



**First authentic record of the freshwater turtle *Mauremys*
from the Upper Pliocene of Italy, with a new occurrence
of the rarely reported ichnotaxon *Thatchtelithichnus holmani***

Alberto COLLARETA^{1, 2}

Simone CASATI^{3, 4}

Marco Alberto Luca ZUFFI^{2, 5}

Andrea DI CENCIO^{3, 6}

Abstract: Nowadays, the living species of the terrapin genus *Mauremys* (Testudinoidea: Geoemydidae) are mostly found in eastern Asia, but three of them inhabit the Western Palearctic ecozone. In Italy, occurrences of living individuals of *Mauremys* are interpreted as records of alien species; however, a growing fossil record demonstrates that this genus has inhabited Italy as recently as the Late Pleistocene. We report on a new fossil specimen of *Mauremys* from the Upper Pliocene (Piacenzian) marginal-marine deposits of Tuscany (central Italy). This find, consisting of a partial plastron and a loose neural, represents the second authentic report of *Mauremys* from the Italian Pliocene, as well as the first one from the Piacenzian of Italy. Therefore, it is a significant fossil that fills a gap in the chronostratigraphic distribution of Italian fossil *Mauremys*, helping – together with the Lower Pliocene holotype of *Mauremys portisi* – to bridge the rich Miocene and Pleistocene segments of this record. Moreover, two unusual scars observed on the external surface of the studied plastron are here referred to the ichnospecies *Thatchtelithichnus holmani*. These traces represent one of the few records worldwide of this rarely identified ichnospecies, as well as its geologically youngest published occurrence. Hypotheses regarding the origin of the *Thatchtelithichnus* traces are reevaluated, and an origin as attachment scars of aquatic ectoparasites (possibly ticks, leeches, or flukes) is reaffirmed as probable in cases of traces occurring on the exterior of the plastral bones of turtles.

Key-words:

- Geoemydidae;
- terrapin;
- turtle shell;
- parasitism;
- Piacenzian;
- Tuscany;
- palaeoherpetology;
- ichnology

Citation: COLLARETA A., CASATI S., ZUFFI M.A.L. & DI CENCIO A. (2020).- First authentic record of the freshwater turtle *Mauremys* from the Upper Pliocene of Italy, with a new occurrence of the rarely reported ichnotaxon *Thatchtelithichnus holmani*.- *Carnets Geol.*, Madrid, vol. 20, no. 16, p. 301-313.

¹ Dipartimento di Scienze della Terra, Università di Pisa, via Santa Maria 53, 56126 Pisa (Italy)

alberto.collareta@unipi.it

² Museo di Storia Naturale, Università di Pisa, via Roma 79, 56011 Calci (Italy)

³ Gruppo Avis Mineralogia e Paleontologia Scandicci, p.za Vittorio Veneto 1, Badia a Settimo, 50018 Scandicci (Italy)

⁴ simonecasati@alice.it

⁵ marco.zuffi@unipi.it

⁶ Studio Tecnico Geologia e Paleontologia, via F.lli Rosselli 4, S. Casciano Val di Pesa, 50026 Firenze (Italy)

andreadicencio@geologiaepaleontologia.eu





Résumé : Première découverte attestée de la tortue d'eau douce *Mauremys* dans le Pliocène supérieur d'Italie, avec un nouveau signalement de *Thatchtelithichnus holmani*, un ichno-taxon rarement mentionné. - De nos jours, les espèces du genre de tortues d'eau douce *Mauremys* (Testudinoidea : Geoemydidae) vivent principalement en Asie orientale, mais trois d'entre elles habitent l'écozone paléarctique occidentale. En Italie, les découvertes d'individus vivants de *Mauremys* sont interprétées comme des signalements d'espèces étrangères ; cependant, un nombre croissant de fossiles montre que ce genre était présent en Italie dès le Pléistocène supérieur. Nous signalons un nouveau spécimen fossile de *Mauremys* provenant de dépôts marginaux marins du Pliocène supérieur (Plaisancien) de Toscane (Italie centrale). Cette découverte, comprenant un plastron partiel et une neurale désarticulée, représente le second signalement confirmé de *Mauremys* dans le Pliocène italien et le premier dans le Plaisancien d'Italie. Ainsi, ce spécimen représente un fossile significatif puisque, avec l'holotype zanzibien de *Mauremys portisi*, il comble la lacune entre les segments miocène et pléistocène dans la distribution chronostratigraphique des fossiles italiens de *Mauremys*. En outre, deux cicatrices insolites observées sur la surface externe du plastron étudié sont attribuées ici à l'ichno-espèce *Thatchtelithichnus holmani*. Il s'agit d'un des rares signalements de cette ichno-espèce à l'échelle planétaire et aussi de son occurrence stratigraphique la plus jeune. Les hypothèses concernant l'origine des traces de type *Thatchtelithichnus* sont reconsidérées à la lumière de notre découverte et leur interprétation en tant que traces cicatricielles d'attachement d'ectoparasites aquatiques (probablement des tiques, des sangsues ou des douves) est réaffirmée comme probable dans le cas de traces situées sur la face externe des plaques plastrales des tortues.

Mots-clefs :

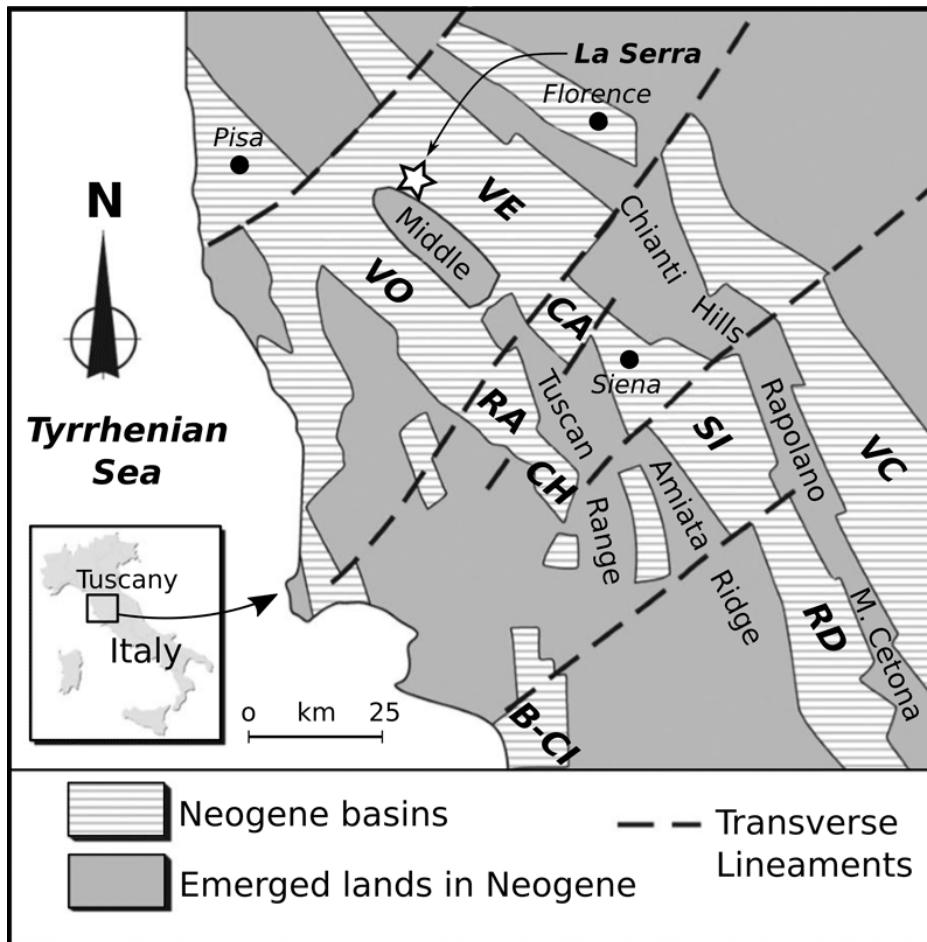
- Geoemydidae ;
- terrapène ;
- carapace de tortue ;
- parasitisme ;
- Plaisancien ;
- Toscane ;
- paléoherpétologie ;
- ichnologie

1. Introduction

The extant terrapin genus *Mauremys* belongs to Geoemydidae, a family of testudinoid cryptodirans consisting of approximately 60 species in 25 genera (BARTH *et al.*, 2004). Currently, the living species of *Mauremys* exhibit a strongly disjunct distribution; they are mostly found in eastern Asia, but three of them – *Mauremys caspica*, *Mauremys leprosa*, and *Mauremys rivulata* – are distributed in the Western Palearctic ecozone. Two of these species, *M. leprosa* and *M. rivulata*, are found along the coasts of the Mediterranean Sea, the former in western North Africa (Morocco to western Libya) and the Iberian Peninsula (KELLER & BUSACK, 2001), and the latter along the Mediterranean coast of the Balkan Peninsula, on several islands of the Eastern Mediterranean, in the coastal regions of western and southern Turkey, and along the Levantine coast (BARTH *et al.*, 2004). In Italy, where the only native freshwater turtles are *Emys orbicularis* and *Emys trinacris*, discoveries of living individuals of *Mauremys* are interpreted as records of alien species (PANZERI *et al.*, 2014). However, a growing fossil record demonstrates that terrapins of the genus *Mauremys* have inhabited Italy as recently as the Late Pleistocene (CHESI *et al.*, 2007) and the Italian Peninsula might even have been the route of a dispersal of *Mauremys* from the Mediterranean into the North African and Arabian domains in Late Miocene times (CHESI *et al.*, 2009; GEORGALIS *et al.*, 2020).

