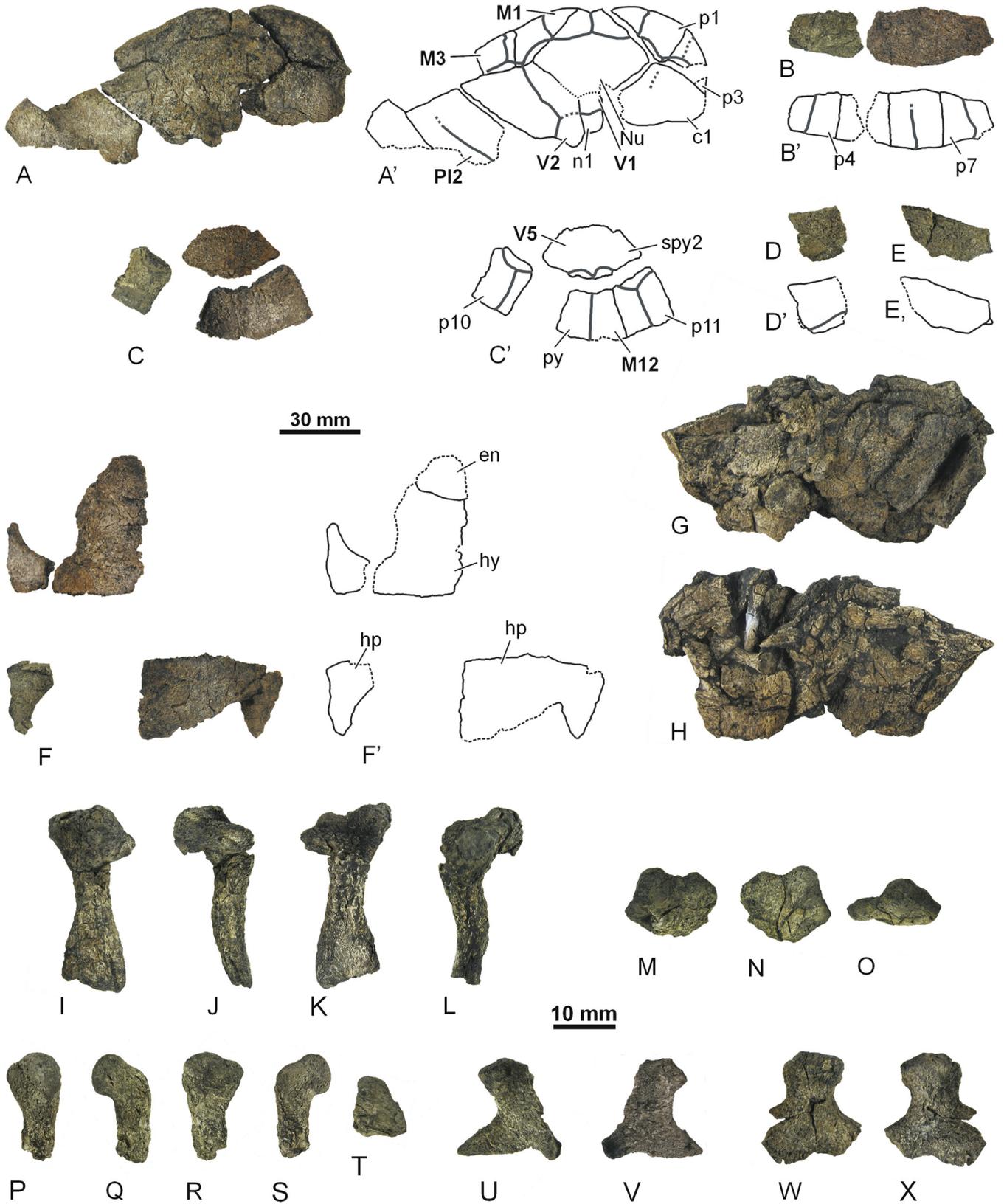


Fig. 3. AR-1-4863, paratype of *Toremys cassiopeia*, gen. et sp. nov., from the lower Albian of Ariño (Teruel Province, Spain). A, anterior region of the carapace, in dorsal view. B, left peripherals of the bridge area, in lateral view. C, posterior region of the carapace, in dorsal view. D–E, distal region of two costals, in dorsal view. F, partial plastron, in ventral view. G–H, two views of a block containing, in situ, other plates of the carapace and plastron, and also appendicular elements. I–L, right humerus, in dorsal (I), anterior (J), ventral (K) and posterior (L) views. M–O, proximal region of the left humerus, in dorsal (M), ventral (N), and medial (O) views. P–T, proximal half of the right femur, in dorsal (P), anterior (Q), ventral (R), posterior (S), and medial (T) views. U–V, right ilium, in dorsal (U), and ventral (V) views. W–X, right pubis, in dorsal (W), and ventral (X) views.

