# Analysis of the Iberian Aragonian record of *Paleotestudo*, and refutation of the validity of the Spanish '*Testudo catalaunica*' and the French '*Paleotestudo canetotiana*'

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## ABSTRACT

Information about the small Testudinidae taxon or taxa (i.e. with a length less than 30 cm) recorded in the Aragonian of the Iberian Peninsula was, until now, very limited. The references to '*Paleotestudo catalaunica*' were regarded as possibly the only valid systematic identifications. That species corresponds to a tortoise defined in the Aragonian of Spain (Sant Quirze del Vallès, Barcelona). New material of tortoises, from several Spanish Aragonian regions, is analyzed here. The specimens from the type locality of '*Paleotestudo catalaunica*' and from other Spanish sites, as well as those from two other European late Aragonian sites (Sansan in France and Hohenhöwen in Germany, where two taxa represented by several specimens were described) are reviewed here. This study refutes the validity of the taxa described in Sant Quirze del Vallès and in Sansan, being recognized as junior synonyms of the German *Paleotestudo antiqua*. This species is the only one recognized in the Aragonian of Spain.

**Keywords:** Testudinidae, *Paleotestudo antiqua*, middle Miocene, Europe, Spain.

## RESUMEN

La información sobre el taxón o taxones de testudínidos de talla pequeña (es decir, de no más de 30 cm de longitud máxima) registrados en el Aragoniense de la Península Ibérica era, hasta ahora, muy limitada. Únicamente se consideraban como posiblemente válidas las referencias a '*Paleotestudo catalaunica*', un quelonio definido en el Aragoniense superior español (Sant Quirze del Vallès, Barcelona). Nuevo material, proveniente del Aragoniense de varias regiones españolas, es aquí analizado. Para su estudio se revisa el material proveniente de la localidad tipo de '*Paleotestudo catalaunica*' y el de otras localidades españolas, así como los de dos localidades europeas del Aragoniense superior (Sansan en Francia y Hohenhöwen en Alemania), donde se describieron dos taxones representados por varios ejemplares. Este trabajo permite refutar la validez de los taxones descritos en Sant Quirze del Vallès y Sansan, reconociéndose como sinónimos de la especie definida en Alemania *Paleotestudo antiqua*. Esta especie es la única reconocida en el Aragoniense español.

**Palabras clave:** Testudinidae, *Paleotestudo antiqua*, Mioceno medio, Europa, España.

# 1. INTRODUCTION

The fields in which Miocene vertebrates are represented are very numerous in the Iberian record. Turtles, and especially the terrestrial forms (Testudinidae), are one of the best-represented clades. However, despite the abundance of turtle remains, and the generally good preservation, the information available was, until recently, very limited. In fact, although several representatives were defined in the Aragonian levels, they lacked diagnosis or the proposed diagnosis needed to be updated. In addition, the generic attribution, and even the specific validity of many of these forms, was problematic.

On the one hand, the remains of large turtles (i.e., specimens with a carapace length of the adult individuals greater than one meter, and even than 1.5 m) are very common in Iberian Aragonian levels. The presence of these turtles is known for over 150 years (Pérez-García & Vlachos, 2014). These large turtles had been originally referred to *Testudo* Linnaeus, 1758, the genus to which all tortoises were traditionally attributed. However, the large tortoises identified from the early Miocene to the early Pleistocene in both Europe and the western region of Asia have been recently assigned to the new genus *Titanochelon* Pérez-García & Vlachos, 2014. A single species of this genus is now recognized in the Spanish Aragonian and Vallesian record: *Titanochelon bolivari* (Hernández-Pacheco, 1917).

Furthermore, the findings of remains of considerably smaller testudinids (i.e., specimens with a carapace length shorter than 30 cm) are also very common in Iberian Aragonian sites. Evidence about the discovery of these forms is known since the first half of the twentieth century (Pérez-García & Murelaga, 2013) (Fig. 1). These forms, also originally attributed to *Testudo*, have been recently reassigned to *Paleotestudo* Lapparent de Broin 2000 (Pérez-García & Murelaga, 2013). Pérez-García & Murelaga (2013) recognize the presence of this genus in all Aragonian and Vallesian biozones of the Iberian Peninsula. Three representatives of this clade had been defined at these levels: '*Paralichelys catalaunicus*' Bergounioux, 1951, from the early Aragonian (MN4) of Can Mas (Barcelona); '*Testudo catalaunica*' Bataller, 1926, defined on the basis of material from the late Aragonian (MN7/8) of Sant Quirze del Vallès (Barcelona); and '*Testudo catalaunica* var. *irregularis*' Bergounioux, 1958, proposed from a specimen found in the same locality. In addition, the presence of potentially new Spanish Aragonian species, which could be related to '*Testudo catalaunica*', had been indicated from remains from the late Aragonian (MN6) of Paracuellos del Jarama and Henares 1, both sites in Madrid (Jiménez Fuentes, 1985). Pérez-García & Murelaga (2013) refuted the validity of '*Paralichelys catalaunicus*', reassigning the holotype and the only known specimen to *Paleotestudo* sp. These authors reported the

presence of intraspecific variability in the case of '*Testudo catalaunica*', refuting the validity of '*Testudo catalaunica* var. *irregularis*', and questioning the previous allusions to potentially new forms proposed by Jiménez Fuentes (1985). Furthermore, that study highlighted the need to review the validity of the species '*Testudo catalaunica*', this taxon being a species lacking a diagnosis that allowed distinguish it from other species defined in other European regions.
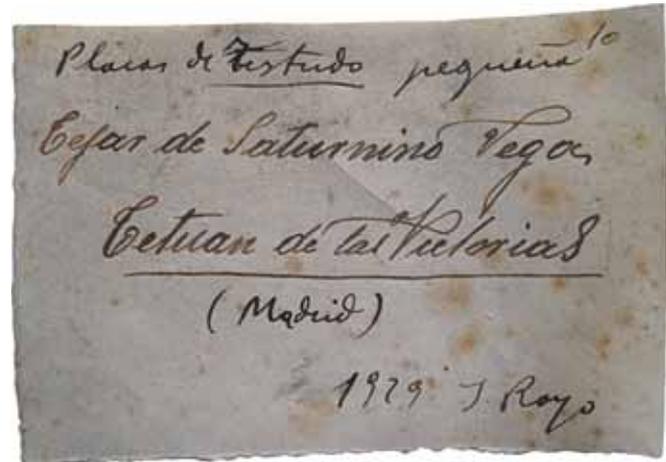


**Figure 1.** Handwritten label by the Spanish paleontologist José Royo y Gómez (1895-1961) corresponding to the discovery of several plates of a 'small *Testudo*' from Tetuan de las Victorias (Madrid), in 1929.

Pérez-García & Murelaga (2013) identified the presence of *Paleotestudo* in several Iberian Aragonian sites. Subsequent studies allowed the identification of specimens attributable to this genus in other middle and late Aragonian sites (MN5-MN6) of Madrid: Somosaguas, O'Donnell and El Pardo (Pérez-García, 2013, 2014; Pérez-García & Vlachos, 2014). New material attributable to *Paleotestudo* is presented here. These specimens come from various Spanish middle and late Aragonian sites where, until now, no reference to turtles had been made (La Barranca, Nombrevilla 2 and Torralba de Ribota 1-3, in Zaragoza; Moratilla 2, in Teruel; Valdemoros 3, in Madrid), or the only previously identified taxon was *Titanochelon* (Illescas, in Toledo; Barajas, Puente de los Franceses and Puente de Vallecas, in Madrid) (Pérez-García & Vlachos, 2014). As in Somosaguas (Pérez-García, 2013), the study of turtles from one of these locations where this group was unpublished (La Barranca) also allows me the identification of material assignable to *Titanochelon*.

The type species of *Paleotestudo*, '*Paleotestudo canetotiana*' (Lartet, 1851), was defined from material found on the late Aragonian (MN6) site of Sansan (Gers, France) (Lapparent de Broin, 2000). Other species defined

in the European late Aragonian (MN7/8) is '*Testudo*' *antiqua* Bronn, 1831, from Hohenhöwen (Engen, Germany). Lapparent de Broin *et al.* (2006a) identified the German species as a potential member of *Paleotestudo*. However, these authors had access to scarce material. Several specimens from Hohenhöwen have recently been published (Corsini *et al.*, 2014). Relevant intraspecific variability can also be identified comparing the specimens from that locality. However, these specimens have not been thoroughly compared with those from other European regions. A high variability can be also identified comparing the *Paleotestudo* individuals from Sansan, and also by the study of the specimens from other Iberian localities where several specimens are recognized (Lapparent de Broin, 2000; Pérez-García & Murelaga, 2013). The study of new Spanish Aragonian material, together with the review of the previously published remains (especially those from the type locality of '*Testudo catalaunica*'), and the comparison of all these specimens with those from Sansan and Hohenhöwen, allows me evaluating the validity of both the Spanish and the French taxa. Thus, a new hypothesis about the diversity of the Iberian Aragonian small testudinids is proposed here.

**Institutional abbreviations.** FFSM, Fürstlich Fürstenbergisches Sammlung Donaueschingen, Donaueschingen, Germany; MGM, Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain; MGSB, Museo Geológico del Seminario de Barcelona, Barcelona, Spain; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN.F, Paleontological collection of the Muséum National d'Histoire Naturelle, París, France; MT, Museum de Toulouse, Toulouse, France; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; STUS, Sala de las Tortugas de la Universidad de Salamanca, Salamanca, Spain; UFGC, University of Freiburg, Colecciones Geológicas, Freiburg, Germany.

