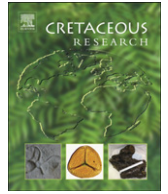


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Turtles from the Lower Cretaceous of the Cameros Basin (Iberian Range, Spain)

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ABSTRACT

Knowledge of the turtle fauna from the Lower Cretaceous of the Iberian Peninsula has been very limited until now. There are several fossil sites where Lower Cretaceous associations of continental vertebrates have been found. Although turtles have been identified in some of them, most of these specimens have not been studied, so the diversity is unknown. Among all these findings, the turtles from the Cameros Basin are considered particularly relevant, both in their abundance and diversity. Their study has allowed the identification of several taxa. At least one representative of Solemydidae and three taxa of Eucryptodira are recognized. This study establishes kinship and biogeographic relationships between the taxa in Cameros with those found in other Spanish fossil sites and with those of other European regions.

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1. Introduction

There are numerous European locations where Lower Cretaceous continental vertebrates have been found, with turtles being one of the most abundant groups (Hirayama et al., 2000). They are generally represented by isolated and fragmented material that is difficult to identify. Although comprehensive studies have been conducted on much of the vertebrate groups represented in many of these places (e.g., at the Spanish site of Galve (Teruel)) (Ruiz-Omeñaca et al., 2004; Sánchez-Hernández et al., 2007), the poor preservation of the turtle fossils has generally hampered their study, with knowledge of the diversity represented being very limited (Danilov, 2005; Lapparent de Broin, 2001). Consequently, the study of new material can greatly expand our knowledge about this group.

Elements assigned to turtles have been found in several Lower Cretaceous fossil sites in the Iberian Peninsula. This record is usually made up of disjointed and poorly preserved elements, and a high percentage of the material found has not been studied. In fact, very few taxa have been identified, with some of the determinations made being wrong, such as the allusions to *Hylaeochelys* Lydekker (1889a), *Tretosternon* Owen (1842) (Royo y Gómez, 1927a, b; see discussion in Pérez-García, 2009a), and *Trachyaspis* Meyer

(1843) (Bergounioux, 1957; see discussion in Lapparent de Broin, 2001).

All discoveries of Early Cretaceous turtles of the Iberian Peninsula have been made in the Iberian Range. The findings from the Cameros Basin are of particular relevance due to the diversity of taxa represented and to their state of preservation (Pérez-García et al., 2010a, b). Numerous plates from this basin are here assigned to Solemydidae, with its record being the best known of the group in the Lower Cretaceous of the Iberian Peninsula, where until now very scarce diagnostic material had been identified. In addition, three taxa assigned to Eucryptodira (sensu Joyce et al., 2004) are identified there, all of which are recognized from articulated shell elements, which is exceptional for the Iberian record. One of them is *Salasemys pulcherrima* Fuentes Vidarte, Meijide Calvo and Meijide Fuentes, 2003 a taxon defined in the western region of this basin from a single specimen (Fuentes Vidarte et al., 2003), but that has recently been reported in the eastern region from fragmentary elements (Pérez-García et al., 2010b). The other two taxa, one in the eastern Cameros Basin and the other in the western Cameros Basin, cannot be ascribed to any known genus. The presence of three relatively complete eucryptodiran carapaces in the Cameros Basin, and their identification as three taxa not known outside this basin, is indicative of the limited information on European Lower Cretaceous turtles.

The attribution of Lower Cretaceous material to Pelomedusoides (Eupleurodira) (Jiménez Fuentes, 1992) and the assignment of

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fragmentary material to Pleurosternidae (Paracryptodira) (Viera and Torres, 1996) are also discussed in order to understand the diversity of turtles represented in the Cameros Basin. This is important because it involved the first reference to Pelomedusoides in Europe and one of the most recent assignments to Pleurosternidae on this continent.

Therefore, this paper analyses the variability of turtles recorded in a European Cretaceous basin, specifically in the Cameros Basin. Within this basin, the record of its two margins (eastern and western) is correlated and compared. After describing and discussing this record, the information is compared with that of the taxa identified in other Iberian regions and with the European record. Palaeobiogeographic relationships are established through recognition of shared or closely related taxa with those of the palaeocheloniofauna of other Spanish or European localities, and that of other taxa hitherto endemic to this basin, including new species. These studies reveal the importance of the record of the Spanish Lower Cretaceous turtles.

Institutional abbreviations. BMNH, British Museum of Natural History, London, England; CPT, Museo Fundación Conjunto Paleontológico de Teruel, Teruel, Spain; ICIPLR, Igea, Centro de Interpretación Paleontológico de La Rioja, La Rioja, Spain; MCNA, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, País Vasco, Spain; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MDS, Museo de Dinosaurios de Salas de los Infantes, Burgos, Spain; STUS, Sala de las Tortugas, Universidad de Salamanca, Salamanca, Spain.

2. Palaeontological context

Although Pancryptodira and Panpleurodira have been recognized in the European Lower Cretaceous record, the latter group has only been identified from scarce and disarticulated elements from the late Barremian deposits of Vallipón (Teruel, Castellote Sub-basin, Maestrazgo Basin, Central Iberian Range, Spain). An undetermined representative of Dortokidae has been assigned to Panpleurodira, being the oldest known record of this group of endemic European turtles (Murelaga Bereikua, 1998). A possible representative of Pelomedusoides has also been preliminarily identified in the Lower Cretaceous of El Cogorro (Burgos, western Cameros Basin, NW Iberian Range) (Jiménez Fuentes, 1992), a group not known in other European sites prior to the Campanian (Gaffney et al., 2006; Lapparent de Broin, 2001; Pérez-García et al., 2010c). Therefore, if confirmed, this attribution would imply that this group (which originated in Gondwana) arrived in Europe earlier than is interpreted at other European sites. This material is studied here, confirming its attribution to this group, but also finding that, in fact, it comes from the Late Cretaceous.

The other turtles identified in the European Lower Cretaceous correspond to Pancryptodira. Solemydidae is a basal pancryptodiran group whose precise systematic position remains uncertain (Danilov, 2008; Lapparent de Broin and Murelaga, 1999). Its oldest reference is from the Late Jurassic of North America and Europe, with several representatives being recognized in the European Lower Cretaceous. The validity of some of the Lower Cretaceous attributions has been questioned as some of the identified specimens (many unpublished) cannot be ascribed to any defined taxa (Lapparent de Broin, 2001). Owing to the generally fragmented nature of its record and to the lack of knowledge of many of the represented taxa, no hypothesis has been put forth that shows the relations between the taxa of Solemydidae or to the other basal pancryptodiran representatives.

In the European Lower Cretaceous, Paracryptodira is represented by Pleurosternidae, with the record of *Pleurosternon* Owen (1853), being relatively abundant. However, other lesser-known taxa that

may belong to this group have also been identified, as is the case of *Desmemys* Wegner, 1911 or "*Glyptops*" *typocardium* (Seeley, 1869) (Milner, 2004; Pérez-García and Ortega, 2011; Wegner, 1911). Pleurosternidae has been identified in Europe from the Middle Jurassic of Kirtlington (Oxfordshire, England) (Gillham, 1994; Scheyer and Anquetin, 2008), and its presence is recognized in North America from the Late Jurassic (Brinkman et al., 2000; Gaffney, 1979).

