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The Youngest European Record of the Chelonian Family Trionychidae (Calabrian, Central Italy) Offers New Clues on the Quaternary Extirpation History of the Softshell Turtles

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Abstract: We report on the geologically youngest occurrence of the softshell turtle family Trionychidae in Europe, from middle Calabrian (Emilian) strata cropping out at Montalto, Pisa Province (Tuscany, central Italy). This record indicates that the softshell turtles survived well past the glacial pulse at ca. 1.8 Ma. That the most recent finds of Trionychidae all over Europe come from mainland Italy further evokes the role of the Apennine peninsula as a refugium for humid-dwelling herpetofaunas through most of the Plio-Pleistocene. Reduced humidity associated with the intensified cool stages at the beginning of the Early–Middle Pleistocene Transition may have been behind the demise of the last European softshell turtles.

Keywords: Early–Middle Pleistocene Transition; Early Pleistocene; Emilian; Fauglia; Late Villafranchian; Montalto; palaeoecology; palaeoherpetology; *Trionyx*; Tuscany

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1. Introduction

Softshell turtles (Testudines: Cryptodira: Trionychidae) are a bizarre family of freshwater chelonians in which the carapace lacks keratinous scutes, hence its leathery aspect. The shell of trionychids is also flexible due to its reduced skeleton that lacks peripherals, pygals and an ossified bridge [1]. Numbering some 35 species, the extant members of Trionychidae are rather widely distributed throughout the tropical to warm-temperate regions of Africa, Asia, New Guinea and North America [2–4].

Because of the idiosyncratic sculpturing on the external surface of their shell bones, the softshell turtles (including both stem- and crown-group trionychids) are readily recognised as such in the fossil record [1]. The oldest fossils of this kind suggest that the softshell turtle clade originated during the Early Cretaceous in Asia and then colonised all continents but Antarctica [1,5]. The oldest European fossils of (Pan-)Trionychidae date back to the Late Cretaceous of Sweden [6]. Softshell turtles remained widespread throughout Europe during the Paleogene, when they were found as far north as England and Denmark, but their range contracted southward during the Neogene, and the group eventually disappeared continent-wide [1]. That said, the Nile softshell turtle (*Trionyx triunguis*) still inhabits some of the Mediterranean coasts of the Near East [7], from where some individuals may reach the Greek islands of the Dodecanese [8].

In Italy, softshell turtle fossils are known from some 40 localities ranging in age from the Eocene to the Early Pleistocene and include some of the youngest European records of Trionychidae [1,9]. Here, we describe and figure a new trionychid find from upper Lower Pleistocene (Calabrian) strata cropping out at Montalto, Pisa Province (Tuscany, central Italy). The case is made for this specimen to represent the youngest softshell turtle occurrence in Europe. The paper concludes with a discussion of the timing and mechanisms leading to the extirpation of the European trionychids.

2. Geological Setting and Age

The study site is located within a large quarried area at Montalto (coordinates: 43°33′52″ N, 10°31′53″ E), in the Municipality of Fauglia (Pisa Province, Tuscany, central Italy) (Figure 1A). The national, regional and local geological cartographies agree that the marine deposits cropping out at the Montalto quarry belong to the local Lower Pleistocene succession, and specifically to the Sabbie di Nugola Vecchia Formation [10–12]. This formational assignment has been embraced by most recent works, albeit at times somewhat tentatively [13–16].

