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The last giant continental tortoise of Europe: A survivor in the Spanish Pleistocene site of Fonelas P-1

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ABSTRACT

The presence of remains of a giant tortoise in the lower Pleistocene site of Fonelas P-1 (Guadix Basin, Betic Ranges; Granada, southeastern Spain) is reported and analyzed herein for the first time. This finding represents the youngest evidence of a large tortoise in continental Europe, dating the age of extinction of this successful lineage as several hundred thousand years younger than previously thought. So far, the most recent record known for continental Europe was at least 400,000 years older than the occurrence reported herein (Vaterá, Greece), that for the Spanish record being about 1.3 million years older (Las Higueruelas). This finding is justified as the youngest evidence of *Titanochelon*, a genus recorded in Europe since the beginning of the Miocene, which includes the largest terrestrial turtles known for the entire European fossil record. The decrease in the biogeographical distribution area and the final extinction of these temperature-sensitive animals in Europe is here recognized as a result of the climate changes documented during the Pliocene and lower Pleistocene. The identification of taxa with environmental and ecological requirements as restrictive as those known for the extant and extinct large tortoises, living in continental Europe 2.0 Ma, has important consequences. Thus, although the paleoclimatic inferences generally assumed for the whole of Europe interpret cooler and drier conditions at the end of the Pliocene, by the increase of the seasonality and the beginning of the glacial activity in the Northern Hemisphere, the record of Fonelas P-1 indicates that, in southern Europe or, at least, in the endorheic basins of the Betic Ranges, warmer climatic conditions than in the rest of the continent continued being present in these chronologies of the lower Pleistocene, being favorable for the persistence of these large tortoises.

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1. Introduction

Testudinidae is one of the most abundant and diverse groups of turtles living today, also being very abundant in the Cenozoic fossil record of most continents (Hay, 1908; de Lapparent de Broin, 2001; Gmira et al., 2013; van Dijk et al., 2014; Rhodin et al., 2015). Although some representatives of this terrestrial lineage are forms of relatively small size (e.g. *Chersine hermanni* (Gmelin, 1789) and *Testudo graeca* Linnaeus, 1758, the two extant forms that are part of the Iberian fauna, and whose shell does not exceed 30 cm in length), others are recognized as some of the largest turtles of both the Cenozoic record and the extant global biodiversity. Two current forms have shells that exceed 1 m in length, both being restricted to island environments: the members of the *Chelonoidis nigra* (Quoy and Gaimard, 1824) species complex (sensu van Dijk et al., 2014), which inhabit the Galápagos Islands (Pacific Ocean), and *Aldabrachelys gigantea* (Schweigger, 1812), exclusive of

the Aldabra Atoll (Indian Ocean). The continental forms of relatively large size, which can reach or even slightly exceed 70 cm in length, also live in intertropical and warm regions: the South American *Chelonoidis carbonaria* (Spix, 1824) and *Chelonoidis denticulata* (Linnaeus, 1766), and the African *Centrochelys sulcata* (Miller, 1779) and *Stigmochelys pardalis* (Bell, 1828). Both the extant forms as those exclusive of the fossil record show that the increase in size in Testudinidae, experienced by several lineages and taxa, in several continents, is limited to warm weather conditions (see, for example, the distribution area of the Pleistocene to Holocene large and giant tortoises in Hansen et al., 2010; Rhodin et al., 2015; and also Hibbard, 1960; Holman, 1971, 1976; Auffenberg, 1974; Estes and Hutchison, 1980, and references in these papers). Indeed, the survival of the forms of relatively large size requires higher temperatures that those in which the representatives of small size can be distributed (e.g. southern Europe is currently only part of the distribution area of small forms, but large taxa also lived there in warmer Cenozoic periods; see van Dijk et al., 2014). Thus, the European Paleogene record includes several forms of relatively large size, as the Eocene *Pelorochelon eocaenica* (Hummel, 1935) and *Pelorochelon soriana* Pérez-García et al., 2016, close to

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70 cm, and the Oligocene *Taraschelon gigas* (Bravard, 1844), whose shell reached 80 cm. The favorable climatic conditions for this group of reptiles during the Cenozoic of Europe also enabled the development of taxa with larger sizes. In this sense, during the Neogene, some members of *Titanochelon* Pérez-García and Vlachos, 2014 reached a length of about 2 m.

