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Presence of several clades of continental turtles in the Lutetian (Middle Eocene) of the Sobrarbe Formation (Ainsa Basin, South-Central Pyrenees, Northeast Spain)

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ABSTRACT. The presence of continental turtles in the Ainsa Basin (south-central Pyrenees, northeast Spain) is reported here for the first time. These specimens come from the middle-late Lutetian of the Sobrarbe Fm. Four clades are identified there. One of them corresponds to a member of Pleurodira, identified as *Neochelys* cf. *salmanticensis*. The others are cryptodiran turtles, recognized as an indeterminate member of Testudinidae, and two soft-shelled turtles: the carettochelyid *Allaeochelys* sp. and the trionychid *Trionyx* sp. This association of turtles is the most diverse identified in the Lutetian of the Iberian Peninsula. The identification of a member of Testudinidae corresponds to the oldest Iberian record of this clade. This turtle fauna is more similar to that present in the Iberian Duero Basin than in any other European region.

KEYWORDS: Palaeogene, Iberian Peninsula, Chelonii, Podocnemididae, Carettochelyidae, Trionychidae, Testudinidae

1. Introduction

The European Eocene fauna of continental turtles is composed of members of several clades, most of them not recognized in this continent in the pre-Eocene record (Lapparent de Broin, 2001; Pérez-García, 2012). One of the regions where a high abundance and diversity of continental turtles is recorded is the Duero Basin, and more specifically, the Spanish provinces of Zamora and Salamanca. The presence of members of Pleurodira (Podocnemididae) and of several groups of Cryptodira, including both terrestrial (Testudinidae) and aquatic (Carettochelyidae and Trionychidae) forms, has been recognized there (Jiménez Fuentes, 2003). This record contrasts with that of the rest of Spain, where the information on the Eocene pleurodirans and continental

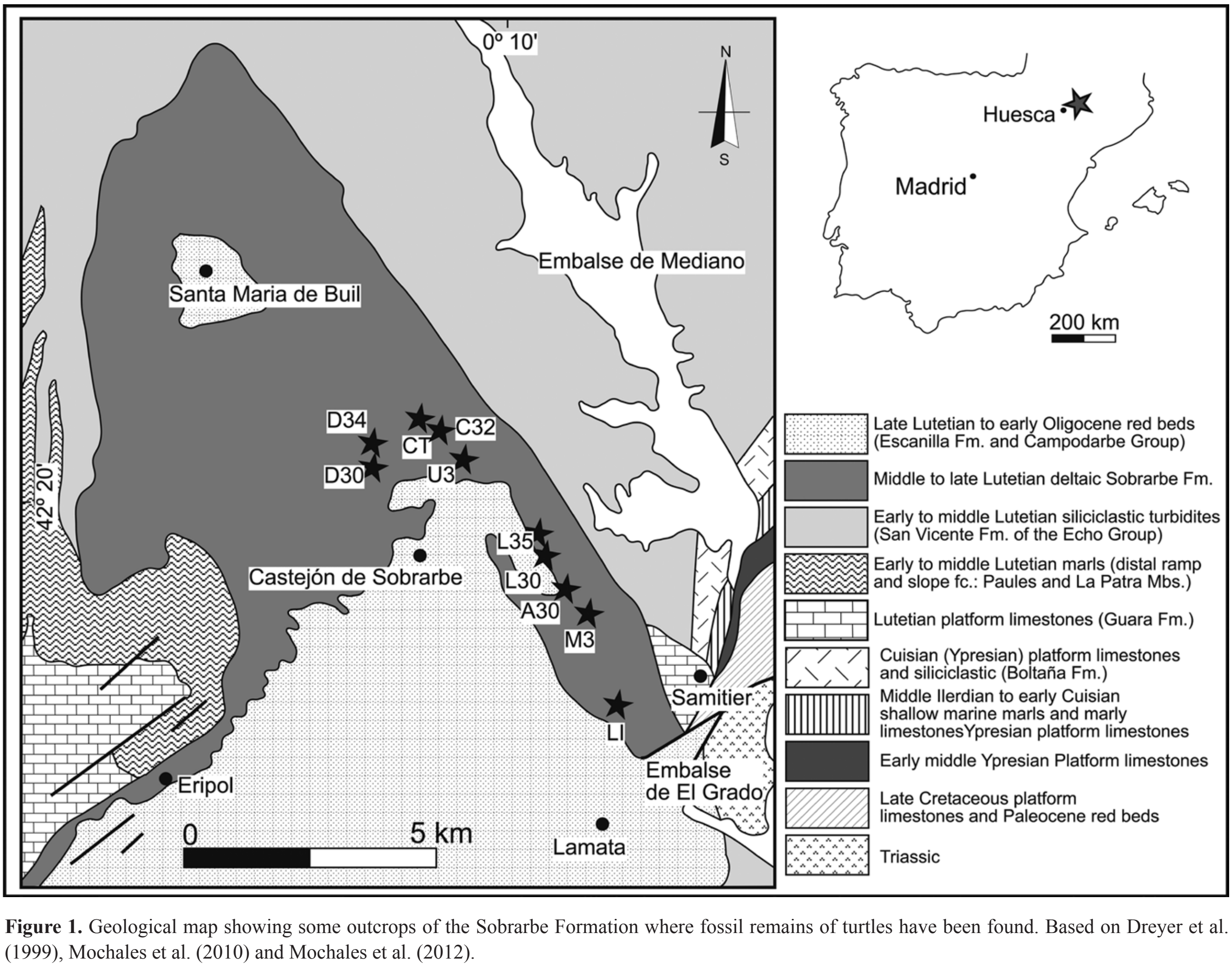

Figure 1. Geological map showing some outcrops of the Sobrarbe Formation where fossil remains of turtles have been found. Based on Dreyer et al. (1999), Mochales et al. (2010) and Mochales et al. (2012).

cryptodiran turtles is limited to the presence of possible aquatic members of Erymnochelyinae, generally poorly preserved, in the Catalonian record (Lapparent de Broin, 2003; Murelaga et al., 2007), and a shell of a terrestrial turtle in Asturias (Bergounioux, 1957).