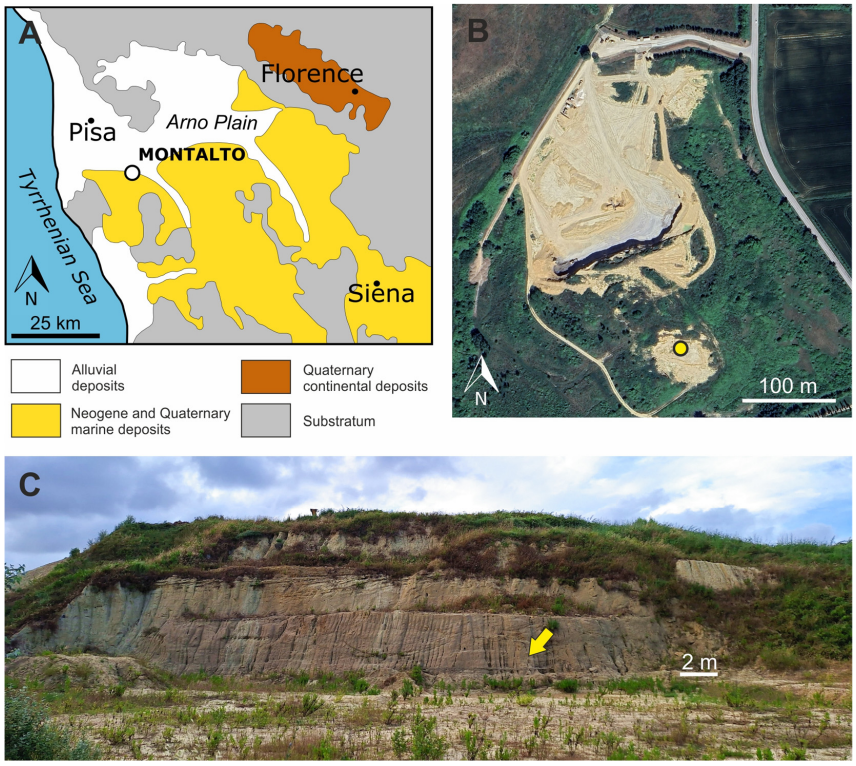

Figure 1. Geographic and geological setting. (**A**). Simplified geological map of Tuscany, showing the location of the study area (Montalto). (**B**). Satellite image of the Montalto quarry (after Google Earth); the yellow circle marks the outcrop that yielded the new trionychid find dealt with herein. (**C**). Landscape view of the quarry wall that yielded the new trionychid find dealt with herein, whose approximate discovery point is indicated by a yellow arrow.

The Sabbie di Nugola Vecchia Formation comprises fine, yellowish sands interbedded with conglomerates and calcarenites that have been referred to the Emilian substage of the 'Italian Mediterranean Marine Stages' regional scheme [17], which corresponds to the middle Calabrian (ca. 1.5–1.2 Ma [18]) [10,19–21]. Although uncertainties exist about the exact dating of these shallow-marine deposits, that the Sabbie di Nugola Vecchia Formation overlies basal Emilian sediments elsewhere along the Tuscan coast [10] can be taken as a further indication that the fossil-bearing strata dealt with herein are most likely younger than the Santernian substage (lower Calabrian; ca. 1.8–1.5 Ma).

A detailed characterisation of some of the deposits cropping out at Montalto (Figure 1B) was recently provided by Bosio et al. [14] and subsequently expanded by Mariani et al. [15]. The sedimentary succession described by these authors consists of alternations of sand and silt that feature an exceptionally preserved seagrass (*Posidonia oceanica*) meadow, an extensive coral (*Cladocora caespitosa*) bank and an oyster (*Ostrea edulis*) reef, in ascending stratigraphic order. These fossil-bearing strata testify to a marginal-marine, somewhat protected palaeoenvironment that became progressively shallower, from 10–35 m water depth (estimated for the seagrass meadow) to less than 5–10 m water depth (estimated for the oyster reef) [14–16]. The few vertebrate finds that are known to date from the Montalto quarry include an isolated monachine seal calcaneum [13] and rare elasmobranch teeth [14,22].

