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Iberoccitanemys atlanticum (Lapparent de Broin & Murelaga, 1996) n. comb.: new data on the diversity and paleobiogeographic distributions of the Campanian-Maastrichtian bothremydid turtles of Europe

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ABSTRACT
Bothremydidae is the most abundant clade of turtles in the Campanian and Maastrichtian (Upper Cretaceous) fossil record of southwestern Europe. Several members of Foxemydina Gaffney, Tong & Meylan, 2006 are known in an area that includes Southern France and the North-Eastern half of Spain. The problematic '*Polysternon*' *atlanticum* is the worst characterized, lacking a diagnosis that allows its specific validity to be confirmed, and whose generic attribution has been recognized as doubtful. Its presence was exclusively proposed in its type locality, the upper Campanian quarry of Laño, in Treviño County (Burgos Province, North of Spain). Despite the fact that knowledge about Bothremydidae has markedly increased after the description of '*Polysternon*' *atlanticum* Lapparent de Broin & Murelaga, 1996, no new information about this species has been published since the 1990s. The analysis of abundant unpublished material of the bothremydid from Laño allows us to confirm the validity of this species. As a consequence of this study, it is not only identified in its type locality, but also in other Spanish regions and in the south of France. The diversity of Bothremydidae Baur, 1891 in the Upper Cretaceous of Europe is lower than previously considered. Thus, the species '*Iberoccitanemys convenarum*' (Laurent, Tong & Claude, 2002), originally defined for the French record, and subsequently also identified in Spain, is identified here as a synonym of the species described in Laño. An emended diagnosis for the upper Campanian to upper Maastrichtian, *Iberoccitanemys atlanticum* (Lapparent de Broin & Murelaga, 1996) n. comb., is proposed.

KEY WORDS
Pleurodira,
Bothremydidae,
Foxemydina,
'*Polysternon*' *atlanticum*,
'*Elochelys convenarum*',
Late Cretaceous,
new combination.

RÉSUMÉ
Iberoccitanemys atlanticum *n. comb. : nouvelles données sur la diversité et les répartitions paléobiogéographiques des tortues bothremydidés du Campanien et Maastrichtien de l'Europe.*
Les Bothremydidae est le groupe de tortues le plus abondant dans les gisements du Campanien et Maastrichtien (Crétacé supérieur) du Sud-Ouest de l'Europe. Plusieurs membres de Foxemydina Gaffney, Tong & Meylan, 2006 ont été identifiés dans le Sud de la France et la moitié Nord-Est de l'Espagne. L'espèce la moins bien caractérisée est le taxon problématique '*Polysternon*' *atlanticum* Lapparent de Broin & Murelaga, 1996. Il s'agit d'une espèce pour laquelle une diagnose adéquate permettant de confirmer sa validité spécifique n'est pas disponible, et pour laquelle l'attribution générique est considérée comme douteuse. Sa présence a été exclusivement reconnue dans sa localité type, la carrière du Campanien supérieur de Laño, dans le Comté de Treviño (province de Burgos, Nord de l'Espagne). Bien que les connaissances sur les Bothremydidae Baur, 1891 aient considérablement augmenté après la description de '*Polysternon*' *atlanticum*, aucune nouvelle information sur cette espèce n'a été publiée depuis les années 1990. L'analyse de nombreux spécimens non publiés du bothremydidé de Laño nous permet de confirmer la validité de cette espèce. Il est non seulement identifié dans sa localité type, mais aussi dans d'autres régions espagnoles et dans le Sud de la France. La diversité des bothremydidés dans le Crétacé supérieur d'Europe est reconnue comme moindre que celle considérée jusqu'à présent. Ainsi, l'espèce '*Iberoccitanemys convenarum*' (Laurent, Tong & Claude, 2002), qui a été définie à partir d'un individu dans le registre français, puis identifiée en Espagne, est reconnue comme synonyme de l'espèce de Laño. Une diagnose modifiée pour l'espèce du Campanien supérieur au Maastrichtien supérieur, *Iberoccitanemys atlanticum* (Lapparent de Broin & Murelaga, 1996) n. comb., est proposée.

MOTS CLÉS
Pleurodira,
Bothremydidae,
Foxemydina,
'*Polysternon*' *atlanticum*,
'*Elochelys convenarum*',
Crétacé supérieur,
combinaison nouvelle.

INTRODUCTION

The pleurodires Bothremydidae Baur, 1891 constitute the most abundant and diverse clade of turtles for the last part of the Cretaceous record (Campanian and Maastrichtian) in Southwest Europe (Lapparent de Broin 2001; Gaffney *et al.* 2006; Pérez-García & Ortega 2018). The currently available fossil record suggests that Bothremydidae reached Europe in the early Late Cretaceous, during the Cenomanian, through the oldest documented dispersal event from Gondwana to Laurasia of a lineage of the crown Pleurodira (Pérez-García 2016, 2018; Pérez-García *et al.* 2017). The first systematic assessment of the Spanish Upper Cretaceous bothremydid record is part of a study on the turtle fauna from the upper Campanian site of Laño, in Treviño County (Burgos Province, North of Spain) (Lapparent de Broin & Murelaga 1996). In addition to the identification of turtles corresponding to other clades (the stem Testudines Batsch, 1788, Helochelydridae Nopcsa, 1928 and the stem Pleurodira Cope, 1864, Dortokidae Lapparent de Broin & Murelaga (1996)), a new member of Bothremydidae was recognized (Lapparent de Broin & Murelaga 1996). Only three valid representatives of Bothremydidae were known in the Upper Cretaceous record of Europe at that time, all of them from the Campanian-Maastrichtian interval: *Rosasia soutoi* Carrington da Costa, 1940, restricted to the Portuguese area of Beira Litoral (Carrington da Costa 1940; Antunes & Broin 1988; Gaffney *et al.* 2006); and two forms exclusively identified in Southern France, *Elochelys perfecta* Nopcsa, 1931 and *Polysternon provinciale* (Matheron, 1869) (Nopcsa 1931; Broin 1977; Buffetaut *et al.* 1996; Gaffney *et al.* 2006). Lapparent de Broin & Murelaga (1996) attributed the new form from Laño to the genus *Polysternon* Portis, 1882, defining the new species '*Polysternon*' *atlanticum* Lapparent de Broin & Murelaga, 1996.