The currently monotypic ichnogenus *Thatchtelithichnus* was erected by ZONNEVELD *et al.* (2015) for circular to subcircular, ring-shaped grooves incised on the external surface of plastral bones of geoemydid turtles from the Eocene of Wyoming, USA. These traces were originally interpreted as the attachment scars of aquatic ectoparasites (possibly ticks, leeches, or spirorchid liver flukes) that infected the turtle while the latter was still living (ZONNEVELD *et al.*, 2015). More recently, WISSHAK *et al.* (2019) reinterpreted *Thatchtelithichnus* as a bioclastration structure and, as such, not a valid ichnotaxon. Later, ZONNEVELD and BARTELS (2020) provided new arguments in support of both the origin of *Thatchtelithichnus* by emplacement of ectoparasites and its ichnotaxonomic validity. In spite of their highly idiosyncratic aspect, to date, *Thatchtelithichnus* traces have only been reported by ZONNEVELD *et al.* (2015) and ZONNEVELD and BARTELS (2020).

In the present work, we report on a new fossil record of *Mauremys* from the famous fossiliferous Pliocene deposits of the Valdelsa Basin (Tuscany, Italy), which has previously yielded significant remains of continental and marine vertebrates (e.g., AZZAROLI, 1992; ABBAZZI *et al.*, 2008; DOMINICI *et al.*, 2018; COLLARETA *et al.*, 2020). This new specimen is here described and illustrated, and its palaeontological implications are discussed in the broader framework of the Italian fossil record of *Mauremys*. Furthermore, two unusual traces observed on this specimen are here characterised and referred to the only ichnospecies that is currently included in *Thatchtelithichnus*, i.e., *Thatchtelithichnus holmani*. This record is also discussed and its palaeobehavioural significance is evaluated.



◀ **Figure 1:** Location of La Serra, where the fossil terrapin described herein was found (white star), and schematic regional geological map. B-CI = Baccinello-Cinigiano Basin; CA = Casino Basin; RD = Radicofani Basin; SI = Siena Basin; VC = Val di Chiana Basin; VE = Valdelsa Basin; VO-RA-CH = Volterra-Radicondoli-Chiusdino basins. After COLLARETA *et al.* (in press).

2. Geological and palaeontological framework

The fossil terrapin described herein was discovered by three of us (A.C., S.C. and A.D.C.) at an active quarry at La Serra village near San Miniato (Pisa Province, Tuscany, central Italy) (Fig. 1). The GPS geographic coordinates of this quarry are 43° 39' 28" N; 10° 48' 57" E. La Serra quarry lies at the northwestern corner of the Valdelsa Basin, a 25 × 60 km, NW-SE elongated extensional basin filled with some 1000 m of Upper Neogene and Quaternary deposits (BENVENUTI *et al.*, 2014). The sedimentary succession exposed at this site has been referred by DOMINICI *et al.* (2018) to the S6 Synthem recognised in the Valdelsa Basin by BENVENUTI *et al.* (2014). The S6 Synthem is a large-scale depositional sequence that consists mostly of fluvial coarse-grained sandstones, intertidal or coastal lagoon deposits, and shoreface and delta-front sandstones (BENVENUTI *et al.*, 2014). At La Serra quarry, a 25-m-thick stratigraphic section was measured by GARASSINO *et al.* (2012), who recognised the following informal units:

- "Unit 1" (from the base of the section to 8 m above it). This unit consists of mixed sand and silt, cross-stratified sand, and massive clay. "Unit 1" was interpreted by GARASSINO *et al.* (2012) as representing an estuarine or deltaic environment with interspersed marshes and ponds.
- "Unit 2" (from 8 to 14 m). This is a thick sand body. According to GARASSINO *et al.* (2012), it testifies to a barrier island environment, where both submarine longshore dunes and subaerial aeolian dunes were active.
- "Unit 3" (from 14 to 19.5 m). This unit consists of intercalated silt and clay. "Unit 3" was referred by GARASSINO *et al.* (2012) to a sheltered lagoon depositional setting.
- "Unit 4" (from 19.5 m to the top of the section at ~25 m). This unit consists of highly fossiliferous clayey sand (including an exceptionally rich decapod assemblage, as well as almost ubiquitous molluscs and rarer dental and dermal remains of elasmobranch cartilaginous fishes; COLLARETA *et al.*, in press). It was interpreted by GARASSINO *et al.* (2012) as a shallowing-upward deposit that formed in a low-energy, shallow-marine palaeoenvironment across offshore transition and lower-shoreface settings.

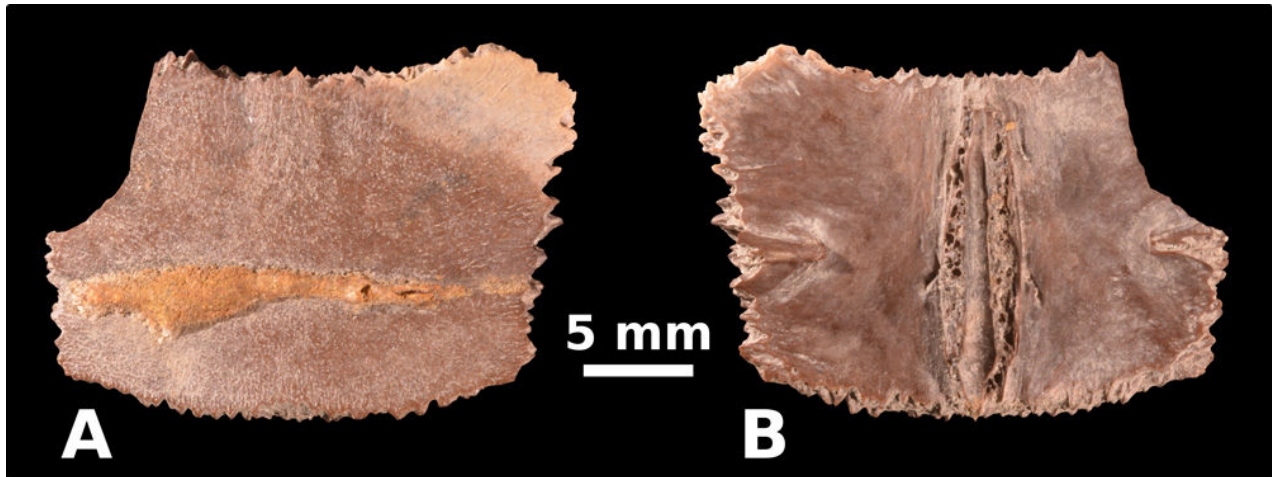


Figure 2: GAMPS-00925, *Mauremys* sp. from the Upper Pliocene of La Serra (Tuscany, central Italy), posterior neural plate in A) dorsal (external) and B) ventral (visceral) views.

GARASSINO *et al.* (2012) reported that fossils of continental vertebrates (*i.e.*, indeterminate remains of cervids and turtles) occur in "Unit 2" ~10 m above the base of their stratigraphic log, in a bed that also features abundant woody remains. The terrapin fossil described herein instead came from a bed of deltaic/estuarine sands of "Unit 1" ~7 m above the base of the section measured by GARASSINO *et al.* (2012).