The turtle fossil dealt with in the present paper was collected by one of us (S.C.) from a newly investigated outcrop in the southern sector of the Montalto quarry (coordinates: 43°33′48″ N, 10°31′56″ E) (Figure 1B). Here, channeled sandy deposits occur along a vertical quarry wall (Figure 1C). The floor of the channels is mantled by rounded pebbles, and cross-stratification is widespread (Similar structures have been reported from other outcrops of the Sabbie di Nugola Vecchia Formation, and interpreted as testifying to beach cusps [10]). Macrofossils, consisting of common oysters and much rarer pectinids, are especially frequent in the conglomeratic bodies (note that oysters and pectinids are the commonest macrofossils throughout the Sabbie di Nugola Vecchia Formation [10]). Marine bioerosional traces (*Entobia* and *Gastrochaenolites*) are often observed on the oyster valves. This cross-stratified interval is capped by an oyster reef consisting of clusters of small oysters with rarer pectinids and encrusting barnacles. Overall, these deposits were laid down in a high-energy, marginal-marine, very shallow setting, not deeper than 5–10 m in occurrence of the oyster reef. Geometric considerations suggest that the sediments exposed at this outcrop may be partly laterally equivalent to those figured by Chirli and Forli ([23]: Figure 2), which in turn occur at a nearby quarry sector that is now largely covered by vegetation.

3. Methods

Photographs of the specimen were taken with a Nikon© D850 camera equipped with an AF-S VR Micro-Nikkor 105 mm f/2.8 G IF-ED macro lens. A textured 3D model was elaborated in the Agisoft Metashape software (v. 1.6.0) by masking and aligning 102 photographs. This photogrammetric model can be downloaded from the Supplementary Material File S1. Digital renderings of the photogrammetric model were obtained with Blender 3.6.9 and then assembled with Inkscape 1.3.1 to build up Figure 2.

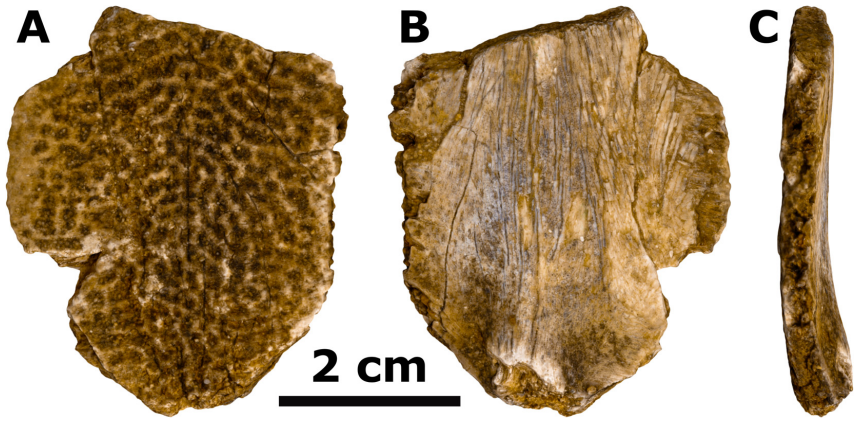

Figure 2. GAMPS-01943, costal plate of Trionychidae gen. et sp. indet. from the Lower Pleistocene (Emilian, middle Calabrian) of the Montalto quarry (Municipality of Fauglia, Pisa Province, Tuscany, central Italy), in (**A**) dorsal, (**B**) visceral and (**C**) profile views. All views are digital renderings of the photogrammetric model.

4. Systematics

Testudines Batsch, 1788 [24]
Cryptodira Cope, 1868 [25]
Trionychidae Bell, 1828 [26]
Trionychidae gen. et sp. indet.
(Figure 2).

4.1. Material

A fragmentary costal plate, currently stored at Badia a Settimo (Scandicci, Italy), in the permanent exhibition of "Gruppo AVIS Mineralogia e Paleontologia Scandicci" (=GAMPS), under accession number GAMPS-01943.

4.2. Occurrence

Lower Pleistocene (Emilian, middle Calabrian) deposits exposed at the Montalto quarry (coordinates: 43°33′48″ N, 10°31′56″ E).