Subsequent studies, in many cases based on the discovery of new remains, but also other studies related to the analysis of previously known specimens, have significantly improved knowledge about the European record of Bothremydidae for the Campanian-Maastrichtian interval. In 1998, just two years after the establishment of '*Polysternon*' *atlanticum*, a new form was described for the upper Campanian to lower Maastrichtian record in Southern France: *Foxemys mechinorum* Tong, Gaffney & Buffetaut, 1998. The biogeographic distribution of this species has recently been expanded, being recognized in central Spain, in the upper Campanian to lower Maastrichtian site of Lo Hueco (Cuenca) (Pérez-García & Ortega 2018). Another new taxon, '*Elochelys convenarum*' Laurent, Tong & Claude, 2002, was defined by a single shell, found in the South of France, in upper Maastrichtian levels (Laurent *et al.* 2002). This species was also subsequently identified in Lo Hueco (Pérez-García *et al.* 2010), but also in the upper Campanian site of Armuña, central Spain (Segovia) (Pérez-García *et al.* 2016). The detailed revision of this species, thanks to the Spanish findings, allowed its reassignment to the new genus *Iberoccitanemys* Pérez-García, Ortega & Murelaga, 2012, with the new combination '*Iberoccitanemys convenarum*' (Laurent, Tong & Claude, 2002) being proposed (Pérez-García *et al.* 2012). A putative new Spanish species

of the genus *Polysternon*, '*Polysternon isonae*' Marmi, Luján, Riera, Gaete, Oms & Galobart, 2012, was defined based on two specimens from the Maastrichtian of Lleida (Northeast Spain) (Marmi *et al.* 2012). However, its validity was subsequently refuted (Pérez-García 2017). The strata that yielded the remains of the French taxon '*Tretosternum*' *ambiguum* Gaudry, 1890 (from Marne, North France) have recently been re-dated (Montenat & Merle 2018; Lapparent de Broin *et al.* 2018). As a consequence, this turtle, previously considered as Palaeocene (Broin 1977), is now recognized as an Upper Cretaceous form, from the Maastrichtian (Pérez-García 2020). Its recent detailed study has allowed the proposal of the new genus *Eotaphrosphys* Pérez-García, 2020, with the new combination *Eotaphrosphys ambiguum* (Gaudry, 1890) having been established (Pérez-García 2020). Therefore, seven forms of Bothremydidae are currently considered in the Campanian-Maastrichtian interval of Europe, all of them restricted to the South-Western region of the continent (France, Spain, and Portugal). Only one of them corresponds to a member of Taphrosphyini: *Eotaphrosphys ambiguum* (Pérez-García 2020). The other six species are part of Bothremydini. The two clades that compose this taxon are represented: Foxemydina and Bothremydina. Among these European forms, *Rosasia soutoi* is the only member of Bothremydina. Therefore, Foxemydina shows the greatest diversity, five putative valid forms being currently identified: *Elochelys perfecta*, *Foxemys mechinorum*, '*Iberoccitanemys convenarum*', *Polysternon provinciale*, and '*Polysternon*' *atlanticum* (Gaffney *et al.* 2006; Pérez-García *et al.* 2012).

The currently poorest-known member of Foxemydina from the Campanian-Maastrichtian interval in Europe is '*Polysternon*' *atlanticum*. In fact, its generic attribution has been considered as doubtful, and probably erroneous (Gaffney *et al.* 2006). Its presence has not been confirmed outside its type locality (Pérez-García 2017). Poorly informative elements to establish its systematic position within Bothremydini were used for the definition of this taxon, carried out in a short paper by Lapparent de Broin & Murelaga (1996). Subsequently, this taxon was described in more detail by Lapparent de Broin & Murelaga (1999) but based on the same remains. In fact, this problematic form is the only one that has not been included in phylogenetic analyses (see Pérez-García *et al.* 2012 and references therein). Thus, because of the very limited available information on '*Polysternon*' *atlanticum*, it has been barely considered, or even totally ignored, in subsequent works in which new European bothremydids were defined, or where the information on previously described forms was updated (e.g. Tong *et al.* 1998; Laurent *et al.* 2002; Pérez-García *et al.* 2012). In this sense, a currently valid diagnosis for '*Polysternon*' *atlanticum* is not available.

Considering the nature of the record of Bothremydidae found in the Campanian-Maastrichtian interval of Europe, comparative and systematic studies, the proposal of phylogenetic relationships, and the diagnoses of these forms are mainly based on shell characters. Fortunately, many unpublished plates of the taxon from Laño have been prepared and are studied here. They come from the reference collection for this form (MCNA), but found after the publication in which this taxon was defined (Lapparent de Broin & Murelaga 1996); and also from the collection of another institution (STUS), having been collected in the 1980s but remaining unpublished until now. These remains include osseous elements of the shell hitherto unknown for this taxon. The different remains allow the identification of intraspecific variability and even of anomalies in plates and in scutes. The study of these remains, together with the review of those considered by Lapparent de Broin & Murelaga (1996, 1999), allows us to evaluate the validity of '*Polysternon*' *atlanticum*, as well as to establish the systematic position of the bothremydid from Laño, taking into account current knowledge on the other European representatives. As a consequence, the faunal list referring to the members of this lineage recorded in the last two stages of the Cretaceous of Europe is updated.

INSTITUTIONAL ABBREVIATIONS

MCNA	Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz;
STUS	Sala de las Tortugas de la Universidad de Salamanca, Salamanca.