The European Lower Cretaceous record of Pancryptodira is also composed of members of Eucryptodira. One is a basal representative of this node, *Brodiechelys* Nopcsa, 1928. This taxon is known from shells and fragments from the Barremian of the Isle of Wight, England (Nopcsa, 1928). Although it has been considered to be closely related to Plesiochelyidae (a group of European turtles very abundant in the Upper Jurassic), or included in that group (Lapparent de Broin, 2001), available information on this taxon is very limited. Consequently, in several papers *Brodiechelys* has been interpreted as a genus very close to Xinjiangchelyidae (turtles known from the Middle Jurassic to the Early Cretaceous of Asia) or even as a member of this group (Danilov, 2005, 2008; Hirayama et al., 2000). In the Cryptodira node (sensu Joyce et al., 2004), two Lower Cretaceous European taxa have been assigned to Trionychoidea, which are the oldest European references of this group. One is *Peltochelys* Dollo, 1884, identified in the middle Barremian–early Aptian deposits of Bernissart (Belgium) (Joyce, 2007; Meylan, 1988), which can only be identified from one shell (Pérez-García and Ortega, 2010). The other taxon identified is *Sandownia* Meylan Moody, Walker and Chapman, 2000, represented only by one skull from the Lower Aptian of the Isle of Wight (Meylan et al., 2000). This specimen has generally been assigned to the Trionychoidea node (Danilov, 2005; Lapparent de Broin, 2001; Meylan et al., 2000). Nevertheless, this taxon has recently been interpreted as a basal eucryptodiran turtle (Joyce, 2007). Other turtle taxa of uncertain affinities, and undefined taxa, are also recognized, generally represented by fragmentary material. Although these specimens have traditionally been referred to as representatives of "Macrobaenidae" (Fuentes Vidarte et al., 2003) or as turtles with a "chelydroid" appearance (Lapparent de Broin, 2001), they are not considered to be related to Chelydridae, a node identified in Eurasia since the Eocene (Danilov, 2005), and that may belong to several groups so far undefined. Therefore, despite the relatively high diversity of turtles in the Lower Cretaceous of Europe, this group of reptiles has received little attention, mostly owing to poor preservation, with several of the taxa being represented by only one or just a few specimens. Besides the existence of endemic groups, such as Dortokidae, the position of Europe allowed it to share with North America the presence of representatives of Paracryptodira and with Asia that of Eucryptodira (Hirayama et al., 2000).

There are several Iberian sites where Lower Cretaceous associations of continental vertebrates have been found. Although turtles have been identified in some of them, most specimens have not been studied, so their diversity is not known and, in fact, very few taxa have been recognized. For instance, "*Trachyaspis*" *turbulensis* Bergouxioux, 1957 has been identified from four fragmentary but articulated peripheral plates from the Aptian of Gargallo (Teruel, Oliete Subbasin, Maestrazgo Basin). This material can be considered as an indeterminate representative of Solemydidae, not assignable to *Trachyaspis* (Lapparent de Broin, 2001), which is a representative of Cheloniidae. The absence of diagnostic elements does not allow any comparison and discussion with other representatives of Solemydidae. Another taxon has also been described in the Iberian Lower Cretaceous: *S. pulcherrima*, from the late Hauterivian–Barremian deposits of Tenadas del Jabalí (Salas de los Infantes, Burgos, western Cameros Basin). This taxon was described with only one specimen (Fuentes Vidarte et al., 2003) preserving a high percentage of skeletal elements. Its accurate systematic

position within Eucryptodira is uncertain. The other turtles from the Iberian Lower Cretaceous are generally very fragmented specimens that are difficult to assign, and in some cases more complete shells that have not been studied. In Lower Cretaceous levels of different age from the area of Galve (Teruel, Galve Subbasin, Maestrazgo Basin), several chelonian taxa have been identified from isolated and fragmentary material. The presence of Solemydidae, Pleurosternidae, and Eucryptodira indet. have been preliminarily recognized there (Pérez-García et al., 2010d). Pleurosternidae has also been preliminarily recognized in the Lower Cretaceous of the eastern Cameros Basin (Viera and Torres, 1996). Four turtle taxa have been cited in the Lower Aptian of the area of Morella (Castellón, Morella Sub-basin, Maestrazgo Basin) (Ortega et al., 2006; Pérez-García et al., 2008; Pérez-García, 2009a). However, only an indeterminate basal member of Eucryptodira (Pérez-García et al., 2008; Pérez-García and Ortega, 2009,) and a solemydid that could be *Helochelydra* Nopcsa, 1928 (Ortega et al., 2006; Pérez-García, 2009a) have been identified. A solemydid turtle, preliminarily assigned to *Trachydermochelys* Seeley, 1869, has been identified in the Albian of Cabezo de las Eras (Teruel, Oliete Subbasin) (Canudo et al., 2005). The taxon identified at the site of Las Hoyas (Serranía de Cuenca Basin, southwestern Iberian Range) has been cited in several publications since the 1980s. It was considered to be an undefined form related to different groups of Pancryptodira, such as Toxochelyidae, Cheloniodea, Centrocryptodira, or a turtle “chelydroid” in appearance, but without the autapomorphies of the family Chelydridae (Jiménez-Fuentes, 1995; Lapparent de Broin, 2001; Ortega et al., 1999; Sanz et al., 1988). It has recently been attributed to a new basal representative of Eucryptodira, *Hoyasemys jimenezi* Pérez-García, de la Fuente and Ortega, in press a. Apart from the reference to Dortokidae in Vallipón, the presence of a “chelydroid” turtle was mentioned, represented by a few plate fragments (Murelaga Bereikua, 1998). Plate fragments from the area of Uña (Serranía de Cuenca Basin) have also been assigned to an indeterminate turtle with that appearance (Krebs, 1995), probably *Hoyasemys* (Pérez-García et al., in press-a). Although these three localities are dated as late Barremian, the poor preservation of the specimens from Vallipón and Uña do not allow an assessment of whether they are of the same taxon.

Therefore, the Spanish Lower Cretaceous turtle record is composed of generally poorly preserved specimens from different basins of the Iberian Range. In this context, the Cameros Basin turtles provide important data to the little-known European Lower Cretaceous record and, especially, to the Iberian record. These turtles are noted for their preservation, with abundant Solemydidae plates recognized with several characters so far unknown in representatives of the Iberian Lower Cretaceous, and relatively complete carapaces of several eucryptodiran taxa.

3. Geographic and geological context

The Cameros Basin is the most north-western basin of the Iberian rift system. This rift system initially developed during the break-up of Pangea in the Late Permian–Triassic, forming several NW–SE basins (Salas et al., 2001). During the second rifting phase, related with the opening of the North Atlantic Ocean in the Upper Jurassic–Lower Cretaceous, non-marine deposits started to accumulate in the Cameros Basin. The second rift phase extended to the middle Albian, and during the Late Cretaceous thermal subsidence allowed the deposition of marine deposits until Campanian times (Floquet, 1998). During the Maastrichtian, alluvial and lacustrine/palustrine sedimentation took place in the Cameros area prior to the main tectonic events of the Alpine orogeny (Floquet and Meléndez, 1982).

The compression of Iberia between Africa and Eurasia during the Alpine Orogeny in the Cenozoic led to the tectonic inversion of

the main extensional Mesozoic faults (Casas-Sainz, 1993; Casas-Sainz and Gil Imaz, 1998; Guimerá et al., 1995). The Cameros Basin has a syncline geometry that developed on an extensional fault that, during its extension, favoured the migration of the depocentre northwards (Mas et al., 1993).

The first stratigraphic studies in the basin, and the unique geological map of the entire basin to the present day, were carried out by Beuther (1966) and Tischer (1966) (Fig. 1A), who proposed a lithostratigraphic division into five groups, from base to top: Tera, Oncala, Urbión, Enciso, and Oliván. During the 1980s and 1990s, after the appearance of sequence stratigraphy, several stratigraphic and sedimentologic studies divided the sedimentary record into formations and alloformations (Clemente and Alonso, 1990; Clemente and Pérez Arlucea, 1993; Gómez Fernández and Meléndez, 1994; Martín-Closas and Alonso Millán, 1998; Platt, 1986, 1989a), and others divided it into depositional sequences (Mas et al., 1993; Salas and Casas, 1993) (Fig. 1B). The age of the Cameros sediments has been determined mainly on the basis of charophyte and ostracod biostratigraphy (Martín-Closas and Alonso Millán, 1998; Schudack and Schudack, 2009). The recent paper of Schudack and Schudack (2009) maintains the previous chronostratigraphy in the western basin, but proposes some changes in the eastern part. The main change is that the classic Urbión Group and associated formations are younger than the Valanginian, and the base of the Enciso Group is proposed as middle Valanginian and the top as late Barremian.

The Cameros Basin sediments consist of alluvial fan, fluvial, carbonate-precipitating lacustrine environments, and playa-lakes. The latter were only present in the eastern basin. The turtle remains in the eastern basin have been recovered from the Enciso Group, in the towns of Torremuña and Igea (Fig. 1A), which is dominated by carbonate-precipitating lake deposits with siliciclastic supplies (Doublet and Garcia, 2004). The remains from Tenadas del Jabalí and Monte Puente Ballesta (Salas de los Infantes) in the western basin belong to the Pinilla de los Moros Formation, which traditionally has been included in the Tera Group (Fig. 1A and B). The remains from La Tejera and Tenada Rosada appeared in the Castrillo de la Reina Formation and Pantano de la Cuerda del Pozo Formation, which are part of the Urbión Group. These formations are present in the Salas area (Arribas et al., 2003), but the great differences between the fluvial deposits of the Salas area and those of the stratotype of the Pantano de la Cuerda del Pozo Formation do not allow their differentiation.