On the basis of sparse data on the ostracod and calcareous nannoplankton content of some samples, GARASSINO *et al.* (2012) regarded the sediments of La Serra quarry as not younger than the Early Pliocene (*i.e.*, Zanclean) in age. More recently, building upon basin-wide correlations, biochronological considerations, and biostratigraphic analyses on several outcrops from throughout the Valdelsa successions, BENVENUTI *et al.* (2014) and DOMINICI *et al.* (2018) referred the S6 Synthem to the upper Piacenzian-lower Gelasian – an interpretation supported by the Piacenzian age of the underlying S5 Synthem, as well as by the detection of the Gauss-Matuyama reversal at Montopoli, some 6 km north of La Serra (LINDSAY *et al.*, 1980). In particular, DOMINICI *et al.* (2018) assigned a latest Piacenzian age to the invertebrate accumulation observed in the "Unit 4" deposits exposed at La Serra. Considering that the latter is stratigraphically higher than "Unit 2", a late Piacenzian age can be inferred for the terrapin fossil described herein.

From a palaeontological point of view, besides a rich record of marine vertebrates (*e.g.*, CAPELLINI, 1905; BIANUCCI, 1996; DANISE & DOMINICI, 2014; COLLARETA *et al.*, 2016, 2017, 2020; DOMINICI *et al.*, 2018; COLLARETA, 2020), remains of continental vertebrates have been abundantly documented from the Pliocene deposits of the Valdelsa Basin (AZZAROLI, 1992; BENVENUTI & DOMINICI, 1992; DOMINICI, 1994; BENVENUTI *et al.*, 1995a, 1995b, 2007; DOMINICI *et al.*, 1995; RUSTIONI & MAZZA, 2001; ABBAZZI *et al.*, 2008). These fossils have mostly been referred to the Triversa and Montopoli Faunal Units, which correspond to the

Upper Pliocene-lowermost Pleistocene Mammal Neogene (=MN) zones 16a and 16b (*e.g.*, ESU & CIANGHEROTTI, 2004).

3. Systematic palaeontology

TESTUDINES BATSCH, 1788

CRYPTODIRA COPE, 1868

TESTUDINOIDEA GRAY, 1825

GEOEMYDIDAE THEOBALD, 1868

***Mauremys* GRAY, 1869**

Type species. *Emys fuliginosus* GRAY, 1860

***Mauremys* sp.**

(Figs. 2 - 4)

Referred material and repository. One loose neural plate and one partial plastron, thought to originate from the same individual, currently kept at Badia a Settimo (Scandicci, Italy) in the permanent exhibition of "Gruppo AVIS Mineralogia e Paleontologia Scandicci" (=GAMPS) under accession number GAMPS-00925.

Occurrence. Upper Pliocene (upper Piacenzian) dune sand exposed at La Serra, Pisa Province, Tuscany, central Italy.

Descriptive remarks. Among several minute carapace bone fragments, a single element was determined anatomically thanks to its significant completeness degree. This element (Fig. 2) consists of a bony plate that lacks its left anterolateral corner. It is hexagonal in outline and displays a short anterolateral margin. It is significantly wider than long (estimated maximum transverse width: 25 mm; maximum anteroposterior length: 18 mm), with a slightly concave anterior margin that is slightly shorter than the slightly convex posterior margin. The dorsal surface of the plate is gently convex upwards; on its anterior half, it shows traces of a sagittal keel, whereas a near-straight epidermal sulcus, mostly lined by indurated sediment, extends transversely at about one



third of the anteroposterior length of the plate (measured from its posterior margin). Viscerally, remains of the attachments of the thoracic vertebrae are clearly observable. The plate exhibits its minimum dorsoventral thickness (about 1.5 mm) at its periphery, whereas it significantly thickens sagittally. Based on its general morphology, as well as on the observation of remains of the attachments of the thoracic vertebrae, this carapace element is interpreted as a neural plate. This disjunct neural is attributed to *Mauremys* on the basis of the co-occurrence of the following characters: plate hexagonal in outline, wider than long; anterolateral margins short; anterior and posterior margins anteriorly concave, displaying different lengths; and medial keel and sagittal thickening present (ERNST & BARBOUR, 1989; HERVET, 2000; LI *et al.*, 2015; GEORGALIS *et al.*, 2019). In light of the shape and proportions of this bone, which are strongly reminiscent of a mid-position neural plate, the epidermal sulcus that ornaments the dorsal surface might be interpreted as dividing the third vertebral scute (V3) from the fourth one (V4). In the extant species *Mauremys leprosa*, V3-V4 is observed on the fifth neural (Ne5), as is also the case for the extinct species *Mauremys massiliensis*, *Mauremys thaninensis*, *Mauremys campanii*, and *Mauremys gaudryi*, among others (HERVET, 2000, 2003; CLAUDE *et al.*, 2007; CHESI, 2009; CHESI *et al.*, 2009; VLACHOS *et al.*, 2019). Given these observations, the neural plate from La Serra is here interpreted as Ne5.

Some plastral bones were found in association with the aforementioned neural plate (Fig. 3). These include the slightly damaged left and right hypoplastra, as well as the substantially complete left and right xiphiplastra. Although disarticulated, these four bones can be easily recombined along their mutual sutures to reconstruct the original aspect of the middle and posterior portions of the plastron, whose ventral surface was almost perfectly flat. The anterior margin of the hypoplastra is only partially preserved, but it seems to have been more or less straight and transversely oriented; furthermore, its morphology demonstrates that a hyo-hypoplastral hinge was not present. The right hypoplastron is 48.5 mm long (measurement taken along the medial margin of the plate) and has a maximum transverse width of 42 mm posterior to the partly preserved inguinal process. The inguinal process occurs at about mid-length of the hypoplastron. Posterior to this level, the posterolateral margin of the hypoplastron is weakly bowed laterally. In ventral view, the abdominal-femoral sulcus crosses the hypoplastra horizontally in its median tract, whereas its distal portions are anterolaterally directed. The abdominal-femoral sulcus terminates just posterior to the inguinal process, where a strongly reduced, barely discernible inguinal notch occurs. The anterior margin of the xiphiplastra is gently bowed anteriorly and, in dorsal

view only, it displays an anteriorly convex tract close to the anterolateral corner of the bone. The right xiphiplastron exhibits a medial length of 32.5 mm and a transverse width of 40.5 mm. In ventral view, the lateral margins of the xiphiplastra distinctly converge backwards; they exhibit obvious, broad, fan-shaped notches in occurrence of the distal terminations of the femoral-anal sulcus. The latter consists of two near-straight, anteromedially projecting segments that meet each other sagittally – *i.e.*, on each xiphiplastron, the femoral-anal sulcus runs nearly perpendicular to the posterolateral margin of the bone. On the right xiphiplastron, the femoral-anal sulcus meets the medial margin of the plate 18 mm anterior to the apex of the anal notch. The latter is formed by the converging posterior margins of the xiphiplastra. The anal notch is narrow and deep, its apex being located 11 mm anterior to the level of the caudal terminations of the posterolateral processes of the constituent plates, which are rather sharply pointed backwards. Facing each other, the posterior margins of the xiphiplastra are slightly concave posteromedially and meet at an angle of about 90°. On the whole, the posterior lobe of the plastron is long and displays a distinctly rounded outline. The visceral view of the posterior lobe shows that the femoral and anal scutes covered the dorsomarginal portions of both the hypoplastra and xiphiplastra, as reflected by the presence of a ridged elevation that runs close to the outer margins of these plates. This elevation is posterior to the inguinal processes and extends all around the hypoplastra and xiphiplastra, to disappear only near the apex of the anal notch. The studied plastron belongs to the genus *Mauremys* on the basis of the following combination of characters: absence of a hyo-hypoplastral hinge; inguinal notch strongly reduced; posterior lobe long and well-rounded; femoral scutes overlapping the dorsomarginal portions of the hypoplastra; femoral-anal sulcus running nearly perpendicular to the lateral edge of the plate; lateral margins of the xiphiplastra distinctly converging posteromedially; anal scutes relatively short; and anal notch narrow and deep (ERNST & BARBOUR, 1989; HERVET, 2003, 2004; CLAUDE *et al.*, 2007; CHESI, 2009; CHESI *et al.*, 2009; GÓMEZ de SOLER *et al.*, 2012; LI *et al.*, 2015; VLACHOS *et al.*, 2015, 2019; VLACHOS & DELFINO, 2016).