SYSTEMATIC PALAEONTOLOGY

Order TESTUDINES Batsch, 1788
Sub-order PLEURODIRA Cope, 1864
Hyperfamily PELOMEDUSOIDES Cope, 1868
Superfamily PODOCNEMIDOIDEA Cope, 1868
Family BOTHREMYDIDAE Baur, 1891
Infrafamily BOTHREMYDODDA Gaffney, Tong & Meylan, 2006
Tribe BOTHREMYDINI Gaffney, Tong & Meylan, 2006
Subtribe FOXEMYDINA Gaffney, Tong & Meylan, 2006
Genus *Iberoccitanemys* Pérez-García, Ortega & Murelaga, 2012

Iberoccitanemys atlanticum
(Lapparent de Broin & Murelaga, 1996) n. comb.
(Figs 1-3)

Polysternon atlanticum Lapparent de Broin & Murelaga, 1996: 731.

Elochelys convenarum Laurent, Tong & Claude, 2002: 465 **n. syn.**

Iberoccitanemys convenarum – Pérez-García *et al.* 2012: 223 **n. syn.**

TYPE LOCALITY AND HORIZON. — North Spain, Burgos Province, Treviño County, Laño quarry. Late Campanian, Late Cretaceous (Pereda Suberbiola *et al.* 2015).

HOLOTYPE. — MCNA 6316, a nuchal plate (Fig. 1H).

DISTRIBUTION. — Late Campanian to late Maastrichtian of Southern France (identified in the Haute-Garonne Department) and Sorthern and central Spain (known in the Provinces of Burgos, Cuenca and Segovia) (Lapparent de Broin & Murelaga 1996, 1999; Laurent *et al.* 2002; Pérez-García *et al.* 2010, 2012, 2016).

EMENDED DIAGNOSIS OF THE GENUS AND SPECIES (MODIFIED FROM PÉREZ-GARCÍA *ET AL.* 2012). — Member of Foxemydina with the following autapomorphies: carapace rectangular with straight or slightly depressed anterior margin; maximum carapace width in its posterior half; presence of six neurals and, therefore, sagittal contact of the last three pairs of costals; square first pair of marginals, covering more than half the lateral nuchal length. In addition, it is characterized by the following unique character combination: nuchal approximately as wide as long, with a short anterior margin (shared with *Polysternon provinciale* and *Foxemys mechinorum*); slightly curved lateral margins of the posterior plastral lobe (shared with *Foxemys mechinorum*); shallow and wide anal notch (shared with *Foxemys mechinorum*); large intergular, reaching the pectorals and preventing medial contact between the humerals (shared with *Elochelys perfecta*); pectoral-abdominal sulci very close to the anterior mesoplastral margins (shared with *Polysternon provinciale* and *Foxemys mechinorum*).

SHELL REMAINS FROM THE TYPE LOCALITY STUDIED HERE. — More than 200 plates from Laño, deposited in the MCNA and STUS collections, are attributable to *Iberoccitanemys atlanticum* n. comb. All of them are prepared and have been analyzed in detail to carry out this study. The main elements considered here, given the relevant characters from a systematic point of view (see Discussion), are those represented in Figures 1 to 3: two nuchals, MCNA 8599 (Fig. 1C) and MCNA 6316 (Fig. 1H); three neurals, STUS 15710 (Fig. 1G), STUS 15726 (Fig. 1M), and MCNA 7096 (Fig. 3L, M); a suprapygal, MCNA MCNA 16165 (Fig. 3K); nineteen costals, MCNA 7033 (Fig. 1E), STUS 15630 (Fig. 1F), MCNA 6984 (Fig. 1K), STUS 15684 (Fig. 1L), MCNA 16177 (Fig. 1N), MCNA 16157 (Fig. 1O), MCNA 16171 (Fig. 1P), MCNA 16149 (Fig. 1Q), MCNA 7052 (Fig. 1R), MCNA 7051 (Fig. 1S), STUS 15647 (Fig. 1T), STUS 15652 (Fig. 1U), STUS 15655 (Fig. 1V), STUS 15702 (Fig. 1W), STUS 15674 (Fig. 1X), STUS 15698 (Fig. 1Y), STUS 15690 (Fig. 1Z), STUS 15682 (Fig. 1AA), and STUS 15646 (Fig. 3N); five elements corresponding to peripherals, MCNA 7006 (Fig. 1A), STUS 15759 (Fig. 1B), three articulated plates numbered as MCNA 16123 (Fig. 1D), MCNA 7048 (Fig. 1I), and STUS 15753 (Fig. 1J); nine epiplastra, MCNA 16126 (Fig. 2A), STUS 15618 (Fig. 2B), MCNA 16139 (Fig. 2G), STUS 12104 (Fig. 2H), MCNA 7098 (Fig. 2I), MCNA 6320 (Fig. 2J), STUS 15616 (Fig. 2K), MCNA 7120 (Fig. 2L), and STUS 12105 (Fig. 2M); an entoplastron, STUS 12106 (Fig. 2C); seven hyoplastra, STUS 12193 (Fig. 2D), STUS 15607 (Fig. 2E), MCNA 16175 (Fig. 2O), STUS 15604 (Fig. 2P), STUS 15605 (Fig. 2Q), MCNA 16127 (Fig. 2R) and MCNA 7035 (Fig. 3O); two mesoplastra, MCNA 7076 (Fig. 2F) and MCNA 6323 (Fig. 2N); and five xiphiplastra, MCNA 6324 (Fig. 3A, B), MCNA 14167 (Fig. 3C, D), MCNA 16178 (Fig. 3E, F), MCNA 788 (Fig. 3G, H) and MCNA 6993 (Fig. 3I, J).