4.3. Description

GAMPS-01943 (Figure 2) is a relatively small proximal fragment of a costal plate. Its anteroposterior length, measured perpendicular to the direction of the costal rib, is 36 mm, whereas its maximum preserved mediolateral width is 44 mm. Most of the margins of GAMPS-01943 are neat broken surfaces due to pre-burial damage, but a sutural edge with an adjacent costal is well preserved overall (Figure 2C). A sculpturing pattern consisting of salient, vermiculating ridges is apparent across the dorsal surface of the bone (Figure 2A). A broken rib process is preserved on the visceral surface of GAMPS-01943, at its proximal preserved end (Figure 2B).

4.4. Taxonomic Identification

The distinct, relatively coarse sculpturing pattern of GAMPS-01943 is consistent with an assignment to the trionychids, rather than with an attribution to other chelonian groups provided with ornamented shells such as the carettochelyids (whose youngest occurrence in the Euromediterranean region dates back to the Middle Miocene of Libya [27]) and some cheloniids (e.g., the Neogene *Trachyaspis* [28]). That the dorsal surface of this fragmentary bone does not feature any epidermal scute sulcus is further suggestive of softshell affinity [28].

Small differences in the sculpturing patterns were once used by vertebrate palaeontologists to distinguish between different fossil taxa of Trionychidae, but these are now known to have limited diagnostic value, which complicates the subfamilial identification of trionychid shell fragments [28–30]. At present, there is no evidence whatever of softshell turtle genera other than *Trionyx* in the Plio-Pleistocene of Europe [1], nor in the whole fossil record of Italy [9]. Therefore, GAMPS-01943 is likely representative of *Trionyx*, whose only extant species (*T. triunguis*) still inhabits some of the Mediterranean coasts of Africa and Asia Minor [7]. That said, GAMPS-01943 does not preserve any character that may be regarded as diagnostic below the family level, hence its referral to Trionychidae gen. et sp. indet.

5. Discussion

GAMPS-01943 does not display the kind of rounded edges and polished aspect that are instead typical of reworked fossil bones [31–34], including turtle shell bones [35]. Thus, the geological age of the sediments from which GAMPS-01943 was collected should be taken as a strong suggestion of the occurrence of softshell turtles in Tuscany as late as the middle Calabrian. The marginal-marine nature of the deposits that yielded this specimen is by no means anomalous, as trionychid fossils are often found in seaborne sediments, either because of occasional marine habits or due to being washed into the sea peri- or post-mortem [1,28]. The peculiar Emilian palaeoenvironment of Fauglia, consisting of a shallow bay protected from strong storm waves [15], is superficially reminiscent of some

marginal-marine settings frequented by the extant *Trionyx triunguis* (e.g., the Luanda Bay of Angola [7]).