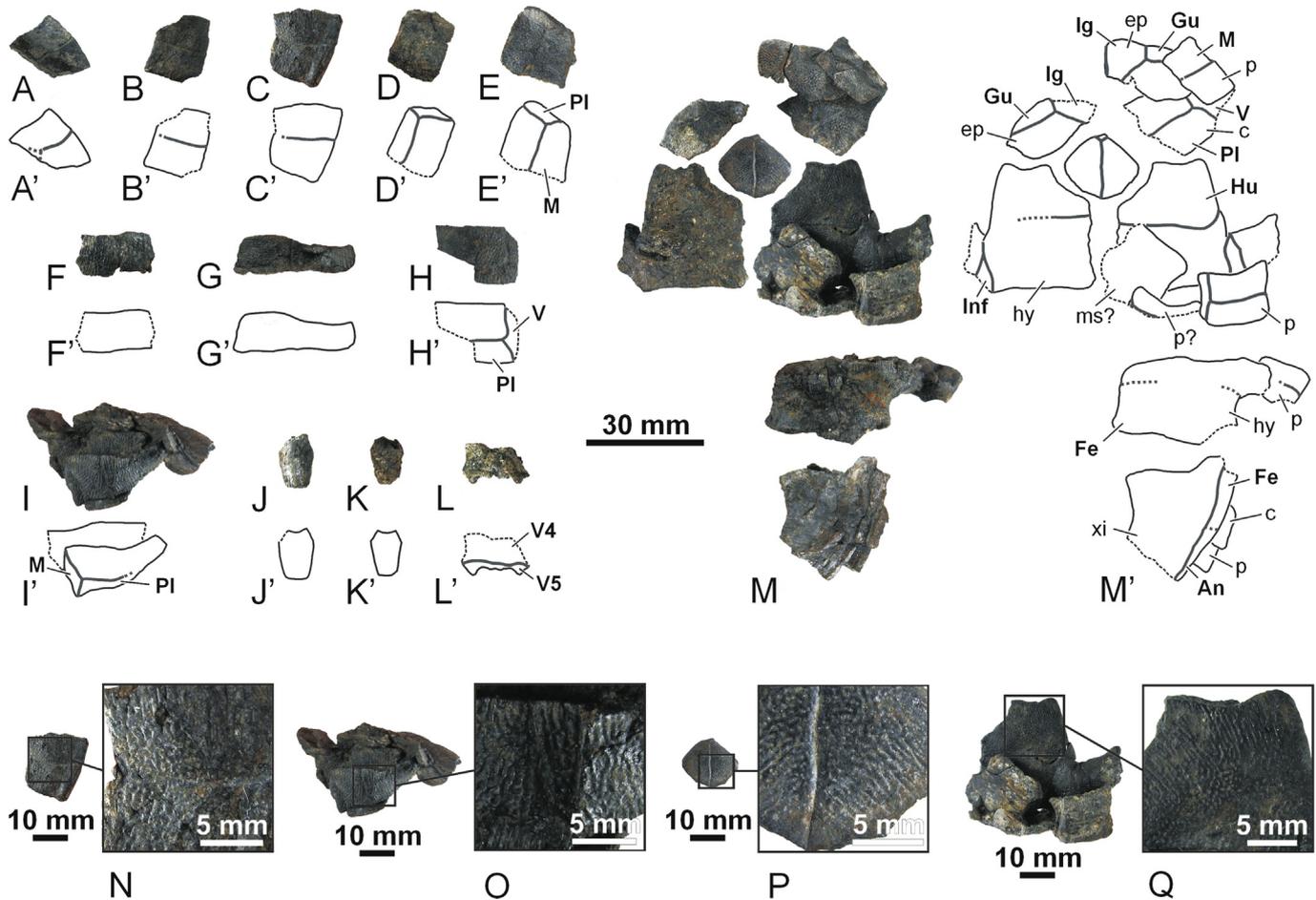


Fig. 4. AR-1-3923, paratype of *Toremys cassiopeia*, gen. et sp. nov., from the lower Albian of Ariño (Teruel Province, Spain). A–E, peripheral plates, in dorsal view. F–I, costal plates, in dorsal view. J–K, neurals, in dorsal view. L, posterior region of a first suprapygal, in dorsal view. M, several elements, including most of the plates of the plastron. All of them are in ventral view except the xiphiplastron, in dorsal view. N–Q, details of the ornamental pattern in the outer surface of several shell regions: a peripheral (N), a costal (O), the entoplastron (P) and the left hyoplastron (Q).

P. bullockii, and *S. lusitanica*); sagittal contact between the mesoplastra (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*); presence of an anal notch (shared with *Do. typocardium* and *P. bullockii*); straight plastral sagittal sulcus (shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, and *P. bullockii*); anal scutes entirely situated on the xiphiplastra (shared

with *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*).

Description. The outer surfaces of all plates of the carapace and plastron of *Toremys cassiopeia* are ornamented by low tubercles, constituting a vermiculate pattern (Figs. 2F–G, 4N–Q). Well-developed fine striations, perpendicular to the margins of all the plates, are present in this taxon. None of the three analysed specimens shows shell fontanelles. The estimated carapace length of these individuals is close to 15 cm. Neither the anterior nor the posterior margins of the shell of *T. cassiopeia* are scalloped (Fig. 5A). A shallow emargination of the anterior region of the carapace is developed on the anterior margin of the nuchal plate and on the antero-medial region of the first pair of peripherals (Figs. 2A, 3A). This taxon lacks a pygal notch (Fig. 3C). The lateral margins of the shell are rounded (Fig. 2A).