Based on comparisons with extant specimens of *Mauremys* kept at the Museo di Storia Naturale dell'Università di Pisa, and considering the dimensions of the preserved plastral bones, a total carapace length of about 175 mm can be reconstructed for GAMPS-00925. Such a size is well within the range of values reported by ERNST & BARBOUR (1989) for the living species of *Mauremys*, as well as close to the typical carapace length of the adults of the extant Mediterranean species *M. leprosa* (160-200 mm according to HERVET, 2000). Attribution of GAMPS-00925 at species level is precluded by the fragmentary na-

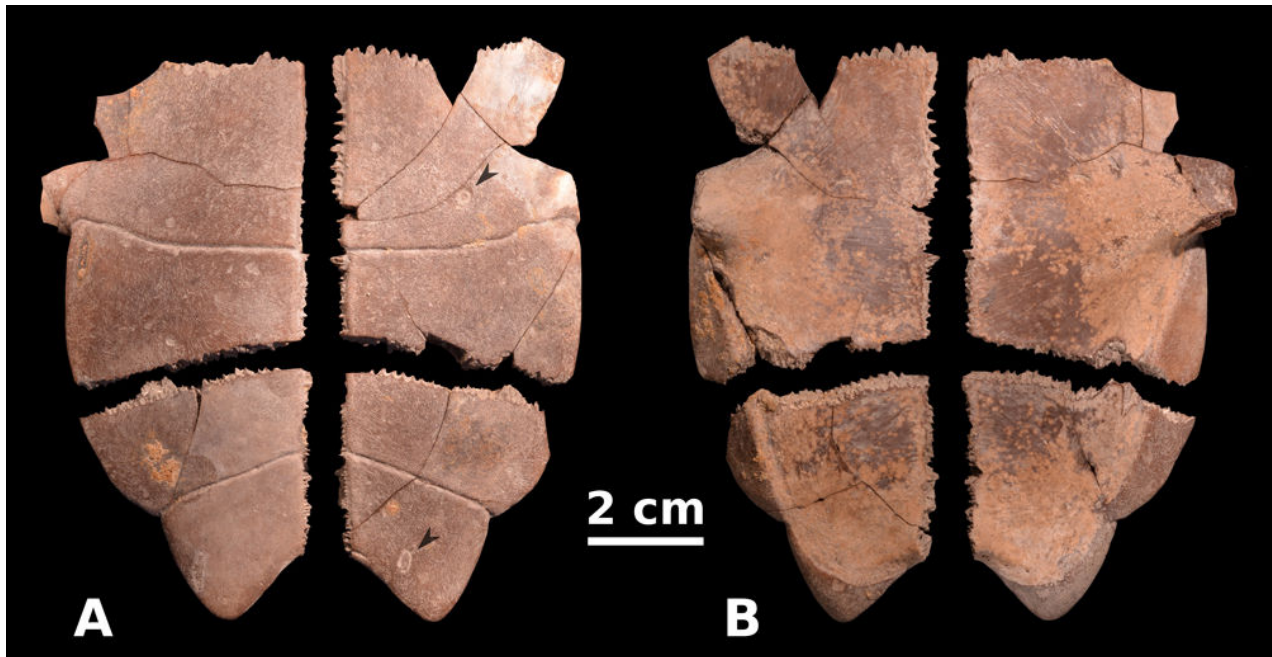


Figure 3: GAMPS-00925, *Mauremys* sp. from the Upper Pliocene of La Serra (Tuscany, central Italy), left and right hypoplastra and xiphiplastra in A) ventral (external) and B) dorsal (visceral) views. The arrowheads superimposed on panel A indicate the location of two *Thatchtelithichnus holmani* traces detailed in Figure 4.

ture of the studied material; nevertheless, this specimen can be distinguished from the extinct Italian species *Mauremys campanii*, *M. portisi*, and *M. etrusca*. In particular, it differs: i) from the Late Miocene *M. campanii* in the differing geometry of the abdominal-femoral sulcus, as well as by the more posterior position of the latter; ii) from the Early Pliocene *M. portisi* by the even more reduced inguinal notch; and iii) from the Early Pleistocene *M. etrusca* by the differing geometry of the abdominal-femoral sulcus, as well as by the more anterior position of the latter. In turn, the following features of the plastron establish the similarity of GAMPS-00925 to the extant *M. leprosa*: posterior lobe starting at the level of the distal terminations of the abdominal-femoral sulcus, at about mid-length of the hypoplastra; anal notch angular rather than rounded, depicting an angle of about 90°; and posterolateral processes of the xiphiplastra posteriorly pointed. The fossil record of *M. leprosa* begin in the Lower Pliocene, the oldest remains of this species being known from the Algerian locality of Ain Boucherit [LAPPARENT de BROIN, 2000; but see CHE-SI *et al.* (2009) for a revised chronostratigraphical attribution of these finds].

Ichnological observations. During examination of GAMPS-00925, two unusual scars were observed on the ventral surface of the left hypoplastron and xiphiplastron (Fig. 3.A). In the following section, these scars are briefly characterized.

Thatchtelithichnus
ZONNEVELD *et al.*, 2015

Type ichnospecies. *Thatchtelithichnus holmani* ZONNEVELD *et al.*, 2015

Thatchtelithichnus holmani
ZONNEVELD *et al.*, 2015

(Figs. 3.A, 4)

Descriptive remarks. The ichnogenus *Thatchtelithichnus* was diagnosed by ZONNEVELD *et al.* (2015) as follows: "Circular to subcircular grooves with a central boss or platform, bored into a bone substrate. Grooves penetrate into the cortical layer of the bone. The central platform may consist of an unmodified platform or a rounded nubbin. Boring walls rounded, convex or sharp and perpendicular to the external substrate surface". The diagnosis of *Thatchtelithichnus holmani*, the sole ichnospecies included therein, was provided by the same authors in these terms: "As for the ichnogenus. Non-penetrative borings into a bone substrate, having a ring-like profile, and a central raised boss or pedestal". These descriptions conform well to two scars observed on the plastral scales of GAMPS-00925. The first (Fig. 4.A) is found on the ventral surface of the left hypoplastron on the area that was originally covered by the abdominal scute. It consists of a very shallow, circular depression, measuring ~3 mm in diameter, hosting at its centre a raised, rounded

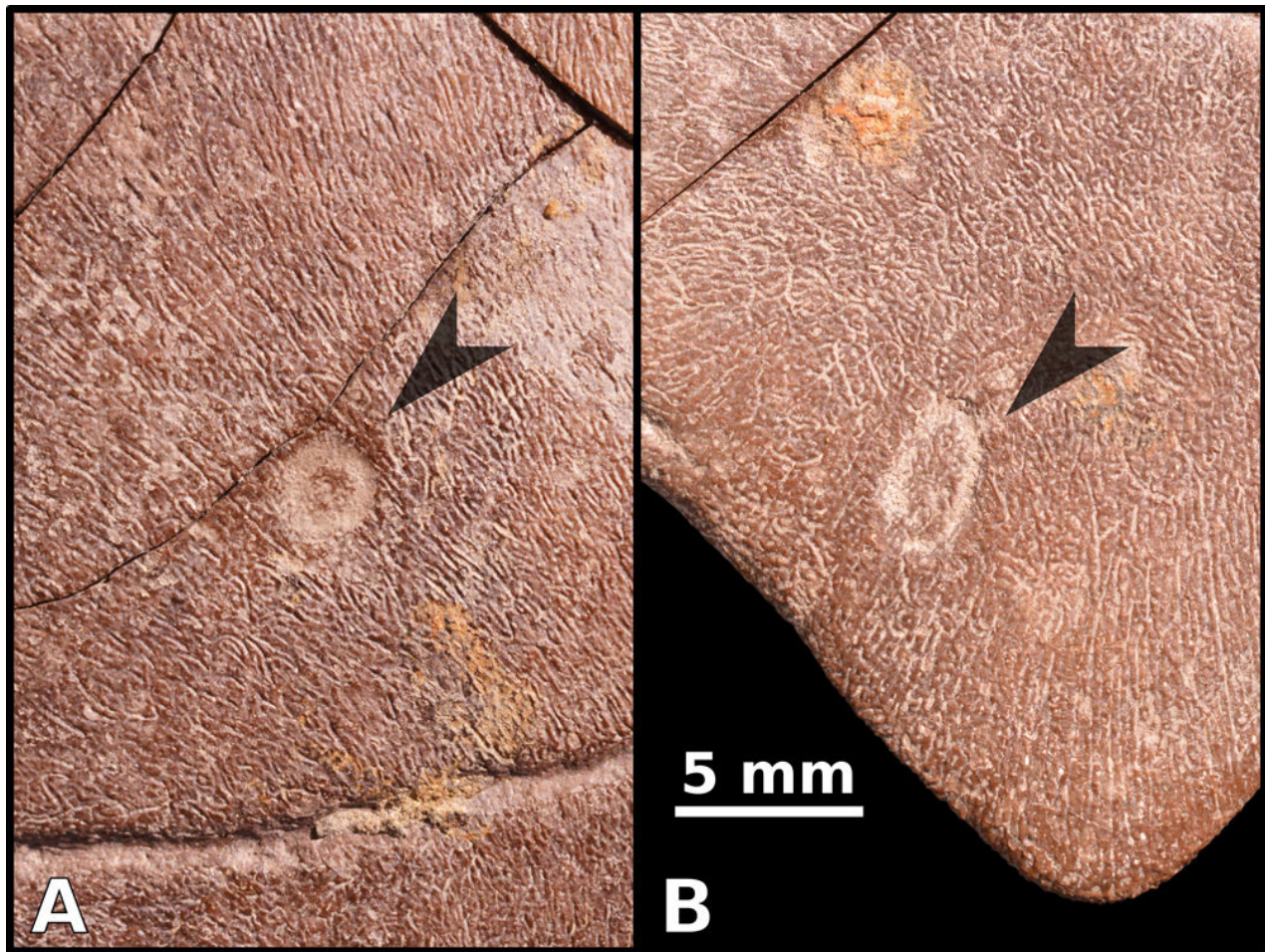


Figure 4: Detail of two *Thatchtelithichnus holmani* traces found on the plastron-bottom of GAMPS-00925, indicated by superimposed arrowheads. A) Circular groove found on the left hypoplastron. B) Elliptical groove found on the left xiphoplastron. The scale bar applies to both panels.