## 2. MATERIALS AND METHODS

As it has been indicated, specimens corresponding to small testudinids from several Spanish sites where this group was not known are presented and studied in this paper. Some of these sites are located in middle Aragonian levels (MN5) of Madrid (Barajas, Puente de los Franceses, Puente de Vallecas and Valdemoros 3). Others belong to Aragón, being located in levels deposited during the early or middle Aragonian (MN4 or MN5) (Torralba de Ribota 1-3, Zaragoza), middle Aragonian (Moratilla 2, Teruel), and late Aragonian, and corresponding to both the MN6 (La Barranca, Zaragoza) and the MN7/8 (Nombrevilla 2,

Zaragoza) biozones. The presence of this group in Illescas (Toledo), is also recognized. Specifically, this finding comes from levels dated as late Aragonian (MN7/8) (Peláez-Campomanes *et al.*, 2003; Sesé, 2003; Astibia & Morales, 2006; García-Paredes *et al.*, 2009; Abella *et al.*, 2011; Domingo *et al.*, 2012; Bastir *et al.*, 2014; Pérez-García & Vlachos, 2014).
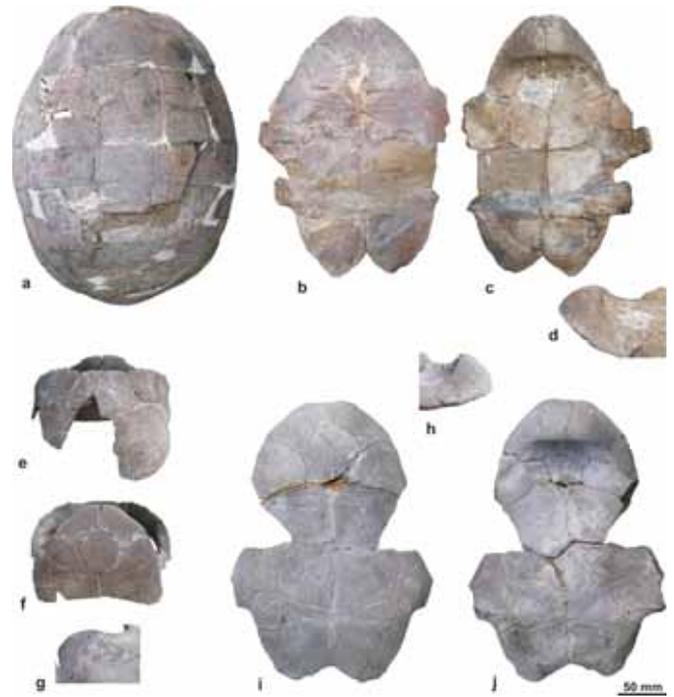


**Figure 2.** French specimens corresponding to the early Miocene (MN2-3) tortoise '*Testudo*' *promarginata*, and to forms closely related to this species. **a-d)** '*Testudo*' *promarginata* (*sensu* Broin, 1977), MNHN.F NEU 55. Neuville-aux-Bois, MN3. Carapace, in dorsal view **(a)**; plastron, in ventral **(b)** and dorsal **(c)** views; and detail of the visceral surface of the anterior plastral lobe, in left lateral view **(d)**. Other figures of this specimen are the plate 32.2 and the figure 112 of Broin (1977). **e-g)** '*Testudo*' *promarginata* (*sensu* Broin, 1977), MNHN.F SG 292. Saint-Gérand-le-Puy, MN2. Anterior region of the carapace in dorsal **(e)** and ventral **(f)** views; detail of the visceral surface of the anterior plastral lobe, in left latero-dorsal view **(g)**. Other figures of this specimen are the plates 31.1 and 31.4-6 of Broin (1977). **h-j)** '*Testudo*' sp. *promarginata* group (*sensu* Broin 1977), MNHN.F SG 326. Saint-Gérand-le-Puy, MN2. Right lateral view of the visceral surface of the anterior plastral lobe **(h)**; plastron, in ventral **(i)** and dorsal **(j)** views. Other figures of this specimen are available in the plate 30.1-2 of Broin (1977).

50 mm
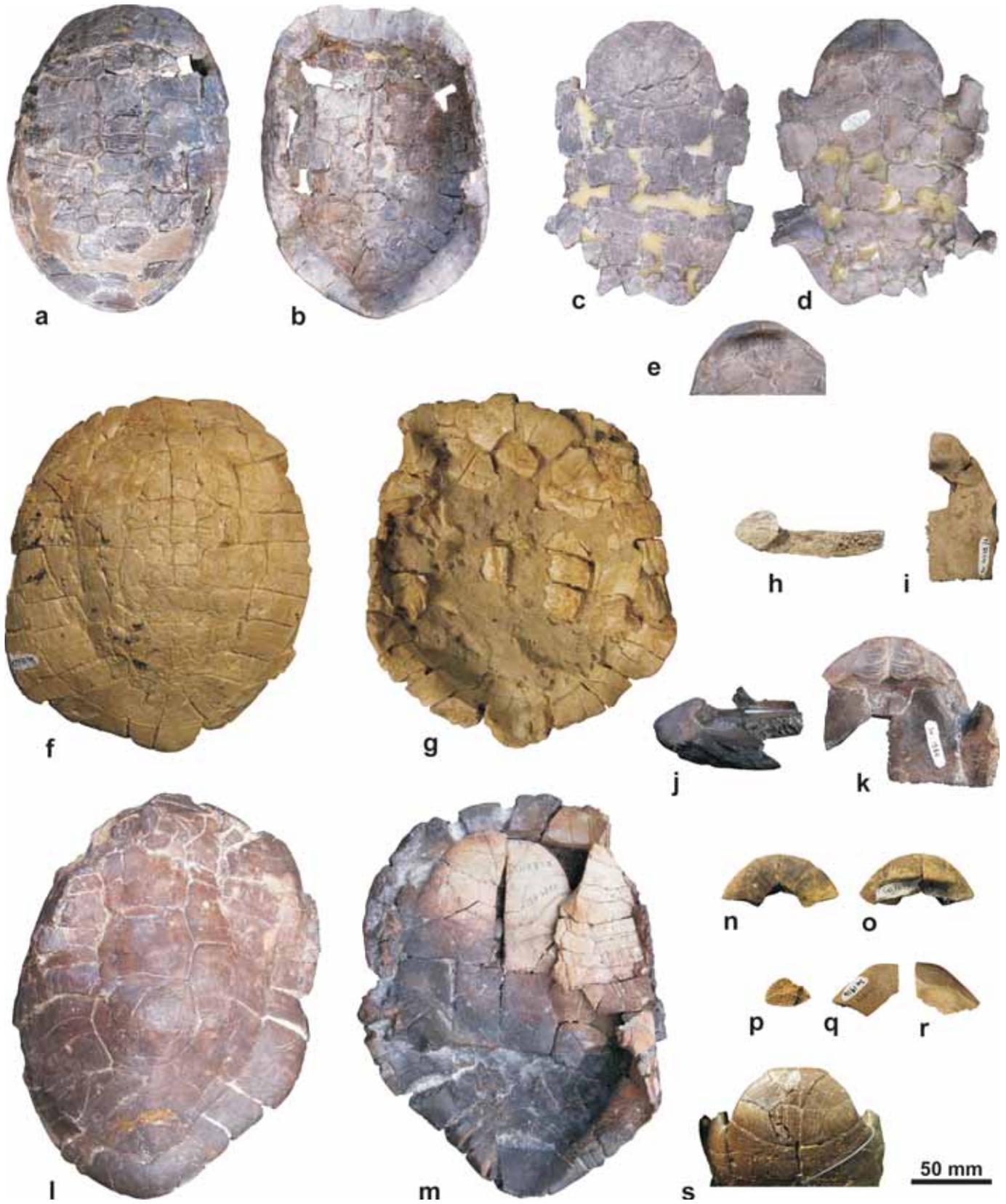
The *Paleotestudo* material from the Iberian record has been compared to several taxa of Testudinidae. Some of the most relevant comparisons are those that have involved the detailed review of specimens attributable to the early Miocene taxon '*Testudo*' *promarginata* Reinach, 1900 (e.g., MNHN.F NEU 55 and MNHN.F SG 292), and of other forms closely related to this taxon, from the MN2 and MN3 of several French sites (e.g. MNHN.F SG 326) (Fig. 2). Indeed, Lapparent de Broin *et al.* (2006a) indicated that '*Testudo*' *promarginata* probably belongs to the same clade that '*Paleotestudo canetotiana*' and '*Testudo*' *antiqua*. The rich collection of specimens of '*Paleotestudo canetotiana*' from the type locality (late Aragonian, MN6; Sansan, France), and those deposited in the MNHN, has been thoroughly revised. Some of the most relevant specimens, including some previously published individuals and many unpublished ones, are: MNHN.F SA 1672-1674, 1677, 1680-1681, 1683, 1686-1687, 1701-1702, 1719-1720, 1722, 1724, 1731-1732, 1737, 1751, 1756-1757, 1764-1765, 1826-1827, 1829-1830, 1832-1840, 1842-1844, 1851-1852, 1855-1858, 1861, 1863, 1866-1869, 1871, 1873, 1878, 1881-1883, 1886, 1903-1904, 1908, 1914-1915, 1918-1919, 1921-1923, 1928, 1945, 1950, 1962-1965, 1967, 1969-1972, 1974-1981, 1983, 1986, 10342, 14501-14502, 14511, 14520, 14523, 14539-14540, 14599, 15108-15112, 15114-15115, 15338, 15341, 15357, 15369-17372, 15375, 15647, 15657, 15682, 15684, 15686-15687, 15690 (Fig. 3). The figures and the detailed descriptions of all the thus far known specimens from the type locality of '*Testudo*' *antiqua* (late Aragonian, MN7/8; Hohenhöwen, Germany), recently published by Corsini *et al.* (2014), have also been considered (i.e., the neotype, MT PAL 2012.0.10, as well as the specimens FFSM 3446.1-3446.4, SMNS 4450, SMNS 51467, SMNS 51469 and UFGC 9). The specimens from the type locality of '*Testudo catalaunica*' (late Aragonian, MN7/8; Sant Quirze del Vallès, Barcelona) have been thoroughly analysed in order to assess the validity of this species (highlighting the lectotype of '*Testudo catalaunica*', MGSB 25324a; the holotype of '*Testudo catalaunica* var. *irregularis*', MGM 1561M; and the specimens MGM 236M and MGSB 25324b) (Figs 4a-4m). All so far cited

specimens of *Paleotestudo* from the Aragonian levels of the Iberian Peninsula (see the compilation of the references and the information corresponding to those numerous specimens in Pérez-García & Murelaga, 2013) have been considered in the comparisons performed here, including the specimen MGSB 24980, i.e. the holotype of '*Paralichelys catalaunicus*' (early Aragonian, MN4; Can Mas, Barcelona) (Figs 4n-4o).

The results obtained by various phylogenetic hypotheses based on molecular data, where the lineages of *Testudo graeca*, *Agrionemys horsfieldi* (Gray, 1844) and *Chersine hermanni* (Gmelin, 1789) (*sensu* Bour & Ohler, 2008) are generally not identified, and all their representatives are grouped under the generic name of *Testudo*, and others in which morphological data are used result in a marked lack of consistency. For that reason, the Turtle Taxonomy Working Group considers valid either the use of *Testudo* for all of them or the use the three generic names: *Testudo*, *Agrionemys* Khosatzky & Mlynarski, 1966 and *Chersine* Merrem, 1820 (van Dijk *et al.*, 2014). The terminology proposed by Lapparent de Broin *et al.* (2006a, 2006b, 2006c) is used here, and the specimens from Hohenhöwen, Sansan and Sant Quirze del Vallès are referred to *Paleotestudo*. Nevertheless, and supporting the ideas of van Dijk *et al.* (2014), the allocation of these specimens to *Testudo* should be performed when the term *Testudo* is used in a broader sense, so it also has to include the representatives of *Agrionemys* and *Chersine*.