The anterior edge of the nuchal plate of *Toremys cassiopeia* constitutes the anterior margin of the carapace (Figs. 2A, 3A, 5A). However, this edge is very narrow in relation to the maximum width of this plate, which is more than four times that of the anterior edge. The width of this plate is considerably less than twice its maximum length. The latero-anterior margins of the nuchal are straight. *Toremys cassiopeia* has eight neurals and lacks supernumerary plates anterior to the neural 1. The neural 1 is rectangular (Figs. 2A, 3A) and is in contact with the costals 1. The other neurals are hexagonal (Figs. 2A, 4J–K) with a latero-anterior margin shorter

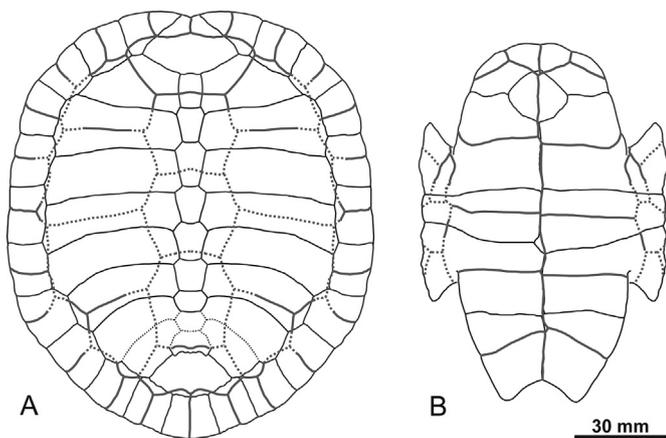


Fig. 5. Reconstruction of the shell of *Toremys cassiopeia*, gen. et sp. nov., from the lower Albian of Ariño (Teruel Province, Spain). A, dorsal view of the carapace. B, ventral view of the plastron.

than the latero-posterior. Each of them contacts with two pairs of costals. Neurals 1–6 are longer than wide. The ratio between the length and width of neurals 7 and 8 is not known due to the poor preservation of that carapace region. *Toremys cassiopeia* lacks a sagittal keel. It has two suprapygal plates (Figs. 3C, 4L, 5A) which the first being much narrower than the second one. *Toremys cassiopeia* has eight pairs of costals and eleven pairs of peripherals. The first dorsal rib is long (Fig. 2B). A slight dorsal curvature of the carapace is developed in the lateral area of the anterior and bridge peripherals (Figs. 2A, 3A, 4A). The last pair of peripherals is longer than wide (Fig. 3C).

Toremys cassiopeia lacks a cervical scute (Fig. 3A). Therefore, the sagittal contact between marginals 1 is visible. Marginals 1 are wider than long. The latero-posterior margins of the vertebral 1 are markedly divergent (Figs. 2A, 3A, 5A) resulting in a maximum width of this scute that is greater than twice the width of its posterior edge. Anterolaterally, this vertebral overlaps the peripheral series (peripherals 1 and 2 in the case of AR-1-4893, Fig. 2A; peripheral 1 in AR-1-4863, Fig. 3A). Medially, the sulcus between vertebrae 1 and 2 is placed on the neural 1. The sulcus between vertebrae 4 and 5 is located on the posterior region of the suprapygal 1 (Figs. 4L, 5A). The vertebral series is relatively narrow, the pleural scutes being wider than long (Figs. 3A, 4H, 5A). The sulci between the pleural and marginal scutes is situated near the suture between the costal and the peripheral plates (Figs. 2A, 3C, 4D–E, 4I, 5A). Marginals 2 do not overlap at the costals 1 (Figs. 2A, 3A). Marginal 11 are not in contact with suprapygal 2 (Figs. 3C, 5A). However, marginals 12 overlap on the postero-medial region of that suprapygal.

Both the lateral and the anterior margins of the anterior plastral lobe of *Toremys cassiopeia* are subrounded (Figs. 2D, 4M, 5B). This taxon lacks well-developed protrusions of the gulars. The entoplastron is rhomboidal, being wider than long. The axillary buttresses of *T. cassiopeia* are poorly developed, only weakly extending onto the first costals (Figs. 2B, 3F, 4M). The inguinal buttresses are in contact with the distal portion of the costals 5. The hypoplastra are longer than the hypoplastra (Figs. 2D, 4M). This taxon has a transversely directed pair of mesoplastra that contact each other sagittally. The lateral margins of the posterior plastral lobe are subrounded. An anal notch, wider than long, is present.

The plastral sagittal sulcus is straight (Figs. 2D, 4M, 5B). *Toremys cassiopeia* has a pair of intergular scutes (Figs. 4M, 5B). These scutes are slightly larger than the gulars. The humero-pectoral sulcus is well posterior to the entoplastron. *Toremys cassiopeia* has inframarginal scutes. The pectoro-abdominal and the abdomino-femoral sulci are straight, and run perpendicular to the axial plane. The anal scutes are entirely situated on the xiphoplastra.

