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A. Pérez-García, E. Vlachos & P. Mocho

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The westernmost records of extinct large European tortoises: the presence of *Titanochelon* (Testudinidae) in the Miocene of Portugal

A. Pérez-García^a , E. Vlachos^b  and P. Mocho^{a,c} 

^aGrupo de Biología Evolutiva, Facultad de Ciencias, UNED, Madrid, Spain; ^bCONICET – Museo Paleontológico Egidio Feruglio, Trelew, Argentina; ^cThe Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, CA, USA

ABSTRACT

The information about the European giant fossil tortoises has been greatly increased in recent years, based on the description of new material and the revision of previously published specimens. A genus with a wide paleobiogeographic and stratigraphic distribution, *Titanochelon*, has recently been described, containing all large testudinids from the European Neogene record. Its type species, *Titanochelon bolivari*, was described in the Spanish record. The presence of this species outside this country had not been justified. In this paper we present and describe fossil material of large testudinids from several sites in the Lisbon District (Portugal), from lower (Quinta da Barbacena; MN4), middle (Charneca do Lumiar and Quinta da Farinheira; MN5) and upper (Aveiras de Baixo; MN9) Miocene levels. This study allows us to confirm the presence of *Titanochelon* in the Portuguese record and justify, for the first time, the presence of *Titanochelon bolivari* outside Spain. Furthermore we are able to discuss the geographical and temporal distribution of the large tortoises in the middle Miocene of Europe, a relevant period for the diversity and evolution of this clade.

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Titanochelon bolivari;
Neogene; Portuguese record;
Lisbon District

Introduction

The crown Testudinidae includes tortoises with almost worldwide distribution and an excellent fossil record. The total clade Pan-Testudinidae is known in Europe since the early Eocene (Broin 1977; Lapparent de Broin 2001; Pérez-García et al. 2016). Small-sized members of this clade (i.e. *Testudo sensu lato* or Pan-*Testudo*), not exceeding 30 cm in shell length, are part of the fauna that inhabits this continent at the present (van Dijk et al. 2014). However, several large taxa are known in the European fossil record, some of them reaching lengths between one and two meters; they all became extinct from continental Europe by the Early Pleistocene (Jiménez Fuentes 1994; Lapparent de Broin 2001, 2002; Pérez-García & Vlachos 2014 and references therein). Information on the taxonomy and systematics of these large forms has been, so far, problematic. In fact, although several Neogene species had been identified, defined in several countries and distributed between the Miocene and Pleistocene, their alpha taxonomy needed a major revision (see also Jiménez Fuentes 1988; Gmira et al. 2013). Many of these species were originally identified as belonging to *Testudo* Linnaeus (1758), a extant small genus to which not only most European tortoises but most known testudinids were traditionally attributed (Lapparent de Broin et al. 2006; Fritz & Havaš 2007). New information about the members of this clade led several authors to reallocate the large European Neogene species to other genera, its assignment to *Cheirogaster* Bergounioux (1935) being very common (e.g.

Bourgat & Bour 1983; Jiménez Fuentes 2000, 2003; Luján et al. 2014; Vlachos et al. 2014). However, *Cheirogaster* corresponds to a more primitive form, defined in the Eocene, and much smaller than those identified in the Neogene (Pérez-García & Vlachos 2014). As such, recent works restricted the use of *Cheirogaster* only for its type species, *Cheirogaster maurini* Bergounioux (1935), a form defined in the upper Eocene (Priabonian) of France (Pérez-García & Vlachos 2014; Pérez-García 2015).

References to the findings of large testudinids in the Iberian Miocene fossil record are known since the nineteenth century (see Prado 1864 and Bolívar 1871; as well as the history of the findings performed in the nineteenth century and the first decades of the twentieth century in Pérez-García & Vlachos 2014), and Hernández-Pacheco (1917) was the first who nominated a species: '*Testudo*' *bolivari*. The material analysed by this author came from several locations from the Aragonian (Orleanian + Astaracian) of the Spanish Castilian Plateau (Alcalá de Henares, Casa de Campo, Vallecas and Los Santos de la Humosa, in Madrid; Cerro del Otero, in Palencia; and Fuensaldaña, in Valladolid). However, a recent study has confirmed that this species was present in many other Spanish locations as well, both in Aragonian and Vallesian levels, with a temporal distribution between the MN5 and the MN10 biozones at least (Pérez-García & Vlachos 2014). Considering the definition of a species for the Spanish material, Zbyszewski (1949) indicated that a large shell found in the Portuguese locality of Aveiras de Baixo (Azambuja Municipality,

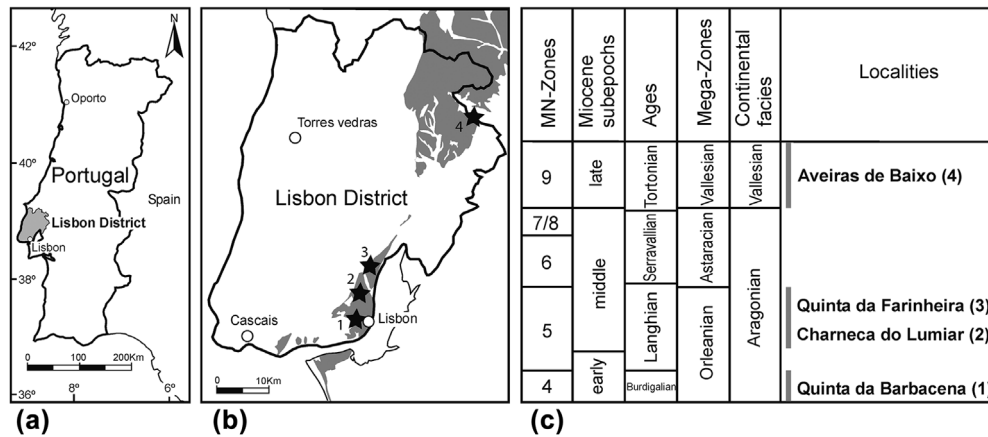


Figure 1. Geographic and stratigraphic position of the Portuguese localities where the remains of the large tortoise *Titanochelon* studied in this paper were found. (a), geographical position of the Lisbon District (Portugal). (b), geographical position of the fossil sites, in a map showing the Miocene outcrops (grey color). 1, Quinta da Barbacena (Lisbon Municipality); 2, Charneca do Lumiar (Lisbon Municipality); 3, Quinta da Farinheira (Loures Municipality); 4, Aveiras de Baixo (Azambuja Municipality). (c), stratigraphic position of these localities.

