



**Terrapin aches and pains:
Parasite borings and other bone modifications
in an Italian Pliocene population of *Mauremys*
(Testudines, Geoemydidae)**

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Abstract: Despite the common and widespread occurrence of turtle shell remains in many fossil vertebrate assemblages worldwide, few palaeontological studies have addressed the palaeoecological significance of turtle bone modification features. Here, we report on ichnofossils occurring on carapacial and plastral bones of the small terrapin genus *Mauremys* (Testudinoidea, Geoemydidae) from Upper Pliocene deposits exposed at La Serra, in the Valdelsa basin of Tuscany (central Italy). The trace fossil assemblage includes *Karethraichnus lakkos*, *Gunnellichnus* cf. *moghraensis*, and *Thatchtelithichnus holmani*, all of which are found on the nonvisceral surfaces of the shell. As observed elsewhere, some of the *Karethraichnus lakkos* borings occur along the epidermal sulci that mark the border between adjacent keratinous scutes. Based on the relevant literature, the studied ichnofossils are interpreted as being due to the parasitic action of leeches/spirorchiid liver flukes (*K. lakkos* and *Thatchtelithichnus holmani*) and to algal/fungal/bacterial (sub)cutaneous infections (*Gunnellichnus* cf. *moghraensis*). The observed stock of bioerosional features compares favourably with the Italian Pliocene climate, which was warmer and wetter than today.

Keywords:

- palaeoichnology;
- *Gunnellichnus moghraensis*;
- *Karethraichnus lakkos*;
- *Thatchtelithichnus holmani*;
- turtle;
- shell;
- Piacenzian;
- Valdelsa basin

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Résumé : Lésions osseuses chez des tortues d'eau douce : Perforations parasitaires et autres modifications osseuses dans une population pliocène italienne de *Mauremys* (Testudines, Geoemydidae).- Malgré la présence fréquente et généralisée de restes de carapace de tortue dans de nombreux assemblages fossiles de vertébrés à travers le monde, peu d'études paléontologiques ont abordé la signification paléoécologique des altérations observées sur les os de tortue. Nous rendons compte ici de la découverte d'ichnofossiles observés sur des os de la dossière et du plastron d'un genre de petite tortue - *Mauremys* (Testudinoidea, Geoemydidae) - provenant de couches du Pliocène supérieur affleurant à La Serra, dans le bassin du Val d'Elsa en Toscane (Italie centrale). L'association de traces fossiles comprend *Karethraichnus lakkos*, *Gunnellichnus* cf. *moghraensis* et *Thatchtelithichnus holmani*, qui se trouvent tous sur les surfaces non viscérales de la carapace. Comme observé ailleurs, certaines des perforations de *Karethraichnus lakkos* se produisent le long des sillons épidermiques qui marquent la frontière entre les écailles kératiniques adjacentes. D'après la littérature spécialisée, les ichnofossiles étudiés sont interprétés comme dus à l'action parasitaire de sangsues/douves du foie (*K. lakkos* et *Thatchtelithichnus holmani*) et à des infections (sous-)cutanées algales/fongiques/bactériennes (*Gunnellichnus* cf. *moghraensis*). L'ensemble des traces bioérosives observées corrobore l'idée que le climat du Pliocène italien était plus chaud et plus humide qu'aujourd'hui.

Mots-clefs :

- paléoichnologie ;
- *Gunnellichnus moghraensis* ;
- *Karethraichnus lakkos* ;
- *Thatchtelithichnus holmani* ;
- tortue ;
- carapace ;
- Plaisancien ;
- bassin du Val d'Elsa

1. Introduction

Turtles are characterised by possessing a peculiar bony shell that includes both dermal bones and highly modified endoskeletal elements (RICE *et al.*, 2016). This shell comprises of a dorsal, dome-shaped armoured element (*i.e.*, the carapace) and a ventral, flattened one (*i.e.*, the plastron), each of which consists of a mosaic of articulating bony plates. In most cases, the external surfaces of both the plastron and the carapace as well as the periphery of the internal surfaces are coated by a layer of keratinised skin, which in turn is typically divided into nonoverlapping epidermal scutes whose often taxonomically informative patterns are reflected by the occurrence of sulci on the underlying bone. Although these epidermal scutes shelter the turtle shell bone from the surrounding environment, they can be infiltrated and bypassed by a wide array of symbionts, which in turn may result in different bone modifications such as pits, holes and grooves. In addition, algal, fungal and bacterial infections may also damage the shell bones (*e.g.*, M.L. FELDMAN & M.B. FELDMAN, 2011; ZONNEVELD & BARTELS, 2019, 2022, 2023; CHRISTIANSEN *et al.*, 2020; ZONNEVELD *et al.*, 2022a). The resulting bone modifications appear to be common in modern turtle populations in both aquatic and terrestrial settings and are likely to be frequent in fossil populations as well. That said, little attention has historically been paid by palaeontologists to the ichnology of the turtle shell (with some remarkable exceptions, *e.g.*, HUTCHISON & FRYE, 2001), though this has dramatically changed lately. Among the several works that have dealt with this issue over the last years (*e.g.*, COLLARETA *et al.*, 2020a, 2022a; SATO & JENKINS, 2020; COLLARETA & BOSSELAERS, 2022; ASCARRUNZ & JOYCE, 2024; GUERRERO

et al., 2024, 2025), those by ZONNEVELD *et al.* (2015, 2022b) and ZONNEVELD and BARTELS (2022, 2023) are particularly relevant in the way they have established an updated ichnotaxonomic framework for dealing with such bone modifications and their fossil diversity.

Our aim here is to report on the bone modifications affecting carapacial and plastral bones of *Mauremys* (Testudinoidea: Geoemydidae) from Upper Pliocene coastal deposits exposed at La Serra (Tuscany, central Italy). The occurrence of *Mauremys* at this locality was recently assessed based on an incomplete skeleton that also features two examples of the parasite boring *Thatchtelithichnus holmani* (COLLARETA *et al.*, 2020a). Including several newly collected plates, the present study reveals a higher diversity of traces, among which are representatives of the ichnogenera *Gunnellichnus* and *Karethraichnus*. Some hypotheses on the identity of the tracemakers are proposed, and the palaeobiological and palaeoenvironmental significance of the studied ichnofossils is briefly discussed.

2. Geological and palaeontological framework

The fossil specimens discussed herein come from an active quarry in the vicinity of La Serra village (San Miniato municipality, Pisa Province; geographic coordinates: [43°39'28"N 10°48'57"E](#)). This quarry lies in the northwestern sector of the Valdelsa basin, a 25×60 km-wide, NW-trending extensional basin in the Northern Apennine hinterland (Fig. 1). The basin fill reaches a maximum thickness of about 2 km, and ranges chronostratigraphically between the Upper Miocene and the Lower Pleistocene (*e.g.*, ABBAZZI *et al.*, 2008; BENVENUTI *et al.*, 2014).