The genus *Titanochelon* is represented by about ten species. It is known from the early Miocene, having been identified in several European countries (Portugal, Spain, France, Switzerland, Germany, Austria, Greece and Bulgaria), as well as in European Turkey and Minor Asia (Pérez-García and Vlachos, 2014). Its younger so far confirmed record was that of the continental site of Vaterá (Lesvos, Greece), with an
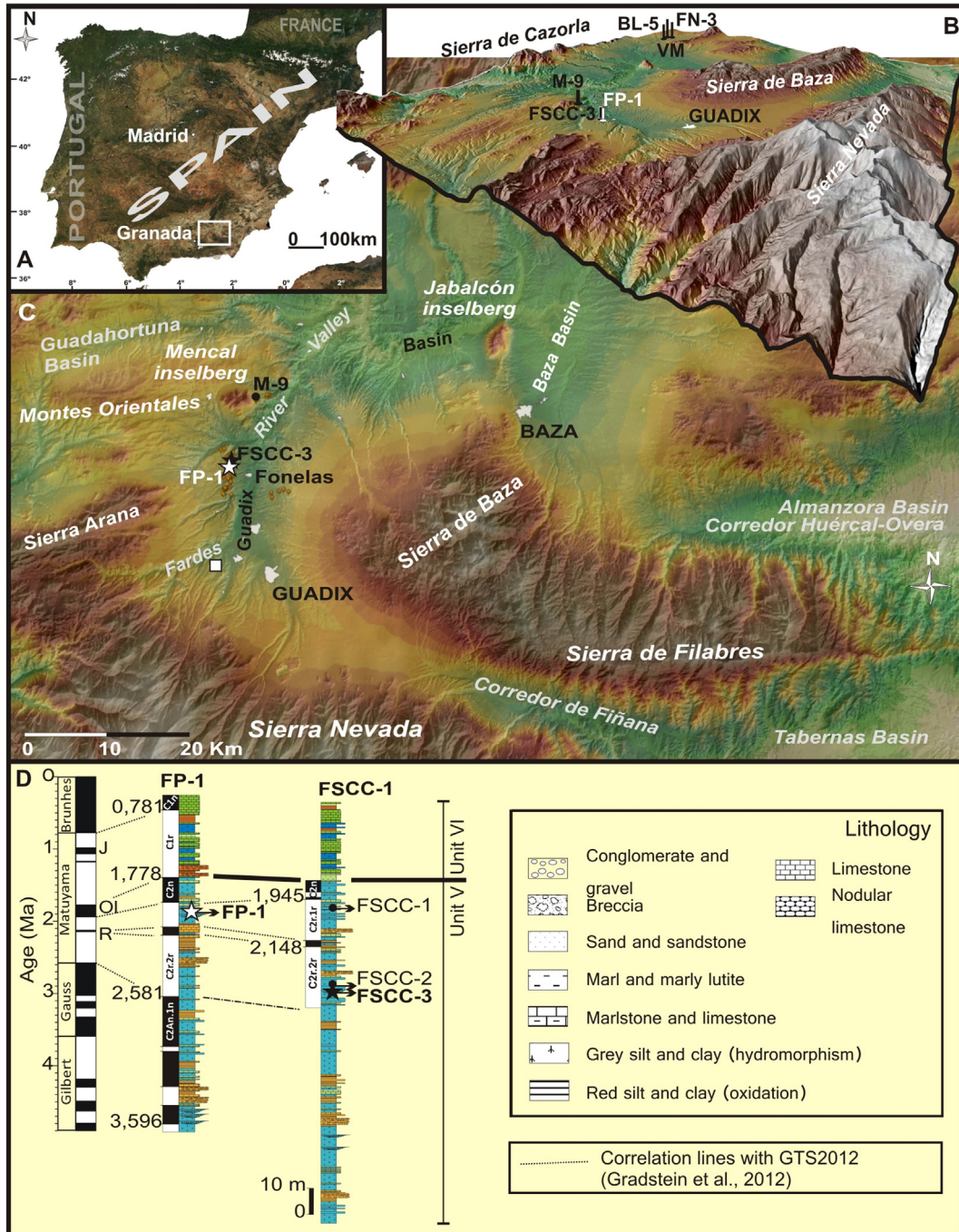

Fig. 1. Geographical and geological setting of the lower Pleistocene Fonelas P-1 site. A, location of the Guadix and Baza Basins (located in the area bounded by a white rectangle) in the southeastern Iberian Peninsula. B, digital elevation model (DEM) of the Guadix and Baza Basins and the high ground surrounding them, in oblique view, in which the altitudinal differences (i.e. the orographic context) can be observed. The position of Fonelas P-1 is indicated along with other important Early Pleistocene sites in the Guadix area (FSCC-3; M-9: Mencal-9), and the three most important in the Baza area (VM: Venta Micena; BL-5: Barranco León-5; FN-3: Fuente Nueva-3). C, DEM of the Guadix and Baza Basin, in cenital view and with a larger scale than in B, showing their Early Pleistocene fossil sites (those listed above along with others, as yet undescribed in the literature, found during the Fonelas Project), plus the area including Paleozoic and Mesozoic ridges and corridors, and associated Neogene basins. The position of the Ruscinian outcrop where the shell giant tortoise have been found is indicated with a square. The current landscape model for the Fardes River Valley includes large expanses of badlands that increase the number outcrops of fossiliferous units and paleontological sites. D, Stratigraphic profiles for Fonelas P-1 and Fonelas SCC-1 (which contain FSCC-3). Magnetostratigraphic information (Arribas et al., 2009; Pla et al., 2011) is provided (modified after Garrido and Arribas, 2014). The sections exclusively corresponding to fluvial sedimentary materials are those in blue.. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

antiquity of at least 2.4 million years (see de Lapparent de Broin, 2002 for description; Koufos, 2006 for the age of the locality; and the Discussion herein). The extinction of this clade from continental Europe is a fascinating question that we aim to explore. Answering this question first requires identifying the last representative of this clade in European continental deposits.

A new finding, which corresponds to the youngest remains of a giant tortoise in continental Europe, is presented and analyzed here. These specimens, coming from the fossil site of Fonelas P-1 (Guadix Basin, Granada, southeastern Spain; Fig. 1), allow recognizing the survival of this group for more than 400,000 years considering the hitherto younger known reference, favored by the favorable climatic conditions in that region of southwestern Europe. This finding, 1.3 million years younger that the youngest so far known Spanish evidence, is discussed within the framework of well-documented extinctions and faunal turnovers of large herbivore mammal groups in the European Mediterranean area.

2. Geographical and geological context of the finding of Fonelas P-1 and taphonomic implications

The material presented here comes from the paleontological site of Fonelas P-1 (Fig. 1). This fossiliferous locality is placed in the Guadix Basin (Granada, Betic Ranges, southeastern Spain) (Arribas et al., 2001). It is interpreted as a hyaenid den, located in a dry flood plain associated with a fluvial course (Viseras et al., 2006). Thousands of fossils that represent a large part of the continental ecosystem of mammals living in the basal lower Pleistocene of Western Europe have been found in this site. Twenty-four species of large mammals have been identified, as well as other vertebrate taxa, including several reptiles: undetermined members of Lacertidae, Anguidae and Viperidae, *Rhinechis scalaris* (Schinz, 1822), and a testudinid of small size (Garrido, 2006; Arribas, 2008; Arribas et al., 2009); the presence of *Titanochelon* is recognized herein for the first time.

Fonelas P-1 site has been dated by biostratigraphy and also using magnetostratigraphy. Its faunal association is exclusive of the Villafranquian (lower Pleistocene) and, more specifically, it belongs to the MNQ18 zone, presenting slightly more derived members than those of the French site of Senèze (Guérin, 1990; Mein, 1990; Arribas et al., 2009; Pla et al., 2011; Nomade et al., 2014). The magnetostratigraphic studies performed in the Guadix Basin, with this site as the main point of interest, have verified that Fonelas P-1 is located in a reversed polarity horizon (subchronozone C2r.1r), between the normal subchrons Reunion and Olduvai, 4 m directly below the base of this last subchron. Therefore, its age is 2.0 million years (Arribas et al., 2009; Pla et al., 2011).