The Pinilla de los Moros Formation and the Castrillo de la Reina Formation/Pantano de la Cuerda del Pozo Formation are interpreted as fluvial environments. The first is dominated by sheet-like channel fills and the second, in the Salas de los Infantes area, is dominated by ribbon-shaped channel fills isolated in red mudstones (Platt, 1989a, b).

The turtle fragments from El Cogorro were found in the lacustrine Maastrichtian deposits that surround the Cameros Basin, in the Santibáñez del Val Formation. These deposits pertain to the post-rift stages of the Iberian Basin.

4. Turtles from the Lower Cretaceous of the Cameros Basin

4.1. Basal pancryptodira: Solemydidae

Testudines Batsch (1788)

Pancryptodira Joyce et al. (2004)

Solemydidae Lapparent de Broin and Murelaga (1996)

aff. *Helochelydra*

Fig. 2A–Q

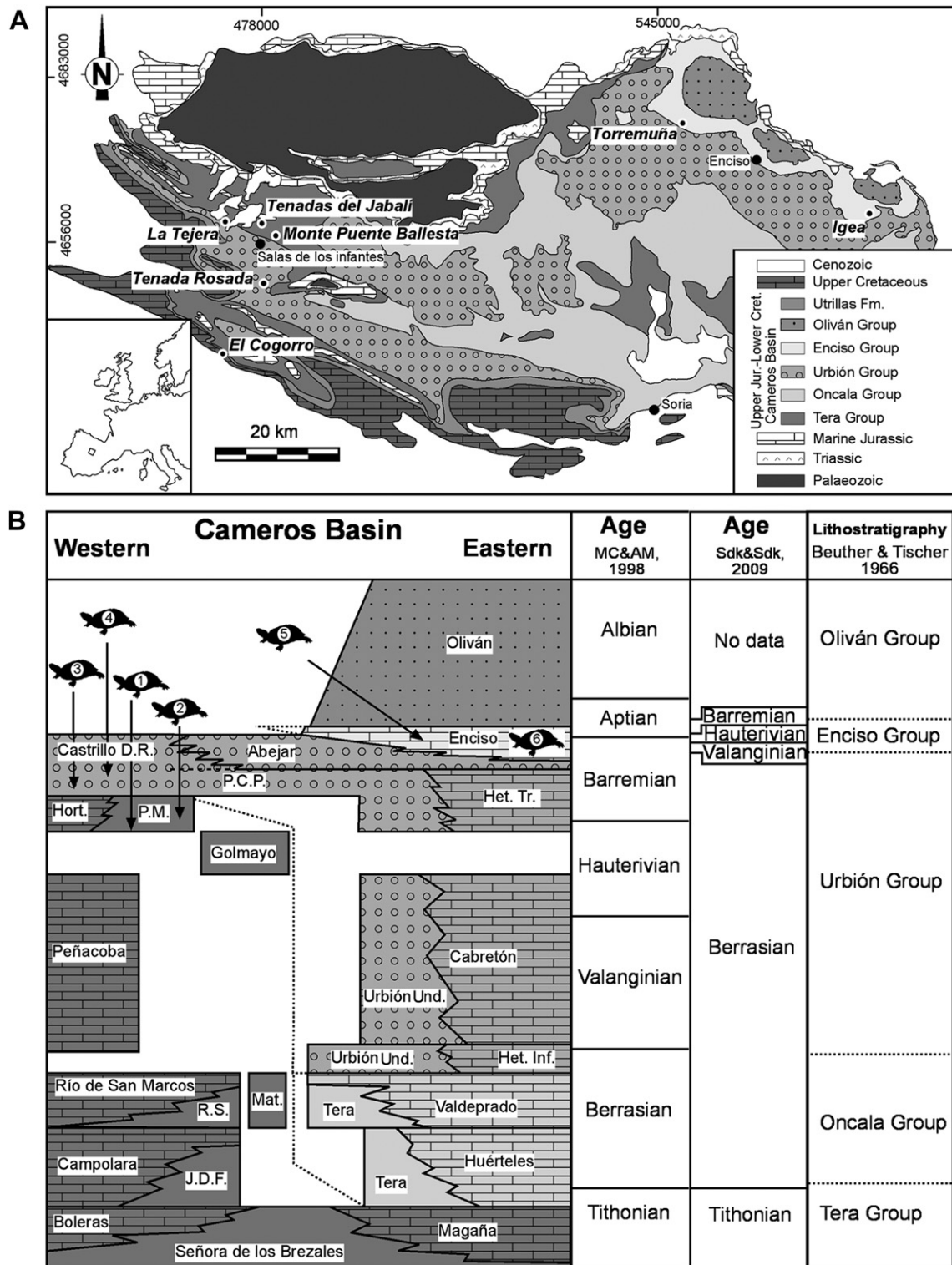


Fig. 1. Geological setting of the sites of the Cameros Basin where turtle fossils have been found. A, Geological map of the Cameros Basin, modified from Beuther (1966) and Tischer (1966). The turtle sites are indicated by black dots with white rims. B, Stratigraphy of the Lower Cretaceous Cameros Basin, modified from Martín-Closas and Alonso Millán (1998). The different formations arranged in the classical Groups of Beuther (1966) and Tischer (1966) (dotted lines and same grey-scale and pattern as in Fig. 1A), indicated in the lithostratigraphy column at the right of the sketch (Beuther and Tischer, 1966). The carbonate-dominated formations are illustrated by the typical limestone pattern. The two age columns reflect the ages proposed by Martín-Closas and Alonso Millán (1998) (MC & AM, 1998) and by Schudack and Schudack (2009) (Sdk & Sdk, 2009). The stratigraphic position of the turtle sites studied are indicated by a turtle symbol. Abbreviations: Castrillo D.R., Castrillo de la Reina; Het. Inf., Heterolítica Inferior; Het. Tr., Heterolítica de Transición; Hort., Hortigüela; J.D.F., Jaramillo de la Fuente; Mat., Matute; P.C.P., Pantano de la Cuerda del Pozo; P.M., Pinilla de los Moros; R.S., Río del Salcedal; Urbión Und., Urbión undetermined. Fossil sites: 1, Tenadas del Jabalí; 2, Monte Puente Ballesta; 3, La Tejera; 4, Tenada Rosa; 5, Torremuña; 6, Igea.