The presence of continental turtles in Eocene levels of another Spanish region, the Ainsa Basin (Huesca, northeast Spain), located in the south-central Pyrenees, is recognized here for the first time. Dreyer et al. (1999) cited the presence of fossil remains of several groups (echinoids, Nummulites, gastropods, ostracods, bivalves and turtles) in the distal delta front deposits of the Sobrarbe deltaic complex. They identified this association as composed by marine taxa. No more information on these turtle remains (the only turtle specimens so far cited in this basin) was provided by these authors. However, due to the identification of several clades of continental turtles in the the Sobrarbe deltaic complex performed in this paper, the attribution of the non-described or figured specimens observed by Dreyer et al. (1999) to marine turtle taxa cannot be confirmed. The identification of the most complete skeletal remains of the European earliest sirenian remains was reported in this region, and specifically in the Sobrarbe Formation (Badiola et al., 2011). However, no other group of vertebrates had been cited there.

The turtles analyzed here come from the Sobrarbe deltaic complex (Sobrarbe Fm., middle-late Lutetian, middle Eocene), which represents the last marine infilling of the Santa María de

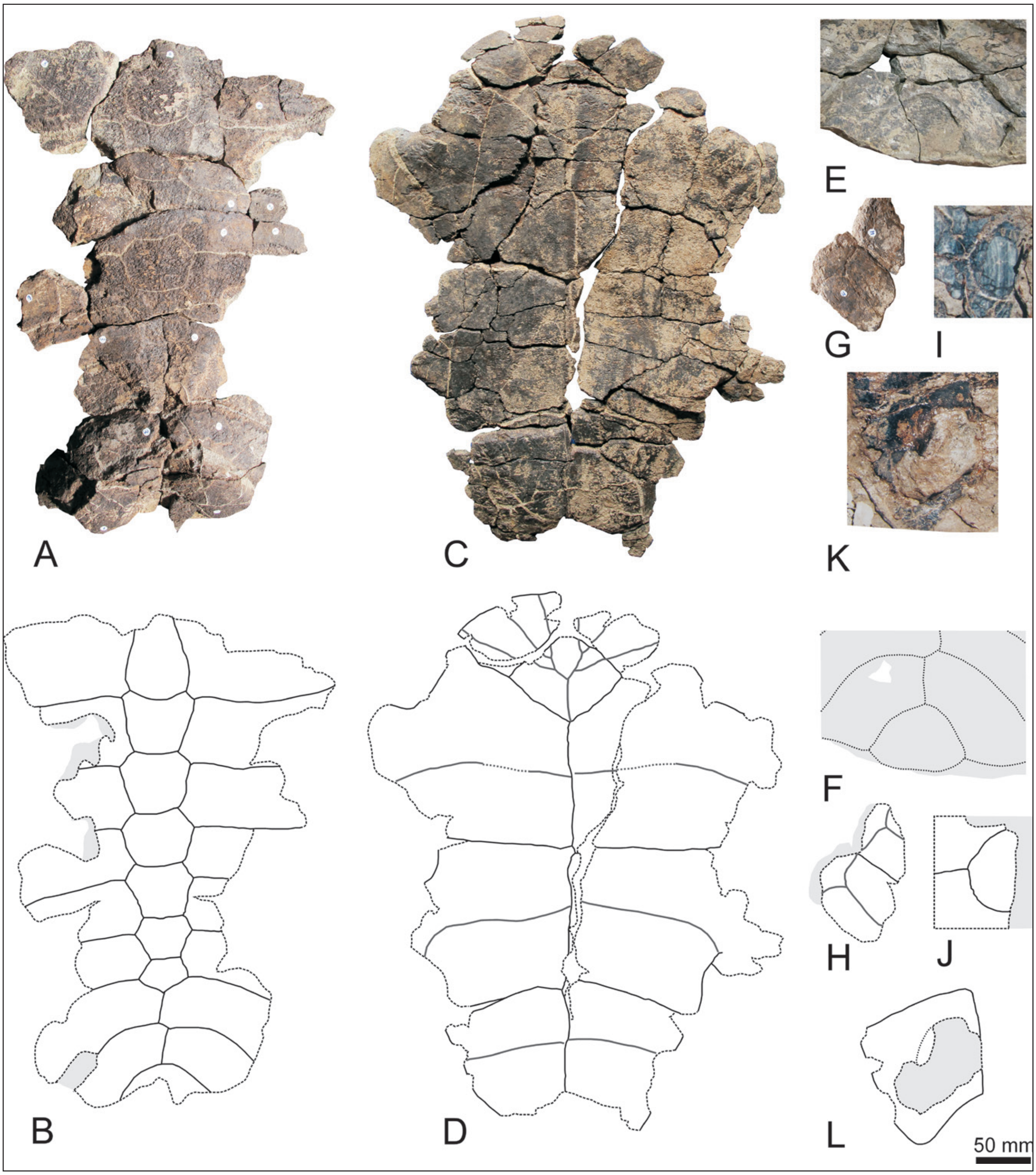

Figure 2. MPS-CT-1, ***Neochelys* cf. *salmanticensis*** (Pleurodira, Podocnemididae), from the Lutetian (Middle Eocene) of the Ainsa Basin. A-B: carapace, in dorsal view; C-D, plastron, in ventral view; E-F, impression of the posterior region of the carapace in the external mold; G-H, posterior peripherals, in dorsal view; I-J, photograph taken in the field, where the dorsal view of the right mesoplastron can be observed; K-L, photograph taken in the field, where the dorsal view of the complete lateral margin of the left xiphiplastron can be observed.

Buil syncline (Fig. 1). The Sobrarbe Fm. overlain the San Vicente (slope marls and deeper marine channalized turbidites) and Guara (marine limestones) Formations (early to middle Lutetian). The continental Escanilla Fm. (late Lutetian to early Oligocene; MP14-20), is overlaing the Sobrarbe Fm., representing the final sedimentary episodes in this area (Dreyer et al., 1999; Beamud, et al., 2003; Mochales et al., 2010, 2012).