The paleontological association of Fonelas P-1 was found in situ, the fossils corresponding to accumulated remains (Viseras et al., 2006; Garrido et al., 2010) (Fig. 2). The femur of *Titanochelon* analyzed here presents the same biostratinomic attributes identified in the fossil bones of large mammals of the site, showing clear evidences of the activity of the hyaenid *Pachycrocuta brevirostris* (Aymard, 1846). The presence of a clear spiral break produced by the nibbling, affecting its diaphysis in the area of contact with the proximal epiphysis (Fig. 3A–F), corresponds to a direct evidence of gnawing on fresh bone (see Palmqvist and Arribas, 2001). Thus, this femur was probably part of a partial hindlimb transported by the hyaenids (of which only the femur and a phalanx have so far been found), and consumed by these animals as a fresh bone immediately prior to its burial and the start of the fossil diagenetic stage, as also happened with the other bones in Fonelas P-1. Taphonomic reelaboration or sedimentary reworking (Murphy and Salvador, 1999) did not affect any bone found in this site (see Garrido et al., 2010).
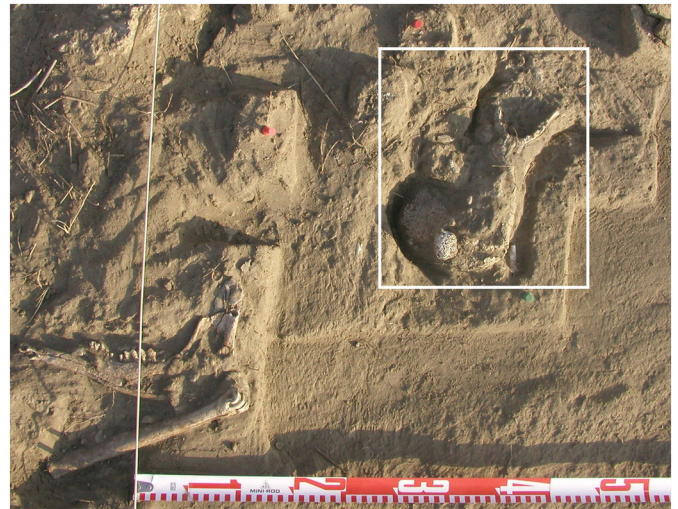

Fig. 2. Cenital view of a part of the (p',-6) excavation grid of the lower Pleistocene site of Fonelas P-1 (Guadix Basin, Granada, southeastern Spain) in the excavation performed in 2007. The femur of *Titanochelon* sp. studied here is in the right half of the image (delimited in the photo with a square), being in its original position and partially covered by sediment. The abundance of stems and roots of the extant *Stipa tenacissima* can be observed.

3. Systematic paleontology

Testudines Batsch, 1788.
Cryptodira Cope, 1868.
Testudinoidea Batsch, 1788.
Testudinidae Batsch, 1788.
Titanochelon Pérez-García and Vlachos, 2014.
Titanochelon sp.

3.1. Material

A left femur that preserves much of its diaphysis and the distal epiphysis (FP1-2007-3535; Fig. 3A–F), and a complete phalanx (FP1-2007-3644; Fig. 3G–L). Both elements come from the fossiliferous unit of Fonelas P-1 (facies association E sensu Viseras et al., 2006) associated with hyaenid activity (Garrido et al., 2010), in the context of the "Salto del Tigre" trench, having been found in the "(p'-6)" excavation grid. Considering the closeness of both findings, the anatomical and in size compatibility, and the taphonomy of the site, they are interpreted as belonging to a single hindlimb. These remains belong to the Fonelas P-1 collection (FP1), housed at the Instituto Geológico y Minero de España, Madrid, Spain.

3.2. Description

The femur was located at a depth of just 40 cm, as a result of the recent erosion of the area where the site is located. The surface of the femur shows evidence of two recent processes of alteration: a brown color as result of the infiltration of meteoric water (instead of white, as is characteristic of the bones of this site when the fossiliferous unit is not altered by recent processes); and marks of roots of *Stipa tenacissima* (Linnaeus, 1755), which grew above this unit and affected the outer cortical surface (Figs 2, 3A–D).