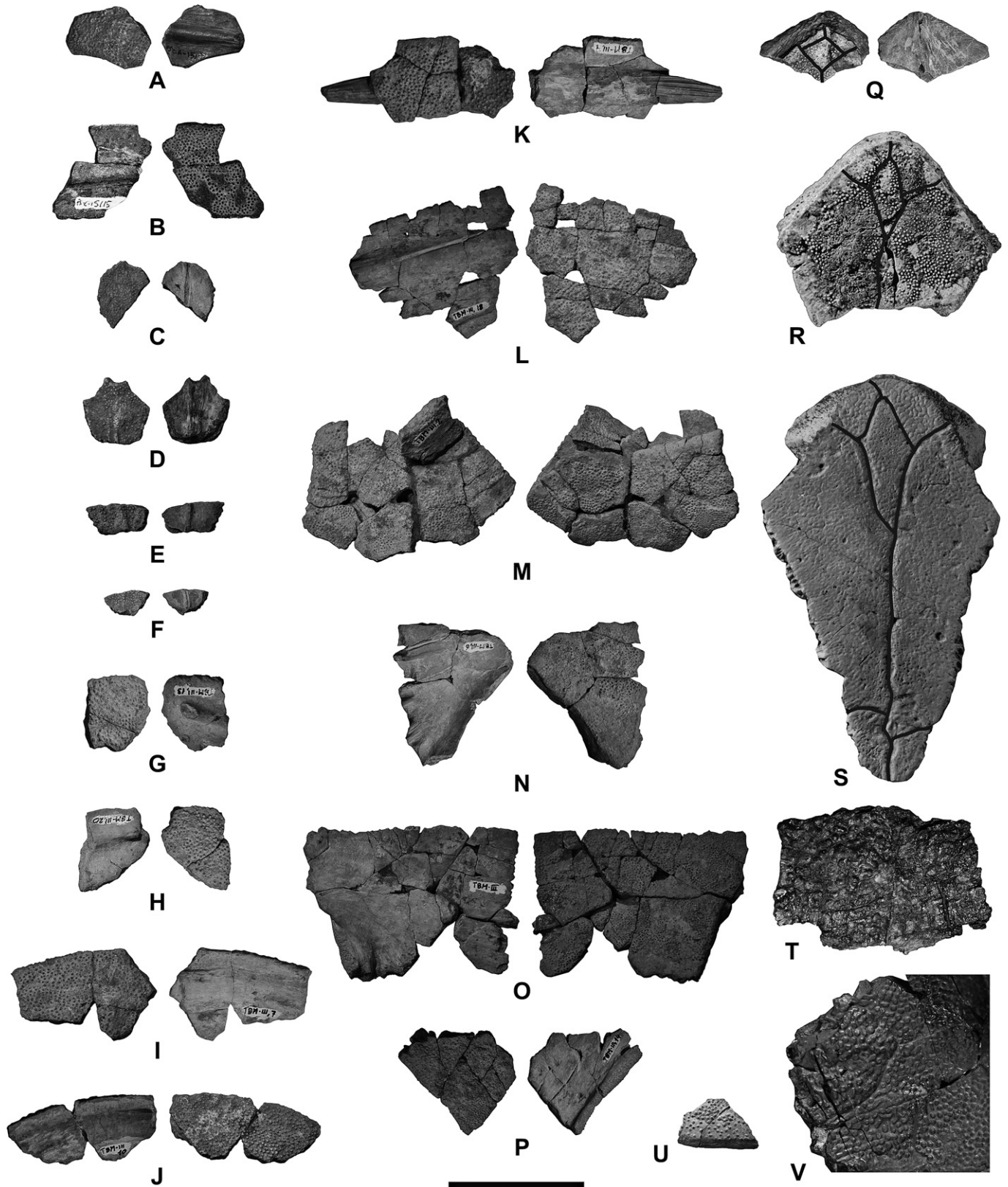


Fig. 2. Solemydidae. A–B, fragments of costal plates of aff. *Helochelydra* from the Lower Cretaceous of Tenada Rosa (Western Cameros Basin, Spain); MDS-C.15. C–Q, fragments of neurals, costals, peripherals, hypoplastra, xiphiplastron and entoplastron of aff. *Helochelydra* from the Lower Cretaceous of La Tejera (Western Cameros Basin, Spain); MDS-TBM-III.319, -III.369, -III.398, -III.399, -III.13, -III.20, -III.7, -III.10, -III.9, -III.18, -III.2, -III.6, -III.1, -III.14, -III.370. R, anterior half of the entoplastron of *Helochelydra nopcsai*, from the Valanginian–Barremian of the Isle of Wight (England); BMNH R171. S, entoplastron of *Solemys vermiculata*, from the late Campanian deposits of Laño (Burgos, Spain); MCNA 7391. T, fragment of costal plate of cf. *Trachydermochelys*, from the Albian of Cabezo de las Eras (Teruel, Spain); CPT-2048.2. U, fragment of peripheral plate of aff. *Helochelydra*, from the Lower Aptian of Morella (Castellón, Spain); MNCN 59517. V, fragment of peripheral plate of “*Trachyaspis*” *turbulensis* from the Aptian of Gargallo (Teruel, Spain); STUS 8371. The limits of the scutes have been painted on the three entoplastra, Q, R and S, in order to be compared the morphology of the entoplastral scute. Scale bar represents 5 cm.

Material. Several disarticulated plates of the carapace and plastron, MDS-C.15, MDS-TBM-III.1, -III.2, -III.6, -III.7, -III.9, -III.10, -III.13, -III.14, -III.18, -III.20, -III.319, -III.369, -III.370, -III.398, -III.399, and other plate fragments deposited in the MDS.

Locality and horizon. La Tejera (Barbadillo del Mercado, Burgos) and Tenada Rosada (Cabezón de la Sierra, Burgos), western Cameros Basin, Castrillo de la Reina Formation/Pantano de la Cuerda del Pozo Formation, Urbión Group.

Solemydidae indet.
 Sánchez Lozano (1894), pl. 4.

Material. A fragment of a peripheral plate, now missing.

Locality and horizon. Sierra de Alcarama (La Rioja), Eastern Cameros Basin, Lower Cretaceous.

Description and comparison. Several specimens collected in two localities of the western Cameros Basin (La Tejera and Tenada Rosada) are here attributed to Solemydidae. Those found in Tenada Rosada (Fig. 2A and B) are scarce, corresponding to indeterminate elements and fragments of costal plates. Numerous elements assigned to the shells of this group of turtles are identified in La Tejera (Fig. 2C–Q). Plates from both the carapace and plastron, and fragmentary elements whose position in the shell is uncertain, are recognized. All except two peripheral plates (Fig. 2M) correspond to disjointed elements. Furthermore, in the eastern Cameros Basin, a fragment of a peripheral plate was recognized, now missing (Pérez-García, 2009a), which was described and figured in the nineteenth century (Sánchez Lozano, 1894) and attributed to “*Hellochelys*” Meyer (1854). This specimen was found in an indeterminate outcrop of the Lower Cretaceous in the Sierra de Alcarama (La Rioja).

All plates from La Tejera, both from the carapace and the plastron, have an ornamentation consisting of isolated tubercles, with a rounded apex, and with a circular to slightly elliptical section. The height of these tubers is usually equal to or slightly less than their width. However, in some regions of the shell, the height can be slightly greater than the width. The diameter is about or just under 1 mm. Although on some of the plates the scute sulci can be recognized, in others they cannot be observed owing to poor preservation and a covering of strongly adhered sediment. The disarticulation and fragmentation of these elements prohibits determination of whether they are all part of the same or of various specimens.

The carapace elements identified are the neural, costal, and peripheral plates. The neural plates belong to different positions of the neural series, including the anterior region of the first neural (Fig. 2C). This plate is elongated, but broken approximately in the region where it was traversed by the sulcus between the first and second vertebral scutes. The other plates of the neural series are hexagonal, and in some of them it can be seen that the antero-lateral margins are shorter than the postero-laterals (Fig. 2D). The most complete neural, the anterior edge, which is the shortest, has a marked concavity (Fig. 2D). Both on this plate and in the posterior region of other neurals preserved (Fig. 2E and F), there is a slight longitudinal thickening in the sagittal region, not present in the first neural. This corresponds to the presence of a medial carina in at least part of the neural series.

Several specimens corresponding to costals are identified, assigned to the proximal, medial, and distal regions of plates between the second and eighth pairs (Fig. 2A and B, G–L). In specimens where the free medial parts of the ribs are preserved, they are not complete. The preserved region indicates that the

vertebra contact should be relatively strong. The distal end of the ribs is well developed.

Two articulated peripheral plates, corresponding to the back half of the carapace, are recognized (Fig. 2M). The greatest length of these plates is the medial-distal.

The preserved plastron plates are the anterior region of the entoplastron, a fragment of the bridge, the proximal half of a hypoplastron, and a fragment of a xifiplastron (Fig. 2N–Q).

The anterior angle of the entoplastron is very obtuse (Fig. 2Q). A small entoplastral scute, slightly wider than long, is situated on its anterior region. The contact suture of the entoplastron with the epiplastra is oblique to the plate surface because the entoplastron slides under the epiplastra. In dorsal view, the area of the anterior interclavicular is slightly grooved. The preserved region of the bridge may be the distal half of the left hypoplastron (Fig. 2N). The area of contact with the carapace plates is very sinuous and low, so union would seem to occur only with the peripheral plates. Although there are some areas where the sulci that delimit the scutes are observable, the poor preservation does not allow reconstruction of the inframarginal morphology, but it can be confirmed that they were present. The proximal half of what is probably the same hypoplastron is identified (Fig. 2O). The abdomino-femoral sulcus, which is perpendicular to the axial axis, is recognized on this plate. The contact of this plate with the other hypoplastron and with the hyoplastra was sutured, without fontanelles. In dorsal view, in the margin of the region covered by the femoral scute, this plate has a lip that is also decorated.

The xifiplastron preserves the antero-lateral area (Fig. 2P). The dorsal lip is also well developed and ornamented.

