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Revision of the extinct Pleistocene tortoise *Testudo lunellensis* Almera and Bofill, 1903 from Cova de Gràcia (Barcelona, Spain)

Massimo Delfino[1,2,*], Àngel H. Luján[2], Raül Carmona[2,3], David M. Alba[2]

1 - Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, 10125 Torino, Italy

2 - Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain

3 - FOSSILIA Serveis Paleontològics i Geològics, S.L. c/ Jaume I núm. 87, 1er 5a, 08470 Sant Celoni, Barcelona, Spain

Abstract. *Testudo lunellensis* Almera and Bofill, 1903 from the Middle Pleistocene of Cova de Gràcia (Park Güell, Barcelona, Spain) is a valid species belonging to the clade of the extant *Testudo hermanni*—a diagnostic feature being the narrowed vertebral scutes. Thanks to still unpublished material, *T. lunellensis* is diagnosed for the first time and its shell morphology described in detail. This species is uniquely characterized, among others, by tall peripheral bones and by a peculiar shape of the anterior lobe of the plastron, somewhat recalling the species referred to *Testudo* s.s. (the clade containing the extant species *Testudo graeca*, *Testudo kleinmanni* and *Testudo marginata*). Given that the purported valid species from Lunel-Viel (Middle Pleistocene, France) is still unnamed and undescribed, *T. lunellensis* from Cova de Gràcia is currently the stratigraphically youngest extinct *Testudo* species. The co-occurrence in *T. lunellensis* of characters typical of both *T. hermanni* and *Testudo* s.s. further testifies the phenotypic plasticity of tortoises and the mosaic distribution of morphological characters, which hinders a clear-cut assessment of the relationships of extant tortoises when based exclusively on morphology. Further analyses of the phylogeny of *Testudo* should consider fossil and extant taxa together, as well as both morphological and genetic

characters.

Keywords: *Testudo hermanni*, *Eurotestudo*, fossil record, shell morphology, phenotypic plasticity.

Introduction

The taxonomy and phylogeny of western Palearctic tortoises, *Testudo* s.l., have been recently the object of morphological and molecular scrutiny. According to the morphological analyses of extant and extinct taxa by Lapparent de Broin et al. (2006) and by Lapparent de Broin, Bour and Perälä (2006a,b), the members of *Testudo* s.l. have a paraphyletic arrangement, and therefore the clade of *Testudo hermanni* Gmelin, 1789 could be referred to a different genus, *Eurotestudo* Lapparent de Broin et al., 2006. Strikingly contrasting are the results of Fritz and Bininda-Emonds (2007), who analyzed approximately two-thirds of all extant testudinid species (including all five *Testudo* species currently recognized) using a five-gene data set. According to their analysis, all the extant *Testudo* species constitute a monophyletic clade. *T. hermanni* and *Testudo horsfieldii* Gray 1844 are grouped in a subclade of their own, which if any nomenclatural distinction was to be made, could be referred to the subgenus *Chersine* Merrem, 1820 (see also Fritz and Kraus, 2008, and references therein). Moreover, Fritz and Bininda-Emonds (2007) and Fritz and Kraus (2008) demonstrated that the name *Eurotestudo* Lapparent de Broin et al., 2006 cannot be used because it is an objective junior synonym of *Chersine* Merrem, 1820 and *Medaestia* Wussow, 1916 (see also Bour and Ohler, 2008).

In agreement with Fritz and Bininda-Emonds (2007) we did not apply the name *Eurotestudo* to *T. hermanni* and its clade.

These taxonomic, phylogenetic and nomenclatural issues aside, the above-mentioned papers by Lapparent de Broin and co-workers offered the most comprehensive description and discussion of the osteological characters and variability of extant and extinct members of *Testudo* s.l. From a palaeontological perspective, a remarkable result obtained by Lapparent de Broin et al. (2006) and

Lapparent de Broin, Bour and Perälä (2006a,b) is that, despite its convoluted nomenclatural history (see Discussion), the extinct *Testudo lunellensis* Almera and Bofill, 1903 from the Middle Pleistocene of Cova de Gràcia (Barcelona, Spain) can be considered a valid species, which still needs to be properly diagnosed. The materials on which this species was based were discovered at the end of the nineteenth century, during the construction of Park Güell, the renowned, iconic urban park designed by the Catalan architect Antoni Gaudí, now a UNESCO World Heritage Site. *T. lunellensis* has been reported only from the type locality, Cova de Gràcia, and its remains are currently housed in three different institutions.

Here we focus on the description of still unpublished remains of this taxon, housed in the collections of the Institut Català de Paleontologia Miguel Crusafont and the Museu Geòlogic del Seminari Conciliar de Barcelona, as well as on the revision of the already described material from the Museu de Ciències Naturals de Barcelona (Museu Martorell, former Museu de Geologia de Barcelona; Almera and Bofill, 1903; Bergounioux, 1958; Gómez-Alba Ruiz, 1997). Our goal is to provide a diagnosis of *T. lunellensis*, on which future comprehensive phylogenetic analyses of the *Testudo* clade could be grounded.