## 3. SYSTEMATIC PALAEONTOLOGY AND DESCRIPTION OF NEW IBERIAN ARAGONIAN SPECIMENS

Order CHELONII Latreille, 1800
Suborder CRYPTODIRA Cope, 1868
Superfamily TESTUDINOIDEA Batsch, 1788
Family **Testudinidae** Batsch, 1788
Genus *Paleotestudo* Lapparent de Broin, 2000

**Figure 3.** Specimens of *Paleotestudo antiqua* from the middle Miocene (MN6) of Sansan (Gers, France), type locality of '*Testudo canetotiana*'. **a-e)** MNHN.F SA 1673. Carapace, in dorsal **(a)** and ventral **(b)** views; plastron, in ventral **(c)** and dorsal **(d)** views; postero-dorsal view of the visceral surface of the anterior plastral lobe **(e)**. See other images of this specimen in figs 113-114 of Broin (1977), fig. 12 of Lapparent de Broin (2000), and figs 2d and 7a of Lapparent de Broin *et al.* (2006b). **f-g)** MNHN.F SA 15657. Shell, in dorsal **(f)** and ventral **(g)** views. **h-i)** MNHN.F SA 14539. Fragmentary anterior plastral lobe, in medial **(h)** and dorsal **(i)** views. **j-k)** MNHN.F SA 1986. Anterior plastral lobe in left lateral **(j)** and dorsal **(k)** views. See other images of this specimen in plate 34.5-6 of Broin (1977). **l-m)** MNHN.F SA 1868. Shell, in dorsal **(l)** and ventral **(m)** views. See other images of this specimen in plate 11.2 of De Stefano (1902), and in fig. 11 of Lapparent de Broin (2000). **n-o)** MNHN.F SA 1674. Articulated epiplastra, in ventral **(n)** and dorsal **(o)** views. **p-r)** MNHN.F SA 1914. Right epiplastron, in medial **(p)**, ventral **(q)** and dorsal **(r)** views. **s)** MNHN.F SA 10342. Detail of the anterior half of the plastron in ventral view.

50 mm
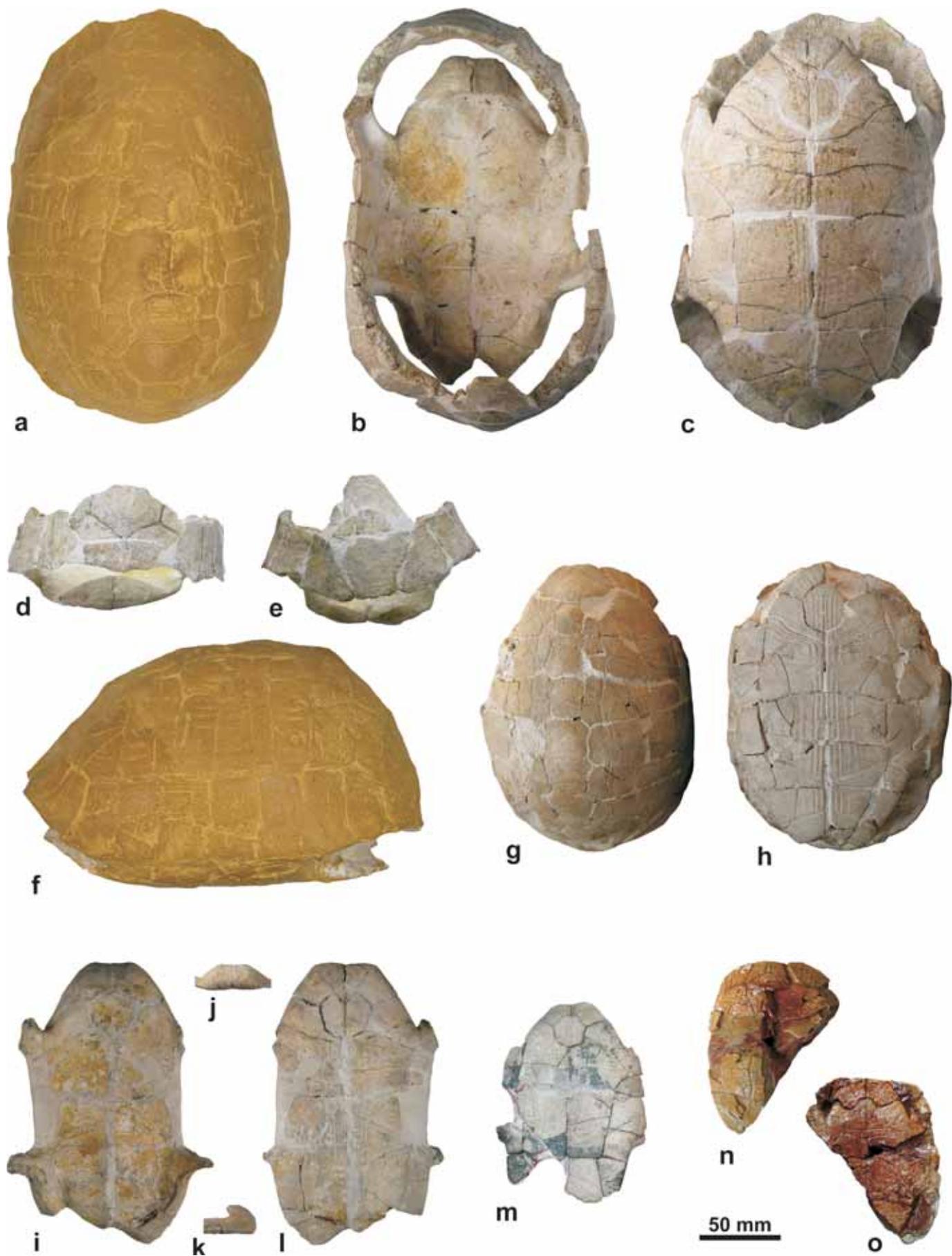
*Paleotestudo antiqua* (Bronn, 1831)
(Figs 5, 6a-6b)

**Material.** A relatively complete shell, MNCN 79862, from Barajas (Madrid) (Fig. 5); a shell that preserves a high percentage of the plastron plates; and the internal mold of its carapace, STUS 14244, from Illescas (Toledo) (Figs 6a-6b).

**Description.** The total length of the shell from Barajas, MNCN 79862, is about 28 cm (Fig. 5). This length is interpreted as greater than that which was the specimen in life, because the diagenetic deformation. The deformation affects most of the shell elements, especially those of the carapace. This shell is relatively narrow, its maximum length being more than 40 % greater than its width. This allows supporting its interpretation as corresponding to a male, as it was proposed for the relatively narrow shells of *Paleotestudo* from the French locality of Sansan and also from those of the Spanish site of Cerro de los Batallones (Lapparent de Broin, 2000; Pérez-García & Murelaga, 2013). The plates of both the carapace and the plastron are relatively thick.

The anterior margin of the nuchal plate is not preserved. However, the preserved region allow interpreting that this plate was wider than long. The neural series, composed of eight plates, is partially preserved. Only a fragment of the first neural, corresponding to the left latero-medial region, can be identified. This fragment is preserved in articulation with the first left costal. The right postero-lateral region of the third neural, rectangular in morphology, is identified. The right half of the fourth neural is also recognized. This plate was octagonal. The preserved region of the fifth neural does not reveal its shape. However, the sixth neural is almost complete. It is hexagonal. The length of the latero-anterior margin is similar to that of the latero-posterior. The seventh neural is missing. Nevertheless, the morphology of the adjacent left costals allows inferring that it was also a hexagonal plate. However, their latero-anterior margins were shorter than the latero-posterior ones. The last neural is also hexagonal, with a morphology similar to that of the previously described neural. This

specimen has two suprapygal plates. Both plates form a trapezoidal structure, longer than wide. The first suprapygal is wider than the second. In fact, this plate encircles the semilenticular second suprapygal, posteriorly contacting the last pair of peripherals and the pygal plate. The pygal is longer than wide. It is also a trapezium, but differs from that constituted by the suprapygals because its anterior margin is wider than the posterior. Viscerally, this plate is concave. Therefore, despite the partial dislocation, its posterior edge is recognized as antero-ventrally directed. The antero-posterior elongation of the suprapygals is recognized as anomalous when this region is compared with that of other specimens of different taxa grouped under *Testudo s.l.* (*sensu* Lapparent de Broin *et al.*, 2006c). In fact, this individual shows several anomalies, both in the plates and in the scutes, related to the morphology of that region. So, a pair of supplementary costals is identified in the posterior region of the carapace. Therefore, MNCN 79862 has nine pairs of costals. Furthermore, a pair of additional peripherals is also identified. A pattern of alternating pairs of costals, some of them with long distal margins and short medial ones, and others showing the inverse condition, is observed. Due to its preservation, the distal margin of the anterior peripherals is unknown. However, a small protrusion at the distal margin of the posterior peripherals, coinciding with the boundary between two marginal scutes, can be recognized (see the left tenth peripheral in Fig. 5a). The anterior margin of the last pair of peripherals is significantly shorter than the posterior. As indicated, this shell is substantially crushed. The peripherals of the bridge region are high relative to its length, corresponding to a relatively high shell, with verticalized lateral margins.

MNCN 79862 has a cervical scute. It is longer than wide. The anomaly observed in the posterior region of the carapace also affects the vertebral, pleural and marginal scutes. Thus, six vertebral scutes are recognized. These scutes are relatively narrow in relation to the pleurals. The first scute is pentagonal. The second to fifth vertebrals are hexagonal. The posterior margin of the fourth vertebral is noticeably narrower than the anterior. This condition is not shared with the other vertebrals, their anterior and