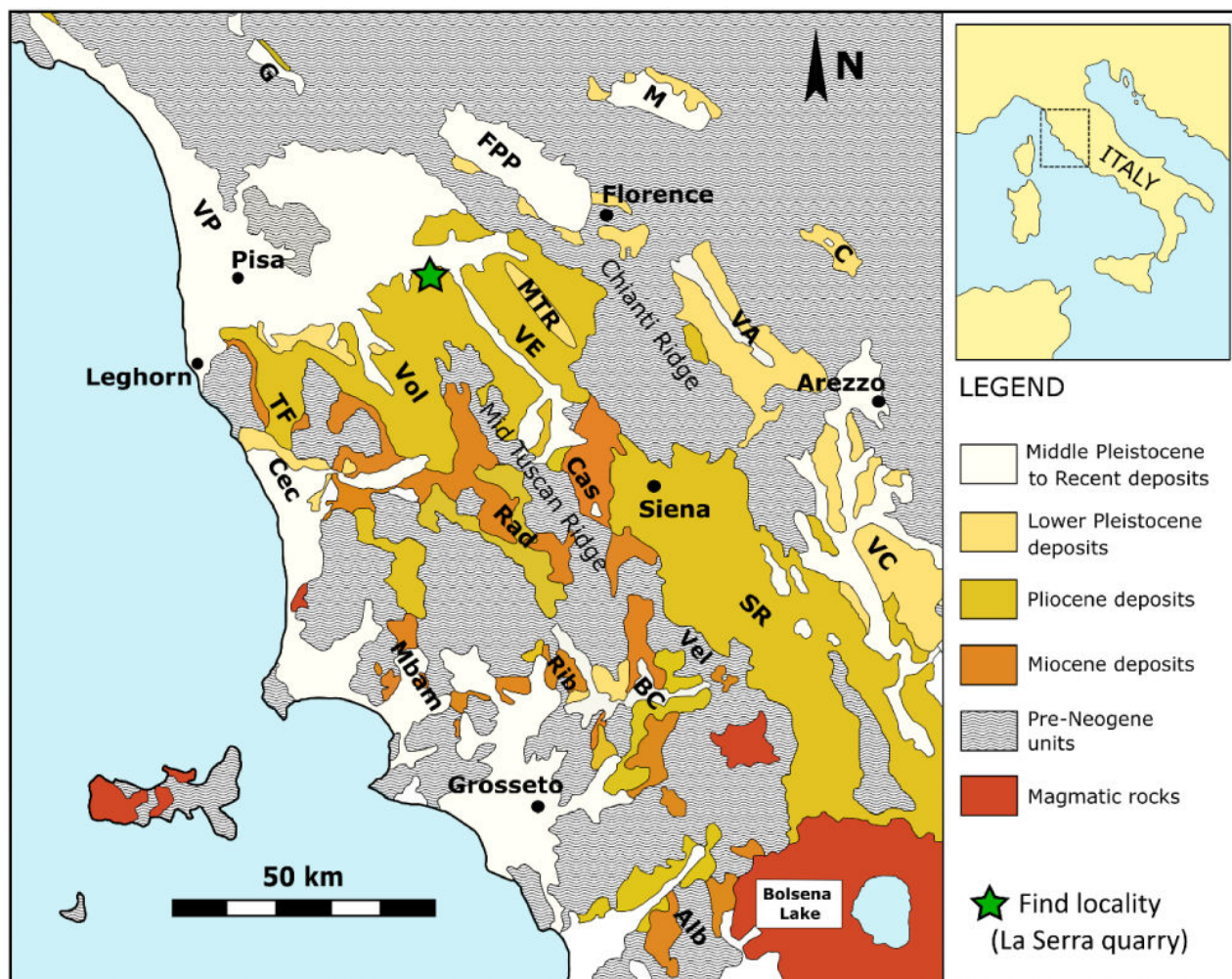


Figure 1: Simplified geological map of Tuscany (central Italy). The star indicates the geographic position of the La Serra quarry (GPS geographic coordinates: $43^{\circ}39'28''\text{N}$ $10^{\circ}48'57''\text{E}$) where the terrapin specimens discussed in the present paper were discovered. Abbreviations: Alb, Albegna basin; BC, Baccinello–Cinigiano basin; C, Casentino basin; Cec, Cecina basin; FPP, Firenze–Prato–Pistoia basin; G, Garfagnana basin; M, Mugello basin; Mbam, Montebamboli basin; MTR, Montespertoli–Tavernelle ridge; Rad, Radicondoli basin; Rib, Ribolla basin; SR, Siena–Radicofani basin; TF, Tora–Fine basin; VA, upper Valdarno basin; VC, Valdichiana basin; VE, Valdelsa–lower Valdarno basin; Vel, Velona basin; Vol, Volterra basin. Redrawn and modified from BENVENUTI *et al.* (2014).

A detailed characterization of the sedimentary succession exposed at La Serra has been provided by GARASSINO *et al.* (2012), who recognised the following informal units:

- "Unit 1", cropping out in the lower part of the quarry, up to 8 m above the base of the section (hereafter, abs). This unit consists of mixed sandstone and siltstone overlain by cross-stratified sandstone and massive claystone. GARASSINO *et al.* (2012) regarded this unit as reflecting an estuarine or deltaic depositional setting punctuated by marshes and ponds;
- "Unit 2" (from 8 m to 14 m abs): a thick sandstone succession with high-angle cross-stratifications, interpreted by GARASSINO *et al.* (2012) as testifying to a barrier island where both submarine longshore dunes and subaerial aeolian dunes were present;
- "Unit 3" (from 14 m to 19.5 m abs): structureless siltstone and silty sandstone that pass laterally into massive claystone. Accord-

ing to GARASSINO *et al.* (2012), this unit was deposited in a sheltered, lagoonal environment that was intermittently connected with the sea;

- "Unit 4" (from 19.5 m abs to the top of the section, ca. 25 m abs): highly fossiliferous, clayey sandstone that testifies to a low-energy, shallow-marine depositional setting.

Over the last few years, the La Serra quarry has yielded a rich assemblage of terrestrial, freshwater and marine vertebrates. GARASSINO *et al.* (2012) were the first to record the occurrence of indeterminate remains of turtles and cervids from Unit 1. Among these finds are plastral and carapacial remains of *Mauremys* sp., some of which have been described elsewhere (COLLARETA *et al.*, 2020a). Tortoise remains have also been recently reported from Unit 1, representing the first unambiguous record of the genus *Testudo* in the Italian Pliocene (MULÈ *et al.*, 2025). Unit 2 is home to fragmentary mandibles and long bones of cervids, postcranial bones and a tooth of proboscidean, and cranial and dental elements of suids (MERELLA

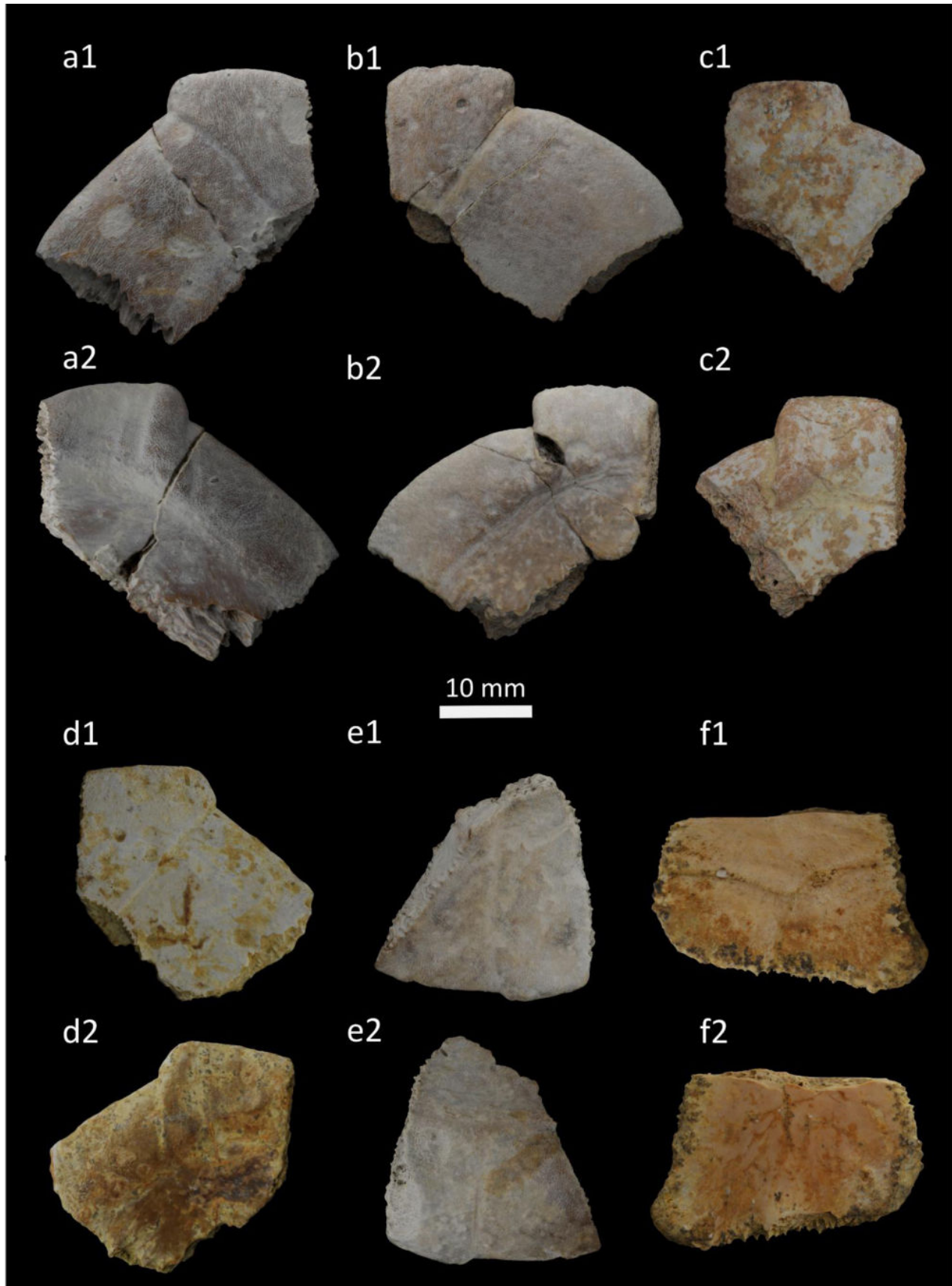


Figure 2: *Mauremys* sp., newly collected carapacial and plastral bones featuring bone modifications from the Upper Pliocene of La Serra. (a1, a2) GAMPS-01987, epiplastron; (b1, b2) GAMPS-01984, epiplastron; (c1, c2) GAMPS-01983, epiplastron; (d1, d2) GAMPS-01967, epiplastron; (e1, e2) GAMPS-01985, peripheral, (f1, f2) GAMPS-01986, costal. External views (a1–f1) and visceral/internal views (a2–f2). All panels are digital renderings of the textured photogrammetric 3D models.