The ornamentation of the plate fragments from Tenada Rosada is compatible with that of the specimens from La Tejera. However, this ornamentation is different from that of the peripheral plate from the eastern Cameros Basin (see Sánchez Lozano, 1894, pl. 4). Although the plate tubers are also separated from each other, and have a diameter of slightly less than 1 mm, those that are well preserved are higher than they are wide and have a superimposed dome of smaller diameter.

4.2. *Eucryptodira*

Testudines Batsch (1788)
 Pancryptodira Joyce et al., (2004)
 Eucryptodira Gaffney (1975)

Salasemys pulcherrima Fuentes Vidarte, Meijide Calvo and Meijide Fuentes, 2003
 Fig. 3C–F

Material. ICIPLR-1, a partial and disjointed carapace; MDS-JTS.V.1–40, a relatively complete skeleton, holotype of this taxon.

Locality and horizon. ICIPLR-1 from Torremuña, eastern Cameros Basin, Enciso Group. The holotype from Tenadas del Jabalí, western Cameros Basin, Pinilla de los Moros Formation, Tera Group.

gen. et sp. indet. 1
 Fig. 3A

Material. MDS-MPBS-6, a partial shell.

Locality and horizon. Monte Puente Ballesta, western Cameros Basin, Pinilla de los Moros Formation, Tera Group.

gen. et sp. indet. 2
 Fig. 3B

Material. ICIPLR-2, a partial shell.

Locality and horizon. Igea, eastern Cameros Basin, Enciso Group.

Description and comparison. In the Cameros Basin there are three representatives of Eucryptodira, turtles with the pelvis not sutured to the carapace and without mesoplastra. The presence of one of them, *S. pulcherrima*, is recognized both in the eastern Cameros Basin (Torremuña) and in the western (Tenadas del Jabalí, Salas de los Infantes). The holotype (Fig. 3F) is a relatively complete specimen from Tenadas del Jabalí (Fuentes Vidarte et al., 2003). A partial, disjointed carapace (Fig. 3C–E), assigned to this taxon, has

recently been identified in Torremuña (Pérez-García et al., 2010b). Of the other two representatives, one is from the eastern region (Igea) (Fig. 3B) and the other from the western (Monte Puente Ballesta, Salas de los Infantes) (Fig. 3A) (Pérez-García and Murelaga, 2010; Pérez-García et al., 2010b). One of these Eucryptodira specimens has a relatively complete articulated carapace and is the holotype of *Salasemys*. However, in this holotype the limits between most of the plates or the scutes cannot be interpreted because of its poor preservation. The Igea carapace lacks most of its margin except that of the right anterior border of the nuchal plate (Fig. 3B). The information available for the Monte Puente Ballesta carapace comes from its posterior half (Fig. 3A).

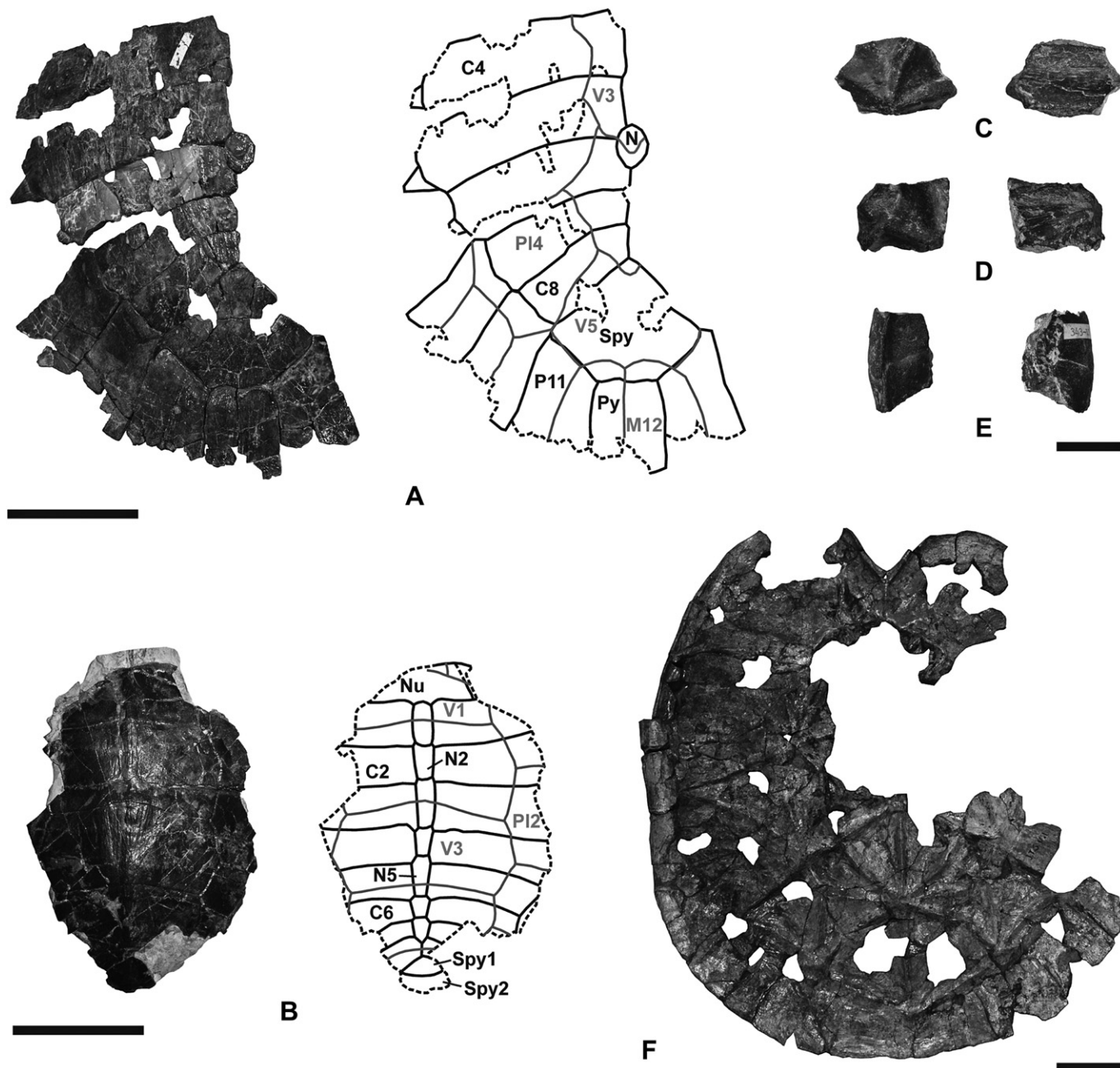


Fig. 3. Carapaces of eucryptodiran turtles from the Cameros Basin (Spain). A, Eucryptodira indet. from the Lower Cretaceous of Monte Puente Ballesta; MDS-MPBS-6. B, Eucryptodira indet. from the Lower Cretaceous of Igea; ICIPLR-2. C–E, fragments of two costal plates and a peripheral plate of *Salasemys pulcherrima*, from Torremuña; ICIPLR-1. F, carapace of the holotype of *Salasemys pulcherrima*, from Tenadas del Jabalí; MDS-JTS.V.1. Some elements not considered by Fuentes Vidarte et al. (2003) have been added, allowing better knowledge of the morphology of its anterior border. Plate abbreviations (in black): C, costal; N, neural; Nu, nuchal; P, peripheral; Py, pygal; Spy, suprapygal. Abbreviations for scutes (in grey and narrower): M, marginal; Pl, pleural; V, vertebral. Scale bars represent 5 cm.

Each of these taxa has a different ornamental pattern. On the carapace of *Salasemys* are relatively high ridges that radiate in different numbers, generating a complex pattern. Furthermore, the distribution of this pattern is not determined by the boundaries between the plates. In the plates from the *Salasemys* specimen from Torremuña, there is a smaller-scale ornamental pattern, not observed in the holotype because of its poor preservation, consisting of slightly elevated and dichotomous discontinuous sulci, mm in size. On the vertebral scutes of the Igea and Monte Puente Ballesta specimens, there is poorly developed ornamentation consisting of sulci that diverge towards the anterior area. In addition, on the peripheral plates of the Monte Puente Ballesta specimen there are some sulci.

The carapace of the Tenadas del Jabalí specimen is over two and a half times longer than that of Igea. The estimated length for the Monte Puente Ballesta carapace is between that of these two, being closer to that of the Tenadas del Jabalí specimen.

Salasemys is a low turtle. The carapaces of the other two specimens belong to taxa with higher shells, particularly that of Monte Puente Ballesta. The morphology of the anterior edge of the *Salasemys* carapace has a deep notch, in contrast to the lack of a notch in the Igea specimen.