DISCUSSION

NEW ANATOMICAL INFORMATION FOR THE BOTHREMYDID FROM LAÑO

Some of the new remains from Laño correspond to specimens slightly longer than the largest known members of this taxon when it was defined (e.g. Fig. 2O). The maximum length of the shell of the new specimens from Laño can be estimated as approximately from 35 to 40 cm instead of the 30 cm calculated for the previously known specimens (Lapparent de Broin & Murelaga 1999). The anterior carapace margin is straight to slightly depressed, lacking a nuchal notch (Fig. 1B-D, J). The width of the anterior margin of the nuchal is equal to or shorter than half of the maximum width of this plate (Fig. 1C, H). More than a dozen specimens from Laño show that the neural series was not complete, the medial region of each sixth costal plate being in contact with the last neural, as well as with the opposite costal (Fig. 1M, N, R-AA). In fact, the proximal region of numerous posterior-most costals from Laño is identified (e.g. Fig. 1O), confirming that the medial contact between each plate of the seventh and eighth pairs of costals, instead of with the neural series, can be recognized. The presence of six neurals and, therefore, the sagittal contact of the last three pairs of costals, contrast with the previous interpretation of the shell of the taxon from Laño, established from fewer remains (the presence of at least seven neurals were interpreted by Lapparent de Broin & Murelaga 1999). A suprapygal plate is identified here for the first time (Fig. 3K). The lateral margins of the first vertebral scute overlap the latero-posterior region of the nuchal plate or are in contact with its lateral margins in some specimens (this condition was the only one previously identified for this taxon; Fig. 1C, H, K). However, these margins cross the posterior end of the first pair of peripherals in others (Fig. 1B, E, F, L). In fact, the first vertebral could even reach the lateral margin of the first pair of peripherals (Fig. 1B, D). Therefore, the lateral margins of the first vertebral are anteriorly divergent. Thus, the width of this vertebral is not markedly less than that of the second vertebral. In addition, the new material from Laño shows that the scutes corresponding to the first pair of marginals were square (Fig. 1B, C). The identification of the entoplastron of the bothremydid from Laño (Fig. 2C), hitherto unknown, shows that, unlike that previous interpretation (see Lapparent de Broin & Murelaga 1999: pl. 4.2), the intergular scute was long, reaching the pectorals and avoiding the medial contact between the humerals. Although the humero-pectoral sulcus is always very close to the contact between the epiplastra and the hyoplastra, its layout shows intraspecific variation. Thus, the humerals can: 1) overlap the posterior region of the epiplastra except the postero-medial area (Fig. 2D, G, Q, R); 2) be in contact with the postero-medial margin of these plates but not overlap them (Fig. 2O); or 3) lack contact (Fig. 2E, P; this last condition having so far been the only one recognized in Laño; see Lapparent de Broin & Murelaga 1999: pl. 4.2). The new material also allows the identification of previously unknown variability related to the overlap of the pectorals onto the mesoplastra. There are specimens: 1) lacking contact between these elements (Fig. 2R); 2) with contact (Fig. 2D); and 3) with a short overlap (Fig. 2F).

The availability of abundant material allows plate and scute anomalies to be identified. In fact, anomalies corresponding to both elements are recognized as relatively frequent in other bothremydids represented by several specimens, as reported, among others, for the oldest European form: the Spanish *Algorachelus peregrina* Pérez-García, 2016 (Pérez-García 2018). A small supernumerary scute was identified, adjacent to the medial region of the left humero-pectoral sulcus, in the most complete known shell of *Iberoccitanemys atlanticum* n. comb., from the Spanish site of Lo Hueco, in the Province of Cuenca (see Pérez-García *et al.* 2010: figs 2.2; 2.4; Pérez-García *et al.* 2012: fig. 3C, D). Some of the scute anomalies at Laño correspond to the identification of a medial sulcus on the posterior half of a first neural, generating a vertebral (i.e., the second one)