**Figure 4. a-m)** Specimens of *Paleotestudo antiqua* from the middle Miocene of (MN7/8) Sant Quirze del Vallès (Barcelona, Spain), type locality of '*Testudo catalaunica*'. **a-f)** Holotype of '*Testudo catalaunica* var. *irregularis*'; **b-e)** original specimen, as it is preserved today (MGM 1561M). Figs 4a, 4f show casts performed before the specimen suffered considerable damage (STUS 14245). Shell in dorsal **(a-b)**, ventral **(c)**, anterior **(d)**, posterior **(e)** and left lateral **(f)** views. **g-h)** Lectotype of '*Testudo catalaunica*', MGSB 25324a. Shell in dorsal **(g)** and ventral **(h)** views. See other figures of this specimen in the plates 1-2, 3.3 and 5-8 of Bataller (1926). **i-l)** MGM 236M. Plastron in dorsal **(i)** and ventral **(l)** views, and details of the anterior region of the anterior plastral lobe, in anterior **(j)** and right lateral **(k)** views. **m)** MGSB 25324b. Plastron in ventral view. **n-o)** Specimen of cf. *Paleotestudo antiqua*, MGSB 24980, from the early Aragonian (MN4) of Can Mas (Papiol, Barcelona). This specimen is the holotype of '*Paralichelys catalaunicus*'. Partial carapace, in dorsal **(n)** and ventral **(o)** views. See other figures of this specimen in the plates 1-2 of Bergounioux (1951), and in the fig. 10 of Bergounioux (1958).
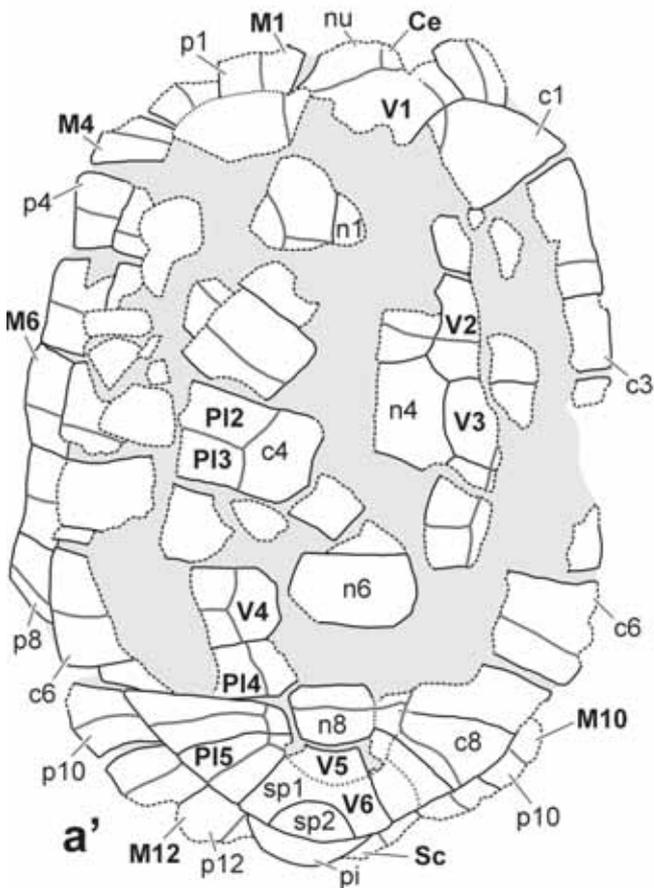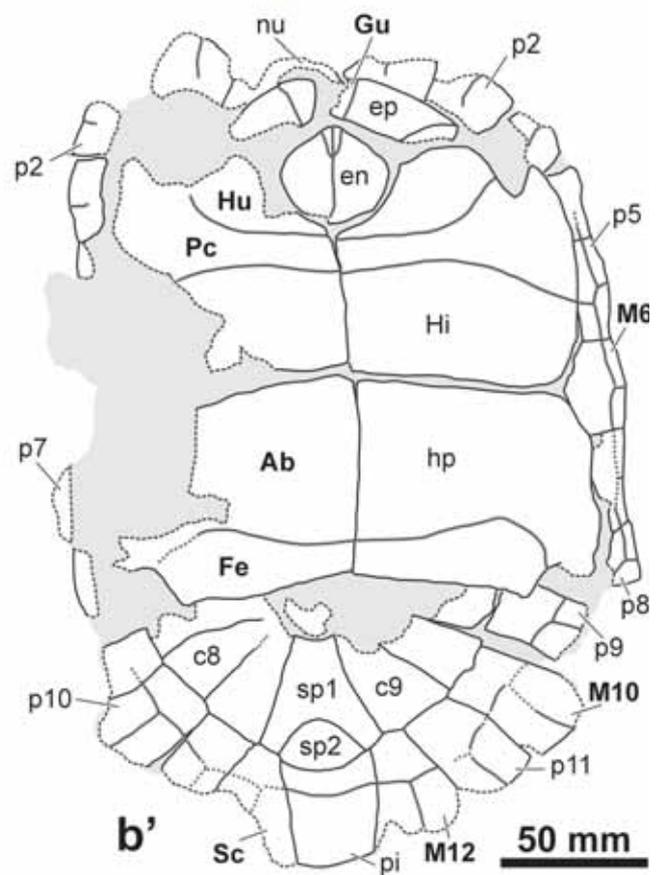
posterior margins being similar in length. The last vertebral is trapezoidal, posteriorly much wider than anteriorly. The boundary between the first and second vertebrals is placed on the medial region of the first pair of costals and of the first neural. That between the second and the third vertebrals is on the third costals and third neural. That between the third and fourth vertebrals crosses the fifth costals and the fifth neural. The boundary between the fourth and fifth vertebrals is located on the seventh costals and the eighth neural. The contact between the additional vertebral scute (i.e., the fifth) and the last one is placed on the last pair of costals and on the first suprapygal. The boundaries between the first four pairs of pleurals, as well as the posterior margin of the fourth vertebral, are located in the standard position for this group of turtles: the middle and distal region of the second, fourth, sixth and eighth costals. The boundary between the fourth and the extra pleural is located on the most posterior pair of costals. The contact between the vertebral and the marginal scutes coincides with the suture between the costal and the peripheral plates along its entire path.

All elements of the plastron are complete or nearly complete except for the xiphiplastra, which have not been found. The anterior plastral lobe is relatively short and wide. Its anterior margin is slightly trapezoidal, the lateral margins being rounded. The entoplastron is subrhombic, slightly wider than long. The hyoplastra are longer than the hypoplastra. A sutured contact is present between the hypoplastra and the xiphiplastra. The visceral region of the epiplastra is not known. However, the presence of a well-developed dorsal epiplastral lip is recognized in anterior view.

The gular scutes overlap the anterior third of the entoplastron, constituting a very acute triangle. Ventrally, a positive relief is observed in the area covered by the gulars. The sulcus, which forms the boundary between the humerals and the pectorals, is concave towards the anterior region. Sagittally, the pectorals are located near the entoplastron. However, they do not contact this plate. The pectorals are very short in the medial region. The abdomino-femoral sulcus does not contact the xiphiplastra, and is not located next to this pair of plates. Considering this, and the sutured contact described between the xiphiplastra and the hypoplastra, the absence of a hinge is recognized.

Due to its preservation, the internal mold of the carapace of the specimen from Illescas, STUS 14244, does not provide relevant information from a systematic point of view. The anterior plastral lobe is trapezoidal. The lateral margins are slightly curved (Figs 6a-6b). The epiplastral symphysis is almost as long as the entoplastron. The anterior margin of the entoplastron is subperpendicular to the axial plane. A well-developed epiplastral dorsal lip is observed in visceral view. Its dorsal surface is convex. This structure is longer than the epiplastral symphysis, so it overlaps the anterior region of the entoplastron. A relatively well-developed gular pocket is present on the posterior surface of the lip. The length of the hyoplastra is similar to that of the hypoplastra. The xiphiplastra is as long as wide. The anal notch is more than twice as wide as long.

Due to its preservation, the boundary between the gular and the humeral scutes is not identifiable in ventral view. Despite being small, the sagittal distance between the pectoral scutes and the entoplastron is greater than that observed in the specimen from Barajas. Medially, the pectoral scutes are also very short. The humero-pectoral sulcus is concave. The abdomino-femoral sulcus is also concave medially, but it is laterally convex, contacting the inguinal notches. However, its sagittal distance to the xiphiplastra is less than that observed in the individual of Barajas. The morphology of this sulcus, and the nature of the contact between the xiphiplastra and the hypoplastra, also involve a union lacking a hinge. The femoro-anal scute is convex throughout its entire path. The anal scutes are short, because that sulcus is located on the posterior half of the xiphiplastra.

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cf. *Paleotestudo antiqua* (Bronn, 1831)
(Figs 6c-6ac)

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**Material.** Plates, usually disjointed, from several localities: a) Puente de los Franceses (Madrid) (Fig. 6c): two plates, MNCN 48293 and MNCN 48294, corresponding to a partial nuchal and a partial peripheral; b) Valdemoros 3 (Madrid) (Fig. 6d): a peripheral, MNCN 35698; c) Puente de Vallecas (Madrid) (Figs 6e-6g): five plates, some of them are complete but others are partial elements, corresponding to the carapace of one or, probably (taking into account the differences in the size and preservation between the specimens),

**Figure 5.** Specimen of *Paleotestudo antiqua* from the middle Aragonian (MN5) of Barajas (Madrid, Spain). MNCN 79862. Shell in dorsal **(a)** and ventral **(b)** views. Abbreviations for the plates (lowercase): c, costal; en, entoplastron; ep, epiplastron; hi, hyoplastron; hp, hypoplastron; n, neural; nu, nuchal; p, peripheral; pi, pygal; sp, suprapygal. Abbreviations for the scutes (in bold and capitals): Ab, abdominal; Ce, cervical; Fe, femoral; Gu, gular; Hu, humeral; M, marginal; Pc, pectoral; Pl, pleural; V, vertebral.