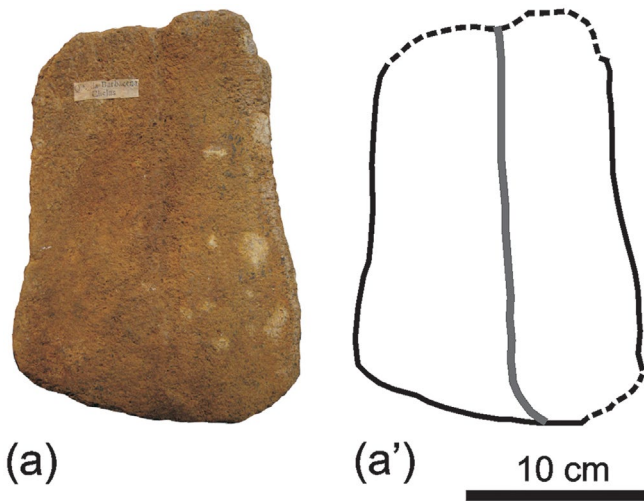


Figure 2. MG 25219, peripheral plate of *Titanochelon* cf. *bolivari*, from the biozone MN4 (upper Burdigalian, lower Miocene) of Quinta da Barbacena (Lisbon Municipality, Lisbon District), in external view.

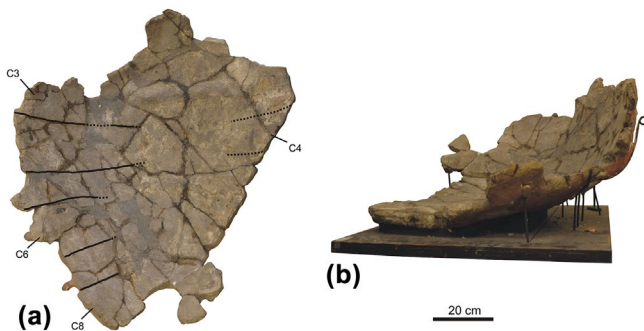


Figure 3. MG 918, partial carapace of *Titanochelon* cf. *bolivari*, from the biozone MN9 (lower Tortonian, upper Miocene) of Aveiras de Baixo (Azambuja Municipality, Lisbon District), in visceral, (a), and anterior, (b), views.

Note: Abbreviations for the plates: C, costal.

Lisbon District; Figure 1), and considered by him as of Pliocene age, corresponded to '*Testudo*' *bolivari*. However, this determination was not justified by anatomical information. More recently,

Crespo (2001) includes this reference in a list on the paleoherpetafauna from Portugal, reallocating it to *Cheirogaster*, as other authors had done with the other European large species. He indicated that this specimen came from lower/middle Miocene levels. This author did not provide any new information on this fossil, which remained undescribed until now. Pérez-García and Vlachos (2014) attributed all species of large testudinids distributed between the lower Miocene and the Pliocene of Europe to a new genus, *Titanochelon*. Although Pérez-García and Vlachos (2014) considered that *Titanochelon* could be present in Portugal as well, they not justified this attribution nor discussed the possible affinity to specific level.

Several specimens of large testudinids from the Miocene of Portugal are studied here, given the significant increase in the information on the European Neogene forms recently published (Pérez-García & Vlachos 2014; Luján et al. 2014; Vlachos et al. 2014). The specimens analysed here come from four sites of the district of Lisbon (Figure 1): the shell from Aveiras de Baixo (upper Miocene) cited in previous papers (Zbyszewski 1949; Crespo 2001), and several unpublished remains from Quinta da Barbacena (lower Miocene), Quinta da Farinheira (middle Miocene) and Charneca do Lumiar (middle Miocene). The systematic allocation of these specimens is discussed. Overall, the combined information presented herein improve significantly our knowledge of the evolution and distribution of large testudinids in the Miocene of Europe, a period that is important for the evolutionary history of this clade.

Institutional abbreviations

MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisbon, Portugal.

Systematic Paleontology

Testudines Batsch, 1788
 Cryptodira Cope, 1868
 Testudinoidea Batsch, 1788
 Pan-Testudinidae Batsch, 1788