Although the boundaries between the plates of *Salasemys* are barely visible, it is interpreted that the last neural contact is with the suprapygal plate. In the Igea specimen, the sagittal contact occurs between the last pair of costals. In that of Monte Puente Ballesta, this contact occurs between the last three pairs.

Although it is not known whether *Salasemys* has one or more suprapygal plates, it is observed that the Monte Puente Ballesta specimen has only one, but that of Igea has two. The contact between the plastron and the carapace, with a ligamentous link in *Salasemys*, is sutured in the other two taxa. The posterior peripheral plates are longer in the Monte Puente Ballesta specimen than in *Salasemys*. The vertebral scutes are much wider in the Igea specimen than in that from the Monte Puente Ballesta. Furthermore, their morphology and the relationship of the contact of the fourth and fifth scutes with the last costal and the suprapygal plates are different. Therefore, the significant differences between the three specimens allow them to be regarded as belonging to three different taxa.

5. Discussion

5.1. Solemydidae

The characters observed in the La Tejera (Fig. 2C–Q) specimens fit well with those recognized in *Solemys vermiculata* Lapparent de Broin and Murelaga, 1996 (see diagnosis of Solemydidae), such as: the presence of an ornamental pattern consisting of granulations, the presence of a dorsal lip around the plastral lobes, and the presence of an entoplastral scute. Despite the limited record from Tenada Rosada (Fig. 2B) and from Sierra de Alcarama, the ornamental pattern also allows its allocation to Solemydidae.

Solemydidae is a group of primitive cryptodiran turtles, with mesoplastra that join medially. Although several taxa have been identified, available information on most of them is very limited. In fact, the only shell that is well known is that of the type genus, *Solemys*, found in Campanian and Maastrichtian sites (Lapparent de Broin and Murelaga, 1996, 1999). Other genera attributed to this family are the American taxon *Naomichelys* (Late Jurassic, Montana), the European taxa *Helochelydra* (Valanginian–Barremian, Isle of Wight, England), *Helochelys* (early Albian, Kelheim, Germany), and *Trachydermochelys* (middle Albian–early Cenomanian, Cambridge Greensand, England), and other poorly known taxa such as “*Trionyx*” *turbulensis*, from the Aptian of Gargallo (Spain) or

“*Trionyx*” *bakewelli* Mantell (1833), from the Berriasian–Barremian of Cuckfield (Sussex, England). Some taxa may be synonymous with previous ones, as might be the case of *Plastremys* Owen, 1881 (in Parkinson, 1881), from middle Albian–early Cenomanian deposits of the Isle of Wight (England). In addition, others identified lack sufficient characters to be diagnosed as new taxa owing to limited findings, as is the case of some specimens from the French Upper Jurassic, the English Lower Cretaceous, and the French Cenomanian (Lapparent de Broin, 2001; Lapparent de Broin and Murelaga, 1996, 1999; Vullo et al., 2010).

In relation to the ornamentation, the Solemydidae is diagnosed by the presence of granulations, close or separated, and of vermiculations (Lapparent de Broin and Murelaga, 1996, 1999). However, the morphology, size, density, and relationship of the tubercles, and the arrangement of the vermiculations, are specific to each taxon or may even vary slightly in different shell areas of the same taxon.

The tubercles of the solemydid of La Tejera differ from those in the genus *Solemys* Lapparent de Broin and Murelaga, 1999, consisting of rounded ridges 1.5–2 mm wide (Lapparent de Broin and Murelaga, 1999). It is also different from that observed in one of the undetermined morphotypes of the Cenomanian of France, with very close granulations (Vullo et al., 2010). Isolated tubercles have been observed in taxa such as *Helochelydra*, *Naomichelys*, *Trachydermochelys*, and *Helochelys*, and in several poorly known taxa (Lapparent de Broin and Murelaga, 1999). *Helochelydra* is a taxon decorated with tubercles with a thickness similar to that of the specimens analysed here, around 1 mm wide. It is considered that the tubercles of *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999 are relatively high, much more than described for *Helochelydra anglica* Milner, 2004. However, there is also some variation in the ratio of the width/length of the tubercles of this taxon, depending on the position in the shell, and this variability is similar to that observed in the La Tejera specimens. The tubercles of *H. nopcsai* and that of the La Tejera taxon differ from those of the other morphotype recognized in the Cenomanian of France (Vullo et al., 2010), with wider tubercles, around 1.5 mm in diameter, and lower. These are similar to those of some British forms that have been mistakenly included under the name of *Tretosternon*, as is the case of “*Trionyx*” *bakewelli* Mantell, 1827 (Lapparent de Broin and Murelaga, 1999; Vullo et al., 2010). However, the analysed material differs from this taxon, actually considered to be an indeterminate solemydid (Vullo et al., 2010) and not a representative of *Helochelydra* (Milner, 2004), for which it has been described that, at least in the plastron, the ventral surface is covered with low tubercles tending to coalesce into groups of two or three (Milner, 2004). In *Helochelys*, the tubercles are also wider and lower than in *Helochelydra*, being much wider in *Trachydermochelys*, in which they are also relatively low (Lapparent de Broin and Murelaga, 1999). Therefore, based on the ornament pattern, it can be considered that the plates of Solemydidae from the western Cameros Basin (La Tejera and Tenada Rosada) could belong to the same taxon. However, the ornamentation of the specimen from the eastern Cameros Basin differs, perhaps because it was a different taxon; however, the scarcity of material at this site does not allow exclude the possibility that it could be due to intra-taxon variability.

The arrangement of the vermiculation varies considerably among different solemydid taxa. In *Helochelydra*, it are scarcely developed, but the tubercles are generally joined in thin vermiculated ridges towards the medial parts of the costal plates (Lapparent de Broin and Murelaga, 1999). However, the Cameros Basin specimens lack vermiculation. In the neurals of La Tejera there is a carina, which is shared with *Solemys* and with the solemydid of Charentes with small tubercles (Lapparent de Broin and Murelaga, 1999; Vullo et al., 2010). However, in these taxa,

especially in *Solemys*, the shell surface has many vermiculations. The neural plates of Cameros lack the fine longitudinal granulated ridges, which radiate from the front, present in the neurals of Charentes (Vullo et al., 2010). In some British specimens from the Lower Cretaceous, as is the case of that assigned to *Trachydermochelys rutteri* Andrews (1920), the shell is longitudinally carinated (Lapparent de Broin and Murelaga, 1999; Milner, 2004).

The morphology of the preserved region of the first neural plate is similar to that observed in some Solemydidae representatives, as is the case of some *Solemys* specimens (see Lapparent de Broin and Murelaga, 1999, pl. 6, fig. 6). However, it was found that the morphology of the anterior region of this plate in *Solemys* can vary considerably, being either narrow or wide anteriorly (Lapparent de Broin and Murelaga, 1999). The morphology of the first neural plate of the solemydid from La Tejera differs from that of *Helochelydra*, a taxon in which it is hexagonal (Nopcsa, 1928).

As in other solemydids, for example, in *Solemys* or in *Helochelydra*, the free medial parts of the ribs that make contact with the vertebrae are strong. As in *Solemys* and in *Helochelydra*, the dorsal plastral lips are wider than those of *Helochelys* (Meyer, 1856; Lapparent de Broin and Murelaga, 1999).

Although some solemydids with relatively small entoplastral scutes are known, such as *Solemys* (Fig. 2S) or *Helochelydra* (Fig. 2R), the scute observed on the entoplastron of La Tejera is very short, differing from these because it is wider than long and because it is located in the anterior region of this plate. However, the entoplastral proportions can be highly variable within a given taxon, as observed in *Solemys* (Lapparent de Broin and Murelaga, 1999).

In the analysed material, the lateral processes of the hyohypoplastra are limited by wide indentations and coarse denticles for a ligamentous link with the carapace, as in the other solemydids. In all of them, the contact of the plastron with the carapace is produced exclusively in the peripheral plates.