Postcranial elements include some generally poorly preserved appendicular bones associated with AR-1-4893 and AR-1-4863 (Figs. 2H–J, 3I–X). The diaphysis of the humerus is more curved than that of the femur. The proximal and distal regions of the humerus are wider than those of the femur. The proximal head of the femur carries a wide depression which separates the two trochanter (Figs. 2H–J, 3I–T). The preserved pelvic elements are relatively flat (Fig. 3U–X). The contacts of these elements with the plastron were ligamentous attachments.

3. Discussion

3.1. Comparison of *Toremys cassiopeia* with other members of *Paracryptodira*

General comparisons. *Toremys cassiopeia* differs from the representatives of Compsemydidae, the sister group of Baenoidea, by the lack of intergulars significantly larger than the gulars, and of a

wider than long neural 5. Furthermore, it does not share most of the morphological features of the exclusive combination of characters described for Compsemydidae (sensu Pérez-García et al., in press) such as the presence of straight lateral shell margins, no contact of the nuchal with the anterior shell margin, presence of a markedly sinuous sagittal plastral sulcus, no contact of the pleuro-marginal sulcus with the costals.

The availability of characters in *Toremys cassiopeia* allows its identification as a taxon which differs from Baenidae by the absence of a scalloped posterior carapace margin; contact of neural 5 with costals 5 and 6; presence of eleven pairs of peripherals; axillary buttresses only weakly extending onto the costals; inguinal buttresses contacting the distal portion of the costals; long first dorsal rib. This combination of characters allows the attribution of the turtle from Ariño to Pleurosternidae, the only clade of Paracryptodira known in the Mesozoic levels of Europe.

The presence of well-developed fine striations perpendicular to the margins of the carapace and plastron plates is shared with the pleurosternids *Glyptops plicatulus* (Cope, 1877), *Dorsetochelys typocardium*, *Riodevemyx inumbragigas*, *Pleurosternon bullockii*, and *Selenemys lusitanica*. The occurrence of low tubercles forming a vermiculate pattern is present in *Dinochelys whitei* Gaffney, 1979, *G. plicatulus*, *Do. typocardium*, and *R. inumbragigas*, the ornamentation being less developed in *Dinochelys whitei*.

All the known specimens of *Toremys cassiopeia* are interpreted as adult or subadult individuals due to the ossification of their carapaces. Carapace length is less than those of the adult specimens of other so far defined pleurosternids (e.g. the size of the shell of *S. lusitanica* is about 25 cm, but that of *P. bullockii* is about 50 cm).

Toremys cassiopeia differs from *Do. typocardium* in the absence of a deep nuchal notch. A shallow emargination of the anterior region of the carapace is present in *Di. whitei*, *G. plicatulus*, *R. inumbragigas*, and some specimens of *P. bullockii*. The slightly notched posterior carapace margin known in *R. inumbragigas* is not present in *T. cassiopeia*.

Carapace plates. The anterior edge of the nuchal plate of *T. cassiopeia* constitutes the anterior margin of the carapace, differing from *S. lusitanica*. The very narrow anterior edge of the nuchal of *T. cassiopeia* relative to the maximum width of this plate is unique in this pleurosternid. The wide nuchal of *Di. whitei*, *Do. typocardium*, and *S. lusitanica* is more than two times as wide as it is long, and differs to that of *T. cassiopeia*. The latero-anterior margins of the nuchal of *T. cassiopeia* are straight, as in all the others pleurosternids except for *R. inumbragigas* and *S. lusitanica*, where it is concave.

The rectangular morphology of the first neural of *T. cassiopeia*, and the hexagonal morphology of the others, are shared with *G. plicatulus*, *R. inumbragigas*, and some specimens of *Do. typocardium*, and *P. bullockii*. The poorly developed sagittal keel on the posterior half of the carapace of *Do. typocardium* is absent in *T. cassiopeia*.

The new taxon shares with *R. inumbragigas*, *P. bullockii*, and *S. lusitanica* a much narrower first suprapygal when compared to the second one. A slight dorsal curvature of the lateral part of the anterior and bridge peripherals is also present in *G. plicatulus*, *Do. typocardium*, and *R. inumbragigas*. The presence of longer than wide peripherals 11 is shared with all pleurosternids except for *R. inumbragigas*.

Carapace scutes. A sagittal contact between the marginals 1, due to the absence of a cervical scute, is shared with *P. bullockii* and *S. lusitanica*. The presence of wider than long marginals 1 differs from the condition in *S. lusitanica*. Relatively narrow vertebrae, and

pleurals wider than long, are shared with *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*.

The presence of the vertebral 1 with the anterior margin significantly wider than the posterior margin is unique for this pleurosternid. Its straight anterior margin differs from that of *Do. typocardium*. A vertebral 1 being wider than the nuchal is shared with all pleurosternids except for *R. inumbragigas* and *S. lusitanica*, taxa in which both elements have a similar width. The overlap of the sulcus between the vertebrae 4 and 5 on the suprapygal 1 is shared with *Di. whitei* and *S. lusitanica*. This overlap occurs on the neural 8 in the other pleurosternids.