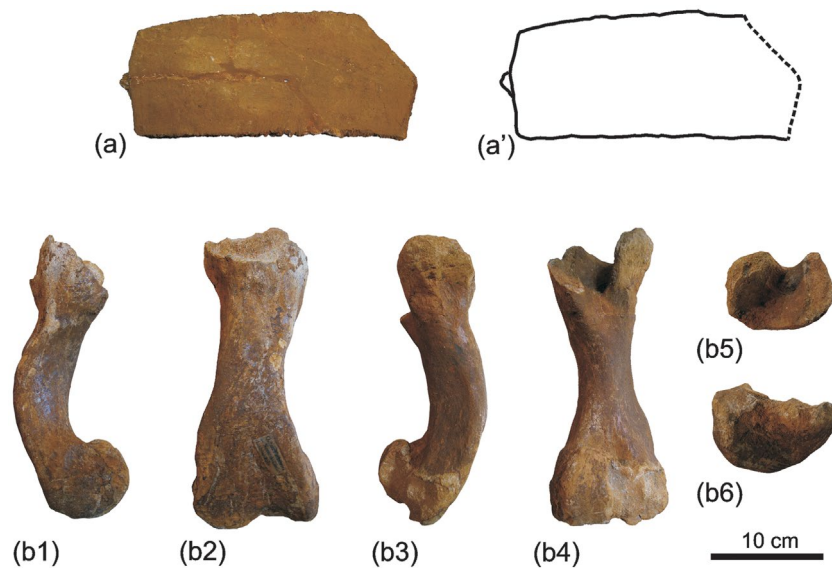


Figure 4. Specimens of *Titanochelon*, from the biozone MN5 (lower Langhian, middle Miocene) of Quinta da Farinheira (Loures Municipality, Lisbon District). (a), MG 4772, distal half of a costal plate of *Titanochelon cf. bolivari*, in external view. (b), MG 4766, right humerus of *Titanochelon bolivari*, in anterior, (b1); dorsal, (b2); posterior, (b3); ventral, (b4); medial (b5); and distal, (b6) views.

Testudinidae Batsch, 1788

Titanochelon Pérez-García and Vlachos, 2014

Titanochelon cf. bolivari (Hernández-Pacheco 1917)

(Figures 2–4(a))

Material: MG 25219 (Figure 2), a peripheral plate from the biozone MN4 (upper Burdigalian, lower Aragonian, lower Miocene) (Antunes & Ginsburg 2003) of Quinta da Barbacena (Lisbon Municipality, Lisbon District) (Figure 1); MG 30490 (Figure 3), a partial carapace from the biozone MN9 (lower Tortonian, lower Vallesian, upper Miocene) (Antunes & Mazo 1983; Antunes et al., 2003) of Aveiras de Baixo (Azambuja Municipality, Lisbon District) (Figure 1); MG 4772 (Figure 4(a)), a partial costal plate from the biozone MN5 (lower Langhian, middle Aragonian, middle Miocene) (Pais et al. 2012) of Quinta da Farinheira (Loures Municipality, Lisbon District) (Figure 1).

Description: The plate from Quinta da Barbacena is a free right peripheral (Figure 2). Its medio-distal width is significantly greater than its anteroposterior length. The outer surface is rough. A sulcus corresponding to the contact between two marginals is recognized. Its path, except at its distal region, is subparallel to the anterior and posterior margins of the plate. No protrusion is noted on the edge of the peripheral. The proximal edge of the peripheral is not preserved. However, the available information indicate that the marginal scutes overlapped to all or most of the dorsal surface of the plate.

The specimen of Aveiras de Baixo is a partial articulated carapace (Figure 3). Due the mounting position and the preparation of the dorsal surface, covered by plaster, only the visceral surface is available for observation. The anteroposterior length of the preserved region is about 115 cm. However, the length of the complete carapace was significantly greater, as neither the anterior nor the posterior regions are preserved. Because of its relatively poor preservation, and the fusion between many of the plates of this adult specimen, the only partially recognizable sutures are those located between the third and the last costals

from the right side, and those between the third and the fifth costals from the left side. Based on the preserved information of this specimen, an alternation of short medially and long laterally costals (pairs) and medially long and laterally short plates (odd) is evident. Although the neural outlines are not visible, traces of the attachment of the dorsal vertebras are evident on the midline.

The plate from Quinta da Farinheira (Figure 4(a)) corresponds to the middle and distal part of a costal plate. The anterior and posterior borders are not parallel, and the antero-posterior length of the costal decreases toward the lateral region. Also no trace of the sulcus between the pleurals is found. Based on all the above, it is identified as an odd plate (i.e. costal 3 or 5 most probably), but further identification is not possible.

Titanochelon bolivari (Hernández-Pacheco 1917)

(Figures 4(b)–5)

Material: MG 4766 (Figure 4(b)), a relatively complete right humerus from the biozone MN5 (lower Langhian, middle Aragonian, middle Miocene) (Pais et al. 2012) of Quinta da Farinheira (Loures Municipality, Lisbon District) (Figure 1); MG 30491 (Figure 5), numerous fragmentary pieces that are part of the shell of a single individual, from the biozone MN5 (lower Langhian, middle Aragonian, middle Miocene) (Antunes & Ginsburg 2003; Pais et al. 2012) of Charneca do Lumiar (Lisbon Municipality, Lisbon District).

Description: The right humerus from Quinta da Farinheira (Figure 4(b)) preserves the diaphysis, as well as most of its distal region and part of the proximal portion. The minor trochanter is complete. Both the humeral head and the major trochanter are broken. However, the available information indicates that the minor trochanter did not reach the level of the maximum height of the humeral head. The preserved region of the major trochanter allow observing that both trochanters were slightly divergent towards the proximal region. The diaphysis shows a relatively well-developed sigmoid curve. The cross-section of