et al., 2023). A fairly diverse marine vertebrate fauna comes from Unit 4, including shark teeth as well as the longest stingray stinger ever described from the fossil and modern records (COLLARETA *et al.*, 2020b). Invertebrate remains occur throughout the succession, with Unit 4 preserving an exceptionally rich decapod fauna (GARASSINO *et al.*, 2012) as well as the youngest lingulid brachiopods known from the Mediterranean Sea (DI CENCIO *et al.*, 2021).

The chronostratigraphic assignment of the aforementioned sediments and fossils is somewhat debated. According to the biostratigraphic results presented by GARASSINO *et al.* (2012), the La Serra section should be referred to the Lower Pliocene, with Unit 1 being possibly as old as the uppermost Miocene (Messinian). This interpretation clashes with previous studies that have placed the La Serra section well into the Pliocene (*e.g.*, BENVENUTI *et al.*, 1995a, 1995b; DOMINICI *et al.*, 1995; ABBAZZI *et al.*, 2008). Building upon basin-wide correlations, biochronological considerations, and biostratigraphic analyses from many different sites of the Valdelsa basin, this succession was assigned by DOMINICI *et al.* (2018) to their S6 Synthem, which in turn would have deposited during the late Piacenzian and early Gelasian. More specifically, DOMINICI *et al.* (2018) and DOMINICI and DANISE (2023) assigned Unit 4 of GARASSINO *et al.* (2012) to the uppermost Piacenzian, which indicates that the quarry section should be entirely referred to the Upper Pliocene. This chronostratigraphic interpretation appears to be consistent with (i) the Piacenzian age of the underlying S5 Synthem; (ii) the recognition of the GAUSS–MATUYAMA palaeomagnetic transition at Montopoli, c. 6 km from La Serra (LINDSAY *et al.*, 1980); and (iii) the subsequent recognition of a simplified nannoplankton assemblage consistent with the CNPL zones 3 (*p.p.*), 4 and 5 (*p.p.*), encompassing the upper part of the Zanclean as well as the whole Piacenzian, in the sediments of Unit 4 (DI CENCIO *et al.*, 2021). It is also worth noting that the San Miniato area is the source of historical terrestrial vertebrate faunas belonging to the Triversa and Montopoli faunal units, which in turn correspond to the Early–Middle Villafranchian mammal age, embracing the Late Pliocene and earliest Pleistocene (*e.g.*, RUSTIONI & MAZZA, 2001; ROOK *et al.*, 2017; BARTOLINI-LUCENTI *et al.*, 2022). In light of the above considerations, we regard the La Serra section as entirely belonging in the Upper Pliocene.



3. Materials and methods

DESCRIPTIVE ICHNOLOGY

The ichnological nomenclature is mostly derived from ZONNEVELD *et al.* (2015, 2022b) and ZONNEVELD and BARTELS (2022, 2023). According to these studies, penetrative traces ("holes") pass through the whole thickness of a given bone, whereas non-penetrative traces ("pits") do not. "Shallow" pits end within the cortical bone layer, whereas "deep" pits penetrate into the internal cancellous bone layer. Individual traces are identified with Greek letters (*e.g.*, "α", "β", etc.).

REPOSITORY AND MATERIAL

The fossil specimens discussed herein are housed at Badia a Settimo (Scandicci, Florence Province), in the permanent exhibition of "Gruppo AVIS Mineralogia e Paleontologia Scandicci" (=GAMPS). They consist of one isolated peripheral, one isolated costal, one incomplete plastron and four incomplete epiplastra, originating from a minimum of five turtle individuals.

Specifically, GAMPS-01985 (Fig. 2.e1-2) is a peripheral, whereas GAMPS-01986 is a distal fragment of a costal (Fig. 2.f1-2). GAMPS-01987 is an isolated right epiplastra, whereas GAMPS-01967, GAMPS-01983 and GAMPS-01984 are isolated left epiplastra. GAMPS-01984 and GAMPS-01987 are essentially complete (Fig. 2.a1-2, .b1-2), whereas GAMPS-10967 and GAMPS-10983 lack their posterolateral corners (Fig. 2.c1-2, .d1-2). Finally, GAMPS-00925 (see COLLARETA *et al.*, 2020a: Figs. 2-3) consists of carapacial and plastral bones from a single turtle individual, including the slightly damaged left and right hypoplastra as well as the essentially complete left and right xiphiplastra.

All the aforementioned plates are thin and slender, as usual for freshwater turtles, and compare favourably with published illustrations and descriptions of the shell bones of *Mauremys* (*e.g.*, CHESI, 2009; CHESI *et al.*, 2009; COLOMBERO *et al.*, 2017; GEORGALIS *et al.*, 2019; VLACHOS *et al.*, 2019). In particular, the epiplastra (Fig. 2.a-d) are characterised by a marked anterior expansion of the area covered by the gular scutes; they display no gular pocket; and a small, elongated bulge is present medial to the gular-humeral groove (*e.g.*, HERVET, 2000). Furthermore, the xiphiplastra (COLLARETA *et al.*, 2020a: Fig. 3) exhibit a very deep anal notch and a straight femoral-anal sulcus.

PHOTOGRAPHY AND 3D IMAGING

Photographs of all specimens were taken at Dipartimento di Scienze della Terra, Università di Pisa, using a Nikon D850 camera equipped with a Nikon Micro Nikkor AF-S 60 mm f/2.8 G ED macro-lens and a Zeiss Axio Zoom.V16 microscope equipped with a Zeiss Axiocam 305 color camera. The latter instrument is connected to a computer running the ZEN core 3.10 software and allows for automated focus stacking as well as for elaborating depth maps and topographic cross-sections over small surfaces.