Abbreviation

Anatomical abbreviations: **ed**, epiplastral depression; **ento**, entoplastron; **ep**, epiplastral pads; **epi**, epiplastron; **gp**, gular pocket; **hyo**, hyoplastron; **hypo**, hypoplastron; **xiphi**, xiphiplastron.

Institutional abbreviations: **ICP**, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Spain; **IPS**, collections of the ICP (formerly Institut de Paleontologia de Sabadell); **MGB MGC**, Museu Martorell (former Museu de Geologia de Barcelona), Museu de Ciències Naturals de Barcelona, Spain; **MSCB**, Museu Geològic del Seminari Conciliar de Barcelona, Spain; **MTD**, Museum für Tierkunde Dresden, Germany; **NHMW**, Naturhistorisches Museum Wien, Austria.

Systematic account

Testudines Batsch, 1788

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758

Testudo lunellensis Almera and Bofill, 1903

(figs 1–4)

Testudo lunellensis Almera and Bofill, 1903:454, pl. 1 fig. 3, pl. 2 fig. 2, pl. 3 fig. 4,5 (original description).

Testudo ibera Pallas, 1814: Almera and Bofill, 1903:456.

Testudo lunellensis Almera and Bofill, 1903: Depéret, 1906: 12

Testudo lunellensis Almera and Bofill, 1903: Bataller, 1956:22.

Testudo lunellensis Almera and Bofill, 1903: Bergounioux, 1958:203, figs 27-28.

Testudo lunellensis Almera and Bofill, 1903 var. *ibera* Bergounioux, 1958:208, figs 29,30; pl. 43, 44.

Testudo lunellensis Almera and Bofill, 1903: Auffenberg, 1974:203.

Testudo hermanni lunellensis Almera and Bofill, 1903: Jimenéz Fuentes and De Jesús, 1991:98.

Eurotestudo lunellensis (Almera and Bofill, 1903): Lapparent de Broin et al., 2006:804 (new combination).

Eurotestudo lunellensis (Almera and Bofill, 1903): Lapparent de Broin et al., 2006a:274, fig. 9g-i.

Eurotestudo lunellensis (Almera and Bofill, 1903): Lapparent de Broin et al., 2006b:344.

Lectotype. – MGB MGC 6101: partial shell (Jimenéz Fuentes and De Jesús, 1991:98).

Paralectotype. – MGB MGC 20642: partial shell, MGB MGC 20838: partial shell (Gómez-Alba Ruiz, 1997:186).

Referred material. – IPS 57549: partial shell; MSCB 25197: partial shell, MSCB 28193: partial shell, MSCB 28194: partial carapace, MSCB 28195: partial shell; MGB MGC 6101: partial shell; MGB MGC 6110: partial carapace, MGB MGC 6202-1/2: femur, MGB MGC 6258-1/4: femur and three long bone fragments, MGB MGC 20839: plastron, MGB MGC 33121: tibia, caudal vertebra, three distal phalanges and six metapodial elements, MGB MGC 33122: fragmentary plastron with femur, MGB MGC 333123: fragmentary carapace, MGB MGC 333124: shell fragment, MGB MGC 333125: partial plastron, MGB MGC 33126: plastron.

Type locality. – Cova de Gràcia, Park Güell, Barcelona, Spain (by original designation; Almera and Bofill, 1903). Also known as Can Montané, Font del Carbó, Can Larrà.

Age: Middle Pleistocene, Toringian, biozone *Arvicola* aff. *sapidus* (Agustí and Moyà, 1992).

Diagnosis: *Testudo lunellensis* differs from all extant and the other extinct species of *Testudo* by the following combination of characters: vertebral scutes narrower than the pleural ones; divided supracaudal scutes (at least externally); peripheral bones very tall; anterior plastral lobe robust and markedly bent dorsally; thick epiplastral pads anteroposteriorly so well developed that their posterior edge is variably convex in dorsal view (reaching the entoplastron but not significantly overhanging it); shallow but evident gular pocket; ventral surface of epiplastra slightly convex in correspondence of the gulars and weakly concave in correspondence of the humerals; xiphoid process present and relatively robust; hypo-xiphiplastral suture (no hinge).

Description of the unpublished materials

The materials of the MGB collection have been listed, figured and at least partly described in several articles (Almera and Bofill, 1903; Bergounioux, 1958; Jimenéz Fuentes and De Jesús, 1991; Gómez-Alba Ruiz, 1997; Lapparent de Broin et al., 2006; Lapparent de Broin, Bour and Perälä, 2006a,b) and therefore they will not be commented in this section. The description below is focused on the most informative remains, which are those at the ICP, and the remains in the collections of MSCB are described just for completing the morphological information provided by the former.