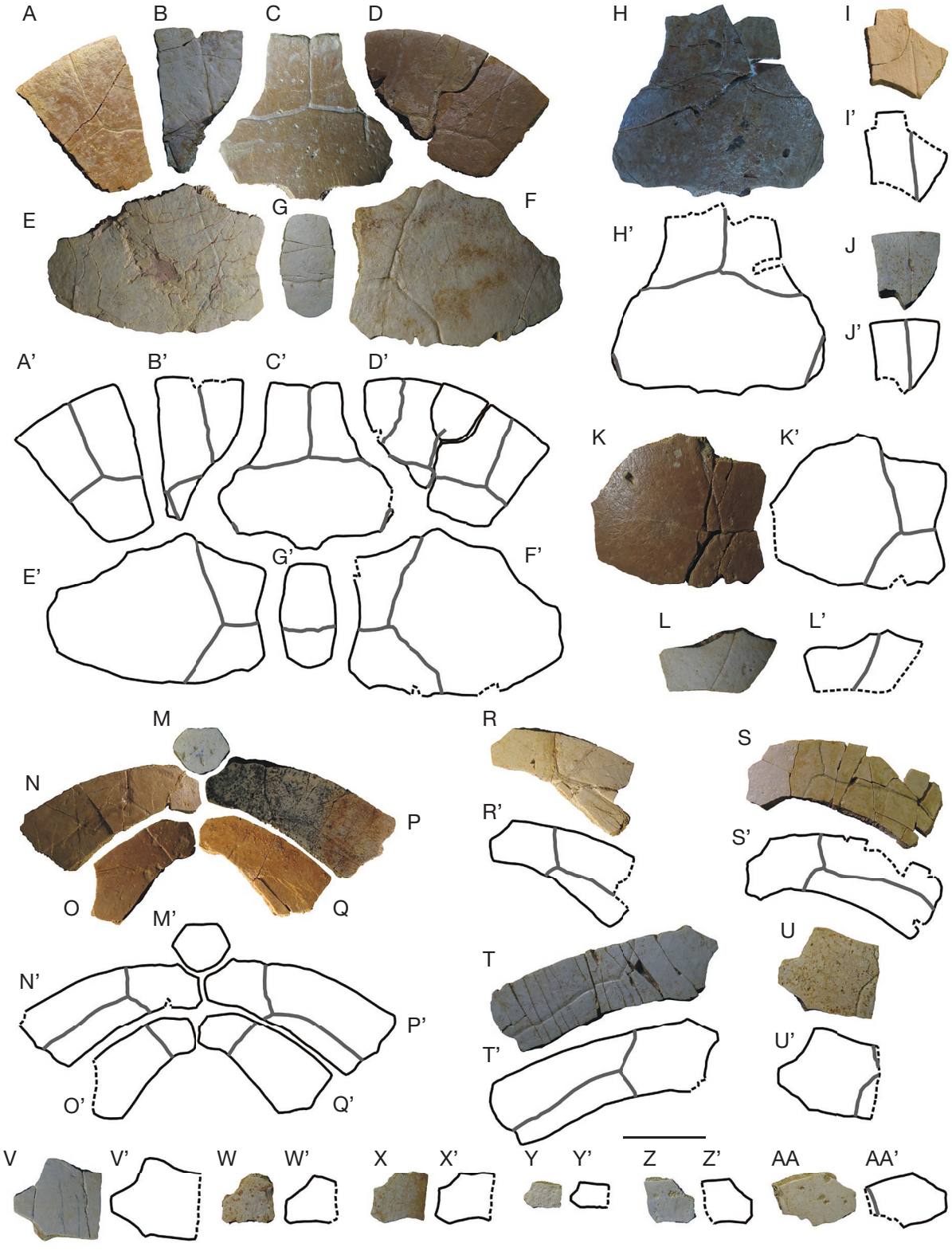

FIG. 1. — Dorsal view of elements of the carapace of the bothremydid turtle *Iberoccitanemys atlanticum* (Lapparent de Broin & Murelaga, 1996) n. comb., from the late Campanian (Late Cretaceous) in the Spanish quarry of Laño (Treviño County, Burgos Province): **A**, second left peripheral, MCNA 7006; **B**, first left peripheral, STUS 15759; **C**, nuchal, MCNA 8599, **D**, first, second and small supernumerary right peripheral, MCNA 16123; **E**, first left costal, MCNA 7033; **F**, first right costal, STUS 15630; **G**, first neural, STUS 15710; **H**, nuchal, MCNA 6316; **I**, first left peripheral, MCNA 7048; **J**, first left peripheral, STUS 15753; **K**, first left costal, MCNA 6984; **L**, first right costal, STUS 15684; **M**, sixth neural, STUS 15726; **N**, sixth left costal, MCNA 16177; **O**, seventh left costal, MCNA 16157; **P**, sixth right costal, MCNA 16171; **Q**, seventh right costal, MCNA 16149; **R**, sixth right costal, MCNA 7052; **S**, sixth right costal, MCNA 7051; **T**, sixth left costal, STUS 15647; **U**, proximal area of a sixth right costal, STUS 15652; **V**, proximal area of a sixth right costal, STUS 15655; **W**, proximal area of a sixth right costal, STUS 15702; **X**, proximal area of a sixth right costal, STUS 15674; **Y**, proximal area of a sixth right costal, STUS 15698; **Z**, proximal area of a sixth left costal, STUS 15690; **AA**, proximal area of a sixth left costal, STUS 15682. Scale bar: 30 mm.