The sedimentary infill of FP1-2007-3535 corresponds the same matrix as that constituting the site (facies association E sensu Viseras et al., 2006), as is also the case in the other bones found in Fonelas P-1. Its surface presents evidences of biological activity produced during the biostratinomic stage. They are basically nibbling marks (Garrido et al., 2010), produced by hyaenids during the feeding (see a summary of the taphonomic activity of *Pachycrocuta brevisrostris* in Arribas and Palmqvist, 1998). There are both a type II spiral fracture (sensu
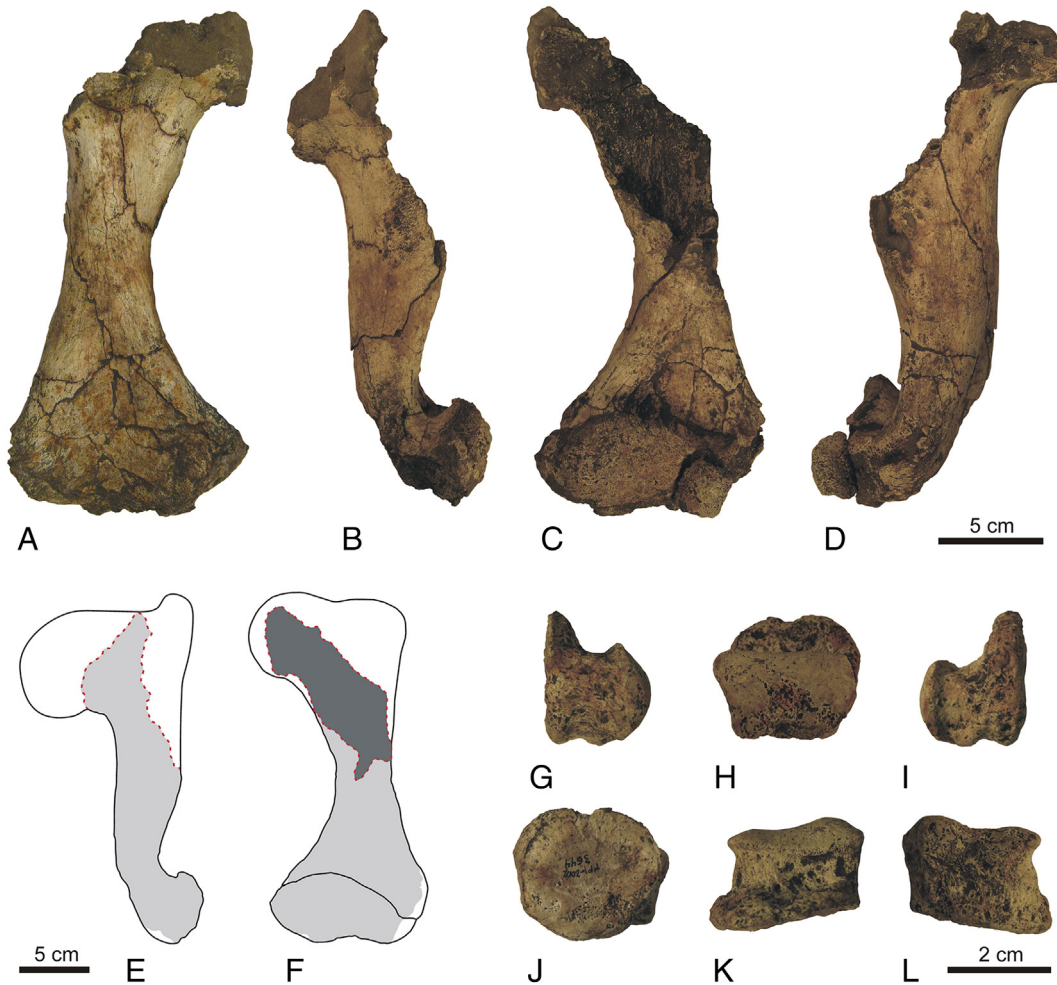
Fig. 3. The remains of *Titanochelon* sp. from the lower Pleistocene site of Fonelas P-1. A-F, FP1-2007-3535, left femur in dorsal (A), posterior (B), ventral (C) and anterior (D) views, and reconstruction of the bone in posterior (E) and ventral (C) views. The red dashed line in E–F represents the spiral break observed in the fresh bone by the nibbling by the hyaenids. G–L, FP1-2007-3644, phalanx in lateral (G), distal (H), lateral (I), proximal (J), probably dorsal (K) and probably ventral (L) views. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Shipman, 1981; Lyman, 1994) of the diaphysis, at its proximal end, as marks (furrows) produced by the premolars (i.e. toothmarks) of hyaenids (Garrido et al., 2010), distributed along that break and also in the diaphysis (Fig. 3A–F).

The bone preserves a length of 256 mm, transversal diameters of 44 mm in the narrowest point of the diaphysis and 128 mm in the widest part of the distal end, and anteroposterior diameters of 46 mm in the diaphysis and 56 mm in the distal region. The diaphysis is slightly curved medially and strongly curved in the distal part. The shape of the cross-section of the diaphysis is circular to elliptical. It has the typical hourglass-shape of the femora of the testudinids, with a widened distal part (Fig. 3A). In lateral view, the distal part of the femur shows a significant degree of curvature (Fig. 3B, D). The anteriorly placed tibial condyle and the posteriorly placed fibular condyle are curved ventrally, defining a well-developed ridge (Fig. 3C). The fibular part of the ridge is taller and thicker compared to the tibial one. A shallow concavity is noted behind the ridge. The distal articular surface shows two convex surfaces, for the tibia and the fibula.

The phalanx is well-preserved (Fig. 3E–J). Due to it was found near the femur, it also shows a brown color, result of the alteration by meteoric water. Hyaenid activity is not recognized in this bone.

FP1-2007-3644 is a short and cubic phalanx, showing a long dorsal extension on the proximal end. This extension is thin and it is developed perpendicular to the main axis. The proximal articular surface is almost flat, whereas the distal one is strongly convex. Due to its general

morphology, and based on its comparisons with the phalanges of other testudinid specimens, it appears to be the first phalanx of the pes.

4. Systematic allocation

The chelonian femora are easily distinguishable among those of other vertebrates based on the morphology of the proximal and distal ends (see Romer, 1956; Zug, 1971, and references therein). The lack of most of the proximal end of the FP-1 femur does not allow the documentation of numerous characters. However, the compressed and widened distal end, with no developed intercondylar fossa and lacking patellar groove, clearly distinguishes this bone from the most common femora in the locality (i.e. those of mammals). Although the missing information on the proximal part does not allow the observation of the fusion of the trochanters of the femur (a clear testudinid character; see Zug, 1971; Auffenberg, 1974; Crumly, 1984; de Lapparent de Broin et al., 2006), the well-developed ridges between the tibial and fibular condyles, the widened distal end and, indirectly, the short and robust phalanx, point out to testudinid affinities. In fact, the comparison of this partial femur with the femora of extant large tortoises (e.g. *Centrochelys sulcata* and *Stigmochelys pardalis*) and extinct members of *Titanochelon* (Fig. 4) shows that FP-1 is remarkably similar to these limb bones, allowing us to confirm that it belongs to a testudinid.