IPS collection

Carapace. The carapace of IPS 57549 (fig. 1A) is represented by the anterior portion up to the fourth neural, fourth costal and seventh peripheral element (a little portion of the eight right peripheral is also preserved). The preserved portion of the carapace, 19.5 cm long and 19.0 cm wide, is highly fractured and part of the left costals and one peripheral have been reconstructed with plaster. The anterior edge of the shell is severely damaged, so that the anterior profile does not correspond to the original shape of the shell. Despite the relatively large size of the carapace, none of its constituting elements is particularly thick. The nuchal bone is only slightly wider than the first vertebral scute. Due to preservation conditions, the cervical scute is visible only on the ventral surface of the nuchal. The maximum thickness of the nuchal is of 12.6 mm. The first neural is much longer (33.3 mm) than wide (21.3 mm); it is approximately rectangular, only weakly tapering anteriorly. In the preserved portion, the neural formula seems to be 4-8-4-8(or 6?) and the typical *Testudo* alternation of approximately trapezoidal costal elements (with dorsal and ventral edges alternatively wide and narrow) is only weakly expressed. The costo-peripheral suture corresponds to the pleuro-marginal sulcus. The peripherals are tall (the mediolateral width of the fourth peripheral is 59.1 mm; the one of the corresponding costal is 93.1 mm). The peripherals from 3 to 7 are involved in the bridge. The axillary buttress contacts the third and the second peripherals, whereas the inguinal buttress contacts the seventh peripheral. Both buttresses did not reach the costals. The maximum width of the second vertebral scute does not exceed the width of the corresponding pleural. A distal fragment of the right acromion is attached to the matrix still adhering to the ventral surface of the first right costal.

Plastron. Despite the fact that the left hypoplastron and right xiphiplastron are incomplete and the left xiphiplastron is missing, the plastron (fig. 1B-E) is relatively well preserved. There are no signs of deformation and the several fractures do not significantly dislocate the bones. The length of the preserved plastral portion is 19.2 cm. The external surface of the plastron is only slightly concave in the region corresponding to the hyo- and hypoplastra, but it is markedly bent dorsally in the area of the epiplastra and the entoplastron. Epiplastra are dorsally bent and very robust as in most specimens of *Testudo graeca* Linnaeus, 1758. They possess a thick dorsal pad (26.5 mm tall) that is considerably developed in anteroposterior direction (29.8 mm long), reaching the entoplastron but not significantly overhanging it. The posterior edge of the epiplastral pads is convex in dorsal view. The area of the pad corresponding to the gular scutes is very weakly concave as is the anterior edge of the epiplastra in dorsal view. A little step is developed at the anterior edge of the epiplastra in correspondence with the gulo-humeral sulcus. On the ventral surface of the epiplastra, the area covered by the gulars occupies about one third of the surface and is very weakly convex; the two thirds not covered by the gulars host a moderate depression. The entoplastron is not entirely located in the anterior lobe of the plastron. It has an approximately triangular outline dorsally and a roundish outline ventrally (40.5 mm wide, 38.2 mm long). The dorsal surface of the entoplastron does not display any marked depression. The remnants of the xiphoid process indicate that it was present and relatively robust. The ventral surface of the anterior half of the entoplastron is curved in dorsal direction; it is crossed by the gular-humeral sulcus (gulars extend to a little more than one fourth of the entoplastron) but not by the humero-pectoral sulcus.

The hyoplastra are characteristically thick and are visibly convex on the dorsal surface (nearly as in most specimens of *T. marginata* Schoepff, 1793). On the ventral surface, the humero-pectoral sulcus medially points in posterior direction, describing a wide curve that is separated by at least 1.5 mm from the suture with the entoplastron; this sulcus reaches the lateral edge of the hyoplastra exactly at the axilla (it turns backward as it approaches the edge of the bone). The pectoro-abdominal sulcus is arched in anterior direction. The interpectoral sulcus is 22.5 mm long. Due to preservation, it is not possible to assess the presence/absence of the axillary scute. The hyo-hypoplastral suture laterally reaches the fifth peripheral. The hypoplastra are much lightly built than the hyoplastra and participate in the posterior lobe. There is no evidence for a hypo-xiphiplastral hinge. On the hypoplastra ventral surface, the abdomino-femoral sulcus is deeply arched laterally, and despite the incompleteness of the hypoplastra it is clear that the sulcus did not reach the hypo-xiphiplastral suture (it was probably separated by about 5 mm). The inguinal scute is clearly present. The fragmentary right xiphiplastron only preserves the thickened anterolateral portion corresponding to the base of the hypoplastral buttress.

MSCB collection

The four tortoise remains from Park Güell housed in the MSCB collections are poorly preserved and therefore very little informative.