nubbin having a diameter of ~ 1.5 mm. This trace is very similar to the holotype of *T. holmani* as figured by ZONNEVELD *et al.* (2015: Fig. 9.1) and ZONNEVELD and BARTELS (2020: Fig. 1D-E, but see also their Fig. 1F). Similar trace fossils, attributed by ZONNEVELD and BARTELS (2020) to *T. holmani*, have also been reported from dinosaur long bones and ribs from the Jurassic of Wyoming (*i.e.*, the "rosettes" of BADER *et al.*, 2009), where they have been interpreted as pupation chambers of dermestid beetles. A similarly shallow second scar (Fig. 4.B) is observed on the ventral surface of the left xiphoplastron on the area that was originally covered by the anal scute. It consists of a rather elongate depression, measuring $\sim 4 \times 2.5$ mm, with a central unmodified platform that extends for a distance of less than 1 mm from the outer edge of the trace. This scar is somewhat reminiscent of a large, roughly elliptical specimen of *T. holmani* figured by ZONNEVELD *et al.* (2015: Fig. 9.1).

4. General discussion and concluding remarks

Scrutiny of the palaeoherpetological literature reveals that fossils of *Mauremys* are known from several Upper Miocene to Upper Pleistocene sites in Italy (Fig. 5 ; Table 1). Most of these occurrences come from Miocene or Pleistocene contexts; in particular, the Miocene segment of the Italian record of *Mauremys* includes both Tortonian and Messinian occurrences, whereas the Pleistocene fossils include Lower, Middle, and Upper Pleistocene instances. Prior to the present note, a single confirmed occurrence of *Mauremys* was known from the Pliocene of Italy, consisting of the holotype and only known specimen of *Mauremys portisi* from Valleandona (Asti Province, Piedmont; SACCO, 1889). The stratigraphic occurrence of the *M. portisi* holotype is somewhat debated; long regarded as "Astian" in age (*e.g.*, HERVET, 2004; CHESI *et al.*, 2007), it was recently referred to the zone MN 13 or 14, *i.e.*, Lower Pliocene (Zanclean),

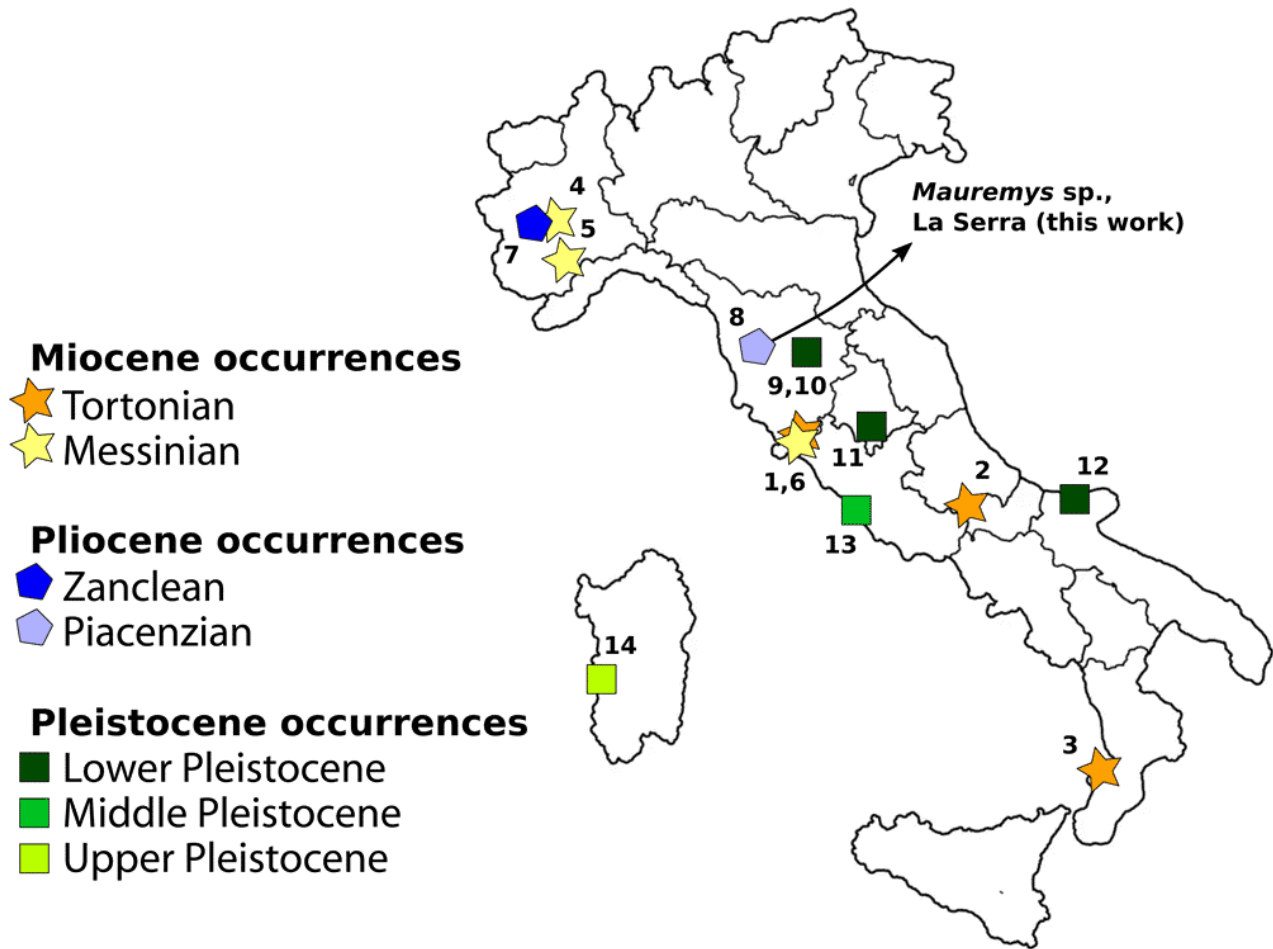


Figure 5: Geographic and stratigraphic distribution of the Italian fossil occurrences of *Mauremys*. Numbers associated with the records refer to Table 1.

by CHESI *et al.* (2009). A second, putative record of *Mauremys* from the Pliocene of Italy, consisting of a partial carapace and associated plastron from Villafranca D'Asti (Asti Province, Piedmont), was reported by AMBROSETTI *et al.* (1996) as belonging to *Mauremys* sp. This specimen, referred to the Upper Pliocene zone MN 16a, was later reattributed to cf. *Geoemyda* sp. by CHESI (2009). Therefore, the Late Pliocene terrapin specimen from La Serra represents the second confirmed occurrence of *Mauremys* in the Italian Pliocene, as well as the first authentic record of this genus from the Piacenzian of Italy. As such, it is an important specimen that fills a gap in the Italian chronostratigraphic distribution of fossil *Mauremys*, and helps – together with the Lower Pliocene holotype of *M. portisi* – bridging the rich Miocene and Pleistocene segments of this record. In light of the above data, it is reasonable to hypothesise that terrapins of the genus *Mauremys* continuously inhabited the Italian peninsula from the Late Miocene to the Middle Pleistocene at least (the sole Late Pleistocene Italian record

of *Mauremys* comes from Sardinia; CHESI *et al.*, 2007). From a palaeoenvironmental point of view, the occurrence of *Mauremys* in the Piacenzian deposits of La Serra does not imply by itself the nearby presence of permanent freshwater ecosystems. Indeed, the extant Mediterranean species of *Mauremys* can respond to prolonged conditions of drought by aestivating (HIGHFIELD, 2002) and they can even survive in brackish waters, including coastal lagoons (SIDIS & GASITH, 1985; ERNST & BARBOUR, 1989; ARNOLD & OVENDEN, 2002; VAMBERGER *et al.*, 2014). The sediments that host the terrapin fossil described herein also feature mesohaline and euryhaline taxa of foraminifers, ostracods, and gastropods, which suggest a brackish lagoonal system, connected with a river mouth and sheltered seawards by a chain of barrier islands (GARASSINO *et al.*, 2012). Such a palaeoenvironmental reconstruction is consistent with the habitat preferences of extant *Mauremys* spp., which are however particularly broad (ERNST & BARBOUR, 1989; HIGHFIELD, 2002).