Although we identify some remains of turtles both in the San Vicente Fm. as in the Escanilla Fm., these specimens correspond to indeterminate fragments. We recognize members of four clades (representatives of Cryptodira and of Pleurodira) in the Sobrarbe Fm., which are discussed herein. The fauna of turtles from the Lutetian of the Ainsa Basin is compared to that recognized in other European regions and, especially, in the Spanish Duero Basin.

All the turtle specimens from the Ainsa Basin studied in this paper are deposited in the Museo Paleontológico de Sobrarbe (MPS) (Lamata, Huesca, Spain).

2. Systematic palaeontology

Order Chelonii Latreille, 1800
Infraorder Pleurodira Cope, 1864
Hyperfamily Pelomedusoides Cope, 1868
Superfamily Podocnemidoidea Cope, 1868
Family Podocnemididae Cope, 1868
Subfamily Erymnochelyinae Broin, 1988
Genus *Neochelys* Bergounioux, 1954
Type species: *Emys capellinii* Zigno, 1889

***Neochelys* cf. *salmanticensis* (Jiménez Fuentes, 1968)**
(Fig. 2)

Referred specimens: Several specimens corresponding to shell elements, from various outcrops, including: MPS-CT-1, a partial shell, from which the complete neural series, the medial region of all the costals, the anterior region of the suprapygal, some peripherals, the plastron and the external mold of much of the carapace are preserved (Fig. 2). MPS-L30-1, a fragmentary and poorly preserved anterior half of a plastron, including the complete anterior margin of the anterior lobe.

Description: The outer surface of the material attributed to this taxon is usually altered, not being possible to recognize the boundary between the scutes in some regions, such as on the carapace of the specimen MPS-CT-1 (Fig. 2 A-B). However, an ornamental pattern consisting of fine and short dichotomic sulci, some of them united in small polygones, can be seen in some regions of its plastron.

It is a pleurodiran member of relative large size compared with most of the European Eocene representatives. The length of the plastron of the specimen MPS-CT-1 is close to 50 cm, being its carapace of at least 55 cm. These dimensions are consistent with those estimated for other specimens found in this region and attributable to the same taxon (for example, the specimen MPS-L30-1).

MPS-CT-1 preserves the entire neural series (Fig. 2 A-B). It has seven neurals. The first one is rectangular, longer than wide, with convex lateral margins. This plate is narrower in the anterior region than in the posterior one. The neurals 2 to 6 are hexagonal, their length being similar to their width. The most posterior neural is pentagonal, wider than long. The last two pairs of costals contact sagittally. The length of the first pair of costals is longer than that of the second pair. This taxon has a single sub-pentagonal suprapygal plate, whose width is slightly greater than its length.

The anterior plastral lobe is wider and shorter than the posterior one. Both lobes are wider than long. The length of the bridge is greater than that of each of these lobes. The anterior lobe is subrounded, being more angular on the specimen MPS-CT-1 than in MPS-L30-1. The lateral margins of the posterior plastral lobe are subrounded. The anal notch is relatively wide, being almost two times wider than long, and wider than each of the xiphiplastra at the femoroanal sulcus. The lateral margins of the xiphiplastra of the specimen MPS-CT-1 are rounded (Fig. 2 K-L). This specimen had a pair of lateral mesoplastra (Fig. 2 I-J), currently not preserved (Fig. 2 C-D). The scar for the suture of the carapace with the axillary processes is present on the distal half of the costals 1. The inguinal processes also suture, medially, with the costal series. The scars for the sutures of the ilia with the carapace are located on the costals 7 and 8, and those of the ischium and pubis with the plastron on the xiphiplastra. The morphology of these scars is not well known due to its preservation.

The pleural scutes overlap the medial region of, at least, the posterior peripheral plates (Fig. 2 G-H). The entoplastral length of the specimen MPS-CT-1 is less than two times its distance with the pectoro-abdominal sulcus (Fig. 2 C-D). The distance between the entoplastron and the hyo-hypoplastral suture is greater than its length. The hyoplastra are longer than the hypoplastra.

This taxon has a single intergular scute (Fig. 2 C-D). The maximal width of the intergular of the specimen MPS-CT-1 is situated on the anterior plastral margin. This width is similar than that of each of the gulars. The intergular scute of that specimen overlaps about half of the length of the entoplastron. Its lateral margins are divergent from its most posterior region to the anterior margin. This scute is in contact with the pectorals. Thus, MPS-CT-1 lacks a medial contact of the humerals. The intergular-pectorals contact is relatively narrow. The gular scutes posteriorly overlap the entoplastron. The humero-pectoral sulcus is significantly anterior to the epi-hyoplastral suture in the described specimen. The order of the plastral scutes, from longer to shorter in the axial plane, is: femorals, abdominals, pectorals, intergular and anals.

Infraorder Cryptodira Cope, 1868
Hyperfamily Trionychoidea Fitzinger, 1826
Superfamily Trionychia Hummel, 1929
Family Carettochelyidae Boulenger, 1887
Subfamily Carettochelyinae Boulenger, 1887
Genus *Allaeochelys* Noulet, 1867
Type species: *Allaeochelys parayrei* Noulet, 1867

***Allaeochelys* sp.**
(Fig. 3)

Referred specimens: Several plates corresponding to elements of the carapace and plastron, belonging to several individuals. These elements include an articulated first and second right peripherals (MPS-A30-18, Fig 3 AC), as well as other disarticulated elements: a first left costal (MPS-A30-10, Fig. 3 D-F), several fragmentary costal plates (MPS-A30-16, MPS-A30-1 and MPS-A30-17, Fig. 3 G-O), some posterior peripherals (MPS-A30-12 and MPS-C32-1, Fig. 3 P-U), the posterior half of a right epiplastron (MPS-A30-14, Fig. 3 V-X), one left hypoplastron (MPS-A30-3, Fig. 3 Y-AA), one right hypoplastron (MPS-A30-4, Fig. 3 AB-AD) and a fragment of a left xiphiplastron (MPS-C32-2, Fig. 3 AE-AG). In addition, a jaw, which preserves the fused dentaries, the relatively complete right coronoid, and a fragment of the left one, is identified (MPS-U30-1, Fig. 3 AH-AM).