MSCB 25197 (fig. 3A) is the best preserved of the specimens, being represented by the anterior portion of the carapace and plastron. However, skeletal elements are partially deformed and their surface altered, so that the sulci are only partly visible. The dorsoventral compression significantly alters the convexity of the carapace. The alternance of the costals is well visible on the right side of the carapace, where the third costal has a ventral edge distinctly narrower than those of the second and fourth. Worth noting is that the entoplastron is not as roundish as in IPS 57549 and has a pointed anterior edge. The humero-pectoral sulcus coincides with the posterior edge of the entoplastron. The shell is filled with matrix and therefore the morphology of the visceral surface of the anterior region of the plastron is not visible.

MSCB 28193 preserves only the right part of a shell with the exception of the gular area, where both the epiplastra are present. A variably thick concretion masks most of the external and internal surfaces except for that of the anterior part of the plastron, which is markedly bent in dorsal direction. The epiplastral pads are developed in a way similar to that of IPS 57549, although they are less thick and their posterior edge is slightly less convex in dorsal view (fig. 4A). Such difference could be likely related to the smaller size of this specimen (the estimated size of the plastron is of about 16 cm). There is no step corresponding to the gular-humeral sulcus (the epiplastral surface covered by the gulars is not significantly convex relative to the uncovered surface).

MSCB 28194 is a small carapace portion preserving only some neural and costal elements of the posterior and left lateral region. The whole ventral surface is covered by matrix. The formula of the preserved neurals appears to be 8-4-6-6. The last of these neurals could be the seventh. The costals show the typical alternation. The position of the vertebral-pleural sulci indicates that the vertebral scutes were narrower than the pleural ones.

MSCB 28195 is a partially preserved shell, missing the dorsal portion of the carapace and the posterior region of both the carapace and plastron. The alteration of most of the surface hinders the evaluation of the morphology of sutures and scute sulci. The visceral surfaces of what remains of the carapace and of the plastron are not visible due to the matrix filling the shell cavity. The xiphiplastra are missing, but on the basis of the suture of the hypoplastra, it is possible to state that there was no hinge. The pectoro-abdominal sulcus is only a little convex (in anterior direction). The abdomino-femoral sulcus is deeply arched anterolaterally and does not reach the hyo-xiphiplastral suture medially.

Discussion

Nomenclatural remarks

Almera and Bofill (1903) named the new species from Cova de Gràcia *Testudo lunellensis* in order to underline its striking similarities with an unnamed species from the Middle Pleistocene (0.30 to 0.34 Ma) of Lunel-Viel (Hérault, France) already figured by Gervais (1859; plate 53, fig. 3), who dubiously referred it to *Testudo hermanni* (at that time named *T. graeca*). Actually, Almera and Bofill (1903) did not see the diagnostic characters of the Cova de Gràcia tortoise (which are present on the dorsal/visceral surface of the plastron) in the plastron from Lunel-Viel depicted in ventral view, and apparently made a connection between the tortoises from Cova de Gràcia and Lunel-Viel only on the basis of the geometric relationships between the entoplastron and the humero-pectoral sulcus (which is quite variable in *T. lunellensis*, compare fig. 3A with 4C). Ironically, the material from Lunel-Viel is now considered as belonging to a new taxon that still has to be named and diagnosed (Lapparent de Broin et al., 2006; Lapparent de Broin, Bour and Perälä, 2006a,b) and therefore the name *T. lunellensis* is currently associated to a form that did not inhabit the Lunel-Viel area. According to the character matrix for the cladistic analysis published by Lapparent de Broin, Bour and Perälä (2006b), the Lunel-Viel *Testudo* differs from *Testudo hermanni* (both *T. h. hermanni* and *T. h. boettgeri*, which were considered in that paper as different species, but whose character coding was identical) for just one character: the neurals were in number of eight in the Lunel-Viel species but are sometimes reduced to seven by fusion of the last two posterior most elements in *T. hermanni*. Worth noting is that such a subtle difference of the Lunel-Viel *Testudo*, if not supported by other, more diagnostic characters, would probably not suffice to solidly diagnose an extinct species different from the extant *T. hermanni.*

Morphological remarks

Contrary to the reports by Almera and Bofill (1903: 455; “el espaldar es notable por su convexidad relativamente poco acentuada y por su anchura”) and by Bergounioux (1958: 207; “carapace relativement peu convexe”) the shell of *Testudo lunellensis* is vaulted and not depressed. The depressed shape of some specimens is clearly due to deformation (particularly MGB MGC 2083, but also MSCB 25197), because the shape of a relatively undeformed carapace (IPS 57549; fig. 1A) is distinctly vaulted thanks to the development of the peripheral elements, a character already noted by Almera and Bofill (1903).