Over the course of the Neogene, the distribution of the European softshell turtles (including the genera *Trionyx* and *Rafetus*) contracted southward, as shown by the fact that Miocene fossils are known from Austria, Cyprus, Czechia, France, Georgia, Greece, Hungary, Italy, Moldova, Portugal, Romania, western Russia, Slovakia, Slovenia, Spain, Switzerland, Turkey and Ukraine, whereas Pliocene fossils are only known from Greece, Italy, France and Romania [1]. Some of the youngest European records of Trionychidae have been recently reappraised by Avrithis and Georgalis [36]. These authors focused on newly reported fossils from the Piacenzian–Gelasian (Mammal Neogene zones MN 16 or 17) of Kos (Dodecanese Islands, Greece) as well as on historical finds from the Lower Pleistocene locality of San Giovanni Valdarno (Tuscany). The former finds come from a setting that was likely connected to the nearby southwestern portion of the Anatolian peninsula (itself part of the present-day range of *T. triunguis* [3,7]) until most of the Early Pleistocene at least. Considering that *T. triunguis* ventures into the marine realm, and that a few neontological observations of vagrant Nile softshell turtles originating from Anatolia exist for the Dodecanese Islands (including the waters off Kos [37]), it may be argued that these fossils could shed more light on the Pleistocene circumstances of the Anatolian trionychids than on the late history of the softshell turtles of mainland Europe. The finds from the Upper Valdarno originate from the western (i.e., Tyrrhenian) side of the Apennine peninsula, which was part of Europe proper in Early Pleistocene times as it is today. The age of the trionychid-bearing outcrops from San Giovanni Valdarno (Montecarlo and Colombaiolo [38]) spans across the Gelasian–Calabrian boundary (ca. 1.9–1.7 Ma [39,40]). Thus, given their earliest Calabrian minimum age, the trionychid fossils from San Giovanni Valdarno are younger than those from Kos but older than the middle Calabrian specimen GAMPS-01943, which in turn represents the youngest European occurrence of the family Trionychidae as well as of the entire clade Trionychia (Trionychidae + Carettochelyidae and basal forms). That the youngest softshell turtles of Europe come from the Apennine peninsula further evokes the latter's role as a refugium for humid-dwelling herpetofaunas through most of the Plio-Pleistocene [36]. That said, the Pleistocene record of Trionychidae is arguably too fragmentary to allow for drawing definitive conclusions on their last European shelters, as shown by the fact that trionychids were not included in Macaluso et al.'s [41] analyses of the palaeoenvironmental suitability of the major Mediterranean peninsulas as biodiversity refugia for reptiles and amphibians due to a shortage of occurrence data.

The tempo and mode of the disappearance of the European Pleistocene softshell turtles remains an open question. According to Georgalis and Joyce [1], the presence of trionychid remains in the fossil record does not reveal much about the corresponding paleoenvironments beyond the presence of permanent bodies of water; in light of this, the quest for the history and causes of the extirpation of the European softshell turtles may prove frustrating. Nonetheless, some potentially insightful considerations can still be drawn based on the life history of the living members of Trionychidae as well as on the available fossil record thereof.

Our find from Montalto indicates that the European softshell turtles survived well past the Gelasian–Calabrian transition and the corresponding early glacial pulse (MIS 64-63-62 [42]) to persist into the middle to late part of what is known among Quaternary palaeontologists as the late Villafranchian Mammal Age [43]. This datum should be read against Georgalis and Joyce's [1] observation that the present-day trionychids occur globally in tropical to temperate regions, including cool continental areas of North America and Asia, and that their northern distribution appears to be limited by the availability of suitable nonfrozen habitat for hibernating in combination with summers of sufficient length to allow the hatchlings to emerge prior to the subsequent winter. Thus, although factors such as predation and interspecific competition may have also been at play, it is tempting to hypothesise that reduced humidity associated with harsher winters at the beginning of the Early–Middle Pleistocene Transition (also known as the Mid-Pleistocene Transition;

ca. 1.4–0.4 Ma [44]) were behind the demise of the last European softshell turtles. Indeed, the Italian pollen record between 1.4 and 1.3 Ma is suggestive of cooling, with winter temperatures decreasing at both interglacial maxima and glacial minima; during the same interval, annual rainfall decreased, with cool stages becoming particularly arid [45]. These new conditions may have proven unsuitable for the persistence of Trionychidae in their southern European strongholds, particularly in periods characterised by relatively short warm seasons in the Northern Hemisphere [46]. If this interpretation is correct, then the European softshell turtles may have become extinct before or about the end of the Emilian.

6. Conclusions

We reported on a fragmentary fossil costal plate belonging to an indeterminate softshell turtle from a middle Calabrian locality of Tuscany, central Italy. Based on stratigraphic considerations, we argued that this specimen represents the geologically youngest find of the family Trionychidae in Europe. The last European softshell turtles may have inhabited the Apennine peninsula at the beginning of the Early–Middle Pleistocene Transition, when reduced rainfall associated with the intensified cooling would have proven unsuitable for these humid-dwelling chelonians, thus leading to their eventual extirpation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/geosciences14090239/s1, File S1: Textured photogrammetric model of GAMPS-01943 (OBJ, MTL and JPG files).

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