Due to the preservation of the Fonelas P-1 femur, only few characters are available for comparison with extant and extinct taxa. Due to
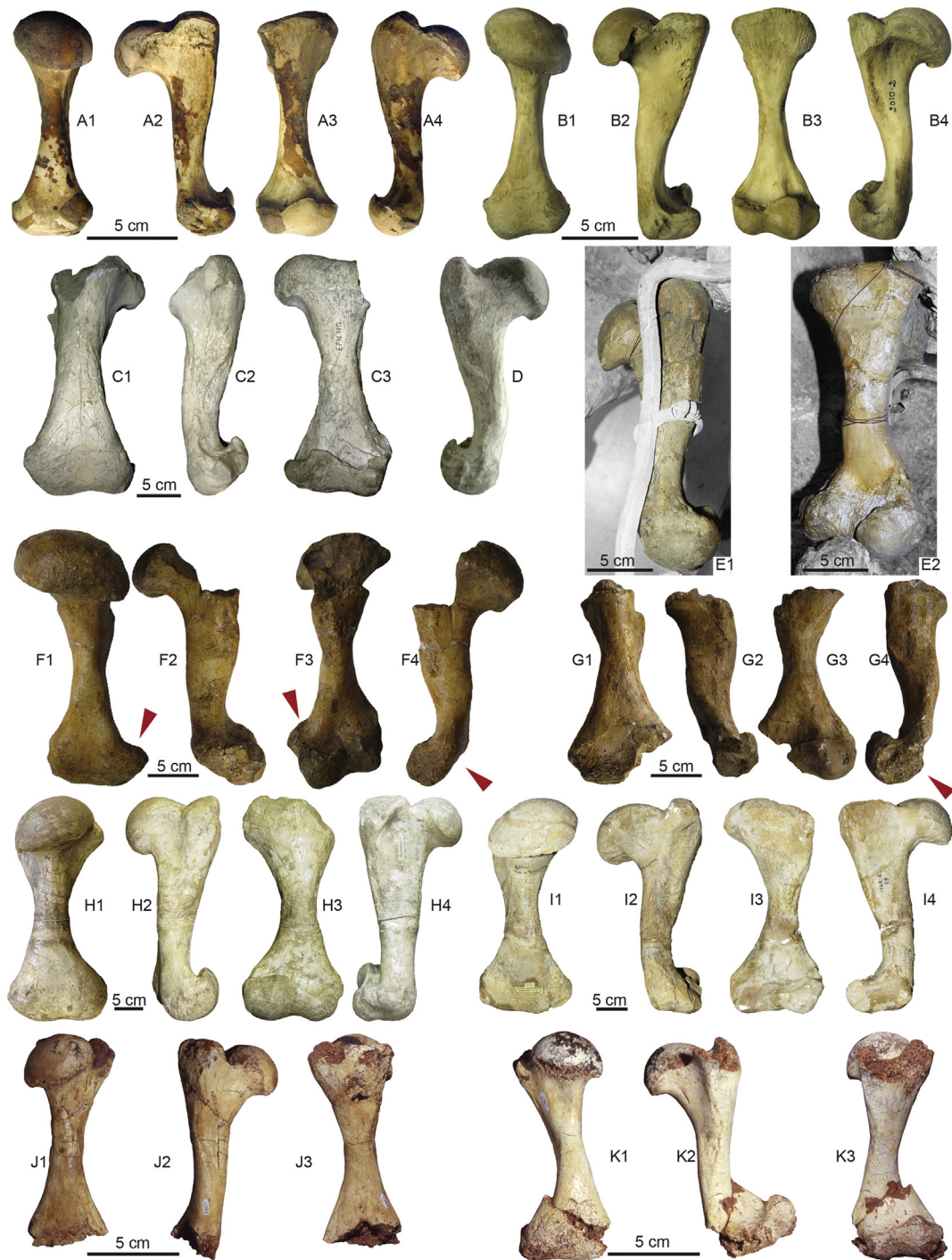
Fig. 4. Comparative information of the femora of extant and extinct large tortoise taxa. A, right femur of the extant *Centrochelys sulcata* (MNCN 58823); B, right femur of the extant *Stigmochelys pardalis* (MNHN ZA AC 2010-2); C, left femur and D, right femur of *Titanochelon bacharidisi* (Pliocene, Greece; LGPUT EPN 107); E, right femur of *Titanochelon perpiniana* (Pliocene, France; MNHN·F 1887-26); F–G, right femora of *Titanochelon bolivari* (Middle Miocene, Spain; MNCN 50228 and MNCN 50268); H, left femur of *Titanochelon schafferi* (Late Miocene, Greece; NHMW 1911/0005/0275); I, left femur of? *Centrochelys punica* (Pliocene, Tunisia; MNHN 1948–2-39); J, left and K, right femur of *Titanochelon gymnesica* (Pliocene, Punta Nati 6, Menorca; IPS 11749 and IPS 307). Institutional Abbreviations (only for this figure): IPS, collections of the Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Barcelona, Spain; LGPUT, Laboratory of Geology and Paleontology, School of Geology, Aristotle University of Thessaloniki, Greece; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN·F, Paleontology Collection of the Muséum national d'Histoire naturelle, Paris, France; MNHN ZA AC, Anatomie Comparée, Muséum national d'Histoire naturelle, Paris, France. Red arrows indicate some characters discussed in the text, such as the lateral extension of the fibular condyle (in dorsal and ventral views, F1 and F3) and the curved distal part (in posterior views, F4 and G4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most of the large fossil tortoises preserve the femur, extensive comparisons have been done based on this element (see de Lapparent de Broin, 2002). de Lapparent de Broin (2002) recognized two morphotypes considering the curvature of the shaft: almost straight femora as in *Centrochelys sulcata*, and curved ones as in *Stigmochelys pardalis* (see Figs. 16 and 17 respectively in de Lapparent de Broin, 2002, and Fig.

4A–B here). The presence of a curved diaphysis of the femur is a character included in the diagnosis of the genus *Titanochelon* (Pérez-García and Vlachos, 2014), and shared with the Fonelas P-1 specimen. The large size of this bone (its complete size being estimated as close to 275 mm) is much higher than those of these extant African taxa, being compatible with those of the members of *Titanochelon*. The strong

curvature in its distal part allow its attribution to *Titanochelon*. Among the representatives of *Titanochelon*, a relatively straight medial region of the femur can be recognized in the Late Miocene *Titanochelon schafferi* (Szalai, 1931), from Samos (Greece; Fig. 4H). The remaining so far known femora of *Titanochelon* display a high degree of curvature in this region (see Fig. 4C-G, I-K). The highest known degree of distal curvature is noted in *Titanochelon bolivari* (Hernández-Pacheco, 1917), from the Aragonian to early Vallesian of Spain (Fig. 4F-G), being similar to that present in the femur from Fonelas P-1. Further similarity between the two taxa is noted in the lateral extension of the fibular condyle which, compared to the remaining taxa, show a more symmetrical distal end (see Fig. 4F1 and F3). The morphology described for the phalanx is also compatible with those of *Titanochelon*. Considering the scarce remains of large tortoises found in Fonelas P-1, and the limited information provided by these two bones, these elements are attributed to *Titanochelon* sp.

de Lapparent de Broin (2002) used the dimensions of the complete skeleton of the French Pliocene *Titanochelon perpiniana* (Depéret, 1885) to estimate the shell size of other giant tortoises only known by appendicular remains. Therefore, we can use the same ratio to provide an estimation of the size of the Fonelas P-1 individual. With an estimated length of the femur of 275 mm (see above), and using the ratio proposed by de Lapparent de Broin (2002), the carapace length of this tortoise is obtained as about 142 cm. It is important to note that this method is not based on a large sample, but only on the study of a single individual. New information presented by Vlachos et al. (2014) and Pérez-García and Vlachos (2014) showed significant metrical differences between males and females of the same species of *Titanochelon* (close to 15%). Due to the nature of the preserved remains, no information about the sex of the specimen studied here is available.