50 mm
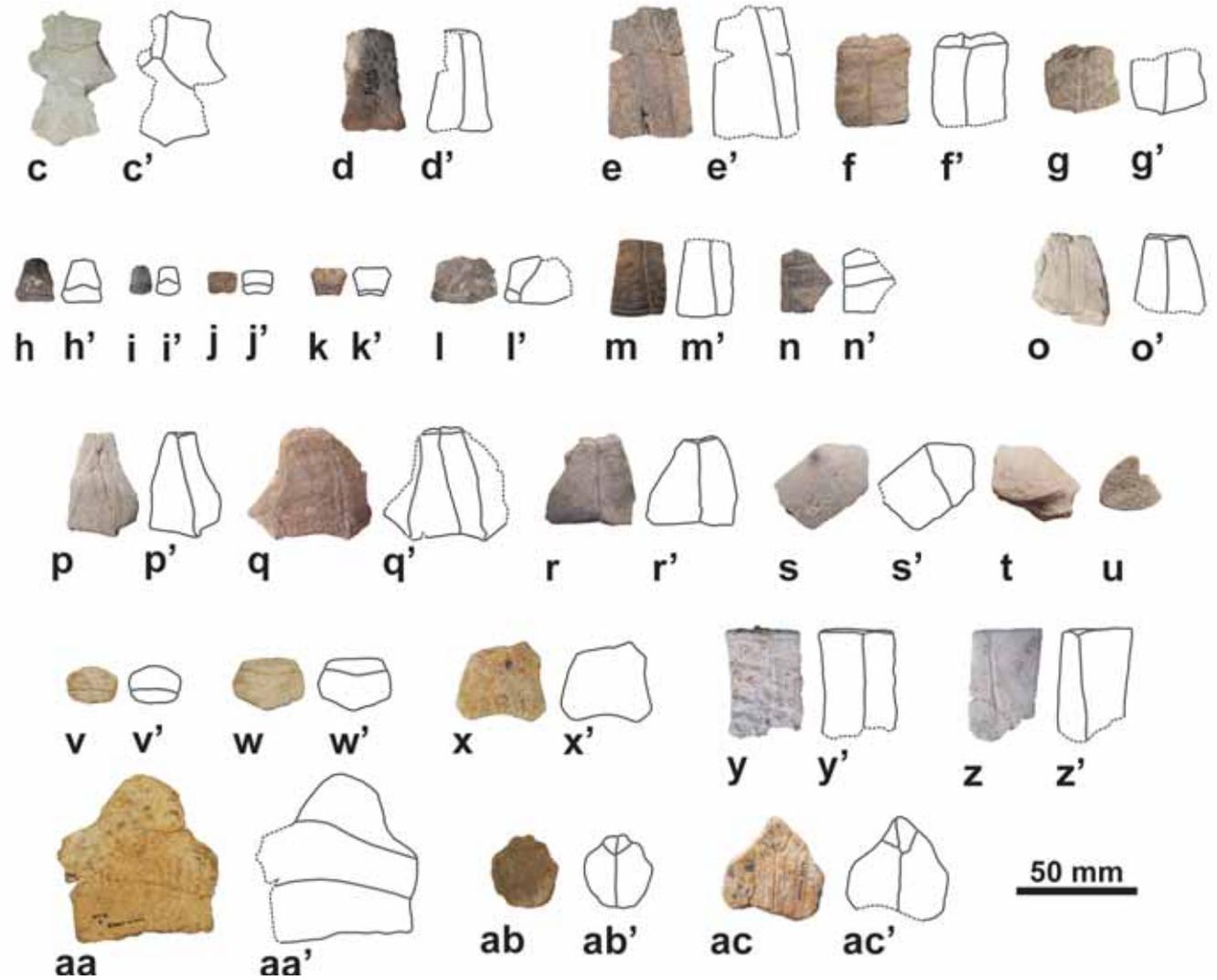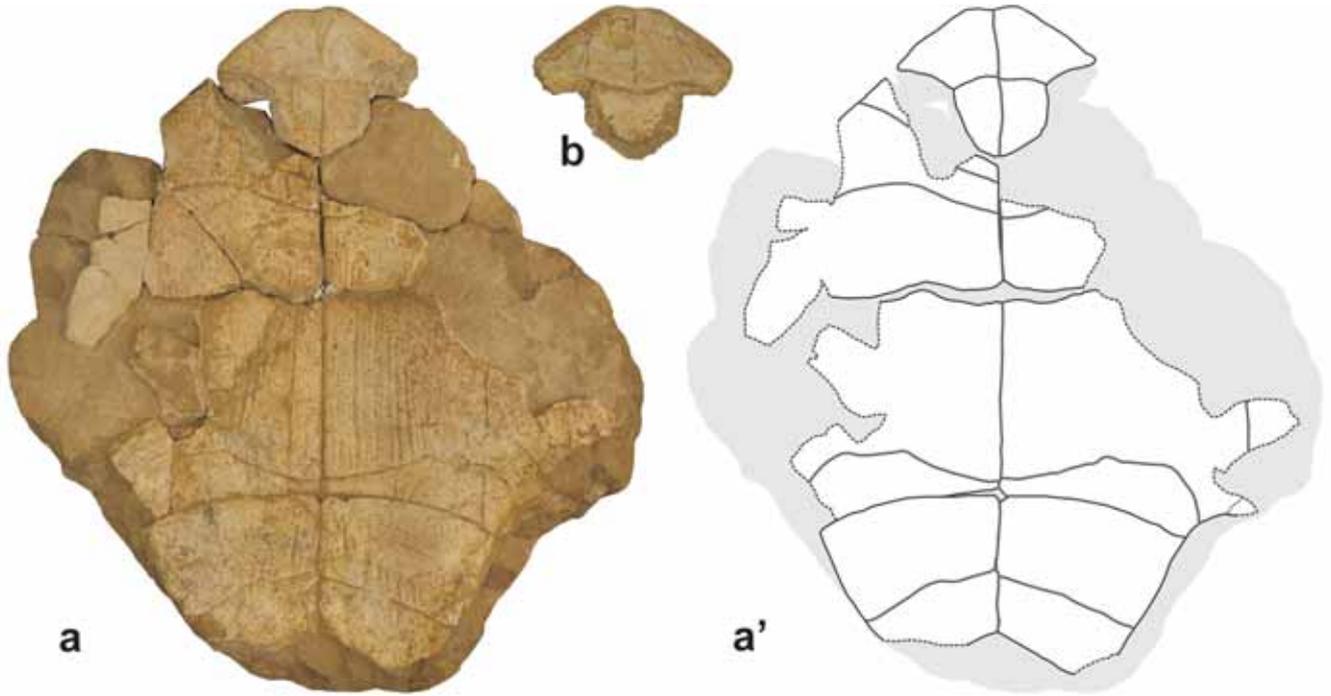
at least two individuals. All of them are numbered as MNCN 49181; d) Moratilla 2 (Teruel) (Figs 6h-6n): nine elements, corresponding to a partial hyoplastron and eight generally complete plates of the carapace. All elements are disjointed. They correspond to, at least, two individuals of relatively small size, one of them being smaller than the other. All these specimens are numbered as MNCN 35679; e) Torralba de Ribota (Zaragoza) (Fig. 6o): a single plate, MNCN 56156, corresponding to a peripheral lacking its distal margin; f) La Barranca (Zaragoza) (Figs 6p-6u): five elements, all of them identified as MNCN 36114. Four of them correspond to peripheral plates. The other is an epiplastron; g) Nombrevilla 2 (Zaragoza) (Figs 6v-6ac): several disjointed plates of the plastron and, especially, of the carapace. They are the neural MNCN 35515 (Figs 6v-6ac), four neurals recognized as MNCN 35527 (Figs 6v-6w), the neural MNCN 57288; the costals MNCN 35521 and MNCN 35523; the peripherals MNCN 35507, MNCN 35509 (Fig. 6y), MNCN 35510, MNCN 35514, MNCN 35516, MNCN 35520 (Fig. 6z) and MNCN 355272; the entoplastra MNCN 35511 (Fig. 6ac) and MNCN 35527 (Fig. 6ab); and the hyoplastron MNCN 35508 (Fig. 6aa).

**Description.** The nuchal plate from Puente de los Franceses, MNCN 48293, lacks the lateral regions (Fig. 6c). Its anterior margin is medially protruding. Its posterior margin shows a medial concavity, which corresponds to the region of contact with the first neural. The presence of a cervical scute is observed. This scute is considerably longer than wide, both dorsally and ventrally. In dorsal view, the anterior margin of the first vertebral scute is considerably coined to its anterior region. As in all testudinids, this plate shows a considerable thickness in the visceral region of the posterior half. The other plate identified in that locality, MNCN 48294, is a free peripheral. It lacks its proximal half. It is a relatively thick plate, showing the granulous outer surface recognized in all testudinids. Both characters are identified in all plates analysed in this paper. However, due to its preservation, any other relevant character from a systematic perspective cannot be identified.

The peripheral of Valdemoros 3 is relatively complete (Fig. 6d). It is a left peripheral and, more specifically, it corresponds to that situated immediately posterior to the plastral bridge. This plate is short but high. The sulcus between two marginal scutes is positioned on the outer surface of the plate, from its distal margin to nearly the proximal. In fact, the boundary between the marginal and the pleural scutes is interpreted as located very close to the suture between the peripheral and the costal series.

One of the elements identified in Puente de Vallecas could correspond to the anterior region of a first suprapygal plate. The morphology of the areas of contact of this plate with the second suprapygal, with the peripheral series and with the pygal is not known because this element is broken. Two costals from this locality are identified. One of them is only represented by its more distal region. However, the other is more complete, since it is the distal half (Fig. 6e). The length of this plate increases distally. Therefore, the costal series was composed by longer distally than proximally plates, alternating with others in which the greatest length was located in the proximal region. Given this character, this plate corresponds to a pair costal. A sulcus is located on this plate, from the preserved proximal margin to the distal. It corresponds to the boundary between two pleural scutes. Therefore, its identification as a pair costal is confirmed. Two peripheral plates from Puente de Vallecas are recognized (Figs 6f-6g). None of them corresponds to the bridge region. One of them lacks its distal margin (Fig. 6f). The other does not preserve its proximal half (Fig. 6g). The boundary between two marginal scutes is observed on both plates. Furthermore, the boundary between two pleural scutes is identified on the plate, which preserves its proximal region (Fig. 6f). The sulcus between the pleural and the marginal scutes is located very close to the costo-peripheral suture. The presence of a protrusion at the distal margin, which coincides with the sulcus developed between two marginals, is observed in the other peripheral.

Most neurals from Moratilla 2 correspond to elements representing different positions in the neural series (Figs 6h-6k). Some of these neurals are rectangular, but others are hexagonal in shape. Sulci corresponding to limits between vertebral scutes are identified on several of these neurals. A first right costal (Fig. 6l), and the distal region of a pair costal (Fig. 6m), are recognized. A peripheral plate, which shows that the pleuro-marginal sulcus was

**Figure 6.** Specimens of *Paleotestudo antiqua* **(a-b)** and cf. *Paleotestudo antiqua* **(c-ac)** from the Aragonian of several Spanish sites. All the elements are in external view, except Fig. 6b and Fig. 6t that are in visceral view, and Fig. 6u in medial view. **a-b)** Illescas, Toledo. STUS 14244. Carapace **(a)**; epiplastra and entoplastron **(b)**. **c)** Puente de los Franceses, Madrid. MNCN 48293. Nuchal. **d)** Valdemoros 3, Madrid. MNCN 35698. Peripheral. **e-g)** Puente de Vallecas, Madrid. MNCN 49181. Costal **(e)**; peripherals **(f-g)**. **h-n)** Moratilla 2, Teruel. MNCN 35659. Neurals **(h-k)**; costals **(l-m)**; medial region of a hyoplastron **(n)**. **o)** Torralba de Ribota 1-3, Zaragoza. MNCN 56156. Peripheral. **p-u)** La Barranca, Zaragoza. MNCN 36114. Peripherals **(p-r)**; right epiplastron **(s-u)**. **v-ac)** Nombrevilla 2, Zaragoza. Neural MNCN 35527 **(v)**; neural 35527 **(w)**; neural MNCN 35515 **(x)**; peripheral MNCN 35509 **(y)**; peripheral MNCN 35520 **(z)**; right hyoplastron MNCN 35508 **(aa)**; entoplastron MNCN 35527 **(ab)**; entoplastron MNCN 35511 **(ac)**.

coincident with the costo-peripheral suture, is identified. The medial region of a hyoplastron (Fig. 6n) shows that the pectoral scutes were medially short. However the length of these scutes was slightly higher than the distance between them and the entoplastron.

The plate from Torralba de Ribota corresponds to a free peripheral (Fig. 6o). This plate was wider than long. It is crossed by a sulcus that separates two marginal scutes. The pleuro-marginal sulcus is recognized near its proximal margin.

All peripherals from La Barranca are free peripherals. In most of them, the distal margin experienced a marked protrusion close to the contact with the sulcus between the marginal scutes (Figs 6p-6q). This condition is not shared with the last peripheral (Fig. 6r). This plate allows inferring that the distal margin of the carapace of the analyzed taxon was not dorsally directed, but was highly verticalized. Indeed, the other preserved peripherals are very high but slightly curved, indicating that the lateral margins were also verticalized. The pleuro-marginal sulcus overlaps the costo-peripheral suture. The eleventh pair of marginal was noticeably distant from the pygal plate. The anterior margin of the epiplastron undergoes a change of curvature where it contacts the gulo-humeral sulcus (Figs 6s-6u). Thus, the morphology of the anterior plastral lobe was trapezoidal. The epiplastral symphysis was relatively long. The gular scutes overlap the entoplastron. A marked thickening of the epiplastra, from the anterior margin to near of the contact area with the entoplastron, can be observed in visceral view. The dorsal surface of the generated structure is convex. An epiplastral pocket, very shallow, is present.

Neural plates with different morphologies are identified in Nombrevilla 2: octagonal, hexagonal, rectangular and even subpentagonal (Figs 6v-6x). Sulci between the vertebral scutes are recognized in some of those plates. The morphology of the identified fragments of costals corresponds to a taxon that had both medially short and distally long costals, as others showing the opposite condition. The peripheral plates are high (Figs 6y-6z). All of them are traversed by a sulcus separating two marginals or, in the case of the most posterior peripheral, are located between the last pair of marginals and the supracaudal scute. The pleuro-marginal sulcus was approximately coincident with the costo-peripheral suture. Each of the two entoplastra found in Nombrevilla 2 has a different morphology. One is subrounded (Fig. 6ab). However, the other was probably pentagonal, with an anterior acute angle. The gular scutes overlap the anterior region of these plates. Medially, the pectoral scutes were located very close to the entoplastron, as can be seen in the preserved hyoplastron. The length of these scutes was slightly higher than that of the abdominals. The humero-pectoral sulcus is medially concave. However, it is slightly convex in the lateral regions.