Conversely, it is not clear why Bergounioux (1958) wrote that the neural elements of *T. lunellensis* are hexagonal. *Testudo* species are characterized by the alternation of octagonal and rectangular neurals. Even though some variation occurs in the neural formula—e.g., *T. h. hermanni* NHMW 13246:1 = 4-7-4-6A-6A-6-6A-6; *T. h. hermanni* NHMW 13246:2 = 6P-6P-4-8-4-6A-6A-6; *T. h. boettgeri* NHMW 34392 = 4-8-4-6A-6A-6A-5-6—and some hexagonal elements can be present mostly in the posterior sector of the carapace (Amiranashvili, 2000, reports 4-8-4-8-4-6-6-6 and 4-8-4-6-6-6-6-6 in *T. h. boettgeri*), the specimens of *T. lunellensis* IPS 57549 and MSCB 25197 clearly have at least one octagonal neural (see fig. 2A).

As in extant *T. hermanni* (see, among others, Cheylan, 1981; Amiranashvili, 2000; Hervet, 2000), sexual dimorphism of *T. lunellensis* is expressed in both the pygal and xiphiplastra. According to Gómez-Alba Ruiz (1997), MGB MGC 6101 and MGB MGC 20642 are males, whereas MGB MGC 20838, MGB MGC 33122, MGB MGC 33123, and MGB MGC 33126 are females. Such distinction has been based on the shape of the pygal, which is more convex in males (MGB MGC 6101) than in females (MGB MGC 20838, MGB MGC 33123, MGB MGC 33126), as well as on the fact that xiphyplastra are generally shorter in males (both MGB MGC 6101 and

MGB MGC 20642) than in females (MGB MGC 33122) (see fig. 2B for the male and fig. 3B for the female morphology).

Taxonomic remarks

Some scholars (Gómez-Alba Ruiz, 1997, and Morales Pérez and Serra, 2009, following Jimenez Fuentes and De Jesus, 1991) referred the Cova de Gràcia tortoise to *Testudo hermanni*, distinguishing it only at subspecies rank, i.e. *Testudo hermanni lunellensis*. Even if *Testudo lunellensis* clearly shows many characters in common with *T. hermanni* (narrowing of the vertebral scutes, supracaudal scutes divided at least externally, triangular entoplastron in ventral view, relatively well-developed xiphoid process, shape and position of the abdomino-femoral sculcus, presence of hypo-xiphyplastral suture) such taxonomic framing is discouraged here, because the referral of the Cova de Gràcia tortoise to a subspecies of *Testudo hermanni* would contrast with the definition of the morphological boundaries between the extant *Testudo* species. In particular, the morphology of the epiplastra (namely the development of the epiplastral pads and their pocket) clearly distinguishes extant *T. hermanni* from that of other *Testudo* species (among others, Cheylan, 1981; Amiranashvili, 2000; Hervet, 2000; Delfino, Chesi and Fritz, 2009) and the development of the epiplastra and hyoplastra in *T. lunellensis* definitely exceeds the variability of *T. hermanni*, being close to that of *T. graeca* and *T. marginata* (see Appendix 1 for the list of comparative material analyzed for this study). The inclusion of *T. lunellensis* in *T. hermanni* at subspecific rank would require a general redefinition of the diagnostic characters of all the extant *Testudo* species. Conversely, its full specific status is congruent with the mosaic distribution of morphological characters found among *Testudo* species, as summarized in detail by Lapparent de Broin, Bour and Perälä (2006a,b).

It is worth mentioning that, according to both Almera and Bofill (1903) and Bergounioux (1958), two taxa would be recorded in the Cova de Gràcia assemblage. Beside *Testudo lunellensis*, these authors discussed the presence of a second tortoise taxon somehow related to *Testudo graeca* (at that time named *Testudo ibera* Pallas, 1814; this name is currently applied to the subspecies

Testudo graeca ibera). The former authors considered it as a variety of *Testudo graeca*, whereas the latter author erected a new variety within *T. lunellensis*: *T. lunellensis* var. *ibera*. According to Almera and Bofill (1903), the form from Cova de Gràcia would be larger than the extant *T. graeca* but similar to it in the following characters: shape of the entoplastron, anal scute, and abdomino-femoral sulcus (only weakly arched laterally). These authors did not mention any catalogue number and did not figure the referred specimens. Bergounioux (1958: 208) stated that the second taxon from Cova de Gràcia was similar to *T. lunellensis*, but agreed with Almera and Bofill (1903) that it also showed some similarities with *T. graeca*, “faisant le passage progressif” with the latter. Hence, Bergounioux (1958) referred two specimens, MGB MGC 20839 (20639 in his paper; see also Gómez-Alba Ruiz, 1997, for corrections to Bergounioux’s numbers) and MGB MGC 6110, to *Testudo lunellensis* var. *ibera* (as remarked by Auffenberg, 1974, *Testudo lunellensis* var. *ibera*. is not a subspecies but just the designation of a morphotype). Regarding its taxonomic validity, according to Bergounioux, who published an interpretative drawing of both specimens (Bergounioux, 1958; figs 29 and 30), the main purported distinguishing characters of this nominal taxon would be the subcircular entoplastron, and the plastron anteriorly truncated and posteriorly only weakly notched. Direct observation of MGB MGC 20839 (fig. 4B,C) indicates that the posterior tip of the plastron is actually missing, and that therefore the morphology of the anal notch cannot be evaluated (the drawing published by Bergounioux is actually based on the shape of the counter slab, which is not present anymore, but it is highly improbable that the original shape was the one depicted). The characters shown by MGB MGC 20839 and 6110 are here considered as comprised in the variability of *T. lunellensis* and therefore just one tortoise taxon in considered present in the Cova de Gràcia fossil assemblage.