The overlap of vertebral 1 on the peripheral series is shared with all pleurosternids except for *S. lusitanica*. Marginals 2 do not overlap on costals 1, a feature that is shared with *Di. whitei*, *G. plicatulus*, and *Do. typocardium*. The boundary between the pleural and marginal scutes near the suture between the costal and the peripheral plates is shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*. The absence of overlap of the marginals 11 on the suprapygal 2 is shared with *Di. whitei*, *R. inumbragigas* and *P. bullockii*. The overlap of the marginals 12 on the suprapygal 2 is shared with *Do. typocardium*, *P. bullockii*, and *S. lusitanica*.

Plastron plates. The subrounded and anteriorly convergent lateral margins of the anterior plastral lobe are shared with *G. plicatulus*, *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*. The absence of the anterior margin of this lobe perpendicular to the axial plane is shared with *G. plicatulus*, *Do. typocardium*, *P. bullockii*, and *S. lusitanica*. The well-developed gular protrusions observed in *Di. whitei* are unique for this taxon within Pleurosternidae.

Toremys cassiopeia has a wider than long entoplastron, which is also present in *Do. typocardium*, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*. Its rhomboidal morphology is similar to that known in *Do. typocardium*, *P. bullockii*, and *S. lusitanica*.

The sagittal contact between the mesoplastra is shared with all pleurosternids except for *R. inumbragigas*, in which these plates undergo marked wedging towards the medial region, which prevents the sagittal contact. The presence of an anal notch is shared with *Do. typocardium* and *P. bullockii*.

Plastron scutes. A straight or slightly sinuous plastral sagittal sulcus is shared with *Di. whitei*, *G. plicatulus*, *Do. typocardium*, and *P. bullockii*. The location of the anal scutes, entirely situated on the xiphiplastra, differs only from the condition in *Di. whitei*.

3.2. Phylogenetic analysis

Methods. In order to establish the systematic position of *Toremys cassiopeia*, this taxon was coded in the data matrix proposed by Pérez-García et al. (in press), in which the phylogenetic relationships of the Paracryptodira representatives were analysed. As in Pérez-García et al. (in press) the baenid *Scabremys ornata* (Gilmore, 1935) was excluded from the analysis due to it was identified as a wild card taxon using the application of the TNT program's "Pruned trees". A total of 123 characters and 30 taxa were analysed. Due to the preservation, 49 characters of this matrix can be encoded for *T. cassiopeia* (Appendix 1).

The analysis has been performed with TNT v. 1.0 (Goloboff et al., 2008) using a traditional search which a tree-bisection algorithm with 10,000 replicates. All characters were considered unordered and equally weighted. Both the majority rule and the strict consensus trees are presented here (Fig. 6A–B). Bootstrap frequencies and Bremer support have also been calculated, using TNT. The equal of or greater than 50 absolute frequencies of the bootstrapped values, obtained using 10,000 replicates, are shown in the strict consensus tree (Fig. 6B). Bremer support (Bremer, 1994),

obtained through the script provided by TNT v.1.1, uses a combination of heuristic searches saving suboptimal trees and negative constraints for monophyly, which are also shown in the strict consensus tree (Fig. 6B). The synapomorphies are obtained using the tool "List common synapomorphies" of TNT.

Results. The topology of the majority rule tree is very similar to that obtained by Pérez-García et al. (in press) (Fig. 6A). The strict consensus tree is very similar too (Fig. 6B), but the hypothesis on the phylogenetic relationships among the Pleurosternidae members cannot be resolved here. In this regard, two polytomies are identified. This analysis resulted in 30 most parsimonious trees, each with a length of 286 steps (CI = 0.486; RI = 0.736; RC = 0.358).

Toremys cassiopeia is identified as a pleurosternid both in the majority rule tree as in the strict consensus tree. As in Pérez-García et al. (in press), the node Pleurosternidae is defined in the majority rule tree by: strongly hooked premaxillae (character 75, state 1); dorsal skull roof not reaching the anterior edge of the premaxillae (character 77, state 1); anterior plastral lobe larger than the posterior one (character 98, state 1); suprapygal 1 as wide or nearly as wide as suprapygal 2 (character 105, state 1), a character state not present in the European pleurosternids *Riodevemys inumbragigas*, *Pleurosternon bullockii*, *Selenemys lusitanica* or *Toremys cassiopeia*; rounded lateral shell margins (character 106, state 1); and skull length greater than 1.45 times its width (character 123, state 1). In the strict consensus tree, Pleurosternidae is defined by some of the cited character states (those corresponding to characters 75, 77, 98 and 106), but also by: oblong and rounded anteriorly skull (character 1, state 1); palatines not or very lightly contributing to the triturating surface (character 10, state 1); parietals thin out towards their posterior edge (character 23, state 1); poorly developed contact between the pterygoids and the basioccipital (character 29, state 0); small supraoccipital exposure on the skull roof (character 69, state 1); small fenestra perilymphatica (character 87, state 1); and pronounced fine striations perpendicular to the plate margins (character 109, state 1), a character state not shared with *Dinochelys whitei*.