# 4. DISCUSSION

## 4.1. *Paleotestudo antiqua*

### 4.1.1. *The specimens from Sant Quirze del Vallès (Spain)*

The new analysis of the material of Testudinidae from Sant Quirze del Vallès (Barcelona), type locality of '*Testudo catalaunica*', allows me making the detailed review of the taxon from this locality. '*Paleotestudo catalaunica*' has never been included in a cladistic analysis. However, the specimens from both Sansan (i.e. '*Paleotestudo canetotiana*') and Hohenhöwen (i.e. '*Testudo*' *antiqua*) were recently considered in two phylogenetic proposals. One of them is the modified version of the data matrix published by Lapparent de Broin *et al.* (2006a, 2006b) recently proposed by Corsini *et al.* (2014) (the encoding of the last character being excluded from this analysis due to the problems indicated by Pérez-García *et al.*, 2015). The other is that proposed by Vlachos & Tsoukala (2016). The characters used in both analyses are considered in this morphological characterization of the material from Sant Quirze del Vallès.

The shell of '*Paleotestudo catalaunica*' is identified as relatively high considering its length; it has a subquadrangular general morphology in dorsal view; and it is not a testudinid with a very narrow or very wide shell (character 1 in Corsini *et al.*, 2014; state 2) (Figs 4a, 4g). The plastral bridge is low, significantly lower than the height of the peripheral plates (character 2 in Corsini *et al.*, 2014; state 0) (Fig. 4f). The posterior edge of the carapace is verticalized, lacking the postero-dorsal expansion present in many testudinids (Fig. 4f). Therefore, this edge is barely visible in dorsal view (character 3 in Corsini *et al.*, 2014; state 2. Character 26 in Vlachos & Tsoukala, 2016; state 0) (Figs 4a, 4g). This taxon lacks a carapacial hinge (character 25 in Vlachos & Tsoukala, 2016; state 0), and a plastral hinge (character 4 in Corsini *et al.*, 2014; state 0. Character 37 in Vlachos & Tsoukala, 2016; state 0). Thus, the contact between the hypoplastra and the xiphiplastra corresponds to a sutured attachment (Figs 4b-4c, 4h-4i, 4l-4m). The sulcus between the pleural and the marginal scutes is coincident or nearly coincident with the suture between the costal and the peripheral plates along its entire path (character 5 in Corsini *et al.*, 2014; state 1. Character 19 in Vlachos & Tsoukala, 2016; state 1) (Fig. 4f). The posterior sulcus of the fifth vertebral coincides with the suprapygal-pygal suture (character 16 in Vlachos & Tsoukala, 2016; state 2). The nuchal plate is hexagonal (character 1 in Vlachos & Tsoukala, 2016; state 0), being markedly wider than long (character 2 in Vlachos & Tsoukala, 2016; state 0) (Figs 4a, 4d, 4g).

This taxon lacks a nuchal notch (character 4 in Vlachos & Tsoukala, 2016; state 0). The neurals form a continuous series, from the contact with the nuchal plate to the first suprapygal, preventing the medial contact of the costal plates (character 12 in Vlachos & Tsoukala, 2016; state 0) (Figs 4a, 4g). The neural series consists of eight plates in all specimens where it is known (character 6 in Corsini *et al*., 2014; state 0. Character 6 in Vlachos & Tsoukala, 2016; state 1). The first neural is rectangular (character 7 in Vlachos & Tsoukala, 2016; state 1). The second neural is octagonal (character 8 in Vlachos & Tsoukala, 2016; state 3). The third one is rectangular (character 9 in Vlachos & Tsoukala, 2016; state 1). The fourth is hexagonal in some specimens (Fig. 4g), but octagonal in others (Fig. 4a) (character 10 in Vlachos & Tsoukala, 2016; states 1 and 2). The morphology of the fifth neural is also recognized as variable, being recognized as hexagonal (Fig. 4g) or rectangular (Fig. 4a) (character 10 in Vlachos & Tsoukala, 2016; states 0 and 1). The suprapygals form a trapezoid, with straight lateral margins, and with the posterior margin coinciding with the posterior edge of the fifth vertebral scute (character 7 in Corsini *et al*., 2014; state 2) (Fig. 4e). Further, the second suprapygal is semilenticular, being anteriorly surrounded by the first one (character 8 in Corsini *et al*., 2014; state 1. Character 13 in Vlachos & Tsoukala, 2016; state 1) (Fig. 4e). The pygal plate is trapezoidal, lacking small latero-anterior edges (character 9 in Corsini *et al*., 2014; state 0. Character 14 in Vlachos & Tsoukala, 2016; state 0) (Fig. 4e). The presence of protrusions on the peripherals, at the limit with the sulci between the marginals, is observed (Figs 4a, 4g). They are poorly developed in some specimens, but well developed in others (character 20 in Vlachos & Tsoukala, 2016; states 0 and 1). Dorsally, this taxon has a well-developed convex epiplastral lip (character 29 in Vlachos & Tsoukala, 2016; state 1). This lip shows an uniform thickening from the lateral margins to the medial region, and also from the anterior margin to near its posterior margin. From that region, the thickening is slightly reduced. Thus, the lip has a subrounded section, being convex (character 10 in Corsini *et al*., 2014; state 2. Character 30 in Vlachos & Tsoukala, 2016; state 1) (Figs 4b, 4d, 4i-4k). The posterior region of the epiplastral lip overlaps the most anterior area of the entoplastron in some specimens. A gular pocket is recognized in the medial region of the posterior face of the lip of these specimens (character 11 in Corsini *et al*., 2014; state 3) (Figs 4b, 4i). The morphology of the anterior lobe is subrounded in some specimens (Fig. 4h), but trapezoidal on others (Figs 4c, 4l-4m) (character 27 in Vlachos & Tsoukala, 2016; state 0). Therefore, a well-developed gular protrusion is absent (character 28 in Vlachos & Tsoukala, 2016; state 0). The gulars cover the anterior area of the entoplastron (character 31 in Vlachos & Tsoukala, 2016; state 2) (Figs 4c, 4h, 4l-4m). The angle between the sagittal axis and the gular-humeral sulcus is more acute then 45º

(character 32 in Vlachos & Tsoukala, 2016; state 1). The median length of the humerals is shorter than that of the gulars (character 33 in Vlachos & Tsoukala, 2016; state 0). The humero-pectoral sulcus is posterior to the entoplastron (character 34 in Vlachos & Tsoukala, 2016; state 0). This sulcus is not perpendicular to the axial plane (character 35 in Vlachos & Tsoukala, 2016; state 0). Medially, the pectorals are relatively short (character 36 in Vlachos & Tsoukala, 2016; state 1). The abdomino-femoral sulcus shows a well-developed medial concavity. Therefore, it is medially positioned near the hypo-xiphiplastral suture. However, this sulcus is recognized as laterally concave. This sulcus is passing beyond the bottom of the inguinal notches at the maximal points of elongation (character 12 in Corsini *et al*., 2014; state 2). The femoro-anal sulcus forms an acute angle with the axial plane (character 38 in Vlachos & Tsoukala, 2016; state 0). The median length of the anals is shorter than that of the femorals (character 39 in Vlachos & Tsoukala, 2016; state 0). A positive relief in the ventral region of the plastron, where the gular scutes were situated, is recognized in some specimens (character 13 in Corsini *et al*., 2014; state 1) (Fig. 4c). The specimens from Sant Quirze del Vallès have a well-developed cervical scute, being longer than wide (character 14 in Corsini *et al*., 2014; state 0. Character 5 in Vlachos & Tsoukala, 2016; state 0) (Figs 4d, 4g). The vertebral series is narrower than that of *Testudo graeca*, but not as narrow as that which characterizes *Chersine hermanni* (character 15 in Corsini *et al*., 2014; state 0. Character 15 in Vlachos & Tsoukala, 2016; state 2) (Figs 4a, 4g). The first pleural overlaps the postero-lateral area of the nuchal in some specimens (Fig. 4d), and touches this plate, not overlapping it in others (Fig. 4g) (character 3 in Vlachos & Tsoukala, 2016; states 0 and 1). The marginals of the last pair are fused together, forming a supracaudal scute, both viscerally (character 16 in Corsini *et al*., 2014; state 1. Character 17 in Vlachos & Tsoukala, 2016; state 1) and dorsally (character 17 in Corsini *et al*., 2014; state 1. Character 18 in Vlachos & Tsoukala, 2016; state 1) (Figs 4c, 4e). This taxon has no contact of the second marginals with the lateral margin of the nuchal (character 21 in Vlachos & Tsoukala, 2016; state 0), of the second marginals with the first vertebral (character 22 in Vlachos & Tsoukala, 2016; state 0), of the fourth marginals with the second pleurals (character 23 in Vlachos & Tsoukala, 2016; state 0), nor of the sixth marginals with the third pleurals (character 24 in Vlachos & Tsoukala, 2016; state 0) (Figs 4a, 4g) (Appendix 1).

The taxon from Sant Quirze del Vallès can be attributed to *Paleotestudo*, the hypothesis proposed by Pérez-García & Murelaga (2013) being confirmed. It shares all the characters considered in the diagnosis of this genus (sensu Lapparent de Broin, 2000): no plastral hinge; moderately broad and moderately long shell, its width being approximately 70 % of its length (around 67 %

in the case of the specimen STUS 14245, Fig. 4a; and around 73 % in the lectotype of '*Testudo catalaunica*', MGSB 25324a, Fig. 4g); maximum length of the shell less than 25 or 30 cm; short posterior plastral lobe, with a maximum length of about nearly 25 % of that of the plastron (26.6 % in the specimen MGM 1561M, Fig. 4c; 24.5 % in 25324a, Fig. 4h; 28.4 % in MGM 236M, Fig. 4l; the length of the posterior plastral lobe being considered from the posterior tip of the xiphiplastra to the contact of the lateral margin of this lobe with the abdomino-femoral sulcus); plastral anterior lobe from rounded (Fig. 4h) to trapezoidal (Figs 4c, 4l-4m); verticalized lateral and posterior margins; well-developed dorsal epiplastral lip, posteriorly overlapped on the anterior region of the entoplastron in some adult individuals; development of a small gular pocket in some specimens.

### 4.1.2. Comparison of the specimens from Sant Quirze del Vallès with those of Sansan (France) and Hohenhöwen (Germany)

'*Paleotestudo catalaunica*' (Sant Quirze del Vallès, Spain) was not compared to '*Paleotestudo canetotiana*' (Sansan, France) or to *Paleotestudo antiqua* (Hohenhöwen, Germany) when it was defined, nor when its diagnosis was proposed (Bataller, 1926; Bergouinioux, 1938). The information about *Paleotestudo antiqua* included in the paper where genus *Paleotestudo* was defined, and where '*Paleotestudo canetotiana*' was reviewed (see Lapparent de Broin, 2000), was extremely limited. '*Paleotestudo catalaunica*' was not cited in that paper. The lack of information generated several problems in the coding of *Paleotestudo antiqua* performed by Lapparent de Broin *et al.* (2006a, 2006b). Some of the encodings were corrected by Corsini *et al.* (2014) in their paper focused on the review of this species (i.e. the condition corresponding to the visceral fusion of the marginals, constituting a supracaudal scute, was considered as not known; and the identification of external fusion of the last pair of marginals was recognized). '*Paleotestudo catalaunica*' was not codified by any of these authors. Corsini *et al.* (2014) did not cite '*Paleotestudo catalaunica*'. Vlachos & Tsoukala (2016) also included *Paleotestudo antiqua* and '*Paleotestudo canetotiana*' in their phylogenetic proposal, but not '*Paleotestudo catalaunica*'. Thus, the comparisons hitherto existing between the material from Sansan and that from Hohenhöwen are extremely limited, as it is also the case of those between the Spanish and French specimens. No comparison between '*Paleotestudo catalaunica*' and *Paleotestudo antiqua* had so far been published. However, Pérez-García & Murelaga (2013) raised doubts about the validity of the species '*Paleotestudo catalaunica*', indicating the need for a detailed comparative study, which is made here.