5. Implications for the survival and extinction of the large tortoises in continental Europe

The youngest so far confirmed reference on the finding of giant tortoises in the Iberian Peninsula corresponded to the material found at the fossil site of Las Higueruelas (Ciudad Real, Spain) (Jiménez Fuentes, 1994). These turtles, that remain unpublished, represent an indeterminate member of *Titanochelon* (Pérez-García and Vlachos, 2014). Las Higueruelas is a site where the remains of *Anancus arvernensis* (Croizet and Jobert, 1828) are very abundant, and whose chronology has been estimated as deposited 3.3 Ma (MNQ 16; Mazo et al., 2003) (Fig. 5).

Considering the entire record of European continental giant tortoises (i.e. *Titanochelon*), the youngest so far confirmed datum was that of Vaterá (F-site; Lesvos, Greece) (de Lapparent de Broin, 2002). Lesvos is now an island but, during Plio-Pleistocene, it was part of the continent being united, at different times, with the Anatolian Peninsula (see Vlachos et al., 2014 and references therein). The faunistic association found in the F-site of Vaterá (studied preliminarily by de Vos et al., 2002) has been assigned to the MNQ17 zone (Koufos, 2006), a fact confirmed by the presence of the genera *Paradolichopithecus* Necrasov et al., 1961, *Nyctereutes* Temminck, 1838, *Gazella* Blainville, 1816 and *Anancus* Aymard, 1855. The presence of *Anancus arvernensis* in Vaterá, in the same unit where the fossil remains of giant tortoises appear, indicates that its youngest possible age is about 2.4 Ma (2.36 ± 0.04 Ma; MNQ17b), according with the latest geochronological revision of the data of last appearance of these mastodons in Europe (*Anancus arvernensis chilhiacensis* Boeuf, 1992 in the French site of Chilhac; Nomade et al., 2014). A similar chronology has been assigned to the last representatives of the species *Anancus arvernensis* in the Iberian Peninsula. This record comes from a new fossil locality in the Guadix Basin, with the most recent record of mastodons known in Spain, was recently published (Garrido and Arribas, 2014). It is the site of Fonelas SCC-3, with an age between 2.5 and 2.4 Ma (MNQ17a, known by magnetostratigraphy), and including the last known fossils of the

lineage of the mastodons in the Iberian Peninsula (i.e. *Anancus arvernensis mencalensis* Garrido and Arribas, 2014) (Fig. 5).

Titanochelon may have also lived in some Mediterranean islands (Pérez-García and Vlachos, 2014). 'Testudo' *gymnesicus* (Bate, 1914) is a large testudinid, which lived in Menorca (Balearic Islands), at levels currently dated as of Pliocene, with a recent estimation as lower Pliocene (Quintana et al., 2011). This form was tentatively proposed as a possible member of *Titanochelon* by Pérez-García and Vlachos (2014), a proposal followed by Rhodin et al. (2015). Although this generic allocation was not justified, the observation of characters shared with the members of *Titanochelon* and included in the diagnosis of this genus (such as, among others, the shell length exceeding 1 m, curved diaphysis of the femur and the well-developed curvature of the distal region on this bone (Fig. 4J-K), curved diaphysis of the humerus, presence of a dorsal convex lip of the epiplastra, absence of ventral relief in the area covered by the gular scutes, angle between the sagittal axis and the gularo-humeral sulcus of 45° or more acute), allow us to support here this generic attribution. However, the presence of *Titanochelon* in insular areas, in post-Pliocene levels, cannot currently be confirmed. Remains of relatively large specimens were identified in Malta, in levels deposited in the middle Pleistocene (sensu Rhodin et al., 2015). 'Testudo' *robusta* Leith-Adams, 1877, 'Testudo spratti' Leith-Adams, 1877 and 'Testudo robustissima' Tagliaferro, 1914 were defined there, these three forms having recently been considered as corresponding to a single species, *Centrochelys robusta* (Leith-Adams, 1877), by Rhodin et al. (2015). The detailed study of these forms, and also that of a not determined synchronous taxon from Sicily (see Rhodin et al., 2015), is necessary to confirm whether this extant African genus (probably known at least since the late Pliocene sensu Gmira et al., 2013) migrated to these European islands, or if they correspond to survivors, in insular territory, of the European lineage of *Titanochelon*. The presence of osseous remains of a Pleistocene medium-sized tortoise (with a length of the shell close to 50 cm) in Ibiza (Balearic Islands), was notified by Bour (1985). Filella-Subirà et al. (1999) recognize the presence of eggs of a medium-sized testudinid in the Pleistocene of the nearby island of Formentera. Bour (1985) does not determine at generic or specific level the finding from Ibiza. Filella-Subirà et al. (1999) indicated that the presence of testudinids of that size in that region (the Pityusic Islands) could be the result of the migration of European or African forms of medium or large size, or of the enlargement in size of a small form of the Balearic Islands. Bour (1985) identify several differences between the medium-sized taxon from Ibiza (recognized by him as represented by an adult individual) and the large tortoises from continental Europe currently attributed to *Titanochelon*. Thus, characters as, among others, the absence of fused astragalus and calcaneum, differ from those that diagnose the genus *Titanochelon*. Thus, the currently limited information available on the taxon from the Pleistocene of the Balearic Islands does not allow us to support a close relationship with this European lineage. Therefore, the finding of *Titanochelon* in Fonelas P-1 presented here not only corresponds to the youngest so far confirmed remain of this successful lineage in continental Europe (this genus being known since the early Miocene), but also to the youngest confirmed evidence, including the insular record. It is important to note here that the smaller-sized tortoise representatives (*Testudo* Linnaeus, 1758 sensu lato or Pan-*Testudo*) were able to survive up to the present in Europe, both as continental and insular forms, with several extant species and numerous extinct ones as well (see de Lapparent de Broin, 2001; van Dijk et al., 2014; Rhodin et al., 2015).