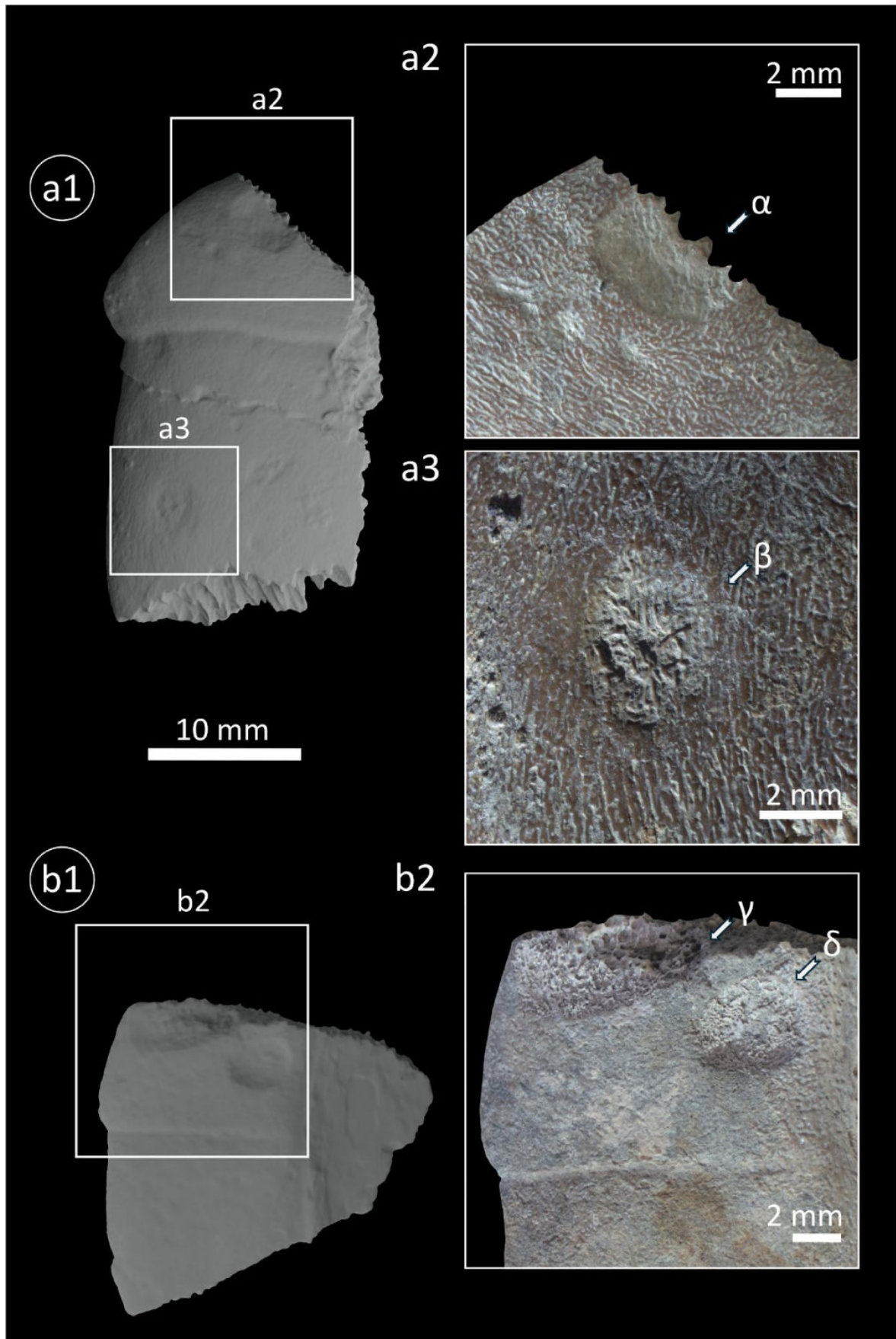


Figure 3: *Gunnellichnus* cf. *moghraensis* borings on plastral and carapacial bones of *Mauremys* sp. from the Upper Pliocene of La Serra. (a1) GAMPs-01987, epiplastron, featuring traces "a" (a2) and "b" (a3) on its external surface. (b1) GAMPs-01985, peripheral, featuring traces "gamma" and "delta" (b2) on its internal surface. Panels a1 and b1 are digital renderings of the textured photogrammetric 3D models. Panels (a2), (a3) and (b2) are photographs taken under annular light (a2, b2) or low-angle artificial light (a3).

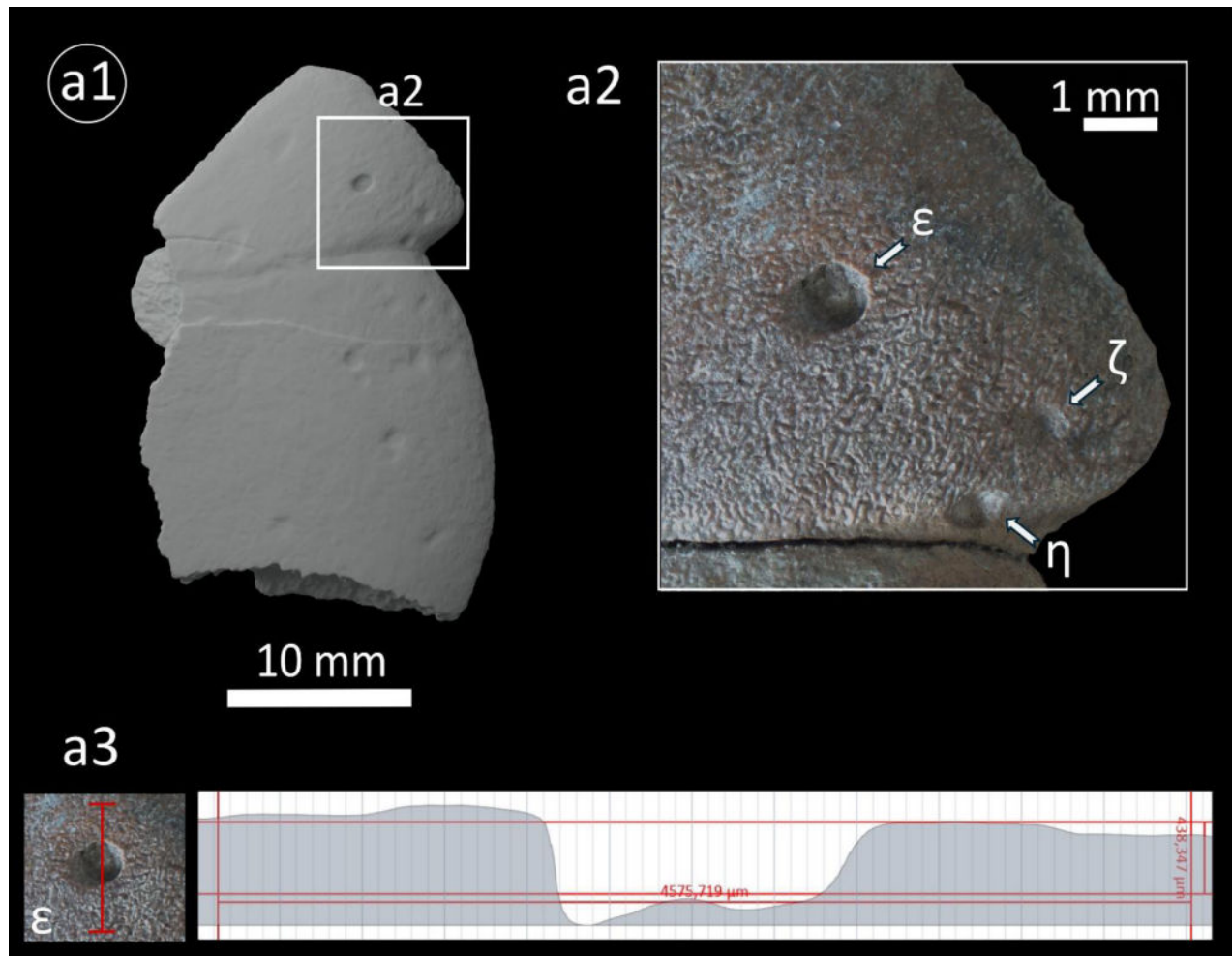


Figure 4: *Karethraichnus lakkos* borings on plastral bones of *Mauremys* sp. from the Upper Pliocene of La Serra. (a1) GAMPS-01984, epiplastron, featuring traces "ε", "ζ" and "η" (a2) on its external surface. Panel (a1) is a digital rendering of the textured photogrammetric 3D model. Panel (a2) is a photograph taken under low-angle artificial light. Panel (a3) is a cross-section of trace ε, featuring a somewhat uplifted terminus.

Textured 3D models of all the trace-bearing bones were elaborated through photogrammetry by using the Agisoft Metashape Standard (64 bit) software. All models were subsequently scaled in Blender 3.6 to their natural size. They are freely available on Figshare at the following web links:

- [10.6084/m9.figshare.28391534](https://figshare.com/figure/10.6084/m9.figshare.28391534) (GAMPS-00925);
- [10.6084/m9.figshare.28391642](https://figshare.com/figure/10.6084/m9.figshare.28391642) (GAMPS-01967);
- [10.6084/m9.figshare.28391615](https://figshare.com/figure/10.6084/m9.figshare.28391615) (GAMPS-01983);
- [10.6084/m9.figshare.28391651](https://figshare.com/figure/10.6084/m9.figshare.28391651) (GAMPS-01984);
- [10.6084/m9.figshare.28391663](https://figshare.com/figure/10.6084/m9.figshare.28391663) (GAMPS-01985);
- [10.6084/m9.figshare.28391666](https://figshare.com/figure/10.6084/m9.figshare.28391666) (GAMPS-01986);
- [10.6084/m9.figshare.28391675](https://figshare.com/figure/10.6084/m9.figshare.28391675) (GAMPS-01987).

Blender 3.6 was also used to elaborate textured and untextured digital renderings of all models as orthographic views under low-angle light.