All characters that were previously considered as different comparing the taxon from Hohenhöwen with that of Sansan are also refuted here, taken into account the currently available material from both locations. Lapparent de Broin *et al*. (2006b, 2006c) considered that the shell of *Paleotestudo antiqua* was wider than that of the French taxon. The observation of the adult and hardly deformed German specimens, and also of those whose original morphology can easily be interpreted (as is the case of FFSM 3446.1, FFSM 3446.4, UFGC 9; see figs 2, 5, 9 in Corsini *et al.*, 2014), allows me observing that the width/length ratio falls within the range of variation known for the French taxon. It is important to note that the females of *Paleotestudo* have been recognized by Lapparent de Broin (2000) wider than the males, this hypothesis being supported here (see a specimen which was recognized as a female in Figs 3f-3g, and two males in Figs 3a-e, 3l-3m). In none of the known German specimens the posterior part of the carapace is preserved in good condition. This taxon was codified by Corsini *et al*. (2014) as having a moderately expanded and dorsally directed posterior edge (character 3, state 0), but not poorly expanded as in the taxon from Sansan (state 2). The described morphology for the German specimens is observed in some carapaces where this region is affected by the deformation (e.g., in the specimens FFSM 344.1, fig. 2 in Corsini *et al*., 2014; UFGC 9, fig. 9 in Corsini *et al*., 2014), being similar to the condition observed in some specimens from Sansan (MNHN.F SA 15657, Figs 3f-3g; MNHN.F SA 1868, Figs 3l-3m). However, it is not recognized in others such as MT PAL.2012.0.10 (fig. 10 in Corsini *et al*., 2014) and SMNS 4450 (fig. 6 in Corsini *et al*., 2014). Corsini *et al*. (2014) recognize the presence of eight neurals in six of the eight shells in which they could observe or interpret the number of these plates. These authors interpret that the individual FFSM 3446.2 could have had seven neurals (fig. 3 in Corsini *et al*., 2014). However, only the internal mold of its carapace is preserved, and its posterior region is not well enough preserved to confirm this hypothesis. Furthermore, these authors interpret the sixth neural of this specimen as anomalous, corresponding to an octagon rather than a hexagon. Only three specimens from Sansan whose neural series is known are identified (Fig. 3). Only two specimens from Sant Quirze del Vallès preserve the carapace (Fig. 4). In both cases, all of them have eight neurals. It is important to note that, for the correct identification of variability in the number of neurals, a large number of specimens could be necessary. Lapparent de Broin *et al*. (2006a, 2006c) indicated that, unlike the generally observed condition in '*Paleotestudo canetotiana*', the German taxon lacked gular pocket. This character is here identified as subject to variability in *Paleotestudo antiqua*, the gular pocket being absent in the specimen FFSM 3446.2 (fig. 3 in Corsini *et al*., 2014), but being present in SMNS 51467 (fig. 7 in Corsini *et al.,* 2014). This character is also

recognized here as subject to variability comparing the specimens from Sansan; absent in some specimens (Figs 3h, 3p) but present in others (Figs 3e, 3j). Lapparent de Broin *et al.* (2006b) considered that the epiplastral lip of *Paleotestudo antiqua* was short on all specimens, its posterior end being away from the entoplastron. This is the present condition in FSM 3446.2 (fig. 3 in Corsini *et al.*, 2014). However, it is not shared with that observed in the other individual from Hohenhöwen, in which this region is known, SMNS 51467 (fig. 7 in Corsini *et al.*, 2014). Indeed, the identification of numerous isolates epiplastra and partial or complete plastra from Sansan allow me to recognize a wide variability in '*Paleotestudo canetotiana*', represented by: short epiplastral lips (Figs 3o, 3r); libs with a longer length, but not contacting the entoplastron (Fig. 3i); lips significantly overlapping this plate (Fig. 3k). The straight anterior margin of the epiplastra of '*Paleotestudo canetotiana*' was recognized by Corsini *et al.* (2014) as possibly different to that of the German taxon. However, the morphology of this region is very variable. Specimens from Sansan where this margin is rounded are identified (Figs 3k, 3m-3n), but also other individuals where this area is markedly trapezoidal (Fig. 3i). The number of specimens of Hohenhöwen in which this margin is known is very limited. However, it is not circular in all of them. For example, the anterior lobe is trapezoidal in FFSM 3446.3 (fig. 4 in Corsini *et al.*, 2014). The identification of the anterior lobe of the French taxon as narrower than that of the German representative, indicated by Corsini *et al.* (2014), cannot be supported here (compare the specimens in Fig. 3 with those in figs. 2-10 of Corsini *et al.*, 2014). Lapparent de Broin *et al.* (2006a, 2006b) did not recognize positive relief on the ventral surface of any plastron from Hohenhöwen, in the area where the gular scutes were placed (character 13, state 0). The description and figuration of new specimens not considered by these authors, but posteriorly presented by Corsini *et al.* (2014), shows the presence of an incipient relief on this area in some specimens (see, for example, the specimen SMNS 51467 in the fig. 7 of Corsini *et al.*, 2014). Most of the specimens from Sansan have not a positive relief. In this sense, Lapparent de Broin *et al.* (2006a, 2006b) indicated that only 3 of the 35 known specimens show a partial relief, being well developed in only 4 individuals.

The better knowledge on the specimens from Sansan and Hohenhöwen also allows me refuting the differences in the encoding of the material from both regions proposed by Vlachos & Tsoukala (2016). The fourth neural was recognized as octagonal (character 10, state 2) for '*Paleotestudo canetotiana*', but as rectangular (state 0), hexagonal (state 1) and octagonal in *Paleotestudo antiqua.* The same variability is recognized here for the specimens from Sansan (e.g., being rectangular in MNHN.F SA 1868, hexagonal in MNHN.F SA 1866, and octagonal in MNHN.F SA 15647 as well as in MNHN.F SA 1673). Between the

scarce shells from Sant Quirze del Vallès presented here, the presence of hexagonal (Fig. 4g) and octagonal (Fig. 4a) fourth neurals is recognized. The fifth neural of the specimens from Sansan and Hohenhöwen was recognized by Vlachos & Tsoukala (2016) as rectangular (character 11, state 1). However, hexagonal and rectangular fifth neurals (states 0 and 1) are identified in each of the three compared locations (e.g., see a specimen from Sant Quirze del Vallès with a hexagonal fifth neural in Fig. 4g, and other with this neural rectangular in Fig. 4a). Vlachos & Tsoukala (2016) considered that the specimens from Sansan and Hohenhöwen have two suprapygals, both elements together constituting one trapeze, the first suprapygal embracing the lenticular second one (character 13, state 1). Significant variability is recorded, as notified by Pérez-García & Murelaga (2013), considering the material from several locations. This is especially relevant in Sansan, due to the large number of suprapygals found there. The second suprapygal could be: semicircular, significantly wider than long, and almost as wide as the first one (MNHN.F SA 1903); significantly wider than long, and significantly narrower than the first one (MNHN.F SA 1867); almost as long as wide, and significantly narrower than the first one (MNHN.F SA 1904); trapezoidal, with its surface being greater than that of the first one, and the suture between them being straight (MNHN.F SA 15647); fused with the first one, resulting in a single element (MNHN.F SA 1908). The presence of specimens with poorly developed protrusions on the peripherals, but also of others with well-developed protrusions, is recognized in the three locations. Vlachos & Tsoukala (2016) characterized the humerals of the specimens from Sansan as equal or smaller than the gulars (character 33, state 0), and those from the German taxon as longer than the gulars (character 1). However, most specimens known from Sansan show humerals significantly longer than the gulars (e.g. MNHN.F SA 1672, MNHN.F SA 1673, MNHN.F SA 1867, MNHN.F SA 10342, MNHN.F SA 15370 MNHN.F SA 15647), the gular scutes being almost as long as the humerals in MNHN.F SA 1868. This is also identified as a variable comparing the specimens from Hohenhöwen, both character states being identified (e.g., state 0 in FFSM 3446.2, see fig. 3 in Corsini *et al.*, 2014; state 1 in MT PAL.2012.0.10, see fig. 10 in Corsini *et al.*, 2014). Although Vlachos & Tsoukala (2016) encoded the specimens from Sansan and Hohenhöwen as having the humero-pectoral sulcus posterior to the entoplastron (character 34, state 0), specimens where this sulcus is medially coincident with the posterior margin of the entoplastron (state 1) are recognized in both locations. Vlachos & Tsoukala (2016) considered the pectorals of the specimens from Sansan as medially long (character 36, state 0), and those from the specimens from Germany as short (state 1). A similar range of variability is identified when all known specimens from both locations are compared. Therefore no differences are

seen, all of them being recognized as having relatively short pectorals compared with those of some testudinids. Vlachos & Tsoukala (2016) recognized the medial length of the anal scutes of the specimens from Hohenhöwen as shorter than the median length of femorals (character 39, state 0), that of the individuals from Sansan being longer than the medial length of femorals (state 1). However, the study of all specimens of Sansan in which this region is known allows recognizing that state of character as shared with that of the German specimens (MNHN.F SA 1672, MNHN.F SA 1673, MNHN.F SA 10342). This and all the other discussed character states are compatible with those recognized in the specimens from Sant Quirze del Vallès, and also with the material from the other Spanish sites presented here and by Pérez-García & Murelaga (2013), including the abundant collection from the MN6-7/8 Spanish site of Can Mata (Barcelona). Therefore, all putative differences between the testudinids defined in the European Aragonian localities of Sansan, Hohenhöwen and Sant Quirze del Vallès, proposed in previous studies, have been refuted here (Appendix 1). In fact, the previously proposed diagnosis for the taxon of each of these localities are also compatible with the material recorded in the others (see Bergounioux, 1938 for '*Paleotestudo catalaunica*', and criticisms by Pérez-García & Murelaga (2013) thanks to the recognition of characters subject to variability, and to the identification of some errors and inaccuracies in the previous interpretations; Lapparent de Broin, 2000 for '*Paleotestudo canetotiana*'; and Corsini *et al*., 2014 for *Paleotestudo antiqua*). The recognition of autapomorphies or of an exclusive character combination for the material found in each of those three locations cannot be done due to the high intraspecific variability recognized in many characters of both the carapace and the plastron. In addition to the variability described in this paper, numerous examples and descriptions of the variability of Spanish and French specimens are explained by Pérez-García & Murelaga (2013). Some characters subject to variability recognized in the German individuals are indicated by Corsini *et al*. (2014) and in this paper. Some of the characters identified as subject to variability in the specimens of the studied localities are: degree of development, or presence or absence, of a nuchal protrusion, and of protrusions on the lateral margins of the anterior peripherals; number of neurals; morphology of the first, fourth and fifth neural plates; morphology of the second suprapygal; developing of growth marks; ratio between the width and length of the cervical scute; overlapping of the first pair of pleurals on the nuchal plate; degree of development, or presence or absence, of gular protrusions and of gular relief; morphology of the entoplastron; degree of overlapping of the gular scutes on the entoplastron; ratio between the length of the gular and the humeral scutes; distance between the pectoral scutes and the entoplastron; ratio between the

length of the pectoral and abdominal scutes. Considering all this, '*Testudo catalaunica*' and '*Testudo canetotiana*' are identified are junior synonyms of '*Testudo*' *antiqua*. Therefore, the presence of *Paleotestudo antiqua* is not only recognized in the late Aragonian of Germany, but also in that of France and Spain. In fact, the synonymy of other European Miocene poorly known taxa with *Paleotestudo antiqua* cannot be ruled out (see Lapparent de Broin *et al*., 2006a, 2006b; Corsini *et al*., 2014).