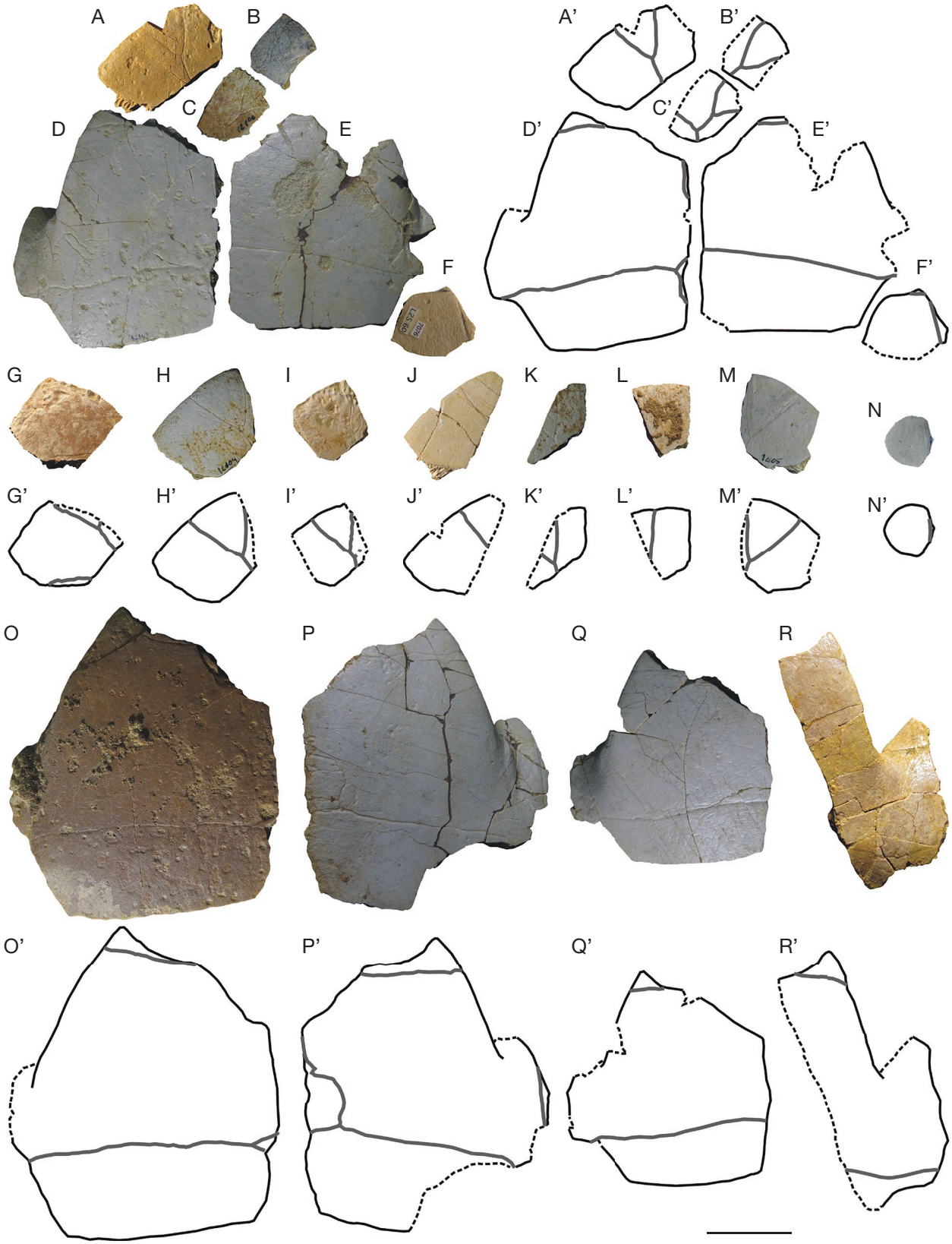

FIG. 2. — Ventral view of elements of the plastron of the bothremydid turtle *Iberoccitanemys atlanticum* (Lapparent de Broin & Murelaga, 1996) n. comb., from the late Campanian (Late Cretaceous) in the Spanish quarry of Laño (Treviño County, Burgos Province): **A**, right epiplastron, MCNA 16126; **B**, left epiplastron, STUS 15618; **C**, entoplastron, STUS 12106; **D**, right hyoplastron, STUS 12193; **E**, left hyoplastron, STUS 15607; **F**, left mesoplastron, MCNA 7076; **G**, right epiplastron, MCNA 16139; **H**, right epiplastron, STUS 12104; **I**, right epiplastron, MCNA 7098; **J**, right epiplastron, MCNA 6320; **K**, right epiplastron, STUS 15616; **L**, right epiplastron, MCNA 7120; **M**, left epiplastron, STUS 12105; **N**, mesoplastron, MCNA 6323; **O**, right hyoplastron, MCNA 16175; **P**, left hyoplastron, STUS 15604; **Q**, right hyoplastron, STUS 15605; **R**, left hyoplastron, MCNA 16127. Scale bar: 30 mm.