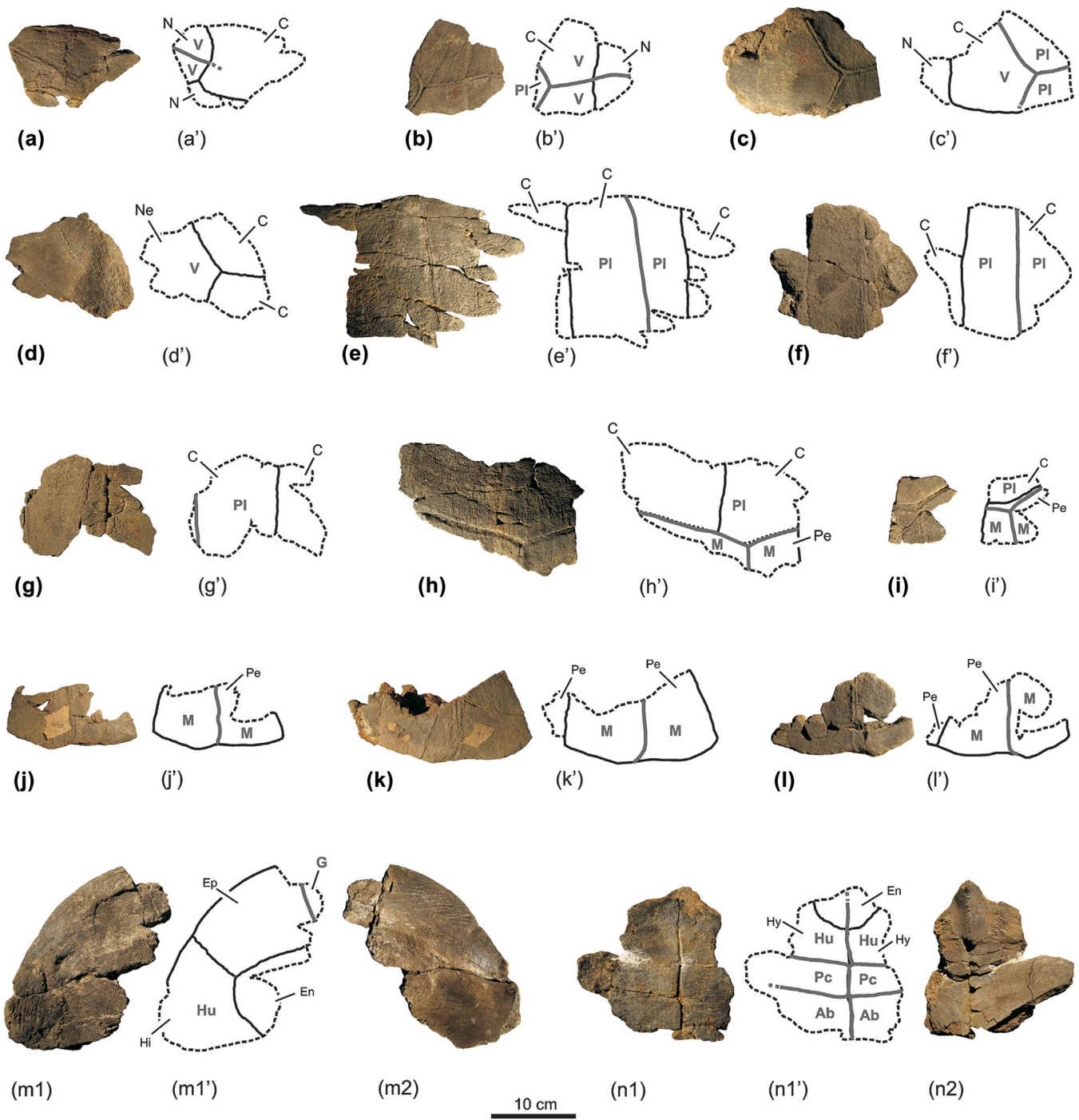


Figure 5. MG 74, selection of some elements of the carapace, (a)–(l), and plastron, (m)–(n) of a specimen of *Titanochelon bolivari*, from the biozone MN5 (lower Langhian, middle Miocene) of Charneca do Lumiar (Lisbon Municipality, Lisbon District). The elements of the carapace are in external view. Those of the plastron are in ventral ((m1), (n1)) and visceral ((m2), (n2)) views.

Notes: The black lines represent the boundaries between the plates and the gray ones, thicker, the margins of the scutes. Abbreviations for the plates (in normal font): C, costal; En, entoplastron; Ep, epiplastron; Hy, hyoplastron; N, neural; Pe, peripheral. Abbreviations for the scutes (in bold and gray): Ab, abdominal; G, gular; Hu, humeral; M, marginal; Pc, pectoral; Pl, pleural; V, vertebral.

the humerus is elliptical in the proximal and distal regions, but subrounded in the central area. A portion of the ulnar condyle is not preserved. The morphology of the distal region of this bone is clearly asymmetrical, due to the different length of the radial and ulnar condyles, the latter being the longest. In dorsal view, the groove separating both condyles is shallow.

The material from Charneca do Lumiar corresponds to a shell of a single individual. The material is highly fragmented,

with some fragments being so small that cannot be identified. Some fragments preserve sutures that correspond to the margins of some plates, but further identification is not possible. Some remains however represent larger portions of the shell, complete plates or plates in association; those fragments are illustrated in Figure 5, summarizing the main anatomical information of this specimen. The estimated length of this shell was certainly greater than one meter but a precise estimation is not possible. Elements