Description: All plates are decorated with granulation and tubercles generating a vermiculate disposition. This taxon lacked keratinous scutes, both on the carapace and on the plastron. The medial margin of the first peripheral plate (Fig. 3 A-C) allows interpreting that the lateral margin of the nuchal plate experienced a marked change of curvature, being its anterior region slightly divergent anteriorly, and the posterior one markedly divergent posteriorly. The distal half of the first costal plate is markedly wedged towards the lateral region (Fig. 3 D-F). Laterally, the free margins of the dorsal ribs are developed as short and sharp apophyses for the contact with the peripherals (Fig. 3 J-L). The medial margin of the peripherals is sinuous, with marked pits where these contact are made (Fig. 3 P-U). The posterior peripherals are posteriorly expanded. The posterior margin of the

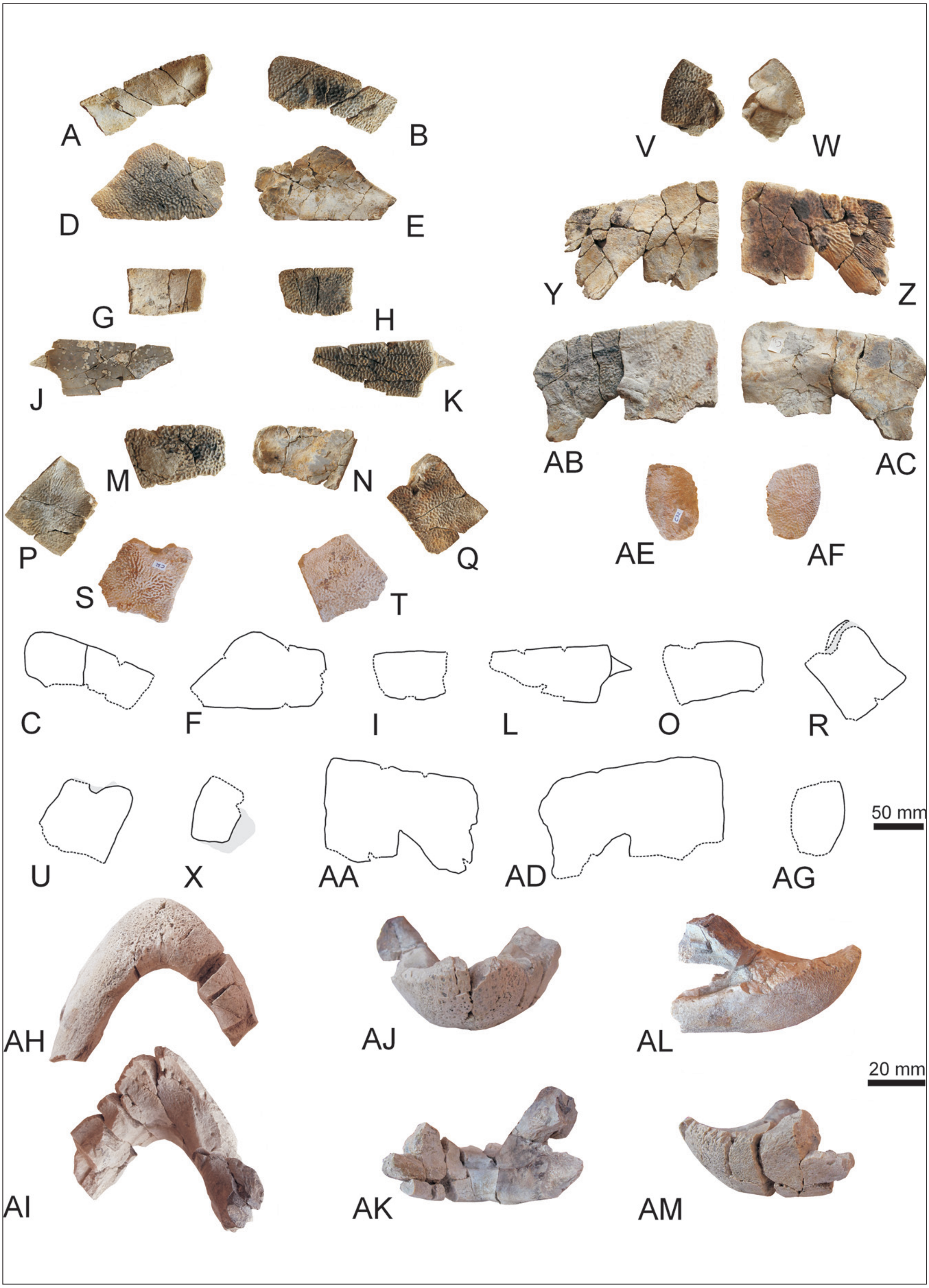

Figure 3. Several elements attributed to ***Allaeochelys* sp.** (Cryptodira, Carettochelyidae), from the Lutetian (Middle Eocene) of the Ainsa Basin. A-C, MPS-A30-18, articulated first and second right peripherals, in ventral (A) and dorsal (B-C) views. D-F, MPS-A30-10 first left costal, in dorsal (D, F) and ventral (E) views. G-O, MPS-A30-16, MPS-A30-1 and MPS-A30-17, several fragmentary costal plates, in dorsal (H-I, K-L, M, O) and ventral (G, J, N) views. P-U, MPS-A30-12 and MPS-C32-1, posterior peripherals, in ventral (P, T) and dorsal (Q-R, S, U) views. V-X, MPS-A30-14, right epiplastron, in ventral (V, X) and dorsal (W) views. Y-AA, MPS-A30-3, left hypoplastron, in dorsal (Y) and ventral (Z-AA) views. AB-AD, MPS-A30-4, right hypoplastron, in ventral (AB-AD) and dorsal (AC) views. AE-AG, MPS-C32-2, left xiphiplastron, in dorsal (AE) and ventral (AF-AG) views. AH-AM, MPS-U30-1, lower jaw, in ventral (AH), dorsal (AI), anterior (AJ), posterior (AK), right lateral (AL) and left lateral (AM) views.