**Table 1:** Geographic and stratigraphic distribution of the Italian fossil occurrences of *Mauremys*. Numbers in the first column refer to Figure 5.

#	Taxon	Locality(ies)	Geological age	Updated literature reference
1	<i>Mauremys campanii</i>	Casteani, Montebamboli	Tortonian	CHESI <i>et al.</i> , 2009
2	<i>Mauremys</i> sp.	Scontrone	Tortonian	PATACCA <i>et al.</i> , 2013
3	<i>Mauremys</i> sp.	Cessaniti	Tortonian	GEORGALIS <i>et al.</i> , 2020
4	<i>Mauremys</i> sp.	Moncucco Torinese	Messinian	COLOMBERO <i>et al.</i> , 2017
5	cf. <i>Mauremys</i> sp.	S. Vittoria d'Alba	Messinian	KOTSAKIS & MORI, 1981
6	<i>Mauremys campanii</i>	Pian Calcinaio	Messinian	CHESI <i>et al.</i> , 2009
7	<i>Mauremys portisi</i>	Valleandona	Zanclean	CHESI <i>et al.</i> , 2009
8	<i>Mauremys</i> sp.	La Serra	Piacenzian	This work
9	<i>Mauremys etrusca</i>	Restoni	Early Pleistocene	KOTSAKIS, 1980
10	<i>Mauremys etrusca</i>	Colombaiolo	Early Pleistocene	KOTSAKIS, 1980
11	<i>Mauremys</i> sp.	Torre Picchio	Early Pleistocene	GIROTTI <i>et al.</i> , 2003
12	<i>Mauremys</i> sp.	Cava Pirro, Cava Dell'Erba	Early Pleistocene	DELFINO & ATZORI, 2013
13	<i>Mauremys</i> sp.	Grotta del Monte delle Gioie	Middle Pleistocene	KOTSAKIS & BARISONE, 2003
14	<i>Mauremys</i> sp.	San Giovanni di Sinis	Late Pleistocene	CHESI <i>et al.</i> , 2007

The two specimens of *Thatchtelithichnus holmani* reported herein represent some of the few records worldwide of this rarely reported ichnotaxon, as well as its geologically youngest published occurrence. The present record stimulates some inferences regarding the *Thatchtelithichnus* tracemaker(s). As mentioned above, ZONNEVELD *et al.* (2015) proposed that these borings were emplacement scars left by invertebrate ectoparasites (or mesoparasites) while the host turtles were living. WISSHAK *et al.* (2019) included *Thatchtelithichnus* in a list of bioclastration structures, which are not regarded as trace fossils. However, a reanalysis of the type series of *T. holmani* performed by ZONNEVELD and BARTELS (2020) revealed that no part of this ichnotaxon involves bioclastration; these authors concluded that the genetic hypothesis formulated by ZONNEVELD *et al.* (2015) for explaining the *Thatchtelithichnus* scars remains the most likely one. With respect to the ring-shaped traces observed by BADER *et al.* (2009) on dinosaur bones from the Jurassic of Wyoming and later attributed to *T. holmani* by ZONNEVELD and BARTELS (2020), an identification as incipient stages in the process of excavation of pupation chambers by dermestid beetles has been proposed. Modern dermestid larvae (and adults as well) feed on the desiccated flesh of carcasses (HINTON, 1945; TIMM, 1982) and might even consume bone when other food sources are not available (HEFTI *et al.*, 1980). After some four

weeks of feeding, the larvae pupate and create chambers in any available compact surface, including desiccated flesh and bone (HINTON, 1945; TIMM, 1982). When severe infestation occurs, bones might become figuratively honeycombed with pupal chambers, their burrows sometimes extending towards the medullary cavity (HUCHET *et al.*, 2013, and references therein). Crucially, however, dermestids are not known to feed on keratin, which constitutes the scutes that coat the plastral bones of turtles. Among extant insects, only some species of tineid moths are specialised in the consumption of the keratinous portions of carcasses, including the turtle shell (DEYRUP *et al.*, 2005). Members of the tineid genus *Ceratophaga* have been reported excavating straight-sided, cylindrical pupation chambers into the astragali of African bovids (HILL, 1987); however, the morphology of tineid moth damage does not match that of *Thatchtelithichnus*. Given these considerations, it is our contention that the *Thatchtelithichnus* traces observed on the exterior of the plastral bones of turtles cannot be interpreted as feeding marks or pupation chambers of insects (whether dermestid beetles, tineid moths, or members of other hexapod lineages). For explaining these scars, we concur with ZONNEVELD *et al.* (2015) and ZONNEVELD and BARTELS (2020) in inferring an origin as attachment traces of aquatic ectoparasites (one of ticks, leeches, or flukes); this interpretation might also better explain the



variation in circularity of the *Thatchtelithichnus* traces found on turtles (e.g., Fig. 4 and ZONNEVELD *et al.*, 2015: Fig. 9.1). On the other hand, it should be noted that severe (yet non-destructive) episodes of septicaemic cutaneous ulcerative disease (=SCUD, or "shell rot"; see e.g., GRANADOS *et al.*, 2013) that penetrate into the plastral scutes to skim the bone surface might also locally produce shallow lesions on the plastral plates of extant freshwater turtles (personal observation by M.A.L.Z.). Recognising that the *Thatchtelithichnus* grooves represent the lesions of a widespread cutaneous disease such as SCUD might also lead to the conclusion that neither *Thatchtelithichnus* nor *T. holmani* should be regarded as valid ichnotaxa (BERTLING *et al.*, 2006). However, the constancy of the ring-like aspect of the *Thatchtelithichnus* scars and their similar occurrence on the plastron-bottom only in different turtle taxa strongly evoke an origin as attachment traces of homotypic organisms rather than as byproducts of extensive, shell-degrading bacterial infections [see also ZONNEVELD *et al.* (2015)]. In conclusion, the ectoparasitic hypothesis currently seems the most parsimonious for explaining the observation of *Thatchtelithichnus*-like structures on the exterior of the plastral bones of fossil chelonians. Nevertheless, additional actualistic observations on living aquatic turtles are clearly needed for confirming or disproving this tantalising conjecture.

Acknowledgments

Our gratitude to Simone FARINA (Museo di Storia Naturale, Università di Pisa) for providing access to the specimens of extant *Mauremys* under his care. Constructive comments by Stephen J. GODFREY (Calvert Marine Museum) and Evangelos VLACHOS (CONICET & Museo Paleontológico Egidio Feruglio) greatly contributed to shape this work into its present form – thank you very much for your support! Not least, thanks are due to Bruno GRANIER (Université de Bretagne Occidentale) and to Stephen CAREY (Federation University Australia) for their valuable and thorough editorial support.