4. Systematic ichnology

Ichnogenus Gunnellichnus ZONNEVELD *et al.*, 2022b

This ichnogenus consists of shallow, narrow to wide, irregularly etched/corroded areas on the external surface of the shell bones. The outer trace margin is smoothly scalloped to gently undulose, and only rarely straight. Marginal troughs deeper than the centre of the trace do sometimes occur. *Gunnellichnus* is typically much wider than deep, with a width-to-depth ratio >10:1 (and commonly >100:1). The absolute dimensions of the trace are variable: the examples described by ZONNEVELD *et al.* (2022b: Figs. 5–7) vary between 2 mm wide and approximately twice as long to 1–2 cm wide and 3–7 cm long. The included ichnospecies are *Gunnellichnus moghraensis* (the type ichnospecies) and *G. akolouthiste* (ZONNEVELD *et al.*, 2022b).

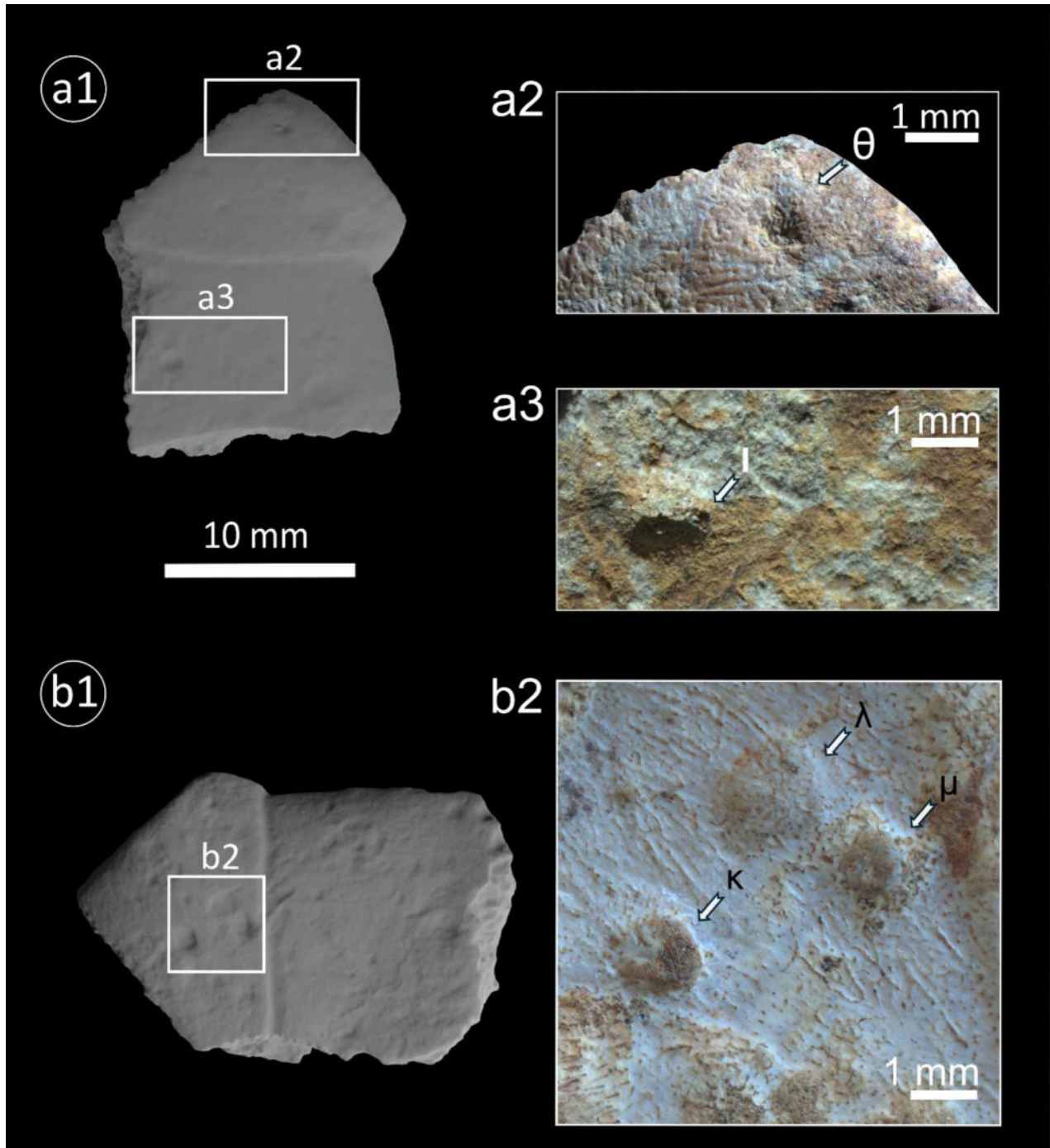


Figure 5: *Karethraichnus lakkos* borings on plastral bones of *Mauremys* sp. from the Upper Pliocene of La Serra. (a1) GAMPS-01983, epiplastron, featuring traces "θ" (a2) and "ι" (a3) on its external surface. (b1) GAMPS-01967, epiplastron, featuring traces "κ", "λ" and "μ" (b2) on its external surface. Panels (a1) and (b1) are digital renderings of the textured photogrammetric 3D models. Panels (a2), (a3) and (b2) are photographs taken under annular light (a3) or low-angle artificial light (a2, b2).

Gunnellichnus* cf. *moghraensis
ZONNEVELD *et al.*, 2022b
 (Fig. 3)

Gunnellichnus moghraensis consists of wide surface etchings. The trace depth is typically submillimetric. The outer trace margin is smoothly scalloped to gently undulose. The width-to-depth ratio is >25:1 and commonly exceeds 100:1. The trace floor is often rough and uneven (ZONNEVELD *et al.*, 2022b).

Fossil occurrences: *Gunnellichnus moghraensis* was first recognised on plastral bones of the extinct terrapin *Erymnochelys* from the Lower Miocene of Wadi Moghra, Egypt (ZONNEVELD *et al.*, 2022b). COLLARETA and BOSSELAERS (2022) recorded the presence of *Gunnellichnus moghraensis* on a cheloniid costal plate from the Middle Miocene of Flanders, Belgium. JANSSEN *et al.* (2013) had previously described similar scars on Upper Cretaceous remains of the sea turtle *Allopleuron hofmanni* from the Maastrichtian type

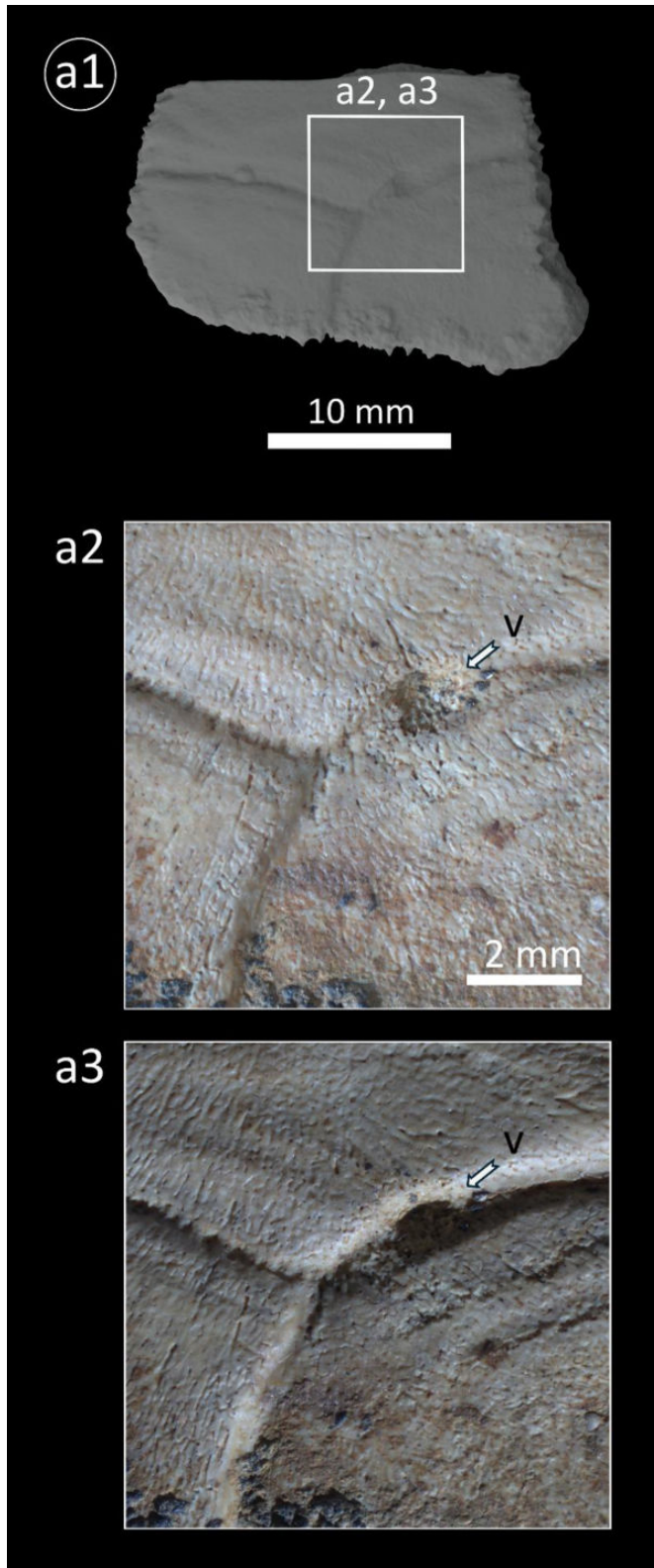


Figure 6: *Karethraichnus lakkos* borings on carapacial bones of *Mauremys* sp. from the Upper Pliocene of La Serra. (a1) GAMPs-01986, costal, featuring trace "v" (a2, 3) on its external surface. Panel (a1) is a digital rendering of the textured photogrammetric 3D model. Panels (a2) and (a3) are photographs taken under annular light (a2) or low-angle artificial light (a3).