of both the carapace and plastron are identified. The outer surface of all these elements is rough, consistent with the shell outer surface of testudinid taxa. The neural/costal association of Figure 5(a) represents fragments of two successive neurals, connected with a costal plate. The neurals are unequal in width, representing most probably rectangular and hexagonal/octagonal neurals. The rectangular one is crossed transversely by the vertebral sulcus. The neural/costal association of Figure 5(b) represents a long neural, probably rectangular, connected with a long costal. The neural is crossed transversely by the vertebral sulcus, whereas a part of the pleural scute is noted as well. The fragment illustrated in Figure 5(c) represents a partial neural, probably rectangular in outline, connected with a costal plate. The costal plate is covered by a vertebral scute and two successive pleurals. The partial neural in Figure 5(d) is either hexagonal or octagonal, connected with two successive costals. No evidence of scute sulci is observed. Numerous fragments of partial costals in association are preserved (Figure 5(e)–(h)), showing an alternating pattern, as that described for the material from Aveiras de Baixo. Several partial peripherals are preserved as well (Figure 5(j)–(l)) lacking protrusions in their distal margins. The grooves delimiting the scutes are relatively deep. Although vertebral scutes are partially preserved, they can be recognized as relatively narrow (Figure 5(b)–(c)). The sulci between the pleural and the marginal scutes coincide with the sutures between the costals and the peripherals, or both structures are very closely located (Figure 5(h)–(i)). The lateral margin of the preserved portion of the right epiplastron and hyoplastron is subrounded (Figure 5(m)). A thick epiplastral lip is present, with a convex dorsal surface. The epiplastral lip were probably about as wide as long. This specimen lacks a well-developed gular pocket. However, a marked change of relief between the dorsal epiplastral lip and the region located behind this structure is present. The entoplastron is subrhombic, with a rounded posterior side (Figure 5(m)–(n)). The sulcus between the gular scutes and the humerals generates a relatively acute angle with the sagittal plane. The humero-pectoral sulcus is located far behind the posterior margin of the entoplastron (Figure 5(n)). In the medial region, the humero-pectoral and the pectoro-abdominal sulci are perpendicular to the axial plane, and the pectoral scutes are medially short.

Discussion

In the following discussion the phylogenies previously presented by Pérez-García & Vlachos 2014; Pérez-García 2015 and Pérez-García et al. 2016 are used as a reference for character distribution and polarity. The material studied here can be attributed to Testudinidae because it shares with the representatives of this clade a unique combination of characters: roughened outer surface of the plates; presence of rectangular, hexagonal and octagonal neurals; alternating pattern in the costal series, composed by medially short and laterally long plates alternating with medially long and laterally short plates; deep sulci corresponding to the lateral margins of the scutes; relatively narrow vertebral scutes; proximity or coincidence of the boundary between the pleural and the marginal scutes with the suture between the costal and the peripheral plates; presence of a thick epiplastral lip; absence of intergular scutes.

The specimens from the Miocene of Portugal are compared with those corresponding to the medium and large

taxa of Pan-Testudinidae recognized in the European record: the Eocene *Fontainechelon cassouleti* (Claude & Tong 2004), *Pelorocheleon eoacaenica* (Hummel 1935), *Cheirogaster maurini* and *Pelorocheleon soriana* Pérez-García, Ortega and Jiménez Fuentes, 2016; the Oligocene *Taraschelon gigas* (Bravard 1844) and ‘*Ergilemys*’ *bruneti* Broin 1977; and the representatives of the Neogene *Titanochelon*.

The size of all analysed specimens from Portugal is consistent with that of a taxon of more than one meter in length, a condition found in the members of *Titanochelon*. The size of the known adult specimens of *Fontainechelon cassouleti* and *Cheirogaster maurini* is about 40 cm; that of *Pelorocheleon eoacaenica* and of *Pelorocheleon soriana* about 70 cm; that of ‘*Ergilemys*’ *bruneti*, about 60 cm; and that of *Taraschelon gigas* about 80 cm. The absence of protrusions in the region of contact of the boundary between the marginal scutes and lateral margin of the peripheral scutes (apomorphic for *Titanochelon*) differentiates the Portuguese material from *Fontainechelon cassouleti* and ‘*Ergilemys*’ *bruneti*. The overlapping or marked proximity of the pleuro-marginal sulci with the costo-peripheral sutures differs from the condition present in *Pelorocheleon eoacaenica*, *Pelorocheleon soriana* and *Taraschelon gigas* (apomorphic for Testudinidae). The absence of a concave dorsal epiplastral lip in the preserved anterior plastral lobe (apomorphic for *Titanochelon*) is shared with all compared taxa, except with *Fontainechelon cassouleti*, *Pelorocheleon eoacaenica* and *Pelorocheleon soriana*. The absence of epiplastral lip significantly wider than long is shared with all analysed taxa except with *Fontainechelon cassouleti* (apomorphic for Testudinidae). The presence of an anterior angle between the gularo-humeral sulcus and the sagittal axis lower than 45° (apomorphic for Testudinidae) is shared with *Taraschelon gigas*, ‘*Ergilemys*’ *bruneti* and the members of *Titanochelon*. The humero-pectoral sulcus perpendicular to the axial plane, in the medial region (apomorphic for Testudinidae), is identified in *Pelorocheleon eoacaenica*, *Pelorocheleon soriana*, ‘*Ergilemys*’ *bruneti* and the representatives of *Titanochelon*. The presence of short medially pectoral scutes (apomorphic for Testudinidae) contrast to the condition seen in the Eocene taxa *Fontainechelon cassouleti*, *Cheirogaster maurini*, and *Pelorocheleon soriana*, and associates the material from Portugal with the Neogene forms. The presence of a well-developed curvature in the humeral diaphysis (apomorphic for Testudinidae) is shared with *Titanochelon*, but differs from the condition present in *Fontainechelon cassouleti*, both taxa being the only discussed testudinids considered here in which appendicular elements have been described. Therefore, all characters discussed above are shared with the representatives of *Titanochelon*. The presence of this genus in the Portuguese record, previously suggested by Pérez-García and Vlachos (2014), is confirmed herein.