Bibliographic references

- ABBAZZI L., BENVENUTI M., CECI M.E., ESU D., FARANDA C., ROOK L. & TANGOCCI F. (2008).- The end of the Lago-Mare time in the SE Valdelsa Basin (central Italy): interference between local tectonism and regional sea-level rise.- *Geodiversitas*, Paris, vol. 30, p. 611-639.
- AMBROSETTI P., AZZAROLI A., FICCARELLI G., MASINI F., SALA B. & TORRE D. (1996).- Vertebrati. *Il Quaternario*, Roma, vol. 9, p. 70-73.
- ARNOLD N.E. & OVENDEN D.W. (2002).- A field guide to the reptiles and amphibians of Britain and Europe.- Collins, London, 288 p.
- AZZAROLI A. (1992).- The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany.- *Palaentographia Italica*, Pisa, vol. 79, p. 1-41.
- BADER K.S., HASIOTIS S.T. & MARTIN L.D. (2009).- Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Jurassic Morrison Formation, northeastern Wyoming.- *Palaios*, Broken Arrow, vol. 24, p. 140-158.
- BARTH D., BERNHARD D., FRITZSCH G. & FRITZ U. (2004).- The freshwater turtle genus *Mauremys* (Testudines, Geoemydidae)- a textbook example of an east-west disjunction or a taxonomic misconception?.- *Zoologica Scripta*, London, vol. 33, p.213-221.
- BATSCH A.J.G.C (1788).- Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere, Vögel, Amphibien und Fische.- Akademische Buchhandlung, Jena, 528 p.
- BENVENUTI M. & DOMINICI S. (1992).- Facies analysis, paleoecology and sequence stratigraphy in a Pliocene siliciclastic succession, San Miniato (Pisa, Italy).- *Bollettino della Società Paleontologica Italiana*, Modena, vol. 31, p. 241-259.
- BENVENUTI M., BERTINI A., CONTI C., DOMINICI S. & FALCONE D. (1995a).- Analisi stratigrafica e paleoambientale integrata del Pliocene dei dintorni di San Miniato.- *Quaderni del Museo di Storia naturale di Livorno*, Leghorn, vol. 14, p. 29-49.
- BENVENUTI M., DOMINICI S. & ROOK L. (1995b).- Inquadramento stratigrafico-deposizionale delle faune a mammiferi villafranchiane (Unità faunistiche Triversa e Montopoli) del Valdarno inferiore nella zona a sud dell'Arno (Toscana).- *Il Quaternario*, Roma, vol. 8, p. 457-464.
- BENVENUTI M., BERTINI A., CONTI C., & DOMINICI S. (2007).- Integrated analyses of litho-and biofacies in a Pliocene cyclothem, alluvial to shallow marine succession (Tuscany, Italy).- *Geobios*, Villeurbanne, vol. 40, p. 143-158.
- BENVENUTI M., DEL CONTE S., SCARSELLI N. & DOMINICI S. (2014).- Hinterland basin development and infilling through tectonic and eustatic processes: latest Messinian-Gelasian Valdelsa Basin, Northern Apennines, Italy.- *Basin Research*, vol. 26, p. 387-402.
- BERTLING M., BRADY R., BROMLEY R.G., DEMATHIEU G., GENISE J., MIKULÁŠ R., NIELSEN J., NIELSEN K., RINDSBERG A., SCHLIRF M. & UCHMAN A. (2006).- Names for trace fossils: a uniform approach.- *Lethaia*, Stockholm, vol. 39, p. 265-286.
- BIANUCCI G. (1996).- A new record of baleen whale from the Pliocene of Tuscany (Italy).- *Atti della Società Toscana di Scienze Naturali, Memorie* (Serie A), Pisa, vol. 102, p. 101-104.
- CAPELLINI G. (1905).- Balene fossili toscane. III *Idiocetus Guicciardini*.- *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna*, vol. 6, p. 71-80.



- CHESI F. (2009).- Il registro fossile italiano dei cheloni.- Ph.D. Thesis, Università degli Studi di Firenze, Florence, 178 p.
- CHESI F., DELFINO, M. ABBAZZI L. & CARBONI L. (2007).- New fossil vertebrate remains from S. Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the central Mediterranean.- *Rivista Italiana di Paleontologia e Stratigrafia (Research in Palaeontology and Stratigraphy)*, Milan, vol. 113, p. 287-297.
- CHESI F., DELFINO M. & ROOK L. (2009).- Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover.- *Journal of Paleontology*, Lawrence, vol. 83, p. 379-388.
- CLAUDE J., SUTEETHORN V. & TONG H. (2007).- Turtles from the late Eocene-early Oligocene of the Krabi Basin (Thailand).- *Bulletin de la Société Géologique de France*, Paris, vol. 178, p. 305-316.
- COLLARETA A. (2020).- Discovery of complementary males in a Pliocene accumulation of *Chelonibia testudinaria* (LINNAEUS, 1758), with some notes on the evolution of androdioecy in turtle barnacles.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 297, p. 193-203.
- COLLARETA A., BOSSELAERS M. & BIANUCCI G. (2016).- Jumping from turtles to whales: a Pliocene fossil record depicts an ancient dispersal of *Chelonibia* on mysticetes.- *Rivista Italiana di Paleontologia e Stratigrafia (Research in Palaeontology and Stratigraphy)*, Milan, vol. 122, p. 35-44.
- COLLARETA A., CASATI S., CATANZARITI R. & DI CENCIO A. (2017).- First record of the knifetooth sawfish *Anoxypristis* (Elasmobranchii: Rhinopristiformes) from the Pliocene of Tuscany (central Italy).- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 284, p. 289-297.
- COLLARETA A., MERELLA M., CASATI S. & DI CENCIO A. (in press).- Did titanic stingrays wander the Pliocene Mediterranean Sea? Some notes on a giant-sized myliobatoid stinger from the Piacenzian of Italy.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart.
- COLLARETA A., MERELLA M., MOLLEN F.H., CASATI S. & DI CENCIO A. (2020).- The extinct catshark *Pachycephalus distans* (PROBST, 1879) (Elasmobranchii: Carcharhiniformes) in the Pliocene of the Mediterranean Sea.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 295, p. 129-139.
- COLOMBERO S., ALBA D.M., D'AMICO C., DELFINO M., ESU D., GIUNTELLI P., HARZHAUSER M., MAZZA P.A.P., MOSCA M., NEUBAUER T.A., PAVIA G., PAVIA M., VILLA A. & CARNEVALE G. (2017).- Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleocological and paleoclimatological implications.- *Palaeontologia Electronica*, vol. 20, article #20.1.10A.
- COPE E.D. (1868).- On the origin of genera.- *Proceedings of the Academy of Natural Sciences of Philadelphia*, Philadelphia, vol. 1868, p. 242-300.
- DANISE S. & DOMINICI S. (2014).- A record of fossil shallow-water whale falls from Italy.- *Lethaia*, Stockholm, vol. 47, p. 229-243.
- DELFINO M. & ATZORI M. (2013).- An update on the early Pleistocene herpetofauna from Pirro Nord.- *Palaeontographica Abteilung A, Paläozoologie-Stratigraphie*, Stuttgart, vol. 298, p. 19-29.
- DEYRUP M., DEYRUP N.D., EISNER M. & EISNER T. (2005).- A caterpillar that eats tortoise shells.- *American Entomologist*, Annapolis, vol. 51, p. 245-248.
- DOMINICI S. (1994).- Regressive-transgressive cycles from the Pliocene of the San Miniato area (Tuscany, Italy): paleoecology and sequence stratigraphy.- *Bollettino della Società Paleontologica Italiana*, Modena, vol. 33 (supplement 2), p. 117-126.
- DOMINICI S., ROOK L., BENVENUTI M. & ABBAZZI L. (1995).- Tapir remains in paralic deposits of Pliocene age in lower Valdarno (Tuscany, Italy): Facies analysis and taphonomy.- *Geobios*, Villeurbanne, vol. 28, p. 131-135.
- DOMINICI S., DANISE S. & BENVENUTI M. (2018).- Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna.- *Earth-Science Reviews*, Amsterdam, vol. 176, p. 277-310.
- ERNST C.H. & BARBOUR R.W. (1989).- Turtles of the world.- Smithsonian Institution Press, Washington - DC, 328 p.
- ESU D., & CIANGHEROTTI A. (2004).- Palaeoecologic and palaeobiogeographic character of Middle Pliocene non-marine mollusc faunas from north-western Italy.- *Rivista Italiana di Paleontologia e Stratigrafia (Research in Palaeontology and Stratigraphy)*, Milan, vol. 110, p. 517-530.
- GARASSINO A., PASINI G., DE ANGELI A., CHARBONNIER S., FAMIANI F., BALDANZA A. & BIZZARRI R. (2012).- The decapod community from the Early Pliocene (Zanclean) of "La Serra" quarry (San Miniato, Pisa, Toscana, central Italy): sedimentology, systematics, and palaeoenvironmental implications.- *Annales de Paléontologie*, Paris, vol. 98, p. 1-61.
- GEORGALIS G.L., VILLA A., MARTIN I., VASILYAN D. & DELFINO M. (2019).- Fossil amphibians and reptiles from the Neogene locality of Maramena (Greece), the most diverse European herpetofauna at the Miocene/Pliocene transition boundary.- *Palaeontologia Electronica*, vol. 23, article #22.3.68, 99 p.
- GEORGALIS G.L., INSACCO G., ROOK L., SPADOLA F. & DELFINO M. (2020).- Turtle remains from the late Miocene of the Cessaniti area, southern Italy- insights for a probable Tortonian chelo-