area, ranging across the Netherlands and Belgium. Other occurrences of *Gunnellichnus moghraensis* are on middle Eocene geoemydid turtles of Wyoming, USA (ZONNEVELD & BARTELS, 2023) as well as on a fragmentary plastron of a 'ptychogasterid' geoemydid from the Eocene of the Messel Pit, in Germany (ASCARRUNZ & JOYCE, 2024).

Material examined herein: "α" and "β", two individual traces on the external surface of epiplastron GAMPs-01987; "γ" and "δ", two individual traces on the internal surface of peripheral GAMPs-01985.

Description: Two relatively large examples of *Gunnellichnus* cf. *moghraensis* occur on the external surface of GAMPs-01987 (Fig. 3.a1). The partly preserved trace α stretches along the suture with the adjoining epiplastron (Fig. 3.a2). Assuming an elliptical outline, the long axis of the trace reconstructs as parallel to the aforementioned suture. This 5.8-mm-long boring displays rather regular margins and a relatively smooth floor. Occurring close to the posterolateral corner of the bone, trace β lies close to the suture with the adjoining hyoplastron (Fig. 3.a3). It measures about 5 mm in maximum length and 3.6 mm in maximum width and penetrates more shallowly than the base of the cortical bone layer. Trace β displays an elliptical outline having its long axis parallel to the lateral margin of the bone. This trace is shallow and provided with a gently scalloped outer margin. A small, irregular, slightly uplifted boss is observed on the trace floor, its outline recalling that of the whole pit. Overall, this trace is similar to a *G. moghraensis* scar described by COLLARETA and BOSSELAERS (2022: Fig. 4.B, trace "δ" therein) on a cheloniid costal plate from the Miocene of Belgium.

Two larger examples of *Gunnellichnus* are present on the internal surface of peripheral GAMPs-01985, indicated herein as γ and δ (Fig. 3.b1). The γ pit lies along the partly damaged suture with an adjoining peripheral (Fig. 3.b2). Measuring about 4.2 mm in length and about 3.7 mm in transverse width, it is wide and shallow, with fairly regular margins. The trace shape is elliptical, the long axis being parallel to the aforementioned suture. Near the γ boring, the larger yet incompletely preserved δ pit occurs close to the outer border of the visceral surface of the bone (Fig. 3.b2). Its morphology and dimensions are similar to those of trace β on GAMPs-01987.

Our Tuscan Pliocene representatives of *Gunnellichnus* include specimens that are morphologically close to *G. moghraensis* but typically characterised by a lower width-to-depth ratio than specified in the original diagnosis of ZONNEVELD *et al.* (2022b), hence our referral to *G. cf. moghraensis*. They are nonetheless consistent with similarly sized traces assigned by ZONNEVELD and BARTELS (2023: Fig. 8) to *G. moghraensis*.



Ichnogenus *Karethraichnus* ZONNEVELD *et al.*, 2015

This ichnogenus is represented by both penetrative holes and non-penetrative pits with a circular or subcircular outline. The latter include shallow, bowl-shaped borings as well as deeper, subcylindrical pits provided with a rounded, blunt, or pointed terminus. The included ichnospecies are *Karethraichnus lakkos* (the type ichnospecies), *K. fiale*, *K. kulindros*, *K. minimum*, and *K. zaratan* (ZONNEVELD *et al.*, 2015; SATO & JENKINS, 2020; MOURA *et al.*, 2021). Of all these ichnospecies, only *K. fiale* conforms to the penetrative morphotype.

***Karethraichnus lakkos* ZONNEVELD *et al.*, 2015 (Figs. 4 - 6)**

This ichnospecies consists of circular, subcircular or irregular pits with a circular outline and a flattened or rounded (*i.e.*, hemispherical) terminus (ZONNEVELD *et al.*, 2015: Fig. 8.1i, 2022a: Fig. 14.A-C). The traces enter the cortical bone and, in some cases, the shallows of the trabecular bone. The diameter ranges widely between about 1 mm and centimetric, and depth is also variable. These traces are often deeper and more circular on tortoise material than on aquatic turtles (width-to-depth ratio range from 1:1 to 5:1) (ZONNEVELD *et al.*, 2022b).

Fossil occurrences: ZONNEVELD *et al.* (2015) first described this ichnospecies from bony elements of the geoemydid terrapin cf. *Echmatemys* from the lower Eocene of Wyoming, USA. COLLARETA *et al.* (2022a) recorded *Karethraichnus* cf. *lakkos* on a cheloniid costal plate from the Upper Miocene of Tuscany (Italy). ZONNEVELD *et al.* (2022b) reported on the presence of this ichnospecies on *Erymnochelys* from the Lower Miocene of Wadi Moghra, Egypt. COLLARETA *et al.* (2022a) dealt with two *Karethraichnus lakkos* borings on a fragmentary sea turtle carapace from the Upper Miocene of the Pisco basin, Peru. ZONNEVELD and BARTELS (2023) recorded this ichnospecies on turtle shell elements of middle Eocene freshwater turtles from Wyoming, USA. EL HEDENY *et al.* (2023) reported on *K. lakkos* borings on Campanian terrapin materials from Kharga Oasis, Egypt. SZCZYGIELSKI *et al.* (2024) detected this ichnospecies on materials of *Proterochersis* from the Upper Triassic of Baden-Württemberg, Germany. Finally, ASCARRUNZ and JOYCE (2024) recorded *Karethraichnus lakkos* on a plastral fragment from the Eocene of the Messel Pit, Germany.

Besides turtles, *K. lakkos* has been recorded on the bones of mosasaurs (as *Gastrochaenolites* isp., JAGT *et al.*, 2020), megatheriids (TRIFILIO *et al.*, 2023), and glyptodonts (ZONNEVELD *et al.*, 2024).

Material examined herein: "ε", "ζ" and "η", three individual traces on the external surface of epiplastron GAMPS-01984; "θ" and "ι", two individual traces on the external surface of epiplastron GAMPS-01983; "κ", "λ" and "μ", three individual traces on the external surface of epiplastron GAMPS-01967; "ν", one individual trace on the external surface of costal GAMPS-01986.

Description: The small pits ε, ζ and η occur on the external surface of epiplastron GAMPS-01984, and specifically in its gular region (Fig. 4.a1-3). Trace ε has a subcylindrical shape and subcircular outline with well-defined margins (Fig. 4.a2). The walls of the boring are subvertical, and its terminus is somewhat lifted above the trace floor (Fig. 4.a3). The diameter of this trace is somewhat shorter than 2 mm and its depth is about 0.5 mm. Not far from trace ε, trace ζ is a shallower pit with a hemispherical shape (Fig. 4.a2). Near the latter lesion, trace η crosses the gular-humeral sulcus (Fig. 4.a2). It is smaller than the former borings but similar in shape to trace ε. A few other bone modifications reminiscent of *Karethraichnus lakkos* occur on the humeral portion of GAMPS-01984, though these are too indistinct to be positively identified as trace fossils (Fig. 4.a1).

The small pits θ and ι occur on the external surface of epiplastron GAMPS-01967 (Fig. 5.a1). The former trace is found close to the inter-epiplastral symphysis. Its outline is subcircular, with a diameter of approximately 1 mm (Fig. 5.a2). Trace ι has an elliptical outline (Fig. 5.a3). It is a shallow, hemispherical depression with a smooth inner surface.