A node that groups all pleurosternids except the North American *Di. whitei* is obtained in the majority rule tree, being defined by the previously described character 109. These pleurosternids are grouped into a third-grade polytomy, composed of *Glyptops plicatulus*, *Dorsetochelys typocardium* and the node grouping the European *R. inumbragigas*, *P. bullockii*, *S. lusitanica*, and *T. cassiopeia*. This node is defined by the presence of suprapygal 1 markedly narrower than suprapygal 2 (character 105, state 0), a character state not shared with *Di. whitei*, *G. plicatulus*, and *Do. typocardium*. It is composed by *T. cassiopeia* and a clade grouping *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*. *Toremys cassiopeia* is defined by an autapomorphy, corresponding to the presence of a trapezoidal first vertebral, with the anterior margin significantly wider than the posterior (character 55, state 2); and by the presence of a well-developed anal notch (character 92, state 1), character state shared with *Do. typocardium* and *P. bullockii*. The other taxa, *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*, are grouped by the following characters: maximum plastron length less than or equal to twice the maximum width of the plastral lobes (character 108, state 0); and presence of overlap of the marginals 2 on the costals 1 (character 118, state 1).

A basal polytomy for Pleurosternidae is obtained in the strict consensus. It corresponds to a fifth-grade polytomy, comprising *Di. whitei*, *G. plicatulus*, *Do. typocardium*, *T. cassiopeia*, and the node grouping *R. inumbragigas*, *P. bullockii*, and *S. lusitanica*. *Toremys cassiopeia* is defined by three character states: those corresponding to the previously described characters 55 and 92, as well as by the

absence of a cervical scute (character 43, state 2), a character that is shared with *P. bullockii* and *S. lusitanica*.

3.3. Systematic and biostratigraphic implications

Toremys cassiopeia is the most recent pleurosternid taxa, coming from the Albian. Before the most recent pleurosternids, *Pleurosternon bullockii* and *Dorsetochelys typocardium* (Fig. 6C), had been described from the Berriasian. The finding of Pleurosternidae in Ariño allows us to extend the known stratigraphic range of this group, that was from the Kimmeridgian to the Barremian (Pérez-García et al., in press), and can now be extended to the Albian.

During the Hauterivian and Barremian of Europe, and especially of Spain, a diverse fauna of freshwater turtles, belonging to Eucryptodira, has been recorded (Pérez-García and Murelaga, 2013; Pérez-García et al., 2014a). One of the most diverse groups is Xingjiangchelyidae, represented by the British taxon *Brodiechelys brodiei* (Lydekker, 1889), and by the Spanish forms *Brodiechelys royoi* Pérez-García, Gasulla and Ortega, 2014a, *Larachelus morla* Pérez-García and Murelaga, 2012a, and *Camerochelys vilanovai* Pérez-García and Murelaga, 2013. *Galvechelone lopezmartinezae* Pérez-García and Murelaga, 2012b is another Spanish turtle that lived in that time interval. These forms, probably belonging to lineages originated in Asia, are not recognized in the European Jurassic record. Other European freshwater turtles are also unique to that time interval, such as the Belgian *Peltochelys duchastelii* Dollo, 1885, the Belgian and Spanish *Chitraccephalus dumonii* Dollo, 1885, and the Spanish *Hoyasemys jimenezi* Pérez-García, de la Fuente and Ortega, 2012. The only European eucryptodiran known from the Upper Jurassic (Tithonian) and the Lower Cretaceous (Valanginian) is *Hylaeochelys*, represented by the British *Hylaeochelys belli* (Mantell, 1844), and by the Portuguese *Hylaeochelys kappa* Pérez-García and Ortega, 2014. In contrast to the previously mentioned forms, *Hylaeochelys* is regarded as probably belonging to an exclusively European lineage (Pérez-García and Ortega, 2014). Despite this diversity, the presence of freshwater eucryptodires between the Barremian and the uppermost Cretaceous of Europe has not been confirmed. The eucryptodires identified in the uppermost Cretaceous, and those from the Paleocene, correspond to other clades, which migrated from several continents (Pérez-García, 2012; Scheyer et al., 2012). The only lineage of freshwater turtles found in Europe in the Lower Cretaceous and in younger levels correspond to Pan-Pleurodira, represented by members of the clade Dortokidae (Murelaga Bereikua, 1998; Pérez-García et al., 2014b). This group is recorded from the Barremian, being relatively abundant in the Campanian and Maastrichtian, and surviving at least until the Paleocene (Lapparent de Broin et al., 2004).

Therefore, the faunas of freshwater turtles identified in the Upper Cretaceous of Europe are very different from those of the Lower Cretaceous. The only exception is the European clade Dortokidae, present during both periods. Information on the transition between the Lower Cretaceous and the uppermost Cretaceous faunas of freshwater turtles is extremely limited. No lineage of European Lower Cretaceous freshwater pan-cryptodires was hitherto known in post-Barremian levels. Pleurosternidae is the only European clade of freshwater turtles identified in both pre-Barremian and post-Barremian levels.