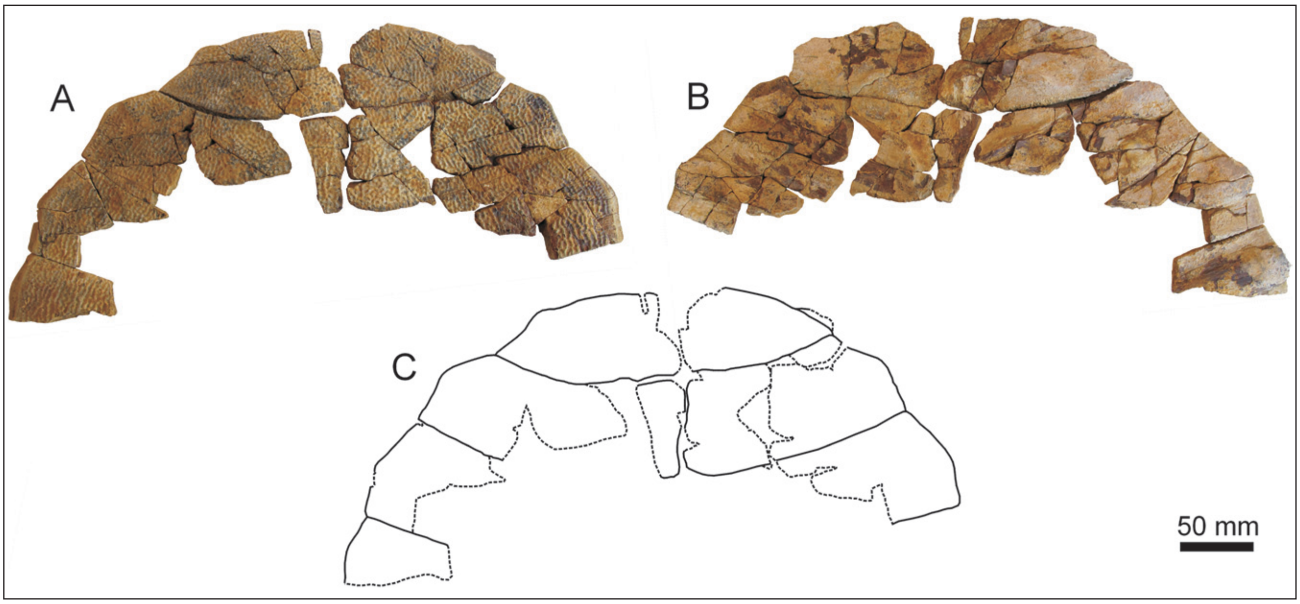

Figure 4. MPS-Li-1, anterior region of a carapace of ***Trionyx* sp.** (Cryptodira, Trionychidae), from the Lutetian (middle Eocene) of the Ainsa Basin. A and C, dorsal view. B, ventral view.

epiplastra is straight, being perpendicular to the axial plane (Fig. 3 V-X). The lateral margin of the posterior region of the epiplastra is subcircular, being much straighter the medial margin. This allows interpreting that the entoplastron was significantly tapered toward the anterior region. The hyoplastron-hypoplastron contact is not perpendicular to the axial plane, but it is postero-laterally directed (Fig. 3 Y-AD). The lateral margins of the plastral processes have short and wide indentations, which only contact with the peripheral plates. The processes of the hypoplastra are long, extending beyond the suture between the hypoplastra and the xiphiplastra. One of the two found hypoplastra (Fig. 3 Y-AA) preserves much of its posterior margin, except the most medial region. The presence of at least one strong denticle, more developed in the visceral view, is observed in this suture. The lateral margin of the identified fragment of xiphiplastron is rounded (Fig. 3 AE-AG).

The preserved region of the mandible (Fig. 3 AH-AM) is triangular in dorsal view. The symphysis is fused. Anteriorly, this region is slightly curved upwards, with a slightly elevated peak in lateral view. Its dorsal surface is slightly concave. It has a single labial ridge. An arc of vascular foramina, arranged on the half of the length of the anterior crushing surface, traversing the symphysis, is present. The splenials are absent. The coronoid processes are high. The sutures between the dentaries and the coronoids, located above these processes, are transversely arranged. A deep external dentary fossa and a relatively large foramen dentofaciale majus are identified.

Family Trionychidae Gray, 1825
Subfamily Trionychinae Fitzinger, 1826
Genus *Trionyx* Geoffroy Saint-Hilaire, 1809
Type species: *Testudo triunguis* Forsskål, 1775

***Trionyx* sp.**
(Fig. 4)

Referred specimens: MPS-Li-1, anterior region of a carapace.

Description: The specimen MPS-Li-1 is the anterior region of a carapace in which the entire dorsal surface of the plates is decorated with irregularly and low ridges, formed by the junction of tubercles. This taxon lacked keratinous scutes. The nuchal plate is very wide. The presence of a rib longer than this plate is observed on the right side. The remaining free regions of the other dorsal ribs are broken. The length of the nuchal is nearly equal to that of the first costal plate, to which is well sutured along its entire rear margin. This margin is concave except in the region where it contacts the first neural plate, where it is slightly convex. This neural lacks the left half. It is a longer than wide plate, being wider in the anterior region than in the posterior one. This taxon lacks a preneural plate as well as fontanelles, at least in the anterior region of the carapace. The almost complete first right costal plate, and the lateral region of the second right costal and of the first to third left costals, are preserved. The lateral margin of these plates is sinuous. This margin was not in contact with any other plate, so that the analyzed taxon lacked peripheral plates.

The width of this specimen, measured in the postero-lateral edge of the second pair of costals, is close to 38 cm. Therefore, it is estimated that its maximum length may be around 50 cm.

Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788

Testudinidae indet.
(Fig. 5)

Referred specimens: MPS-A30-20, proximal region of a costal plate.