Three pits are found on the external surface of epiplastron GAMPS-01967, namely, κ, λ and μ (Fig. 5.b1-2). Trace κ is deeper than the others, whereas traces λ and μ are shallow pits occurring close to the gular-humeral sulcus.

Boring ν occurs on the external surface of costal GAMPS-01986, along the vertebral-pleural sulcus (Fig. 6.a1-3). Its diameter is about 1 mm, and its outline is irregularly subcircular. It is a shallow depression with a flattened floor.

All the studied specimens of *Karethraichnus lakkos* conform to the "Type I" borings of ZONNEVELD *et al.* (2022a: Fig. 14.A), *i.e.*, "shallow (<1 mm) circular pits etched into the external cortex". Trace ε may be an exception, as its 3D morphology is similar to the "Type III" of ZONNEVELD *et al.* (2022a: Fig. 14.C), *i.e.*, "flat-bottomed pits that terminate within the trabecular layer", although it does not penetrate the trabecular bone due to its limited depth.



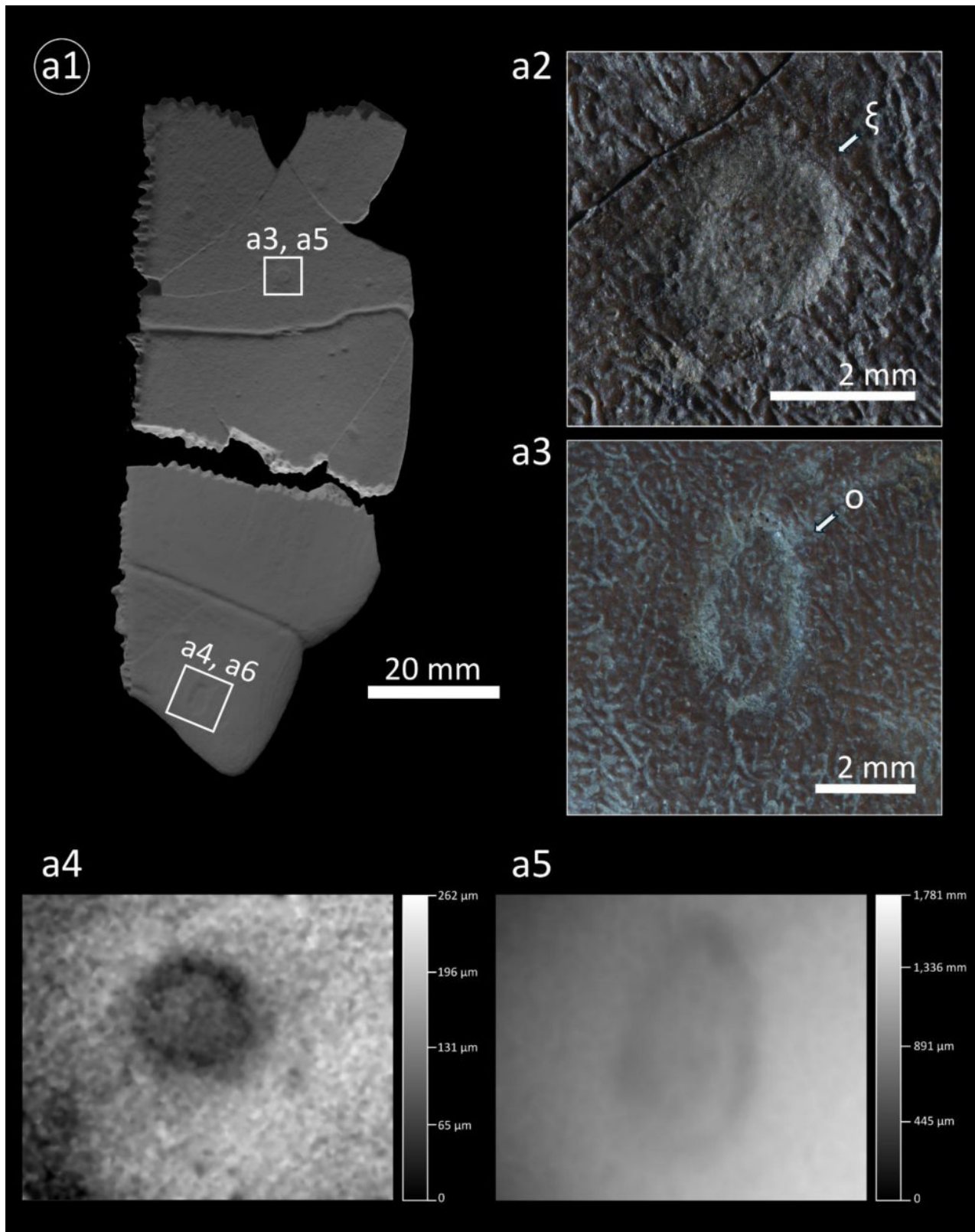


Figure 7: *Thatchtelithichnus holmani* borings on plastral bones of *Mauremys* sp. from the Pliocene of La Serra. (a1) GAMPS-00925, left hypoplastron and xiphiplastron, featuring traces "ξ" (a2) and "o" (a3) on their external surface. Panels a1 is a digital rendering of the textured photogrammetric 3D model. Panels (a2) and (a3) are photographs taken under low-angle artificial light. Panels (a4) and (a5) are depth maps of traces ξ and o, respectively.

**Ichnogenus *Thatchtelithichnus*****ZONNEVELD *et al.*, 2015**

This monotypic ichnogenus is represented by circular to subcircular, ring-shaped grooves that affect the external layer of the cortical bone. The signature character of these borings lies in the presence of an uplifted central element on the trace floor, which consists of an unmodified pedestal or a rounded nubbin. The trace walls are rounded, convex or sharp, and perpendicular to the substrate (ZONNEVELD *et al.*, 2015: Fig. 8.2iv-v, 2022a: Fig. 14.F). The trace may (or may not) penetrate the outer part of the trabecular bone. Its diameter is variable, ranging between 1.5–2 mm on Eocene terrapins from Wyoming, USA (ZONNEVELD *et al.*, 2015) and 7 mm on Miocene freshwater turtles from Wadi Moghra, Egypt (ZONNEVELD *et al.*, 2022b).

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

(Fig. 7)

Fossil occurrences: ZONNEVELD *et al.* (2015) first described this ichnospecies from the external surface of plastral bones of the geoemydid turtles cf. *Echmatemys* from the lower Eocene of Wyoming (USA). ZONNEVELD and BARTELS (2019) reassigned to *Thatchtelithichnus holmani* some rosette-like traces occurring on dinosaur long bones from the Jurassic of Wyoming. Two records reported on by COLLARETA *et al.* (2020a) are rediscussed herein. ZONNEVELD *et al.* (2022b) referred to *T. holmani* some pits observed on the plastron bottom of the terrapin *Erymnochelys* from the Lower Miocene of Wadi Moghra to *Thatchtelithichnus*.

Material examined herein: "ξ" and "o," two individual traces on the external (*i.e.* ventral) surface of partial plastron GAMPs-00925.

Description: COLLARETA *et al.* (2020a) described two shallow, ring-shaped scars occurring on the external surface of the partial plastron GAMPs-00925. These pits are refigured herein with the support of macroscope imaging (Fig. 7.a1-5). Trace ξ, a boring observed in the abdominal area of the left hypoplastron (Fig. 7.a2, .a4), is "a very shallow, circular depression, measuring ~3 mm in diameter, hosting at its centre a raised, rounded nubbin having a diameter of ~1.5 mm" (COLLARETA *et al.*, 2020a). The second scar, trace o, lies in the anal portion of the left xiphiplastron (Fig. 7.a3, .a5). It is "a rather elongate depression, measuring ~4×2.5 mm, with a central unmodified platform that extends for a distance of less than 1 mm from the outer edge of the trace" (COLLARETA *et al.*, 2020a).

**5. Discussion****INFERRED TRACEMAKERS**

Although the aetiology of the pits and holes observed on modern and fossil carapacial and plastral bones remains somewhat conjectural, it has been noted elsewhere that turtles are subjected to a broad spectrum of ecto- and mesoparasites, among which the producers of these bone modifications should be searched for (*e.g.*, M.L. FELDMAN & M.B. FELDMAN, 2011; CHRISTIANSEN *et al.*, 2020; ZONNEVELD & BARTELS, 2022, 2023). That all the traces dealt with in the present paper occur on the nonvisceral surfaces of the bony elements strongly suggests that trace production occurred due to some external agent while the host turtles were alive (ZONNEVELD *et al.*, 2015, 2022b; ZONNEVELD & BARTELS, 2022, 2023: table 2).