Phylogenetic remarks

According to Bergounioux (1935), *T. lunellensis* belongs to the *T. antiqua-graeca* phyletic line (sensu Glaessner, 1933). In fact, as discussed above, he later considered the variety *Testudo lunellensis* var. *ibera* as an intermediate form between *Testudo lunellensis* and *T. graeca*

(Bergounioux, 1958).

As clearly shown by Lapparent de Broin et al. (2006) and Lapparent de Broin, Bour and Perälä (2006a,b), *T. lunellensis* is actually closer to *T. hermanni* than to any other living *Testudo* species (and *Testudo antiqua* Bronn, 1831 belongs to the clade of *T. hermanni*): they share the narrowing of the vertebral scutes. It is noteworthy that the pectoral scutes of *T. lunellensis* are medially shorter than the femoral scutes, a proportion typical of the extant western subspecies, *T. h. hermanni*, and not of the eastern one, *T. h. boettgeri*. In the phylogenetic analysis by Lapparent de Broin, Bour and Perälä (2006a,b), the character coding of *T. lunellensis* differs from that of *T. hermanni* (again, *T. h. hermanni* and *T. h. boettgeri*) for three characters concerning the shape of the suprapygals, pygal, and the epiplastra in the area covered by the gulars. As seen above, more characters could be now considered for *T. lunellensis* (see Diagnosis) for the phylogenetic analysis of the whole *Testudo* clade. Given that the purported valid species from Lunel-Viel (Middle Pleistocene, France) is still unnamed and undescribed, *T. lunellensis* from Cova de Gràcia is currently the stratigraphically youngest extinct member of *Testudo* (including all the extant living species: *T. graeca*, *T. hermanni*, *T. horsfieldi*, *T. kleinmanni* Lortet, 1883 and *T. marginata*). Remarkably, the co-occurrence in the youngest extinct *Testudo* species of characters typical of both *T. hermanni* and of the members of the *Testudo* s.s. group (*T. graeca*, *T. kleinmanni* and *T. marginata*) further testifies the phenotypic plasticity of tortoises and the mosaic distribution of morphological characters that hinders a clear-cut evaluation of the relationships of the *Testudo* species when based exclusively on morphology (for extant *T. graeca* see Fritz et al., 2007). A cladistic analysis based on the morphological characters of Lapparent de Broin et al. (2006) and Lapparent de Broin, Bour and Perälä (2006a,b) is not performed here due to the contrasting results of the genetic analyses by Fritz and Bininda-Emonds (2007) that impose a deep renovation of the matrix based on morphological characters. A thorough analysis of the phylogeny of *Testudo* should consider fossil and extant taxa together, as well as both morphological and genetic characters, as already attempted for other reptilian taxa (e.g., Conrad et al., 2010).

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Appendix 1. Comparative extant specimens examined.

Testudo graeca: NHMW 1236: 1+2, NHMW 28293, NHMW 34354, NHMW 34356, NHMW 37686, NHMW 39096.

Testudo hermanni: NHMW 35605, NHMW 13246:1, NHMW 13246:2, NHMW 34392, NHMW 37898, NHMW 37903, NHMW 37967, NHMW 38614, NHMW 37663.

Testudo horsfieldi: MTD D 3568, MTD D 7679

Testudo kleinmanni: MTD D 26762, MTD D 32832, MTD D 35692, MTD D 38650, MTD D 39221, MTD D 40289, MTD D 44284, MTD D 44285.

Testudo marginata: NHMW 33441, NHMW 33442, NHMW 33443, NHMW 33460, NHMW 33461, NHMW 34244, NHMW 34253, NHMW 34254, NHMW 37154, NHMW 37081, NHMW 38021, NHMW 39095.

Figure legends

Figure 1. *Testudo lunellensis* Almera and Bofill, 1903 from Cova de Gràcia (Barcelona, Spain). **A**, carapace IPS 57549 in right lateral view, showing the high peripherals. **B–E**, plastron of the same specimen, **B**, ventral, **C**, dorsal (detail of the anterior lobe), **D**, anterior, **E**, right lateral. Note that the anterior lobe is dorsally bent and that the epiplastral pads are well developed, with an overhanging convex posterodorsal edge that forms a moderate gular pocket. Scale bar equals 10 cm. [planned for page width]