The absence of a well-developed dorsal epiplastral pocket (apomorphic for Testudinidae) allows to exclude the allocation of the material studied here to the forms of the Miocene record of France *Titanochelon eurysternum*, *Titanochelon ginsburgi* and *Titanochelon leberonensis*, as well as the Greek *Titanochelon bacharidisi*, but not to the Spanish Miocene *Titanochelon bolivari* or to the French Pliocene *Titanochelon perpiniiana*. However, the absence of contact of the humero-pectoral sulcus with the entoplastron (plesiomorphic for *Titanochelon*), known in *Titanochelon bolivari*, is not compatible with the condition

present in *Titanochelon perpiniana* nor in the Greek Pliocene species *Titanochelon bacharidisi*. Furthermore, the marked asymmetry observed in the distal region of the humerus (autapomorphic for *Titanochelon bolivari*) is only shared with *Titanochelon bolivari*, and especially with the humerus from Alcalá 3 from the MN6 of Madrid (Spain; figure 5C1–C4 in Pérez-García & Vlachos 2014). The similarity of the two specimens (compared to other humeri of *Ti. bolivari*) is on the robust diaphyseal and distal part of the bone. The position of the humero-pectoral sulcus relative to the entoplastron is placed more posteriorly in the Portuguese specimen (Figure 5(n)) than in those of *Titanochelon bolivari* figured by Pérez-García and Vlachos (2014). However, the distance of this sulcus to the entoplastron is not only recognized as subject to variability in the large forms of Testudinidae (see Pérez-García & Vlachos 2014), but also in small representatives of this clade, as has been evidenced, for example, by the study of other Iberian Miocene forms (see Pérez-García & Murelaga 2013; Luján et al. 2016; Pérez-García Accepted). Therefore, considering all the available information, the presence of the species *Titanochelon bolivari*, defined in Spain and known in that country from the MN5 to the MN10 biozones (see Pérez-García & Vlachos 2014), is here recognized in the biozone MN5 of Portugal, both in Quinta da Farinheira (Figure 4(b)) as in Charneca do Lumiar (Figure 5). The availability of characters provided by the material from the MN4 biozone of Quinta da Barbacena (Figure 2), and that of the biozone MN9 of Aveiras de Baixo (Figure 3), is compatible with *Titanochelon bolivari*, but is considered too limited to confirm this specific attribution. Therefore, the presence of *Titanochelon* cf. *bolivari* is recognized in these two locations.

The recent advances in our knowledge of the anatomy and taxonomy of the Neogene large testudinids from Europe highlight that the Middle Miocene was an important period for the diversification of this clade. First of all, the tortoises from Europe achieve a large size for the first time in their evolutionary history during the late Langhian–middle Serravallian interval (i.e. the late Orleanian–middle Astaracian, MN5–MN6) (see Pérez-García & Vlachos 2014), following a trend toward increased size known from the Eocene (Pérez-García 2015; Pérez-García et al. 2016). The material described herein represent the westernmost records of *Titanochelon* in the European continent, not only for the Middle Miocene but for all the Neogene. Middle Miocene confirmed records of *Titanochelon* are known in Central Europe, mainly in Germany and Switzerland, with numerous localities including some well-preserved specimens such as those of Sandlezhausen (Germany) (see Schleich 1981) and Winterthur and Zurich (Switzerland) (see Biedermann 1862 and Peyer 1942 respectively). Several localities with *Titanochelon* remains are known between these areas representing the western and eastern known limits for the geographic expansion of the large tortoises in the Middle Miocene (i.e. Portugal and Central Europe). They are located in Spain and France. In Spain, several sites where *Titanochelon bolivari* has been identified are recognized for the MN5 and MN6 biozones (MN5 sites in Barajas, Casa de Campo, Puente de los Franceses and Vallecas; MN6 sites in Coca, Cerro del Viso, Henares 1 and Parla; and MN5 or MN6 sites in Carabanchel, Ciudad Universitaria, El Pardo and Puente de la Princesa referred by Pérez-García & Vlachos 2014). The material from France is more scarce, represented by

species from Bois de Fabrègues, with a uncertain specific allocation (Lapparent de Broin 2002). As such, it is clear that during MN5–MN6 *Titanochelon* achieved a wide geographic distribution, reaching more northern latitudes (Germany, Switzerland) than in previous periods. In subsequent moments of the Neogene large tortoises are still quite widespread, but confined in more southern latitudes (including their occurrences in Greece). Also, in terms of taxonomic diversity of the *Titanochelon* clade, this period is among the richest during the Neogene, with at least two species (i.e. *Titanochelon bolivari* in the Iberian Peninsula and *Titanochelon vitodurana* in Switzerland).

These first two pulses in geographic expansion and higher taxonomic diversity of *Titanochelon* coincides with the Miocene Climatic Optimum (MCO), a period with a warm climate and favorable conditions that was followed by significant cooling and climate change in the Northern Hemisphere (Zachos et al. 2001). During this period the survival of ectothermic vertebrates, including giant turtles, is favored in Central Europe (Böhme 2003). Our results further corroborate these claims and indicate that the Middle Miocene was crucial period for the establishment of the clade *Titanochelon* in Europe.

The material from the MN4 of Quinta da Barbacena joins a list of a few occurrences of large tortoises from the lower Miocene of Europe. These early records come from France, with *Titanochelon ginsburgi* (Broin 1977) from the MN4 of Artenay and *Titanochelon eurysternum* (Gervais 1848–1852) from the MN2 of Saint-Gerard-le-Puy (see Pérez-García & Vlachos 2014 for comments on these taxa). Therefore, although limited, the material from the MN4 presented herein provides new information on the earliest records of this clade in Europe.

Conclusions

The presence of the large testudinid *Titanochelon* is confirmed for the Portuguese record. This generic attribution is justified here for the first time, based on specimens from the lower, middle and upper Miocene (biozones MN4, MN5 and MN9) of the Lisbon District. A humerus and a partial shell from two localities of the MN5 biozone, Quinta da Farinheira and Charneca do Lumiar, are attributed to the species *Titanochelon bolivari*. This species was defined from the Aragonian levels of the Castilian Plateau (Spain), being known from the MN5 to the MN10 biozones. Its presence outside the Spanish record is confirmed here for the first time. In addition, *Titanochelon* cf. *bolivari* is recognized in the Portuguese sites of Quinta da Barbacena (MN4) and Aveiras de Baixo (MN9).