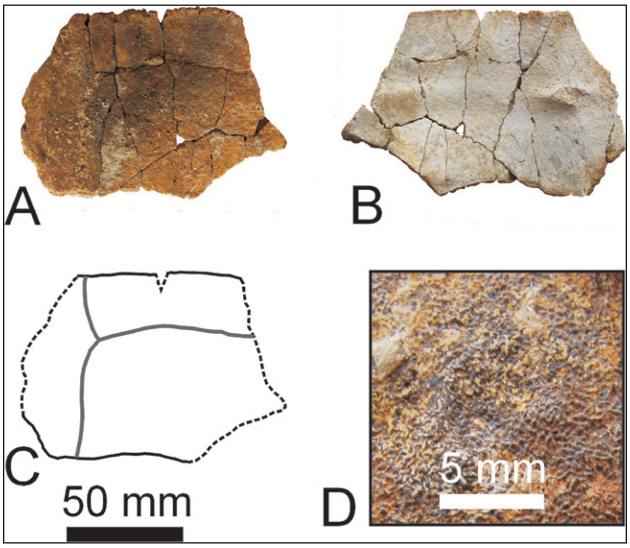

Figure 5. MPS-A30-20, proximal región of a costal plate of an indeterminate member of Testudinidae (Cryptodira), from the Lutetian (middle Eocene) of the Ainsa Basin. A and C, dorsal view. B, ventral view. D, detail of the ornamental pattern.

Description: Besides the three clades hitherto described in the Sobrarbe Fm., each of them characterized by a different ornamental pattern, a fourth taxon is identified (Fig. 5). The ornamental pattern consists of a tiny granulation. The carapace of this taxon was covered with keratinous scutes. The vertebral scute observed in the proximal fragment of the costal plate MPS-A30-20 is narrow. Antero-posteriorly, the dorsal rib is short.

3. Discussion

The presence of sutures of the pelvis with the carapace and plastron, and of mesoplastra, located on the lateral margins of the plastron, allow the assignment of the taxon represented in Figure 2 to Pleurodira. It is assigned to the European taxon *Neochelys* because it shares with its representatives a unique combination of characters (see Broin, 1977 and Lapparent de Broin, 2003 for comparison with other podocnemidids): shell decorated with fine and short dichotomic sulci; costals 1 markedly longer than costals 2; sagittal contact of the posterior costals; axillary and inguinal processes in contact with costals; iliac scars on costals 7 and 8; pleurals widely overlapping the peripherals; broad plastral lobes; anterior lobe shorter than the posterior one; lobes shorter than the bridge; broad and shallow to moderate anal notch; large and rhomboidal entoplastron, posteriorly close to the axillary notch; intergular separating the gulars; humero-pectoral sulcus medially anterior to the epi-hyoplastral suture; postero-lateral boundary of the pectorals located near the anterior margin of the mesoplastra (Pérez-García & Lapparent de Broin, in press).

Neochelys is a diverse freshwater taxon known in Eocene levels of several countries of Europe (Belgium, France, Germany, Italy, Portugal and Spain) (see Lapparent de Broin, 2003; Pérez-García & Lapparent de Broin, in press). In the Spanish record this genus is very abundant in the Duero Basin, where it may be present, with doubts, from the MP7 (earliest Ypresian) to the MP18-20 (Priabonian) (Jiménez Fuentes, 2003). Large forms (e.g., *N. salmanticensis*), and also other much smaller (e.g., *Neochelys zamorensis* Jiménez Fuentes, 1992) are identified there. Furthermore, the presence of at least one undetermined large taxon has been previously notified in Lutetian levels of the northeast of Spain (Lapparent de Broin, 2003).

Several species of *Neochelys* have been described in Europe. However, the size of the specimens from the Sobrarbe Fm. is only compatible with that of *N. salmanticensis* (type locality Teso de la Flecha, Spain, MP16), taxon whose carapace length can reach or exceed 60 cm (Jiménez Fuentes, 2003). The known maximum length of the species *Neochelys arenarum* Broin, 1977 (type locality Rians, France, MP7), *Neochelys liriae* Pérez-García & Lapparent de Broin, in press (type locality Soleillades, France, MP8-9), *Neochelys franzeni* Schleich, 1993 (type locality Messel, Germany, MP11) and *Neochelys zamorensis* (type locality Sanzoles, Spain, MP13-14) is close to 25 cm. Although the representantives of *Neochelys laurenti* (Tong, 1998) (type locality Saint Papoul, France, MP8-9), *Neochelys eocaenica* (De Stefano, 1902) (type locality Pépieux, France, MP10-11) and *Neochelys capellinii* (type locality Purga di Bolca, Italy, MP10-11) are larger than these turtles, their length rarely exceeds 35 cm, being always less than 40 cm (Lapparent de Broin, 2003, Pérez-García & Lapparent de Broin, in press).

The material of *Neochelys* from the Sobrarbe Fm. shares with all the representatives of this genus, except with *N. arenarum*, the presence of seven neurals. The presence of entoplastral length less than two times its distance with the pectoro-abdominal sulcus is shared with *N. eocaenica*, *N. franzeni*, *N. zamorensis* and *N. salmanticensis*. As in all the representatives of *N. arenarum*, *N. laurenti*, *N. liriae*, *N. franzeni* and *N. salmanticensis*, and in some specimens of *N. eocaenica*, the anterior plastral lobe is wider than the posterior one. The presence of a subrounded anterior lobe is shared with all the analyzed taxa except with *N. arenarum* and *N. zamorensis*. Moreover, it differs from *N. zamorensis* due to the absence of straight lateral margins of the posterior lobe. The character states of the intergular-gular complex of the taxon present in the Sobrarbe Fm. fall within the autapomorphic ranges of variability of *N. salmanticensis*: maximum width of the intergular scute similar to that of each gular; gulars superimposed on the anterior region of the entoplastron; intergular overlying the anterior half of the length of the entoplastron; relatively narrow intergular-pectorals contact (Jiménez Fuentes, 1968; Lapparent de Broin, 2003; Pérez-García & Lapparent de Broin, in press).