Figure 2. *Testudo lunellensis* Almera and Bofill 1903 from Cova de Gràcia (Barcelona, Spain). Reconstruction of the shell based on the information provided by the available material. **A-C**, shell in dorsal, ventral, and lateral views; **C,** anterior lobe of the plastron in dorsal view. Note that variability is not represented in this drawing (in particular those of the relationships between the humero-pectoral sulcus and the entoplastron, as well as the configuration of the suprapygal area). [planned for page width]

Figure 3. *Testudo lunellensis* Almera and Bofill 1903 from Cova de Gràcia (Barcelona, Spain). **A**, anterior lobe of the plastron MSCB 25197, showing the relationships between the humero-pectoral sulcus and the entoplastron; **B**, posterior lobe of the plastron MGB MGC 33122 in ventral view, showing the female morphology of the xiphiplastra. Scale bar equals 10 mm. [planned for column width]

Figure 4. *Testudo lunellensis* Almera and Bofill, 1903 from Cova de Gràcia (Barcelona, Spain). **A,B**, anterior lobe of the plastron in dorsal view, showing the thick epiplastral pads variably developed in posterior direction, **A**, MSCB 28193, **B**, MGB MGC 20839. Note that the anterior profile of the lobe is not truncated as in IPS 57549. **C**, ventral view of the anterior lobe of the plastron MGB MGC 20839 with the surface of the epiplastra characterized by a depression (a

character particularly well-developed in this large size specimen, but also present in others). Scale bars equal 10 mm. [planned for column width]