Spanish specimens that can now be assigned to Solemydidae had been reported since the 1920s (Pérez-García, 2009a; Royo y Gómez, 1927a, b). They come from the early Aptian deposits of Morella (Maestrazgo Basin). These were attributed to *Tretosternon punctatum* (Royo y Gómez, 1927a, b), as was the case of other ornamented specimens from the Upper Jurassic and Lower Cretaceous of England and France (see Lapparent de Broin and Murelaga, 1999; Vullo et al., 2010). The Morella specimens are small plate fragments with very few characters that allow comparison with the known representatives of the group. These specimens had been attributed, in a preliminary way, to *Helochelydra*, due to their ornamental pattern (Fig. 2U) and the presence of well-developed dorsal lips (Ortega et al., 2006; Pérez-García, 2009a). These specimens are compatible with those from the western Cameros Basin owing to these characters and to the absence of vermiculation.

This solemydid turtle shares with *H. nopcsai* its morphology, size, and distance between tubercles, as well as wide dorsal plastral lips. It differs from *Helochelydra* in some characters such as the absence of vermiculated ridges towards the medial parts of the costal plates, in the morphology of the first neural plate, and in the morphology and position of the entoplastral scute. It is not possible to know if there is a sagittal carina in *Helochelydra* because the holotype is only partially preserved, and only the first plate of the neural series is preserved (Lapparent de Broin and Murelaga, 1999). Some characters from the *Helochelydra* (Lapparent de Broin and Murelaga, 1999) diagnosis cannot be compared with the Spanish material because of gaps in the record: entoplastron length, width of first vertebral scute, morphology of the anterior carapace edge, morphology of the anterior plastral lobe, relationship between the length of the plastral lobes, and shell height. Therefore, examination of the material from the western Cameros Basin assigns these plates, and possibly that of Morella, to a representative of

Solemydidae, probably closely related to *H. nopcsai*. Owing to the scarce known record of these taxa, knowledge of their variability is very limited. Therefore, the attribution of the Spanish material to this taxon cannot be confirmed, but it is determined as an indeterminate solemydid, probably closely related to it.

This taxon differs from the Spanish taxon "*Trachyaspsis*" *turbulensis* (Bergounioux, 1957), of which only four articulated peripherals are known (Jiménez et al., 1988), with isolated tubercles, low, around 2 mm in diameter, and with vermiculation (Fig. 2V). It is also different from the plate from the Albian of Cabezo de las Eras (Teruel), assigned preliminarily to *Trachydermochelys* sp. (Canudo et al., 2005). This specimen is a fragment of a costal plate, with tubercles of a size similar to those of "*Trachyaspsis*" *turbulensis* (Fig. 2T). The absence of diagnostic characters does not allow a generic allocation or confirm that both Spanish specimens may belong to the same taxon of Solemydidae. Therefore, based on ornament pattern, at least two representatives of Solemydidae are identified in the Lower Cretaceous of Spain.

5.2. Eucryptodira

Some of the plates of the Torremuña carapace (Fig. 3C–E), which are assigned to *Salasemys* based on a shared ornament pattern and the morphology and dimensions of the preserved elements (Pérez-García et al., 2010b), correspond to the material preliminarily identified by Viera and Torres (1996) as Pleurosternidae. This is the only identification of a Paracryptodira representative in the Cameros Basin because the specimens found so far do not allow us to confirm any representatives of this group in the area.

S. pulcherrima had been identified as a representative of "Macrobaenidae" (Fuentes Vidarte et al., 2003). However, "Macrobaenidae" is not a monophyletic group (Gaffney et al., 2007; Parham and Hutchinson, 2003), leaving the precise systematic position of *Salasemys* among the Eucryptodira representatives uncertain (Pérez-García et al., 2010a).

Some fragments of carapace plates recently identified in the Berrasian of northwestern Germany have been assigned, because of ornamentation, to *Salasemys* (Karl and Reich, 2009). In fact, *Salasemys* could be a taxon closely related to the poorly known *Chitraccephalus* Dollo, 1884, represented by a single specimen from the middle Barremian–early Aptian deposits of Bernissart (Belgium) (Dollo, 1884; Karl and Reich, 2009; Pérez-García et al., 2010e). The poor preservation of this specimen and the limited information so far published about *Salasemys* have hampered comparative studies between the two taxa. The detailed study of the holotypes of both taxa, and that of the Torremuña carapace, may provide additional insights into the systematic position of these representatives of Eucryptodira (Pérez-García et al., 2010e).

The taxon of *Igea* (Fig. 3B) shares with the basal European representative of Eucryptodira, *Brodiechelys brodiei* (Lydekker, 1889b), several characters such as the presence of a wide nuchal, two suprapygals, and the morphology of the neural plates (see Lydekker, 1889b). These characters are primitive for node Eucryptodira. However, it differs in other characters, such as the number of neural plates, the sagittal contact at the last pair of costals, the width of the vertebral scutes, and the morphology of the nuchal plate. Although the Eucryptodira, not Cryptodira (sensu Joyce et al., 2004), are relatively abundant in the European Jurassic, and particularly in the Iberian Peninsula (Lapparent de Broin, 2001; Pérez-García, 2009b; Pérez-García et al., 2010f), their presence is very scarce in the Lower Cretaceous of Europe even though this group has many representatives of that age elsewhere such as Asia and North America (Parham and Hutchinson, 2003; Peng and Brinkman, 1993; Rabi et al., 2010). However, an unknown specimen consisting of a very complete shell in the early Aptian deposits of Morella (Maestrazgo Basin) has

been assigned to this group (Pérez-García et al., 2008), as well as an internal cast from the Barremian of the same basin (Pérez-García and Ortega, 2009). The Igea specimen could be closely related to these forms, differing in characteristics such as the number of neural plates or the development of the ornament pattern (Pérez-García et al., 2010b). A detailed study of these specimens is needed, and of other fragmentary specimens also from the Igea area, in order to interpret whether they all belong to the same taxon, with variability in some characters, or whether they should be assigned to more than one taxon. The study of these Spanish specimens, the review of the *Brodiechelys* taxon, and the analysis of unpublished Spanish and British specimens, will allow a determination of the phylogenetic position of these basal representatives of Eucryptodira, a node barely known in the European Cretaceous. The study of these new specimens will enable the assessment of whether, as suggested by some authors, the European Lower Cretaceous could contain representatives of Plesiochelyidae (turtles whose presence has been confirmed only in marine deposits of the European Upper Jurassic) and/or Xinjiangchelyidae (probably a paraphyletic taxon sensu Rabi et al. (2010) whose presence has been confirmed only in the Upper Jurassic and Lower Cretaceous of western Asia), or are representatives of new groups. The preliminary study of these specimens indicates that several of the characters shared with Xinjiangchelyidae or with Plesiochelyidae are, in fact, primitive characters.

The specimen from Monte Puente Ballesta (Fig. 3A) cannot be assigned to any of the known turtle genera (Pérez-García and Murelaga, 2010). The combination of characters for this taxon, including height, the distinctive ornament, the sagittal contact between the last three pairs of costals, the presence of a single and large suprapygal, the length of the posterior peripheral plates, and the distinctive morphology of the vertebral scutes, does not allow its assignment to any of the eucryptodiran groups known in the Lower Cretaceous.

Some specimens with similar ornamentation to that of this carapace have been found in the early Barremian deposits of Galve (Maestrazgo Basin) (Pérez-García et al., 2010d). Because they consist only of plate fragments, this assignment cannot be confirmed.

5.3. Other Cretaceous turtles from the Cameros Basin

In addition to the afore-mentioned turtles, Jiménez Fuentes (1992) cited the presence of a representative of Pelomedusoides

in the Lower Cretaceous of the Cameros Basin. This group of turtles, which originated in Gondwana, has not been recognized elsewhere in Europe before the Senonian (Vullo et al., 2010). Therefore, the confirmation of its presence would have important palaeobiogeographic implications. However, these plates were erroneously considered to be Lower Cretaceous, as was all the other turtle material deposited in the Salas de los Infantes. There are two specimens from the Maastrichtian of El Cogorro (Arauzo de Miel, Burgos). One is a fragment of an indeterminate plate, but the other is the posterior region of a hypoplastron articulated with the anterior region of a xiphiplastron (Fig. 4).