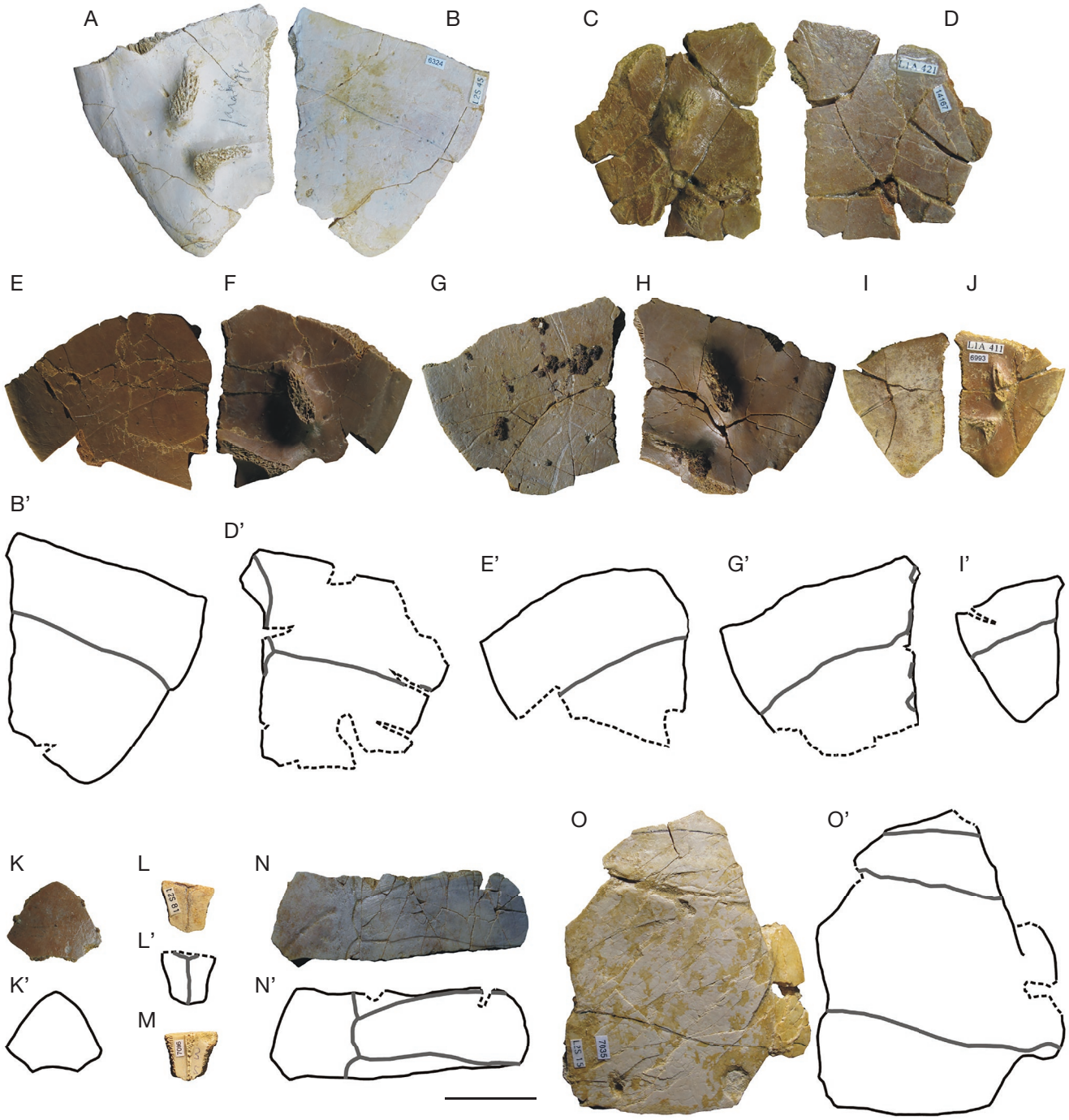

FIG. 3. — Elements of the shell of the bothremydid turtle *Iberoccitanemys atlanticum* (Lapparent de Broin & Murelaga, 1996) n. comb., from the late Campanian (Late Cretaceous) in the Spanish quarry of Laño (Treviño County, Burgos Province): **A**, **B**, left xiphiplastron, MCNA 6324, in dorsal (**A**) and ventral (**B**) views; **C**, **D**, left xiphiplastron, MCNA 14167, in dorsal (**C**) and ventral (**D**) views; **E**, **F**, right xiphiplastron, MCNA 16178, in ventral (**E**) and dorsal (**F**) views; **G**, **H**, right xiphiplastron, MCNA 788, in ventral (**G**) and dorsal (**H**) views; **I**, **J**, right xiphiplastron, MCNA 6993, in ventral (**I**) and dorsal (**J**) views; **K**, suprapygal, MCNA 16165, in dorsal view; **L**, **M**, first neural showing an anomalous scute pattern, MCNA 7096, in dorsal (**L**) and ventral (**M**) view; **N**, second right costal showing an anomalous scute pattern, STUS 15646, in dorsal view; **O**, left hyoplastron showing an anomalous scute pattern, MCNA 7035, in ventral view. Scale bar: 30 mm.

divided into two elements (Fig. 3L); a supernumerary scute on a second costal, short but wide, located between the first and the second right pleurals (Fig. 3N); and a supernumerary scute on the anterior region of a left hyoplastron, completely separating the humeral from the pectoral scutes (Fig. 3O). Osseous anomalies in the shell are often associated with anomalies in the scute pattern, as documented for Bothremydidae (Pérez-García 2018). A small supernumerary plate is located between the first and the second right peripherals of a specimen from Laño, partially preventing the contact between these plates (Fig. 1D). A scute anomaly is also present in that region; a sulcus partially divides the second right marginal.

Systematic discussion

The attribution of the bothremydid turtle from Laño to Bothremydini can be confirmed (following Gaffney *et al.* 2006; Pérez-García *et al.* 2012), differing from the members of Taphrosphyini (a clade represented in the European Maastrichtian record by *Eotaphrosphys ambiguum*), among other characters, by the absence of a strong ornamental pattern on the outer surface of the carapace; relatively wide pubic scars; elongated ischiatic scars, not contacting the anal notch margins; and contact or a short distance between the pectoral scutes and the epiplastra (Gaffney *et al.* 2006; Pérez-García 2020; Pérez-García *et al.* 2020). As indicated (see Introduction) Bothremydini is represented in the Campanian-Maastrichtian interval in Europe by both Bothremydina and Foxemydina. The taxon from Laño cannot be attributed to Bothremydina considering the absence of a relatively long distance between the pectorals and the epiplastra (Fig. 2D, E, O-R), the long overlap of those scutes onto the entoplastron (Fig. 2C-E, O-R) (the pectorals only contact the most posterior end of the entoplastron in the Portuguese form *Rosasia soutoi*; see Carrington da Costa 1940, 1958; Antunes & Broin 1988), and the absence of a long overlap of the pectorals onto the mesoplastra (Gaffney *et al.* 2006; Pérez-García *et al.* 2012). However, the states for all these characters present in the taxon from Laño support its attribution to the sister group Foxemydina.

The diagnosis proposed by Lapparent de Broin & Murelaga (1996) for '*Polysternon*' *atlanticum* was slightly amended by Lapparent de Broin & Murelaga (1999), subsequently being reproduced, without modifications, by Gaffney *et al.* (2006). However, the increase in knowledge about the anatomy and diversity of Bothremydidae since the establishment of the species '*Polysternon*' *atlanticum*, especially considering the record of the Campanian-Maastrichtian interval in Europe (see Introduction), means that the available diagnosis hampers distinguishing the taxon from Laño from all other representatives of this clade. Thus, only three characters were considered by Lapparent de Broin & Murelaga (1999), all of them defined in opposition to the states recognized for *Polysternon provinciale*: smaller shell, between 11 to 32 cm long; narrower first vertebral, not covering all the nuchal posterior border or slightly wider than it; and absence of thin parallel striations on the carapace. As indicated (see above), the maximum shell size of the species from Laño is recognized here as close to 40 cm, a length not only shorter than that of *Polysternon provinciale*, but also than that of *Foxemys mechinorum*, which can reach a length close to 50 cm (Tong *et al.* 1998; Gaffney *et al.* 2006; Pérez-García & Ortega 2018). However, the taxon from Laño is not the only European member of Foxemydina smaller than those species: *Elochelys perfecta* and '*Iberoccitanemys convenarum*' also have smaller shells. The maximum shell size recognized for the Laño taxon is compatible with the range of variability known for the adult specimens of '*Iberoccitanemys convenarum*', but larger than that of *Elochelys perfecta* (Nopcsa 1931; Laurent *et al.* 2002; Pérez-García *et al.* 2012). The high range of variability for the first vertebral scute of the bothremydid from Laño identified here is similar to that recognized in such other European forms as *Foxemys mechinorum*, '*Iberoccitanemys convenarum*' and *Polysternon provinciale* (Tong *et al.* 1998; Gaffney *et al.* 2006; Pérez-García & Ortega 2018). The presence of thin parallel striations on the carapace is recognized as exclusive to *Polysternon provinciale* within Bothremydini, their absence being, therefore, shared between the taxon from Laño and the other forms.