The identification of *Titanochelon* in Fonelas P-1 shows that this lineage survived in the Iberian Peninsula at least 1.3 million years more than hitherto recognized (considering the Las Higueruelas record), and in the whole of continental Europe at least 400,000 years more than was indicated by the so far available evidence. No giant tortoises were previously recognized in the Guadix Basin. However, another recent unpublished finding shows the presence of older populations of these animals. This finding corresponds to two shells, in section, found
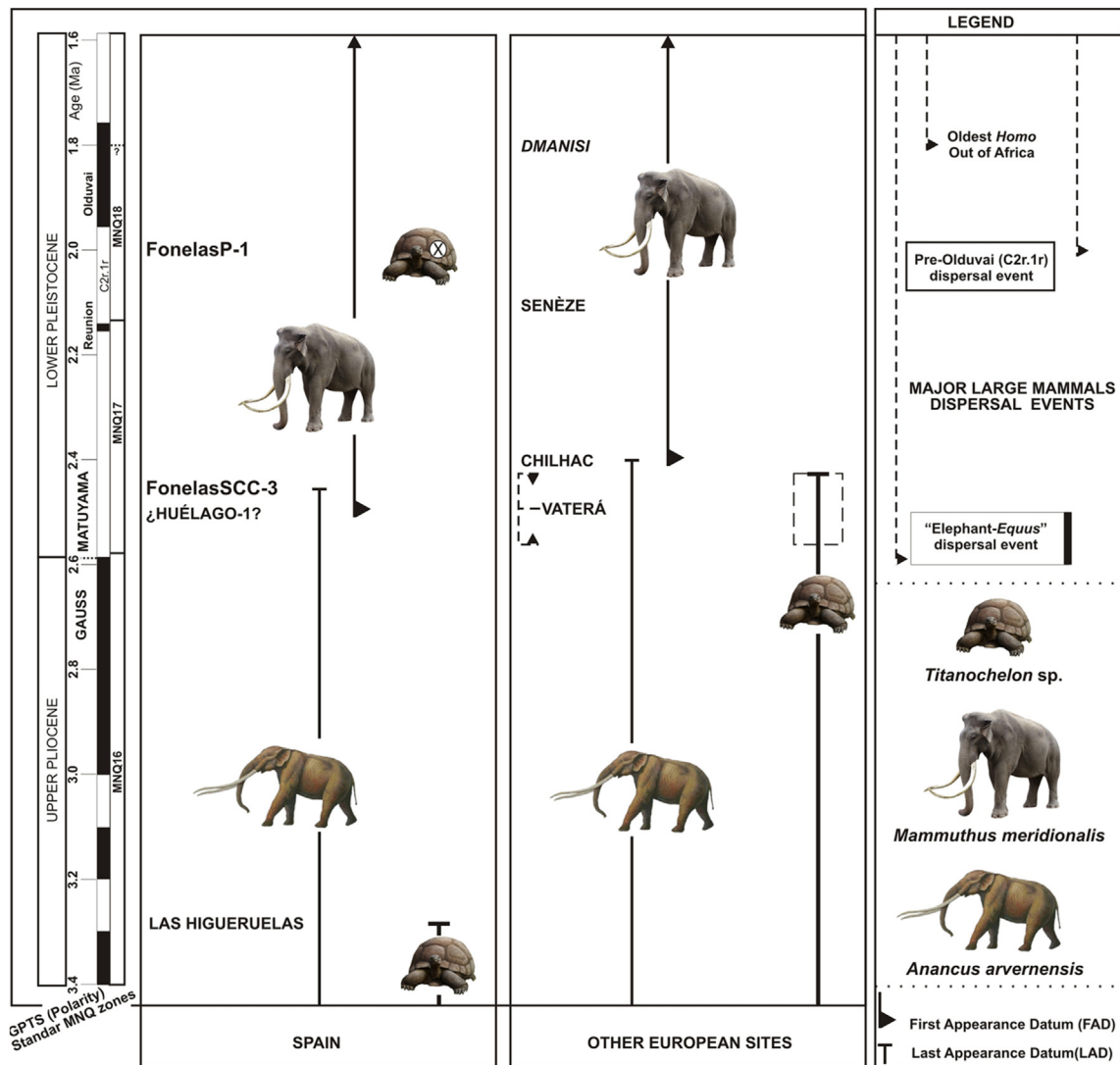
Fig. 5. Figure showing the chronological distribution, in Spain and Europe, of the last representatives of the genus *Anancus* and the first representatives of the genus *Mammuthus* along the late Pliocene and the basal early Pleistocene. In addition, the younger continental representatives of the genus *Titanochelon* (including the new material from Fonelas P-1) are also presented for both contexts. Only the relevant sites for the discussion, based on their record and chronology, are represented. The chronological position of the sites is based on: magnetostratigraphic and biostratigraphic data (Las Higueruelas, Fonelas SCC-3 and Fonelas P-1); geochronological data (Chilhac, Senèze and Dmanisi); and exclusively biostratigraphic data (Huélago-1 and Vaterá). Dmanisi, in the Caucasus, where the first human evidence outside Africa is registered, presents an association of large mammals significantly similar to that identified in Fonelas P-1 (Atlantic Europe). The chronological position of Vaterá is indicated by a dashed rectangle corresponding to the more reasonable chronological interval for its genesis (their faunas, in which *Anancus* and *Titanochelon* coexist, belong to the MNQ17 zone and, within it, they cannot be more modern than 2.4 million years or older than 2.6 million years). The two major mammals dispersal events so far characterized in Europe for the period considered here are also represented (see Arribas et al., 2009; Nomade et al., 2014). Reconstructions of the animals: *Titanochelon* (Mauricio Antón), *Anancus arvernensis* (Alexis Vlachos), and *Mammuthus meridionalis* (Roman Uchytel/EPVRF-IGME).

in a ravine cutting layers corresponding to alluvial fans deposits, in units of "playa-lake" intercalated in proximal facies (internal transverse system sensu Viseras et al., 2006), from the Ruscinian (MN14-MN15; 5.3 to 3.6 Ma), in the area of Cortes and Graena (11 km south of the position of Fonelas P-1) (Figs. 1, 6). Therefore, large tortoises lived in this Basin several million years before the populations of Fonelas P-1.