Several Campanian–Maastrichtian fossil sites have been identified in the Upper Cretaceous of Spain (Pérez-García, 2009b). The presence of Bothremyidae (Pelomedusoides) has been identified in most of them (Pérez-García et al., 2010c, in press-b). This is the most abundant group of turtles in the Campanian–Maastrichtian fossil sites of Western Europe (Gaffney et al., 2006; Lapparent de Broin and Murelaga, 1999). The Spanish taxon *Polysternon atlanticum* had been defined on the basis of abundant disjointed material from the fossil site of Laño (Burgos, Basque–Cantabrian Basin) (Lapparent de Broin and Murelaga, 1996, 1999). However, the fossil site of Lo Hueco (Cuenca, southwestern Iberian Range), is the only one in which articulated remains of individuals of this group of turtles have been found (Pérez-García et al., 2009). At this site, shells of *Iberococcanemys converanum* Pérez-García, Ortega and Murelaga, in press (Pérez-García et al., 2010c, in press-c), and of another undetermined representative of Foxemydina which is not *P. atlanticum* Lapparent de Broin and Murelaga, 1996 (Pérez-García et al., in press-b), have been identified.

The El Cogorro specimen corresponds to a part of the posterior plastral lobe (Fig. 4). It has a scar for the pubis suture, which confirms its assignment to Pleurodira. Its ventral surface is decorated with “pelomedusoid ornamentation” (Broin, 1977; Gaffney et al., 2006) composed of small dichotomous discontinuous grooves that may anastomose forming mm-sized and almost flat polygons. This ornamentation is compatible with that of Bothremyidini (Gaffney et al., 2006), being different from that of some members that could live in marine environments such as *Taphrosphys*. In this specimen, the morphology of the lateral margin posterior to the femoral-anal sulcus and that of the anal notch are unknown. It is not possible to determine the distance between the suture of the pubic and the sagittal plane. The preserved region is compatible with that of Bothremyidae. The study of the material

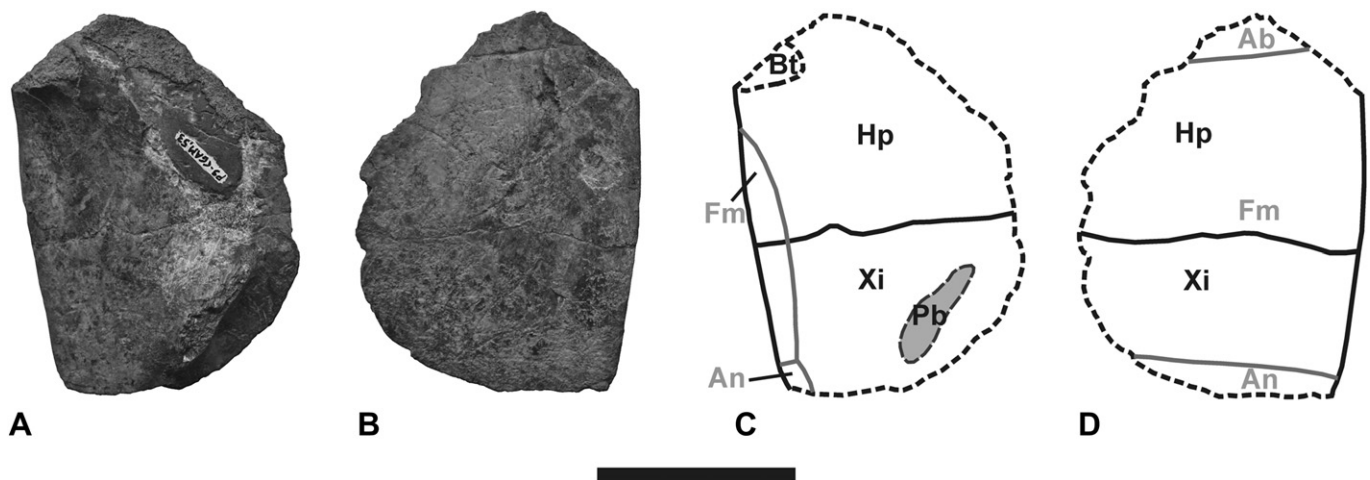


Fig. 4. Fragment of the posterior lobe of the plastron of cf. Bothremyidae, from the Maastrichtian of El Cogorro (Cameros Basin); MDS-CGAM.53. Plate and bony structures abbreviations (in black): Bt, hypoplastral buttress; Hp, hypoplastron; Pb, suture with the pubis; Xi, xiphiplastron. Abbreviations for scutes (in grey and narrower): Ab, abdominal; An, anal; Fe, femoral. Scale bar represents 5 cm.

from Lo Hueco has demonstrated the difficulty of the generic allocation of isolated material. This is due to the expansion of the distribution area of some taxa, the finding of important intraspecific and generic variability, and the confirmation of the coexistence of more than one taxon at a single site (Pérez-García et al., 2010h). Therefore, owing to the presence of several representatives of Bothremydidae in the Spanish Campanian and Maastrichtian, and the absence of characters for comparison with them, this specimen is determined as cf. Bothremydidae indet.

6. Conclusions

The study of the turtles found in the Lower Cretaceous of the Cameros Basin has led to the identification of several taxa, including Solemydidae and three representatives of Eucryptodira. References to Pelomedusoides and to Pleurosternidae in the Lower Cretaceous of that basin are considered erroneous.

So far, limited knowledge of turtles from Spanish Lower Cretaceous sites had not allowed kinship and biogeographic relationships to be established between the taxa found in the various fossil sites or with those of other European regions. The study of the turtles found in the Cameros Basin allows a preliminary analysis of these relationships.

The solemydid taxa to which are allocated the majority of the solemydid plates identified in the basin is probably the same taxon as that found in early Aptian deposits of the Maestrazgo Basin as very fragmentary specimens. The characters available do not allow its generic determination, but it can be regarded as a taxon closely related to the British genus *Helochelydra*. It is not known whether the sole plate from the eastern Cameros Basin assigned to this group might correspond to the same or to another closely related taxon. This is because it is only known from a drawing and descriptions from the nineteenth century and because the observed differences could probably be justified by variability within the taxon or even by the position of this element in the shell. The ornamentation of the Spanish specimen identified as "*Trachyaspis turbulensis*" is also similar to that of other British taxa, such as *Trachydermochelys*. The available information on this specimen is also very limited because it is only represented by some peripheral plates. Its ornamentation is compatible with that of the fragment of costal plate from Cabezo de las Eras (Teruel). Therefore, the current record of Solemydidae in the Lower Cretaceous of Spain, including at least two taxa, suggests that there are many similarities between the Spanish and the British fauna.

The presence of new specimens from the Cameros Basin attributed to *S. pulcherrima* allows a better understanding of this eucryptodiran taxon, whose precise phylogenetic position is uncertain. Fragmented and scarce material from Germany has recently been recognized and attributed to this taxon because of its ornament pattern. However, owing to the limited knowledge of *Salasemys* and other European turtles that might be related to this taxon, it is currently not possible to confirm this conspecific attribution. Specimens that may be closely related to *Salasemys* in Germany and Belgium suggest that this turtle is probably part of a little-known group distributed at least through Western Europe.

A chelonian assigned to an undetermined Eucryptodira basal taxon is recognized in the eastern Cameros Basin. Information on representatives of this node in the Lower Cretaceous of Europe is very limited and, so far, it has not been possible to determine to which groups some of the specimens identified belong. The Cameros specimen has similarities with those found in other regions of Spain, but also in other areas of Europe. Although these specimens share some primitive characters, it is not possible to exclude the possibility that some of them may belong to the same group.

The turtle identified in Monte Puente Ballesta is different from the other taxa so far recognized in the European Lower Cretaceous. However, because of the limitations of this record, the possibility that this turtle also formed part of a group whose distribution may not be restricted to Spain cannot be dismissed.

Therefore, the study of turtle diversity in the Lower Cretaceous of a Spanish region (with notable preservation) makes clear the similarity of these fauna with those of other European areas. The fauna is very different from that of the Iberian Upper Jurassic, with freshwater turtles attributed to Pleurosternidae and a likely representative of Platycheilyidae, and basal members of Eucryptodira represented by coastal marine Plesiochelyidae turtles. In addition, the fauna is different from that of the Upper Cretaceous. The only group recorded in the Cameros Lower Cretaceous that survives is Solemydidae, which occurs with other groups such as Bothremydidae (which originated in Gondwana), also identified in this basin.

In addition to the description of new taxa, further detailed studies of the Spanish Lower Cretaceous turtles will provide new data on certain issues as yet unresolved, such as what group or groups of basal eucryptodiran turtles lived in Europe during the Early Cretaceous and what is the phylogenetic position of some turtles currently assigned to "Macrobaenidae" or identified as "chelydroids" in appearance. It is necessary to resolve these issues in order to determine more precise paleobiogeographic relationships.

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