Gaffney *et al.* (2006) questioned the attribution of '*Polysternon*' *atlanticum* to the genus *Polysternon*, but they did not raise any doubts regarding its specific validity. They proposed the same emended diagnosis for the species *Polysternon provinciale* as for the genus *Polysternon*, characterized by a combination of characters, all of them defined as opposed to those observed in *Foxemys mechinorum*, including four shell characters: the above discussed presence of parallel striations on the carapace, representing an autapomorphy for this species within Foxemydina; as well as the presence of a nuchal notch, rounded lateral borders of the posterior plastral lobe, and a narrow anal notch. The anterior carapace margin of both *Foxemys mechinorum* and '*Iberoccitanemys convenarum*' lacks a well-developed nuchal notch, being straight or only slightly depressed (Tong *et al.* 1998; Pérez-García *et al.* 2012, 2016). This condition is shared with the taxon from Laño (Fig. 1B-D), but differs from that in *Elochelys perfecta*, which shows a convex margin (Nopcsa 1931; Pérez-García *et al.* 2012; Pérez-García & Ortega 2018). The presence of well-developed rounded lateral borders in the posterior plastral lobe of *Polysternon provinciale* is shared with *Elochelys perfecta*, differing from the condition in *Foxemys mechinorum*, '*Iberoccitanemys convenarum*', and in the taxon from Laño (Fig. 3A-J), in which those edges are slightly curved (Nopcsa 1931; Tong *et al.* 1998; Laurent *et al.* 2002; Pérez-García *et al.* 2012, 2016). *Elochelys perfecta* has a narrow anal notch, as in *Polysternon provinciale*, but it is shallower. *Foxemys mechinorum*, '*Iberoccitanemys convenarum*' and the taxon from Laño share a shallow and wide notch, more than twice as wide as it is deep (Tong *et al.* 1998; Pérez-García *et al.* 2012; Pérez-García & Ortega 2018).

The absence of articulated shells of Bothremydidae in Laño does not allow an evaluation of such characters as the general morphology of the carapace, or the relative position between the anterior margin of the carapace and that of the plastron. However, the identification of plates corresponding to all shell elements, most of them represented by several specimens, allows a comparison of the states corresponding to all the other shell characters included in the diagnoses of the members of Foxemydina known in the European Campanian-Maastrichtian interval. The wide anterior margin of the nuchal of *Elochelys perfecta*, greater than half the maximum width of this plate, contrasts with the condition in *Foxemys mechinorum*, '*Iberoccitanemys convenarum*' and *Polysternon provinciale*, but also in the taxon from Laño (Fig. 1C, H) (Nopcsa 1931; Tong *et al.* 1998; Laurent *et al.* 2002; Pérez-García *et al.* 2012). The presence of a suprapygal plate in the taxon from Laño is shared with all these taxa except *Elochelys perfecta* (Nopcsa 1931; Pérez-García *et al.* 2012). The development of nearly parallel lateral margins of the first vertebral of *Elochelys perfecta*, this scute being markedly narrower than the second one, not only contrasts with the condition in the taxon

from Laño (Fig. 1B, C, E, F, H, K, L), but also with that of the other representatives of Foxemydina (Pérez-García *et al.* 2012, 2016). The presence of wider than long mesoplasta, recognized as exclusive to *Elochelys perfecta* within Foxemydina (Nopcsa 1931; Pérez-García *et al.* 2012), is not shared with the taxon from Laño either (Fig. 2F, N). The presence of contact between the intergular scute and the pectorals is exclusively shared by *Elochelys perfecta* and '*Iberoccitanemys convenarum*' within Foxemydina (Nopcsa 1931; Pérez-García *et al.* 2012).

The states recognized in the taxon from Laño for all characters discussed here are compatible with those present in a single known species, whose currently known biostratigraphic (upper Campanian to upper Maastrichtian; Laurent *et al.* 2002; Pérez-García *et al.* 2016) and paleogeographic distributions (Southern France to central Spain; Laurent *et al.* 2002; Pérez-García *et al.* 2010, 2012, 2016) are also compatible with those of the form from Laño: '*Iberoccitanemys convenarum*'. In addition, the presence of six neurals, allowing the sagittal contact of the last three pairs of costals, and that of square scutes corresponding to the first pair of the marginal series, were recognized as autapomorphies for '*Iberoccitanemys convenarum*' within Foxemydina (Pérez-García *et al.* 2012). Therefore, all remains of Bothremydidae from Laño are compatible with a single form, which shows no difference with that found in several regions of South-Western Europe (the French Haute-Garonne Department and the Spanish Cuenca and Segovia provinces). It had originally been defined as '*Elochelys convenarum*', and subsequently reassigned to the new genus *Iberoccitanemys*, by the combination '*Iberoccitanemys convenarum*'. As a consequence of this study on the hitherto poorly known taxon represented in Laño, the European diversity of Bothremydidae at the end of the Cretaceous is reduced, due to the new combination *Iberoccitanemys atlanticum* n. comb.

CONCLUSIONS

Bothremydidae represents the most abundant and diverse group of turtles at the end of the Cretaceous (Campanian-Maastrichtian interval) in South-Western Europe, where it is identified by a representative of Taphrosphyini, a member of Bothremydina, and five putative valid species of Foxemydina. The poorest known member of Foxemydina was the problematic '*Polysternon*' *atlanticum*, which lacked a diagnosis that would confirm its specific validity, and whose generic attribution was doubtful. It was only identified in its type locality: the upper Campanian quarry of Laño, in Treviño County (Province of Burgos, North Spain). Despite the notable increase in knowledge about this lineage, no study on this species has been conducted from the 1990s until the present one. Abundant unpublished material from the bothremydid of this locality is analyzed here. In this way, all elements of the shell of this species are identified, and the states represented for the characters that define the other representatives of the group can be characterized. Furthermore, the abundance of remains makes it possible to identify intraspecific variability, which provides more information for a better understanding of this taxon.

The validity of the species from Laño is confirmed here. However, its attribution to the genus *Polysternon* is refuted. Thus, '*Iberoccitanemys convenarum*' (originally described as '*Elochelys convenarum*') is recognized as recognized here as a synonym of '*Polysternon*' *atlanticum*, thus establishing the new combination *Iberoccitanemys atlanticum* n. comb. Better knowledge about this species allows us to propose its emended diagnosis. The species *Iberoccitanemys atlanticum* n. comb., previously identified as exclusive to its type locality, is recognized both in various Spanish regions (Burgos, Cuenca, and Segovia provinces) and in Southern France (Haute-Garonne Department). The diversity of Foxemydina in the Campanian-Maastrichtian interval of Southwestern Europe is recognized as less than that previously considered, and only two forms are identified in the Iberian Peninsula, *Foxemys mechinorum* and *Iberoccitanemys atlanticum* n. comb., with this latter species being the most common.

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