Some studies suggested that *N. salmanticensis* was represented in both the MP16 reference-level (type locality) as in more ancient levels of the Duero Basin (MP13-14), synchronous to the Sobrarbe Fm. (see, for example, Jiménez Fuentes, 1968, 1977). However, the information on the variability of *N. salmanticensis* is very scarce, and no comparisons of the abundant material of the large *Neochelys* specimens identified in several sites of the Duero Basin are available. For this reason, more recent papers has indicated that cannot be ruled that the material from the MP13-14 reference-levels may belong to an undefined taxon, closely related to *N. salmanticensis* (see, for example, Jiménez Fuentes, 2003, 2007). Thus, although the combination of characters present in the material of *Neochelys* from the Sobrarbe Fm. is only shared with the large taxon of *Neochelys* described in the Duero Basin, we opted here for its determination as *Neochelys* cf. *salmanticensis*. The detailed review of the material of the Duero Basin, currently in progress, will probably confirm this specific determination.

The combination of characters observed in the shell elements of the specimens shown in Figure 3 is unique of Carettochelyidae (see Walther, 1922; Broin, 1977): autapomorphic ornamental pattern; reduction or absence of scutes; presence of peripherals; no sinuous peripheral posterior edge; sinuous medial margin of the peripherals; plastron firmly linked to the carapace by short apophyses contacting the peripherals; anteriorly coined entoplastron; epiplastra-hyoplastra contact perpendicular to the axial plane, allowing the mobility of the anterior lobe. The combination of characters described in the mandibular material found in the Sobrarbe Fm. (Fig. 3 AH-AM) (e.g., triangular morphology, fused symphysis, single labial ridge, absence of splenials, high coronoid processes, deep external dentary fossa, relatively large foramen dentofaciale majus) is also unique to this group (Walther, 1922; Broin, 1977). The absence of keratinous scutes both in the carapace and in the plastron; relatively broad plastron; and long inguinal processes in relation to the position of the hypoplastra-xiphiplastra sutures; allow the allocation of the material found in the Sobrarbe Fm. to *Allaeochelys*, the representative of Carettochelyidae identified in the European record (Broin, 1977).

Carettochelyidae is known in Europe from the lower Eocene (MP7) (Lapparent de Broin, 2001), being its record relatively abundant throughout the Eocene (Broin, 1977; Jiménez Fuentes, 2003; Alonso Santiago & Alonso Andrés, 2005; Alonso Santiago et al., 2008), and having been recognized in the Oligocene (Karl et al., 2006; Karl & Müller, 2008). In the Iberian record, this group is well represented in Lutetian levels (MP13-14) of the Duero Basin (Jiménez Fuentes, 2003; Alonso Santiago & Alonso Andrés, 2005; Alonso Santiago et al., 2008). Two species, hitherto unique of that region, have been described: *Allaeochelys casasecai* Jiménez Fuentes, 1971 and *Allaeochelys jimenezi* Alonso Santiago & Alonso Andrés, 2005.

The maximum length of the more complete hypoplastron found in the Sobrarbe Fm. (Fig. 3 Y-AA), measured parallel to the axial axis, without considering the plastral process, is close to 10 cm. The other identified hypoplastron (Fig. 3 AB-AD) corresponds to a larger specimen. Therefore, the length of material of *Allaeochelys* recognized in this formation falls within the known range of variability for the Spanish species *A. jimenezi*, also being compatible with the size of the taxon from the Lutetian of Belgium *Allaeochelys delheidi* (Dollo, 1886). The plastron length estimated for *A. jimenezi* is about 30 cm (Alonso Santiago & Alonso Andrés, 2005). The length of the first costal plate presented here is also consistent with that of *A. jimenezi*. It has been proposed that its carapace length is about 36 cm (Alonso Santiago & Alonso Andrés, 2005). This contrasts with the size that diagnoses other European species, such as *Allaeochelys parayrei*

Noulet, 1867 (Bartonian of Castres, France), with a maximum length of the shell of 240 mm and of the plastron of 180 mm (Broin, 1977), and *Allaeochelys crassesculpta* (Harrassowitz, 1922) (Lutetian of Messel, Germany), whose size is no greater. The size of the jaw analyzed here, more robust than that of *A. crassesculpta*, is also compatible with a large species.

Several characters related with the sexual dimorphism in the species *A. crassesculpta* has recently been analyzed, being recognized that, in this species, the males are on average 17 per cent smaller than the females. Moreover, the arrangement of the hypoplastra-xiphiplastra sutures of the females are simpler than that of the males, due to the presence of a plastral kinesis, interpreted as useful in oviposition (Joyce et al., 2012). The differences in size between the Spanish species *A. casasecai* and *A. jimenezi* (estimated at 26.19% by Alonso Santiago & Alonso Andrés, 2005), together with the different morphology of the hypoplastra-xiphiplastra sutures, could indicate that both forms actually represent the sexual morphs of a single species. The larger morphotype, *A. jimenezi*, presents a more acute inguinal notch, as in the female of *A. crassesculpta*. However, *A. jimenezi* is diagnosed by the presence of a more complex hypoplastron-xiphiplastron suture than that of *A. casasecai*. The detailed study of abundant unpublished new material from the Duero Basin is need to better understand the range of variability of each of these defined species, and to confirm its validity. In this regard, the number, morphology and arrangement of the neural plates characterizing the large species, *A. jimenezi*, are compatible with those of the Belgian species, *A. delheidi*, which also coincides in the size, similar to that of the specimens from the Sobrarbe Fm. analyzed here. However, the morphology of the hypoplastron-xiphiplastron suture of the only known specimen of *A. delheidi* is similar to that of the small species, *A. casasecai*. In fact, the presence of unjustified identifications of sexual morphs of *A. casasecai* (such as the two specimens of the figure 4 of Jimenez Fuentes, 2003) has been indicated. Several complete skulls from the Duero Basin have been found, whose study will also improve the knowledge on the systematic relationships and on the interspecific and intraspecific variability of these forms. Therefore, and due to the need for a detailed study of the variability, diversity and systematic of the Spanish material, the material from the Sobrarbe Fm. is determined as *Allaeochelys* sp.