The Portuguese material of large tortoises represent the westernmost records of this clade in Europe and further highlight that the favourable climatic and environmental conditions in the Middle Miocene played an important role of the survival, expansion and diversification of this clade in the Neogene of Europe. The material from the MN4 is also among the oldest confirmed records of *Titanochelon* in Europe. The material from Portugal appears to be directly associated with the large tortoise material from Spain, both from a taxonomic as well as from a paleogeographical point of view. The presence of large tortoises in Iberian Peninsula from the MN4 till the Pleistocene provides a rich, mostly uninterrupted, fossil record of large tortoises in Europe, which is crucial for our understanding of the origin,

evolution and extinction of large continental tortoises in the European continent.

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Disclosure statement

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ORCID

A. Pérez-García  <http://orcid.org/0000-0002-9074-6855>

E. Vlachos  <http://orcid.org/0000-0003-3137-8383>

P. Mocho  <http://orcid.org/0000-0002-3348-5572>

References

- Antunes MT, Ginsburg L. 2003. The *Deinotherium* (Proboscidea, Mammalia): an abnormal tusk from Lisbon, the Miocene record in Portugal and the first appearance datum. Evidence from Lisbon, Portugal. *Ciênc Terra*. 15:173–190.
- Antunes MT, Mazo AV. 1983. Quelques mastodontes miocènes du Portugal [Some Miocene mastodonts from Portugal]. *Ciênc Terra*. 7:115–128.
- Antunes MT, Ginsburg L, Mein P. 2003. Mammifères miocènes de Azambujeira, niveau inférieur (Santarém, Portugal) [Miocene mammals from Azambujeira, lower level (Santarém, Portugal)]. *Ciênc Terra*. 7:161–186.
- Batsch GC. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien [An attempt of guide about the knowledge and history of the animals and minerals]. Jena: Ed. Akad. Buchhand.
- Bergounioux FM. 1935. Contribution à l'étude paléontologique des Chéloniens. Chéloniens fossiles du Bassin d'Aquitaine [Contribution to the paleontological study of the turtles. Fossil turtles from the Basin of Aquitaine]. *Mém Soc Géol Fr*. 25:1–216.
- Biedermann WGA. 1862. Petrefakten aus der Umgegend von Winterthur. I. Schildkroten [Petrifications from the surrounding of Winterthur. I. Turtles]. Winterthur: S. Bleuler–Hausheer.
- Bolívar I. 1871. Noticia del hallazgo de restos fósiles de tortuga en el arroyo de los Meaques (Casa de Campo) [News of the finding of fossil remains of a tortoise in the Meaques stream (Casa de Campo)]. *Actas Soc Esp Hist Nat*. 1:19.
- Bourgat R, Bour R. 1983. La Tortue géante de Perpignan: *Cheirogaster perpiniana* (Depèret, 1885) [The giant tortoise from Perpignan: *Cheirogaster perpiniana* (Depèret, 1885)]. *Bull Soc Agric Sci Litt des Pyrénées orient*. 21:167–177.
- Bravard A. 1844. Considérations sur la distribution des mammifères terrestres fossiles dans le département du Puy-de-Dôme [Considerations on the distribution of the fossil terrestrial mammals in the department of Puy-de-Dôme]. *Ann Sci Litt Ind d'Auvergne*. 16:402–439.
- Böhme M. 2003. The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeogr, Palaeoclimatol, Palaeoecol*. 195:389–401.
- Broin F de. 1977. Contribution à l'étude des Chéloniens: Chéloniens continentaux du Crétacé et du Tertiaire de la France [Contribution to the study of the turtles: continental turtles from the cretaceous and tertiary of France]. *Mém Mus Natl Hist Nat*. 38:1–366.
- Claude J, Tong H. 2004. Early Eocene testudinoid turtles from Saint-Papoul, France, with comments on the early evolution of modern Testudinoidea. *Oryctos*. 5:3–45.
- Cope ED. 1868. On the origin of genera. *Proc Acad Nat Sci Philadelphia*. 20:242–300.
- Crespo EG. 2001. Paleo-Herpetofauna de Portugal [Paleo-Herpetofauna of Portugal]. Portugal: Museu Bocage, Museu Nacional de História Natural, Publ. Avulsas.
- van Dijk PP, Iverson JB, Rhodin AGJ, Schaffer HB, Bour R. 2014. Turtles of the World, 7th edition: Annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. In: Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson JB, Mittermeier RA, editors. Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Lunenburg: Chelonian Research Foundation; p. 329–479.
- Fritz U, Havaš P. 2007. Checklist of chelonians of the world. *Vert Zool*. 57:149–368.
- Gervais P. 1848–1852. Zoologie et Paléontologie Françaises (Animaux vertébrés) [French zoology and paleontology (vertebrate animals)]. Paris: Bertrand.
- Gmira S, Broin F de, Geraads D, Lefèvre D, Mohib A, Raynal JP. 2013. Les tortues du Pliocène d'Ahl al Oughlam (Casablanca, Maroc) et de localités Mio-Pliocènes avoisinantes [The Pliocene turtles from Ahl al Oughlam (Casablanca, Morocco) and from neighboring Mio-Pliocene localities]. *Geodiversitas*. 35:691–733.
- Hernández-Pacheco E. 1917. El problema de la investigación científica en España [The problem of scientific research in Spain]. *Asoc Esp Prog Cienc*. 2:63–93.
- Hummel K. 1935. Schildkröten aus der mitteleozänen Braunkohle des Geiseltales [Turtles from the middle eocene lignite of the Geiseltales]. *N Acta Leopold*. 2:457–483.
- Jiménez Fuentes E. 1988. Consideraciones taxonómicas sobre algunos quelonios fósiles de España [Taxonomic considerations on some fossil turtles from Spain]. *Rev Esp Herp*. 3:7–13.
- Jiménez Fuentes E. 1994. Nota preliminar sobre nuevos ejemplares de quelonios fósiles del Plioceno de Las Higuieruelas (Campo de Calatrava: Ciudad Real) [Preliminary note on new specimens of fossil turtles from the Pliocene of Las Higuieruelas (Campo de Calatrava: Ciudad Real)]. *Stud Geol Salmant*. 30:133–138.
- Jiménez Fuentes E. 2000. Tortugas gigantes fósiles de la Provincia de Segovia (Castilla y León, España). Nueva localidad: Chañe [Giant fossil tortoises from the Segovia Province (Castilla y León, Spain). A new locality: Chañe]. *Stud Geol Salmant*. 36:109–115.
- Jiménez Fuentes E. 2003. Quelonios fósiles de la Cuenca del Duero [Fossil turtles from the Duero Basin]. In: Jiménez Fuentes E, Civis Llovera J, editors. Los vertebrados fósiles en la historia de la vida. Excavación, estudio y patrimonio [The fossil vertebrates in the history of life. Excavation, study and heritage]. Salamanca, Spain: Univ. Salamanca; p. 177–195.
- Lapparent de Broin F de. 2001. The European turtle fauna from the Triassic to the Present. *Dumerilia*. 4:155–217.
- Lapparent de Broin F de. 2002. A giant tortoise from the late Pliocene of Lesvos Island (Greece) and its possible relationships. *Ann Geol Pays Hell*. 39:99–130.
- Lapparent de Broin F de, Bour R, Perälä J. 2006. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii). First part *Annlis Paléontol*. 92:255–304.
- Linnaeus C. 1758. *Systema Naturae* [Natural system]. Volume 1. Holmia: Laurentius Salvius.
- Luján AH, Alba DM, Delfino M, Fortuny J, Carmona R. 2014. First cranial remains of *Cheirogaster richardi* (Testudines: Testudinidae) from the late Miocene of Ecoparc de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula): taxonomic and phylogenetic implications. *J Syst Palaeontol*. 12:833–864.
- Luján AH, Delfino M, Robles JM, Alba DM. 2016. The Miocene tortoise *Testudo catalaunica* Bataller, 1926, and a revised phylogeny of extinct