Based on all the above, the extinction of the large tortoises remains as probably one of the most puzzling questions of the evolutionary history of the European testudinids. Recently, the Turtle Extinction Working Group (Rhodin et al., 2015) investigated the global extinction of turtles and tortoises across the Pleistocene and Holocene. They estimated that nearly 25% of the large taxa living in these series have gone extinct. Several reasons prevent a detailed analysis on the extinction of the large tortoises from Europe. First, the absence of detailed chronological information concerning several of the findings (contrasting with the precise dating of Fonelas P-1) excludes the possibility of knowing in temporal detail the timing of the extinctions that occurred. Second,

the fragmentation and limited information provided by the known Pliocene and Pleistocene large tortoise material, and the absence of skull and relevant shell remains, usually does not allow a detailed taxonomic identification. As a result, this problem prevents the inclusion of the fossil individuals into a phylogenetic framework, which would allow a proper diversity and extinction analysis. Finally, the material itself is limited, and disproportionally distributed (both geographically and temporally), especially when compared to the abundant fossil mammal material from that period (e.g. about 20 localities with fossil large tortoises are known versus more than 200 localities with fossil mammals selected by Kahlke et al., 2011).

Two factors may be recognized as the main ones for the global extinction of taxa and lineages of tortoises along the Pleistocene and Holocene. The most important is the role of the humans (see Rhodin et al., 2015 and references therein). It not only can be evidenced in the case of the extinction of many Pacific and Indian island large tortoises, but also globally considering the extinction of turtles and tortoises,

Fig. 6. Section of a shell of a giant tortoise, located in August 2016 on alluvial fans units of Pliocene deposits (Ruscinian). This outcrop is located in a ravine on the southern edge of the Guadix Basin, very close (2 km) to the high paleogeographic areas defined by the Iberian mountain range with the highest altitude (i.e. Sierra Nevada; metamorphic rocks). The sedimentary materials that were deposited in Fonelas P-1 came from these metamorphic areas.

including the continental forms. The current available evidence shows that the earliest human dispersal in Europe occurred after the extinction of the lineage of *Titanochelon* (Dmanisi, Caucasus, 1.8 Ma; Ferring et al., 2011. See Fig. 5), so it cannot be identified as a factor for the extinction of the large tortoises in this continent (in contrast to the situation in other continents with large tortoises and, especially, island regions). The second factor is the temperature decrease. With the beginning of the Pleistocene, the temperature in the Northern Hemisphere started to decrease (Zachos et al., 2001; Zubakov and Borzenkova, 1990; Lisiecki and Raymo, 2005). Several authors (e.g. Hibbard, 1960; Holman, 1971, 1976; Estes and Hutchison, 1980, among others) point out that the presence of large tortoises indicates subtropical climatic conditions or, at least, relatively mild winters, with temperatures well above freezing. As an example, Hibbard (1960) documents that the Galápagos Islands large tortoises cannot survive in the mild climate of the Florida Keys. Auffenberg (1974) showed that the ranges of geographic distribution of several lineages of testudinids were modified during the cooling periods of the Quaternary, the drought and cold conditions in the northern latitudes playing an important role in the extinction of large tortoises. Some small tortoises (*Gopherus* Rafinesque, 1832 and *Testudo*) used burrows to protect themselves from these severe conditions. However, this adaptation is not frequent for large forms, their range of geographic distribution being significantly more limited in periods with relatively low temperatures. Besides the temperature decrease, the increased aridification in Europe during that period (see Kahlke et al., 2011) could also have had significant effects not only in the feeding (linked to changes in plant diversity and systematic composition) but also in the reproduction of these tortoises, due to both the oviposition and the hatching are related with the rainy season in many species (see Swingland and Klemmens, 1989, and references therein). Climate and habitat change also coincide with major changes in other large-sized herbivore groups that were affected as well (e.g. the Elephant-*Equus* dispersal event sensu Azzaroli, 1995). Whereas in rest of Europe this coincidence is clearer, the favorable conditions in the Gaudix Basin allowed the persistence of the giant tortoises for few hundred thousand years more.

The presence of a taxon with environmental and ecological requirements as restrictive as those known for the extant and extinct large tortoises (see introduction, and Hibbard, 1960; Holman, 1971, 1976; Auffenberg, 1974; Estes and Hutchison, 1980), living in the diverse ecosystem developed in Fonelas P-1 two million years ago (with a large variety of herbivores, recorded in an extensive fluvial section showing abundance of water resources in an endorheic basin, with open habitats and patches of woodlands), allows to question the generalization of

paleoclimatic inferences assumed for the whole of Europe at that period of time (i.e. a cooler and drier Europe that at the end of the Pliocene by the increase of the seasonality and the beginning of glacial activity in the Northern Hemisphere; see Palombo and Valli, 2004; Haug et al., 2005; Lisiecki and Raymo, 2007; Kahlke et al., 2011; Solgaard et al., 2011). The record of Fonelas P-1 indicates that in the lower Pleistocene of southern Europe (at least in the endorheic basins of the Betic Ranges) warmer climatic conditions than in the rest of the continent persisted, favoring the survival of large testudinids.

Knowledge about when and why the large tortoises became extinct in different regions of the world is important not only for our understanding of the evolutionary history of this clade but even for broader issues such as a those concerning turtle conservancy, climate change and the effect of human interactions.

6. Conclusions

The last so far known continental large tortoises from Spain were those from Las Higueruelas (3.3 Ma), and those from continental Europe were those from the Greek locality of Vaterá (2.6 to 2.4 Ma). All these testudinids belong to *Titanochelon*, a diverse genus known since the beginning of the Miocene. Here we present new fossil material of a giant tortoise (*Titanochelon* sp.) from the lower Pleistocene Fonelas P-1 site (Guadix Basin, Betic Ranges; Granada, southeastern Spain). The Fonelas P-1 tortoises lived 2.0 Ma. Thus, they represent the last known survivals of this clade in continental Europe, and the youngest so far justified evidence of *Titanochelon*. During the upper Pliocene and lower Pleistocene, important climate events are documented, which are recognized here as the main factor for the extinction of these gigantic reptiles in this continent. The presence of these temperature-sensitive animals in Fonelas P-1 at that period confirm previous claims of a warmer climate in the area, with abundant water resources, as opposed to the rest of Europe where cooler and drier conditions were present.

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