The three ichnotaxa recognised on the Tuscan Pliocene shell bones of *Mauremys* appear to be relatively widespread among extinct and extant turtles, although the studies dealing specifically with these issues remain few in number. *Gunnelllichnus moghraensis* occurs both on Mesozoic and Cenozoic materials as well as both on sea turtle and terrapin shell bones. JANSSEN *et al.* (2013) proposed that these bone modifications may be the result of anchoring by a variety of sessile, epibiotic macro-invertebrates. However, this interpretation has been argued against by several recent studies (ZONNEVELD *et al.*, 2015, 2022b; COLLARETA & BOSSELAERS, 2022; ZONNEVELD & BARTELS, 2022, 2023; GUERRERO *et al.*, 2024), which rather proposed that *Gunnelllichnus*-like traces are due to algal, bacterial and/or fungal infections of the turtle shell. Enlightening comparisons have been recently established with the lesions observed on modern freshwater turtles such as the red-eared terrapin, *Trachemys scripta elegans* (ZONNEVELD & BARTELS, 2022, 2023). Several diseases affecting primarily the epidermal scutes – *e.g.*, carapacial shell disease (CSD), necrotizing scute disease (NSD), pond turtle shell disease (PTSD), ulcerative shell disease (USD) and septicemic cutaneous ulcerative disease (SCUD) – can expand to eventually damage the shell bones in the form of more or less amorphous degradation patches (*e.g.*, LOVICH *et al.*, 1996; GARNER *et al.*, 1997; GRANADOS *et al.*, 2013; ROTHSCCHILD *et al.*, 2013; CHRISTIANSEN *et al.*, 2020). These lesions may be obliterated by subsequent pathological reaction features (*sensu* BERTLING *et al.*, 2006, 2022) (Fig. 8.a).

As for *Karethraichnus lakkos* and *Thatchtelithichnus holmani*, different groups of ecto- and mesoparasites have been proposed as the most likely tracemakers, depending on the hosts' lifestyle and environmental preferences. These include ixodid arachnids (ticks) as well as epizootic barnacles, which are thought to be prominent producers of the aforementioned traces on terrestrial and marine turtles, respectively (COLLARETA *et al.*



	Inferred tracemakers	Ichnotaxon	Description
	Bacteria, algae and/or fungi	<i>Gunnellichnus</i> cf. <i>moghraensis</i>	Shallow, wide depressions etched into the external cortical bone
	Leeches or spirorchid liver flukes	<i>Karethraichnus lakkos</i>	Hemispherical pits that penetrate through the external cortical bone into the underlying trabecular bone, featuring a circular to semicircular outline and smooth margins
	Leeches	<i>Thatchtelithichnus holmani</i>	Circular to subcircular, ring-like grooves etched into the external cortical bone

10 mm

Figure 8: Synoptic overview of the ichnological diversity observed on carapacial and plastral bones of *Mauremys* from the Upper Pliocene of La Serra. The descriptions and sketches of *Karethraichnus lakkos* and *Thatchtelithichnus holmani* are modified after ZONNEVELD *et al.* (2022b: Fig. 14.a). Abbreviations: eco, external cortex; tra, trabecular bone; ico, internal cortex.

al., 2022b; ZONNEVELD *et al.*, 2022a). In freshwater habitats, leeches are the most commonly reported parasites of terrapins (ZONNEVELD & BARTELS, 2022). When feeding, leeches attach themselves to their host with the posterior sucker, whereas a proboscis is extended from the oral opening of the anterior sucker and inserted into the turtle shell (e.g., SIDDAL & GAFFNEY, 2004; FEDIRAS *et al.*, 2017). Feeding is accompanied by the release of salivary secretions that may be capable of bone decalcification and digestion of the connective tissue matrix (SIDDAL & GAFFNEY, 2004), hence the leeches' ichnogenetic potential (ZONNEVELD & BARTELS, 2022). Similarly, some vermiform parasites such as the spirorchid liver flukes may also cause lesions on the carapace and plastron of aquatic turtles (e.g., JOHNSON *et al.*, 1998).

The feeding sites of extant leeches are often located in-between adjacent keratinous scutes (e.g., SIDDAL & GAFFNEY, 2004; FEDIRAS *et al.*, 2017). This is consistent with the observation of ZONNEVELD *et al.* (2015, 2022b) that *Karethraichnus lakkos* traces are especially frequent along the epidermal sulci. We were able to replicate this observation on the Tuscan Pliocene epiplastron GAMPS-01984 (trace η) as well as on the costal GAMPS-01986 (trace v).

Regardless of their taxonomic assignment, the main tracemakers of *K. lakkos* and *Thatchtelithichnus holmani* on turtle bones were likely parasites that prefer plastrons to carapaces, because these borings are more commonly observed on plastral materials. Plastrons provide a more sheltered location, which suggests that the tracemakers may be sensitive to exposure or desiccation (ZONNEVELD & BARTELS, 2022, 2023) (Fig. 8.b-c).

BROADER PALAEOECOLOGICAL INTERPRETATION

According to the palaeoenvironmental reconstruction proposed by GARASSINO *et al.* (2012), the Pliocene population of *Mauremys* discussed herein would have inhabited a coastal lagoon system not far from a river mouth and sheltered seaward by a chain of barrier islands. This is consistent with the broad habitat preferences of modern *Mauremys* spp., which include brackish water bodies such as coastal lagoons (e.g., SIDIS & GASITH, 1985; ERNST & BARBOUR, 1989; HIGHFIELD, 2002; VAMBERGER *et al.*, 2014).

In the present-day Mediterranean region, *Mauremys* is represented by *M. leprosa*, which inhabits the coasts of Northwestern Africa as well as in the Iberian Peninsula (KELLER & BUSAK, 2001), and by *M. rivulata*, which inhabits the Eastern Mediterranean (BARTH *et al.*, 2004). No native populations of *Mauremys* exist to date on the Apennine Peninsula, from which this genus was extirpated during the Pleistocene (CHESI, 2009; CHESI *et al.*, 2009). Previously, in Pliocene times, *Mauremys* inhabited Italy under a warmer and more humid climate than today (e.g., ALBIANELLI *et al.*, 1997; BERTINI, 2010; COMBOURIEU-NEBOUT *et al.*, 2015; PRISTA *et al.*, 2015). These palaeoenvironmental conditions may correlate with the stock of bioerosional features observed on the *Mauremys* shell remains from La Serra. In particular, diseases affecting the epidermal scutes have been proposed to be sensitive to changes in temperature, rainfall frequency and cloud cover as well as to vitamin deficiency (ZONNEVELD & BARTELS, 2023). Nowadays, *Gunnellichnus*-like shell lesions are especially frequent on freshwater turtle populations inhabiting persistently moist settings, where fungal



and bacterial infections do not dry out easily (e.g., ROSE *et al.*, 2001; PARÉ & JACOBSON, 2007) because of a low basking efficacy (ZONNEVELD & BARTELS, 2023).

6. Conclusions

We reported on the occurrence of different bone modifications on newly collected plastral and carapacial bones of the small terrapin, *Mauremys* sp., from Upper Pliocene deposits exposed at La Serra, a recently discovered palaeontological site in Pisa Province (Tuscany, central Italy). The recognised ichnotaxa include representatives of *Gunnellichnus* cf. *moghraensis*, *Karetharichnus lakkos*, and *Thatchtelithichnus holmani*. All the studied traces occur on the nonvisceral surfaces of the bones. As previously observed elsewhere, some *Karetharichnus lakkos* borings occur along the epidermal sulci that mark the border between adjacent keratinous scutes. Based on the relevant literature, the studied ichnofossils are interpreted as due to algal, bacterial and/or fungal infections (*Gunnellichnus* cf. *moghraensis*) as well as to the parasitic action of leeches and/or spirorchid liver flukes (*Karetharichnus lakkos* and *Thatchtelithichnus holmani*). A similar suite of traces has recently been reported from the shell bones of the extant red-eared slider, *Trachemys scripta elegans*, evoking similar tracemakers as well as a comparable ecology for our Tuscan Pliocene population of *Mauremys*. Previous studies have reconstructed the *Mauremys*-bearing strata at La Serra as comprising a brackish lagoon system, which matches well with the broad spectrum of environmental preferences of extant *Mauremys* spp. Our Tuscan Pliocene population of *Mauremys* lived under warm, humid conditions, which compares favourably with the observed stock of bioerosional features.

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