### 4.1.3. A new diagnosis for Paleotestudo antiqua

Considering all discussed characters, *Paleotestudo antiqua* is diagnosed here as: Paleartic European testudinid with a shell rarely exceeding 25 cm in length. Shell subquadrangular in dorsal view. Shell relatively high, but not too wide relative to its length (width generally about 70 % of the length). Verticalized lateral and posterior margins, lacking a postero-dorsal expansion of the distal margin of the posterior peripherals. Low plastral bridge relative to the height of the peripheral plates. Relatively thick carapace and plastron plates. Presence of two suprapygals, the second being generally sublenticular, and the first one postero-laterally contacting the pygal and the peripheral series. Trapezoidal suprapygal series, with straight lateral margins. Trapezoidal pygal plate, wider anteriorly than posteriorly, and lacking small latero-anterior margins. Pygal showing a slight convexity in posterior view, both in males and in females. Narrow cervical scute, both dorsally and ventrally. Vertebral series narrower than in *Testudo graeca*, but wider than that characterizing *Chersine hermanni*. Pleuro-marginal sulcus approximately coincident with the costo-peripheral suture, along its entire path. Posterior margin of the fifth vertebral scute coincident with the posterior margin of the suprapygal plates. Fusion of the last pair of marginals, constituting a single supracaudal scute, both in dorsal and in visceral views. No overlapping of the eleventh pair of marginals on the pygal plate. Trapezoidal to rounded morphology of the anterior plastral lobe. Poorly-developed or absent gular protrusion. Convex and well-developed epiplastral lip, showing a uniform thickening from the lateral margins to the medial region, and also from the anterior margin to near its posterior margin, where the thickening is slightly reduced (resulting in a subrounded morphology in section). Variable posterior expansion of the epiplastral lip, usually being located close to the anterior margin of the entoplastron. Absence or presence of a gular pocket, usually shallow, which can generate an overhang on the entoplastron. Flat visceral medial surface of the plastron posterior to the epiplastral lip. No plastral hinge. Short and wide posterior lobe. Gular scutes overlying the anterior region of the entoplastron. Concave humero-pectoral sulcus, lacking a marked change of lateral curvature, in

contact with the posterior margin of the entoplastron or, generally, not contacting it. Abdomino-femoral sulcus with a strong medial concavity, where it is close to the hypo-xiphiplastral suture, but being laterally concave. Coalescence of the femoral trochanters more developed than in *Testudo graeca*, but less than in *Chersine hermanni*.

## 4.2. Comparison of *Paleotestudo antiqua* with '*Testudo*' *promarginata* and with other testudinids from the early Miocene of Europe

'*Testudo*' *promarginata* (recognized as a taxon closely related to the members of *Paleotestudo* by Lapparent de Broin *et al.*, 2006a) is a form identified in the early Miocene (Aquitanian and Burdigalian) of Germany and France (Fig. 2). Some characters indicated by Broin (1977), Lapparent de Broin (2000) and Lapparent de Broin *et al.* (2006b) allow recognizing some potential differences between '*Testudo*' *promarginata*, as well as specimens probably attributable to this species or closely related to it, as was proposed by Lapparent de Broin *et al.* (2006a), and *Paleotestudo antiqua*. Thus, the distal margin of the posterior peripherals (especially that of the peripherals 9 and 10) is not ventrally directed; the suprapygals are fused or, in the case of some specimens in which this condition is not present, the first suprapygal does not contact the pygal plate nor the peripheral series; the epiplastral lip of the known specimens is not posteriorly recurved, not generating an overhang on the entoplastron, a well-developed gular pocket not being recognized; the visceral surface posterior to the dorsal lip is not flat, but descends progressively until the anterior region of the entoplastron; a relief in the ventral area of the plastron where the gular scutes were situated has not been recognized in any individual; the humero-pectoral sulcus is perpendicular to the axial plane in the medial region, but it generally experiences a well-developed lateral change of curvature (Fig. 2).

Other forms such as the specimen from the early Miocene (Burdigalian) of Austria attributed by Glaessner (1933) to '*Testudo antiqua* var. *noviciensis*' Depéret, 1885 (see figs. 2-3 in the plate 21 of Glaessner, 1933), and recognized by Broin (1977) as probably belonging to *Paleotestudo mellengi* or to a closely related taxa, differ from *Paleotestudo antiqua* in characters such as the presence of a hexagonal pygal, with short latero-anterior margins, and the bell-shaped morphology of its carapace. Therefore, the presence of several species in the European early and middle Miocene is recognized.

## 5. CONCLUSIONS

Several remains corresponding to small testudinids (i.e., less than 30 cm in length of the shell) from various Spanish Aragonian localities, where this group of tortoises was so far unmentioned, are identified in this paper. These specimens share the diagnosis of *Paleotestudo*, a genus defined from a species identified in the French site of Sansan (MN6), i.e. '*Testudo canetotiana*'. The presence of this genus was recently recognized in the Iberian Peninsula, both in Aragonian as in Vallesian levels. The validity of two forms defined in Spanish Aragonian sites had recently been refuted ('*Paralichelys catalaunicus*' and '*Testudo catalaunica* var. *irregularis*'). However, the information needed to confirm or refute the validity of other taxa identified in Spain, i.e. '*Testudo catalaunica*', was not available until now. The review of specimens from the type locality of this species (MN7/8 of Sant Quirze del Vallès, Barcelona) allows me to confirm its attribution to the genus *Paleotestudo*.

Two taxa also defined in the Aragonian levels of Europe, and also represented by several specimens (i.e., '*Paleotestudo canetotiana*', from Sansan, France; and '*Testudo*' *antiqua*, from Hohenhöwen, Germany), are analyzed in detail in order to make detailed comparisons between them, and with the specimens of '*Testudo catalaunica*'. In fact, the comparison between the tortoises from the three localities performed in previous works was very limited. The attribution of '*Testudo*' *antiqua* to *Paleotestudo* is confirmed here.

Pérez-García & Murelaga (2013) recognized that a high range of variability affects the specimens of *Paleotestudo* identified in each locality, and that a similar variability is identified in French and Spanish localities where several individuals were recorded. The new observations here performed on the specimens from Sansan and Sant Quirze del Vallès, but also on others from Hohenhöwen and other Spanish localities, show the presence of a range of variability even greater than that hitherto recognized. All putative differences between these taxa considered in previous papers are refuted here, by the study of the variability recorded in the material in each site. Exclusive characters in the material found in any of the three locations are not recognized. All new Spanish specimens of *Paleotestudo* presented in this paper, as well as all Iberian Aragonian individuals previously mentioned (see Pérez-García & Murelaga, 2013), are compatible with *Paleotestudo antiqua*: the states of characters that can be observed in each one of them are shared with those of the new diagnosis of *Paleotestudo antiqua* proposal here, being part of the range of variation known for this taxon. Therefore, the presence of the same taxon at the three countries (i.e. Spain, France and Germany) is recognized here, i.e. *Paleotestudo antiqua*. '*Testudo catalaunica*' and '*Testudo canetotiana*' are identified as junior synonyms of that species.

All specimens of small testudinids so far recorded in the Iberian Aragonian sites are recognized as compatible with *Paleotestudo antiqua*. Thus, the presence of this species in the middle and late Aragonian of Spain, in localities where relatively complete specimens have been found (e.g., Barajas, in Madrid; Illescas, in Toledo; Can Mata, in Barcelona) is recognized. Specimens that provide less information, recorded in several Iberian Aragonian sites, are attributed to cf. *Paleotestudo antiqua*.

## ACKNOWLEDGEMENTS

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**Appendix 1.** New encodings for the specimens of *Paleotestudo antiqua* from the late Aragonian of Hohenhöwen (Germany) and Sansan (France) in the modified version of the data matrix published by Lapparent de Broin *et al.* (2006a, 2006b) recently proposed by Corsini *et al.* (2014) (the encoding of the last character being excluded from this analysis due to the problems indicated by Pérez-García *et al.*, 2015), and in that published by Vlachos & Tsoukala (2016). The specimens of *Paleotestudo antiqua* from Sant Quirze del Vallès (Spain) are also encoded, the variability corresponding to these characters and recognized in each on these sites being shown. The encoding of the taxon *Paleotestudo antiqua* in both analyzes, considering the observed variability, is done.

Specimens of *Paleotestudo antiqua* from Hohenhöwen in the Corsini *et al.* (2014) data matrix: 20?01 [01]2103 22?00 ?1?

Specimens of *Paleotestudo antiqua* from Sansan in the Corsini *et al.* (2014) data matrix: 20201 02103 22100 111

Specimens of *Paleotestudo antiqua* from Sant Quirze del Vallès in the Corsini *et al.* (2014) data matrix: 20201 02103 22100 11?

*Paleotestudo antiqua* in the Corsini *et al.* (2014) data matrix: 20201 [01]2103 22100 111

Specimens of *Paleotestudo antiqua* from Sant Quirze del Vallès in the Vlachos & Tsoukala (2016) data matrix: 00[01]001131[12] [01]01022111[01] 0000000011 210001000? ?????????? ?????????? ?????????? ?????????? ?

Specimens of *Paleotestudo antiqua* from Hohenhöwen in the in the Vlachos & Tsoukala (2016) data matrix: 00[01]00[12]131[012] [01]01022111[01]    0000000011 21[01][01]01000?????????? ?????????? ?????????? ?????????? ?

Specimens of *Paleotestudo antiqua* from Sansan in the in the Vlachos & Tsoukala (2016) data matrix: 00[01]001131[012] [01]0[012]022111[01]    0000000011 211[01]01000?????????? ?????????? ?????????? ?????????? ?

*Paleotestudo antiqua* in the in the Vlachos & Tsoukala (2016) data matrix: 00[01]00[12]131[012] [01]0[012]022111[01] 0000000011 21[01][01]01000? ?????????? ?????????? ?????????? ?????????? ?