- nian dispersal from Europe to Africa.- *Swiss Journal of Palaeontology*, vol. 139, article #1, 13 p.
- GIROTTI O., CAPASSO BARBATO L., ESU D., GLIOZZI E., KOTSAKIS T., MARTINETTO E., PETRONIO C., SARDELLA R. & SQUAZZINI E. (2003).- The section of Torre di Picchio (Terni, Umbria, central Italy): a Villafranchian site rich in vertebrates, molluscs, ostracods and plants.- *Rivista Italiana di Paleontologia e Stratigrafia (Research in Palaeontology and Stratigraphy)*, Milan, vol. 109, p. 77-98.
- GÓMEZ de SOLER B., CAMPENY VALL-LLOSERA G., VAN DER MADE J., OMS O., AGUSTÍ J., SALA R., BLAIN H.-A., BURJACHS F., CLAUDE J., GARCÍA CATALÁN S., RIBA D. & ROSILLO R. (2012).- A new key locality for the Pliocene vertebrate record of Europe: the Camp dels Ninots maar (NE Spain).- *Geologica Acta*, Barcelona, vol. 10, p. 1-17.
- GRANADOS J.L., MORENO O.G. & BRIEVA C.I. (2013).- Lesiones ulcerativas cutáneas en tortugas dulceacuícolas.- *Revista de la Facultad de Medicina Veterinaria y de Zootecnia*, Bogotá, vol. 60, p. 49-60.
- GRAY J.E. (1825).- A synopsis of the genera of reptiles and amphibia, with a description of some new species.- *Annals of Philosophy*, Edinburgh, vol. 10, p. 193-217.
- GRAY J.E. (1860).- Description of a new species of *Emys* lately living in the gardens of the Zoological Society.- *Proceedings of the Zoological Society of London*, London, vol. 1860, 232-233.
- GRAY J.E. (1869).- Description of *Mauremys laniana*, a new freshwater tortoise.- *Proceedings of the Zoological Society of London*, London, vol. 1869, p. 499-500.
- HEFTI E., TRECHSEL U., RÜFENACHT H. & FLEISCH H. (1980).- Use of dermestid beetles for cleaning bones.- *Calcified Tissue International*, London, vol. 31, p. 45-47.
- HERVET S. (2000).- Tortues du Quaternaire de France : Critères de détermination, répartition chronologique et géographique.- *Mésogée*, Marseille, vol. 58, p. 3-47.
- HERVET S. (2003).- Le groupe "*Palaeochelys* sensu lato-*Mauremys*" dans le contexte systématique des Testudinoidea aquatiques du Tertiaire d'Europe occidentale. Apports à la biostratigraphie et à la paléobiogéographie.- Ph.D. Thesis, Muséum Nationale d'Histoire Naturelle, Paris, 406 p.
- HERVET S. (2004).- Systématique du groupe "*Palaeochelys* sensu lato-*Mauremys*" (Chelonii, Testudinoidea) du Tertiaire d'Europe occidentale : Principaux résultats.- *Annales de Paléontologie*, Paris, vol. 90, p. 13-78.
- HIGHFIELD A.C. (2002).- An introduction to the *Mauremys* turtles of the Mediterranean.- Tortoise Trust online article, available from: <http://www.tortoisetrust.org/articles/mauremys.html>
- HILL A.P. (1987).- Damage to some fossil bones from Laetoli. In: LEAKEY M.D & HARRIS J.M. (eds.), Laetoli: a Pliocene site in Northern Tanzania.- Clarendon Press, Oxford, p. 543-545.
- HINTON H.E. (1945).- A monograph of the beetles associated with stored products, I.- British Museum of Natural History, London, 443 p.
- HUCHET J.B., LE MORT F., RABINOVICH R., BLAU S., COQUEUGNIOT H. & ARENSBURG B. (2013).- Identification of dermestid pupal chambers on southern Levant human bones: inference for reconstruction of Middle Bronze Age mortuary practices.- *Journal of Archaeological Science*, New York, vol. 40, p. 3793-3803.
- KELLER C. & BUSACK S.D. (2001).- *Mauremys leprosa* (SCHWEIGGER, 1812)- Maurische Bachschildkröte.- *Handbuch der Reptilien und Amphibien Europas*, Strasbourg, vol. 3, p. 57-88.
- KOTSAKIS T. (1980).- Révision des tortues (Emydidae, Testudinidae, Trionychidae) du Pliocène de Valdarno supérieur (Toscane, Italie).- *Quaternaria*, Rome, vol. 22, p. 11-37.
- KOTSAKIS T. & BARISONE G. (2003).- Cenni sui vertebrati fossili di Roma.- *Memorie descrittive della Carta Geologica d'Italia*, Rome, vol. 80, p. 115-143.
- KOTSAKIS T. & MORI D. (1981).- Note di paleoerpetologia piemontese. I. I Cheloni del Messiniano superiore di Santa Vittoria d'Alba (Cuneo).- *Rivista Piemontese di Storia Naturale*, Turin, vol. 2, p. 89-98.
- LAPPARENT de BROIN F. de (2000).- African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record.- *Palaeontologia Africana*, Johannesburg, vol. 36, p. 43-82.
- LI L., MO J., HUANG Z., TONG H. (2015).- First fossil turtle from Hainan Island, China.- *Research & Knowledge*, Mahasarakham, vol. 1, p. 48-52.
- LINDSAY E.H., OPDYKE N.D. & JOHNSON N.M. (1980).- Pliocene dispersal of the horse *Equus* and late Cenozoic mammalian dispersal events.- *Nature*, London, vol. 287, p. 135-138.
- PANZERI M., MORI E., MAZZA G. & MENCHETTI M. (2014).- Records of introduced stripe-necked terrapins (*Mauremys* species) in Italy.- *Acta Herpetologica*, Florence, vol. 9, 227-230.
- PATACCA E., SCANDONE P. & CARNEVALE G. (2013).- The Miocene vertebrate-bearing deposits of Scontrone (Abruzzo, Central Italy): stratigraphic and paleoenvironmental analysis.- *Geobios*, Villeurbanne, vol. 46, p. 5-23.
- RUSTIONI M. & MAZZA P.A.P. (2001).- Taphonomic analysis of *Tapirus arvernensis* remains from the lower Valdarno (Tuscany, Central Italy).- *Geobios*, Villeurbanne, vol. 34, p. 469-474.
- SACCO F. (1889).- I Cheloni astiani del Piemonte.- *Memorie della Reale Accademia delle Scienze di Torino (Serie 2)*, vol. 39, p. 427-461.



- SIDIS I. & GASITH A. (1985).- Food habits of the Caspian terrapin (*Mauremys caspica rivulata*) in unpolluted and polluted habitats in Israel.- *Journal of Herpetology*, Columbus, vol. 19, p. 108-115.
- THEOBALD W. (1868).- Catalogue of reptiles in the Museum of the Asiatic Society of Bengal.- *Journal of the Asiatic Society*, Calcutta, Extra number, 88 p.
- TIMM R.M. (1982).- Dermestids.- *Field Museum of Natural History Bulletin*, Chicago, vol. 53, p. 14-18.
- VAMBERGER M., STUCKAS H., AYAZ D., LYMBERAKIS P., ŠIROKÝ P. & FRITZ U. (2014).- Massive transoceanic gene flow in a freshwater turtle (Testudines: Geoemydidae: *Mauremys rivulata*).- *Zoologica Scripta*, London, vol. 43, p. 313-322.
- VLACHOS E. & DELFINO M. (2016).- Food for thought: Sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a glacial refuge for *Emys orbicularis* in Peloponnesus (S. Greece).- *Quaternary Science Reviews*, Amsterdam, vol. 150, p. 158-171.
- VLACHOS E., KOTSAKIS T. & DELFINO M. (2015).- The chelonians from the latest Miocene-earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece).- *Comptes Rendus Palevol*, Paris, vol. 14, p. 187-205.
- VLACHOS E., STERLI J., VASILEIADOU K. & SYRIDES G. (2019).- A new species of *Mauremys* (Testudines, Geoemydidae) from the late Miocene-Pliocene of Central Macedonia (northern Greece) with exceptionally wide vertebral scutes.- *Papers in Palaeontology*, London, vol. 5, p. 177-195.
- WISSHAK M., KNAUST D. & BERTLING M. (2019).- Bioerosion ichnotaxa: review and annotated list.- *Facies*, Erlangen, vol. 65, article #24, 39 p.
- ZONNEVELD J.P. & BARTELS W.S. (2020).- Ichnologic note: in defence of *Thatchtelithichnus* ZONNEVELD, BARTELS, GUNNELL and MCHUGH, 2015.- *Ichnos*, Philadelphia, vol. 27, no. 2, p. 152-155.
- ZONNEVELD J.P., BARTELS W.S., GUNNELL G.F. & MCHUGH L.P. (2015).- Borings in early Eocene turtle shell from the Wasatch Formation, South Pass, Wyoming.- *Journal of Paleontology*, Lawrence, vol. 89, p. 802-820.