4. Conclusions

The turtles from the recently discovered Spanish lower Albian bonebed of Ariño (Teruel Province) are studied here for the first time. This study focuses on the description and analysis of three specimens which preserve elements of the shell as well as some appendicular bones. The three specimens are recognized as

belonging to the same taxon. It is identified as a member of Pleurosternidae (Paracryptodira), a group of European and North American freshwater turtles. The morphology of its nuchal plate (with the width of its anterior margin being less than four times the maximum width of the plate, and constituting the anterior margin of the carapace) and that of the vertebral 1 (with its maximum width greater than twice the width of its posterior edge) are recognized as unique to the turtle from Ariño. Furthermore, it is distinguished from the other pleurosternids by an exclusive character combination. Therefore, it is recognized as a new taxon, *Toremys cassiopeia* gen et sp. nov. *Toremys cassiopeia* is the third pleurosternid identified in the Iberian Peninsula, where the Late Jurassic *Selenemys lusitanica* and *Riodevemys inumbragigas* were described.

The most recent so far described pleurosternids were the European *Pleurosternon bullockii* and *Dorsetochelys typocardium*. Both came from the oldest stage of the Lower Cretaceous (Berriasian). Therefore, *Toremys cassiopeia* is the worldwide most recent known pleurosternid taxa, coming from the youngest stage of the Lower Cretaceous (Albian). Pleurosternidae is identified here as the only European clade of freshwater turtles recognized before and after the Barremian.

This study allows us to observe, for the first time, a partial overlap in the known range of stratigraphic distribution of Pleurosternidae with that of its sister group, the Baenidae (Fig. 6C). However, the distributions of the Cretaceous pleurosternids and that of the baenids were not sympatric: all known Cretaceous pleurosternids were European forms, and all known baenids were North American taxa.

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References

- Alcalá, L., Espílez, E., Mampel, L., Kirkland, J.L., Ortega, M., Rubio, D., González, A., Ayala, D., Cobos, A., Royo-Torres, R., Gascó, F., Pesquero, M.D., 2012. A new Lower Cretaceous vertebrate bonebed near Ariño (Teruel, Aragón, Spain); found and managed in a joint collaboration between a mining company and a palaeontological park. *Geohéritage* 4, 275–286.
- Batsch, G.C., 1788. Versuch einer Anleitung, zur Kenntniss und Geschichte der Thiere und Mineralien. Jena, Akademische Buchhandlung 1, pp. 1–528.
- Bremer, K., 1994. Branch support and tree stability. *Cladistics* 10, 295–304.
- Buscalioni, A.D., Alcalá, L., Espílez, E., Mampel, L., 2013. European Goniopholididae from the early Albian Escucha Formation in Ariño (Teruel, Aragón, Spain). *Spanish Journal of Palaeontology* 28, 103–122.
- Cope, E.D., 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20, 242–300.
- Cope, E.D., 1877. On reptilian remains from the Dakota beds of Colorado. *Proceedings of the American Philosophical Society* 17, 193–196.