- species of genus *Testudo* (Testudines: Testudinidae). *Zool J Linn Soc.* 178:312–342.
- Pais J, Cunha PP, Pereira D, Legoinha P, Dias R, Moura D, Silveira AB, Kullberg JC, González-Delgado JA. 2012. The Paleogene and Neogene of Western Iberia (Portugal): a Cenozoic Record in the European Atlantic Domain. Germany: Springer, Berlin Heidelberg.
- Pérez-García A. 2015. A new genus for '*Testudo*' *gigas*, the largest European Paleogene testudinid. *J Vert Paleontol.* 36. Article ID: 1030024. doi: [10.1080/02724634.2015.1030024](https://doi.org/10.1080/02724634.2015.1030024).
- Pérez-García A. **Accepted**. Analysis of the Iberian Aragonian record of *Paleotestudo*, and refutation of the validity of the Spanish '*Testudo catalaunica*' and the french '*Paleotestudo canetotiana*'. *Span J Palaeontol.*
- Pérez-García A, Murelaga X. 2013. Las tortugas del Vallesense superior del Cerro de los Batallones (Madrid, España): nuevos datos sobre el escasamente conocido género *Paleotestudo* [The turtles from the upper Vallesian of Cerro de los Batallones (Madrid, Spain): new data on the poorly known genus *Paleotestudo*]. *Ameghiniana.* 50:335–353.
- Pérez-García A, Vlachos E. 2014. New generic proposal for the European Neogene large testudinids (Cryptodira) and the first phylogenetic hypothesis for the medium and large representatives of the European Cenozoic record. *Zool J Linn Soc.* 172:653–719.
- Pérez-García A, Ortega F, Jiménez Fuentes E. 2016. Taxonomy, systematics, and diversity of the European oldest testudinids. *Zool J Linn Soc.* 177:648–675.
- Peyer B. 1942. Fossile Riesenschildkröten aus der oberen Süßwassermolasse der Umgebung von Zurich [Fossil giant turtles from the upper freshwater molasse surrounding Zurich]. *Abh Schweiz Paläontol Ges.* 63:1–47.
- Prado C. 1864. Descripción física y geológica de la provincia de Madrid [Physical and geological description of the province of Madrid]. Madrid: Junt. Gen. Estad.
- Schleich H. 1981. Jungtertiäre Schildkröten Süddeutschlands unter besonderer Berücksichtigung der Fundstelle Sandelzhauzen [Late Tertiary turtles from Southern Germany with special reference to those of the Sandelzhauzen site]. *Cour Forsch Senckenberg.* 48:1–372.
- Vlachos E, Tsoukala E, Corsini J. 2014. *Cheirogaster bacharidisi* sp. nov., a new species of a giant tortoise from the Pliocene of Thessaloniki (Macedonia, Greece). *J Vert Paleontol.* 34:560–575.
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science.* 292:686–693.
- Zbyszewski G. 1949. Contribution a la connaissance du Pliocène portugais [Contribution to the knowledge of the Portuguese Pliocene]. *Com Serv Geol Portugal.* 30:5–24.