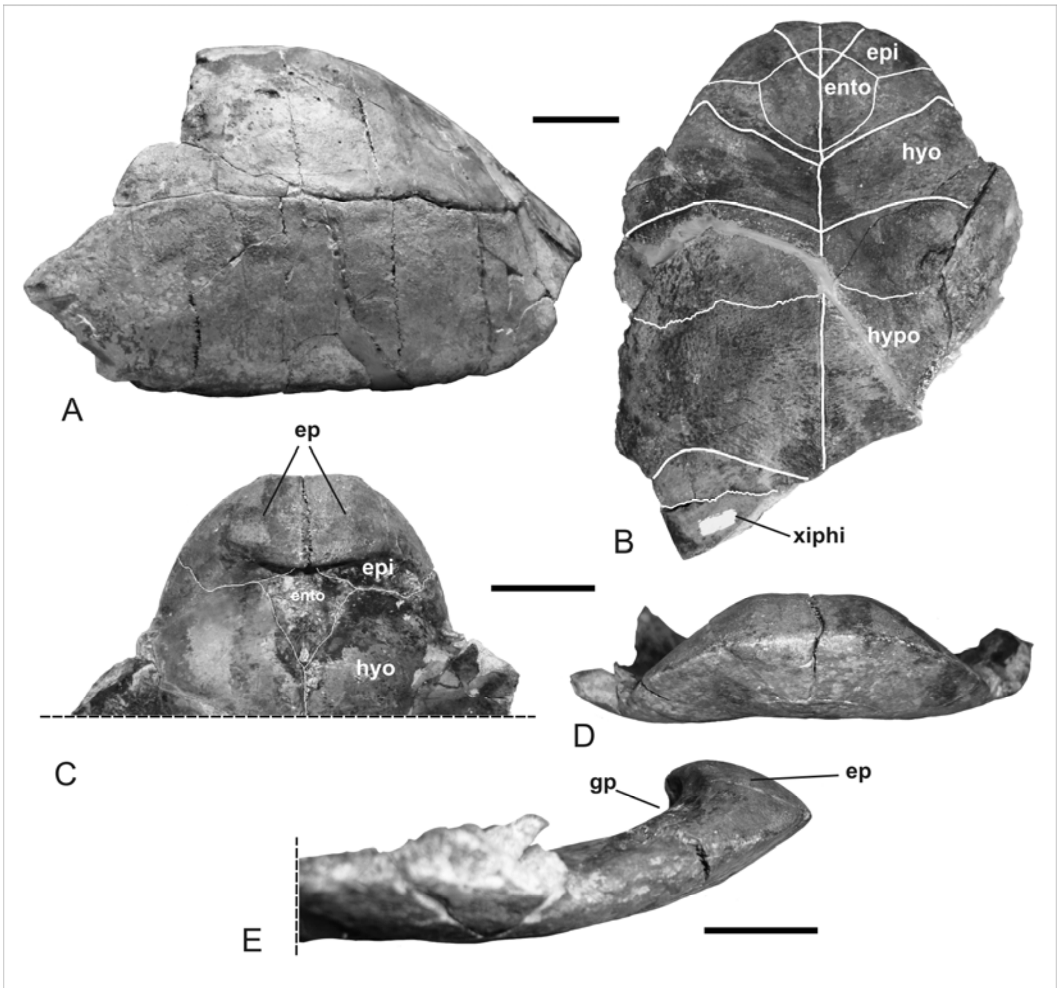

Fig. 1

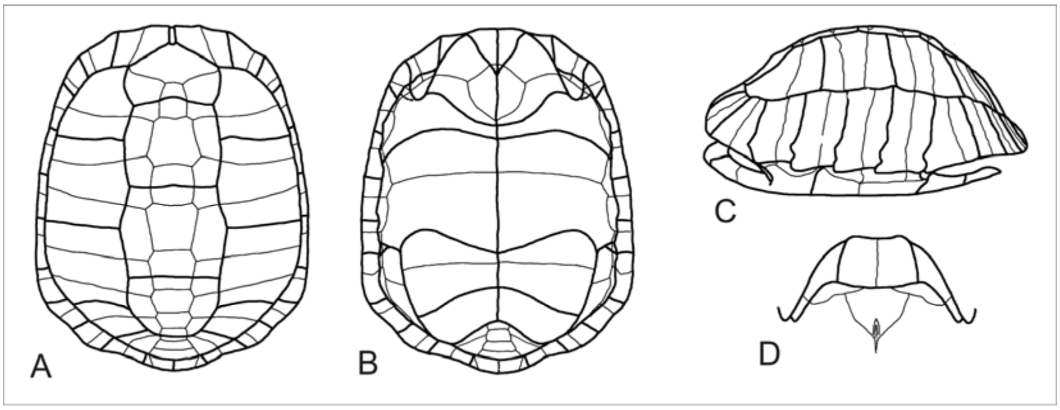

Fig. 2

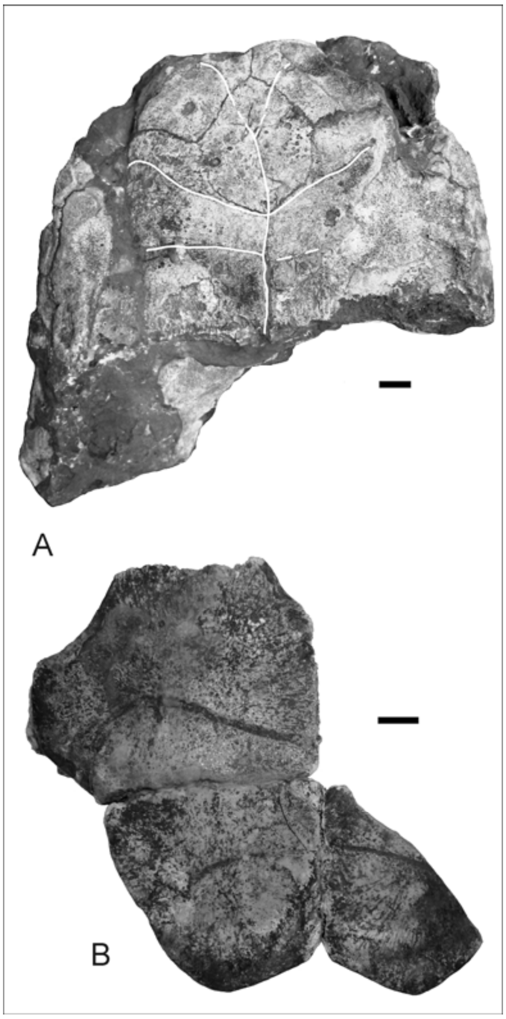

Fig. 3

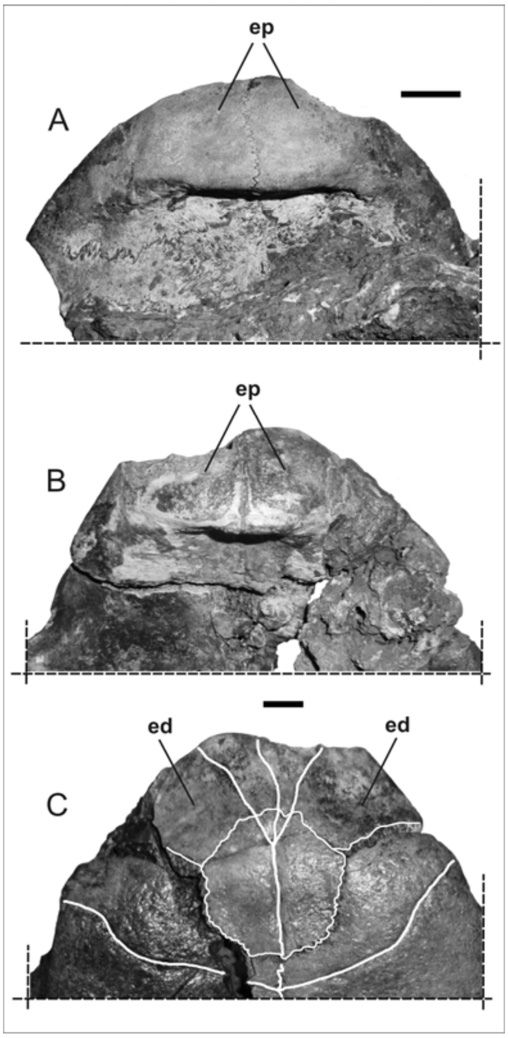

Fig. 4