The characters combination identified in the specimen MPS-Li-1 (e.g., autapomorphic ornamental pattern; very wide nuchal; presence of a pair of ribs with lateral development greater than that of the nuchal plate; sinuous lateral margin of the costals; absence of peripherals) is unique to Trionychinae (Fig. 4). This group is relatively well represented in the European Cenozoic record by at least two lineages, one of large size, which could correspond to the American taxon *Axestemys* or a closely related form (see Hutchison & Holroyd, 2003; Pérez-García, 2012), and a smaller one, identified as *Trionyx*, compatible with the dimensions of the specimen from the Sobrarbe Fm. (Broin, 1977; Jiménez Fuentes & Alonso Andrés, 1994). In addition to its size, the specimen from the Sobrarbe Fm. can be attributed to this second taxon due to several characters: absence of preneural; absence of fontanelles between medial region of the costal plates and the nuchal; nuchal-costals 1 suture along all the anterior margin of this pair of costals; ornamentation developed over the entire dorsal surface of the plates of the carapace; rounded morphology of the carapace.

Indeterminate material, belonging to one or more species compatible with the size of *Trionyx*, has been recognized in the Duero Basin, in various sites between the MP9-14 and the MP18 reference-levels (Jiménez Fuentes, 2003). The only determination at generic and specific level corresponds to the allocation of two hyoplastra, from two sites of the MP13-14, to *Trionyx* cf. *michauxi* (Jiménez Fuentes & Alonso Andrés, 1994). That determination was only based on the sinuous morphology of the anterior margin of those plates, considered as belonging to immature specimens. The decoration attributed by Broin (1977) to the elements of the carapace of *Trionyx michauxi* Broin, 1977 was composed by ridges and tubercles considerably thicker than those of the specimen from the Sobrarbe Fm. Generally undetermined material of *Trionyx*, or of forms close to it, is identified in several Iberian sites from the Eocene to the uppermost Miocene or the early Pliocene (Pérez-García et al., 2011). Due to the poorly knowledge about this group in the Iberian record, and the scarce record from the Sobrarbe Fm., the specimen MPS-Li-1 is attributed to *Trionyx* sp.

The ornamentation of the costal plate MPS-A30-20 (Fig. 5) is compatible with that of some representatives of Testudinidae, especially with the terrestrial forms (Testudininei). As in these taxa, the dorsal ribs are antero-posteriorly short along its entire length, including its proximal region. The presence of narrow vertebral scutes, with little sinuous lateral margins, subparallel to the axial plane, is also characteristic of this group.

The presence of Testudininei in Duero Basin is known from the Late Eocene (MP16-17). There was identified the presence of a single taxon, preliminarily attributed to *Hadrianus* sp. (Jiménez Fuentes, 2003). Its size and the thickness of the plates are greater than that of the specimen MPS-A30-20. Another taxon that may be closely related to the testudininei from the Duero Basin is *Asturichelys multicostatus* Bergounioux, 1957, also from the MP16-17 reference-levels, but from the Oviedo Basin (Asturias, northwestern Spain). The presence of specimens attributed to *Hadrianus* is recorded in Europe from, at least, the Lutetian (Lapparent de Broin, 2001). However, other European representatives of Testudininei have also been recognized throughout the Eocene, having been identified even in older levels, as is the case of the French species *Achilemys cassouleti* Claude & Tong, 2004, from the early Eocene (MP8-9, Ypresian). Due to the limited availability of characters in the material analyzed here, it is attributed to an undetermined representative of Testudinidae, probably belonging to the clade Testudininei.

New palaeontological field works are being carried out in the Ainsa Basin, and mainly in the Sobrarbe Formation. More turtle remains, as well as other vertebrate fossils, have been yielded. New information will probably be obtained by the detailed study of the new turtle remains.

4. Conclusions

The turtles from the Sobrarbe Fm. (Ainsa Basin, south-central Pyrenees, northeast Spain) had not been so far described. We identify members of four clades. One of them is a member of Pleurodira Podocnemididae (*Neochelys* cf. *salmanticensis*), and the others are representatives of Cryptodira, corresponding to both Testudinidae as two groups of Trionychia: the representative of Carettochelyidae *Allaeochelys* and that of Trionychidae *Trionyx*. The information on the Iberian Lutetian record of turtles comes, almost exclusively, from the Duero Basin, and specifically from the provinces of Zamora and Salamanca, where the remains of this group of reptiles are very abundant. These levels included the presence of three groups of turtles: Podocnemididae, Carettochelyidae and Trionychidae. The known record of Testudinidae in the Duero Basin not begin until the Late Eocene (MP16-17), not being identified any terrestrial turtle in the Lutetian. Thus, the fauna of turtles from the Sobrarbe Fm. is the most diverse considering the clades represented in the Lutetian of the Iberian Peninsula. In fact, the presence of Testudinidae in the Lutetian of this basin is the oldest reference reported in the Iberian Peninsula.

The association of turtles recorded in the Sobrarbe Fm. corresponds to a European association unique to the Eocene, probably generated by the immigration of clades from Africa, Asia and North America to Europe: the presence of Podocnemididae, Carettochelyidae and Testudinidae in the European Pre-Eocene record is not known, but neither Podocnemididae is identified in the Post-Eocene record of this continent.

The material of turtles recorded in the Sobrarbe Fm. comes from various outcrops (see the location of some of them in Fig. 1). The only outcrop where the presence of more than one clade is identified is in the site A30, where carettochelyids (aquatic turtles) and testudinids (terrestrial representatives) have been identified.

Some aquatic turtles recorded in the Sobrarbe deltaic complex correspond to taxa that can live in both freshwater and brackish (the representatives of Trionychia: Carettochelyidae and

Trionychidae). However, *Neochelys* corresponds to a freshwater taxon, not having been recognized elements of other representative of Erymnochelyinae, closely related to *Erymnochelys* Baur, 1888, identified in other European regions and more linked to coastal environments.

The presence of a representative of *Neochelys* that probably corresponds to a species so far only recorded in the Duero Basin, and of a member of *Allaeochelys* that may also be represented there, allow recognizing more similarities between the turtle fauna of the Ainsa Basin with that of the Duero Basin than with any other European basin.

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