- Dollo, M.L., 1885. Première note sur les chéloniens de Bernissart. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 3, 63–79.
- Gaffney, E.S., 1975. A phylogeny and classification of higher categories of turtles. Bulletin of the American Museum of Natural History 155, 387–436.
- Gaffney, E.S., 1979. The Jurassic turtles of North America. Bulletin of the American Museum of Natural History 161, 91–136.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.
- Kirkland, J.I., Alcalá, L., Loewen, M., Espílez, E., Mampel, L., Wiersma, J., 2013. The basal nodosaurid ankylosaur *Europelta carbonensis* n. gen., n. sp. from the Lower Cretaceous (lower Albian) Escucha Formation of northeastern Spain. PLoS One 8, e80405.
- Lapparent de Broin, F. de, Murelaga Bereikua, X., Codrea, V., 2004. Presence of Dortokidae (Chelonii, Pleurodira) in the earliest Tertiary of the Jibou Formation, Romania: paleobiogeographical implications. Acta Palaeontologica Romaniaae 4, 203–215.
- 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.
- Mantell, G.A., 1844. The Medals of Creation: or First Lessons in Geology and in the Study of Organic Remains. London, Private edition II, pp. 587–876.
- McDonald, A.T., Espílez, E., Mampel, L., Kirkland, J.I., Alcalá, L., 2012. An unusual new basal iguanodont (Dinosauria: Ornithopoda) from the Lower Cretaceous of Teruel, Spain. Zootaxa 3595, 61–76.
- Murelaga Bereikua, X., 1998. Primeros restos de tortugas del Cretácico Inferior (Barremiense superior) de Vallipón (Castellote, Teruel). Mas de las Matas 17, 189–200.
- Neraudeau, D., Allain, R., Balleve, M., Batten, D.J., Buffetaut, E., Colin, J.P., Dabard, M.P., Daviero-Gomez, V., El Albani, A., Gomez, B., Grosheny, D., Le Loeuff, J., Leprince, A., Martín-Closas, C., Masure, E., Mazin, J.-M., Philippe, M., Pouech, J., Tong, H., Tournepichem, J.F., Vullo, R., 2012. The Hauterivian-Barremian lignitic bone bed of Angeac (Charente, south-west France): stratigraphical, palaeobiological and palaeogeographical implications. Cretaceous Research 37, 1–14.
- Owen, R., 1842. Report on British fossil reptiles. Part II. Report of the British Association for the Advancement of Science 11, pp. 60–204.
- Pérez-García, A., 2012. *Berruchelus russelli* gen. et sp. nov., a paracryptodiran turtle from the Cenozoic of Europe. Journal of Vertebrate Paleontology 32, 545–556.
- Pérez-García, A., 2014. Revision of the poorly known *Dorsetochelys typocardium*, a relatively abundant pleurosternid turtle (Paracryptodira) in the Early Cretaceous of Europe. Cretaceous Research 49, 152–162.
- Pérez-García, A., Murelaga, X., 2012a. *Larachelus morla* gen. et sp. nov., a new member of the little-known European Early Cretaceous record of stem cryptodiran turtles. Journal of Vertebrate Paleontology 32, 1293–1302.
- Pérez-García, A., Murelaga, X., 2012b. *Galvechelone lopezmartinezae* gen. et sp. nov., a new cryptodiran turtle in the Lower Cretaceous of Europe. Palaeontology 55, 937–944.
- Pérez-García, A., Murelaga, X., 2013. *Camerochelys vilanovai* gen. et sp. nov., a new pan-cryptodiran turtle in the Early Cretaceous of the Iberian Range (Spain). Cretaceous Research 41, 143–149.
- Pérez-García, A., Ortega, F., 2011. *Selenemys lusitanica* gen. et sp. nov., a new pleurosternid turtle (Chelonii, Paracryptodira) from the Upper Jurassic of Portugal. Journal of Vertebrate Paleontology 31, 60–69.
- Pérez-García, A., Ortega, F., 2014. A new species of the turtle *Hylaeochelys* (Eucryptodira) outside its known geographic and stratigraphic ranges of distribution. Comptes Rendus Palevol 13, 183–188.
- Pérez-García, A., de la Fuente, M.S., Ortega, F., 2012. A new freshwater basal eucryptodiran turtle from the Early Cretaceous of Spain. Acta Palaeontologica Polonica 57, 285–298.
- Pérez-García, A., Gasulla, J.M., Ortega, F., 2014a. A new species of *Brodiechelys* (Testudines, Pan-Cryptodira) from the Early Cretaceous of Spain: Systematic and palaeobiogeographic implications. Acta Palaeontologica Polonica 59, 333–342.
- Pérez-García, A., Gasulla, J.M., Ortega, F., 2014b. *Eodortoka morellana* gen. et sp. nov., the first pan-pleurodiran turtle (Dortokidae) defined in the Early Cretaceous of Europe. Cretaceous Research 48, 130–138.
- Pérez-García, A., Royo-Torres, R., Cobos, A., 2015. A new European Late Jurassic pleurosternid (Testudines, Paracryptodira) and its inclusion in a new hypothesis on the phylogeny of the paracryptodiran taxa. Journal of Systematic Palaeontology. <http://dx.doi.org/10.1080/14772019.2014.911212> in press.
- Pérez-García, A., Scheyer, T.M., 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.
- Seeley, H.G., 1869. Index to the fossil remains of Aves, Ornithosauria and Reptilia, from the Secondary system of strata arranged in the Woodwardian Museum of the University of Cambridge. Deighton Bell, Cambridge, 143 pp.
- Scheyer, T.M., Mörs, T., Einarsson, E., 2012. First record of soft-shelled turtles (Cryptodira, Trionychidae) from the Late Cretaceous of Europe. Journal of Vertebrate Paleontology 32, 1027–1032.
- Scheyer, T.M., Pérez-García, A., Murelaga, X., 2015. Shell bone histology of solemydid turtles (stem Testudines): palaeoecological implications. Organisms Diversity and Evolution. <http://dx.doi.org/10.1007/s13127-014-0188-0> in press.
- Tibert, N.E., Colin, J.-P., Kirkland, J.I., Alcalá, L., Martín-Closas, C., 2013. Lower Cretaceous Ostracods from the Escucha Formation, Arino, Spain (Iberian Basin): Palaeontological implications for age and depositional environment. Micropaleontology 9, 83–91.
- Williams, E.E., 1950. Variation and selection in the cervical central articulations of living turtles. Bulletin of the American Museum of Natural History 94, 511–561.

Appendix 1

Scored characters for *Toremys cassiopeia*, gen. et sp. nov. into the data matrix proposed by Pérez-García et al. (in press): ?????????? ?????????? ?????????? ?????????? 00100 1021000100 ?0002010?? ?????????? ?????????? ??????????1? 0110111? 11 01?-011110 110-1?1011 0??