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The last of the large-sized tortoises of the Mediterranean islands

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Archaeological investigations carried out in the cave Zubbio di Cozzo San Pietro, Bagheria, Sicily, revealed the presence of a few skeletal elements of a large-sized tortoise in a funerary area dating to the Copper/Bronze Age. The tortoise has been AMS-dated revealing an age of 12.5 ± 0.5 kyr BP and therefore it pre-dates the funerary activities. The morphology of the retrieved skeletal elements differs from that of the only native tortoise currently living in Sicily, *Testudo hermanni*. The tortoise's size significantly exceeds the size range of extant *Te. hermanni* and all *Testudo* spp., as well as that of their known fossils, and suggests a shell length of 50–60 cm. Repeated efforts to obtain DNA sequences from the tortoise of Zubbio di Cozzo San Pietro failed, but the morphology of the femur is distinct enough to allow us to erect a new taxon, ***Solitudo sicula* gen. et sp. nov.**, based on a parsimony analysis. It belongs to a hitherto unrecognized clade that includes other large-sized tortoises from Mediterranean islands, like Malta and Menorca. A review of the pertinent taxa indicates that the remains here described represent the geologically youngest large-sized tortoise of the Mediterranean area.

ADDITIONAL KEYWORDS: ancient DNA – insular faunas – Italy – latest Late Pleistocene – parsimony – Sicily – Testudinidae.

INTRODUCTION

The tortoise family Testudinidae has an almost global distribution and occurs on all continents, except Antarctica and Australia, and on many islands (TTWG, 2021). The group has an extensive fossil record, testament to a former much wider distribution and higher diversity, e.g., Kuhn (1964); Auffenberg (1974); de Lapparent de Broin (2002); Luján *et al.* (2014); Vlachos *et al.* (2014); TEWG (2015); Pérez-García *et al.* (2017); Vlachos & Rabi (2018); Georgalis *et al.* (2021). Large- and giant-sized tortoises, here arbitrarily defined by a straight shell length of 40–75 cm and over 75 cm, respectively, evolved independently in

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several lineages, without a clear connection between large body size and the occurrence on islands (Vlachos & Rabi, 2018, and references therein). Most of these large and giant tortoises are now extinct, and many of these extinction events occurred during the Pleistocene and Holocene, at least in some cases due to human involvement (TEWG, 2015, and references therein).

Thriving for many millions of years in mainland Europe, the circum-Mediterranean area and the Mediterranean islands, large-sized and giant tortoises are today extinct in these regions (Fig. 1); see also de Lapparent de Broin (2002), Pérez-García & Vlachos (2014) and Georgalis *et al.* (2021). The last giant tortoises on the European mainland date to approximately 2.0 Mya (Pérez-García *et al.*, 2017). In the Mediterranean islands, the oldest insular remains of large-sized tortoises are known from the Late Miocene (Tortonian) of the 'palaeo-island' of Scontrone, Italy (Georgalis & Delfino, 2021), but the remainder of the giant or large-sized taxa of these islands occurred much later, with the youngest records being from the Middle Pleistocene of Malta (Leith-Adams, 1877), Sicily (Bonfiglio *et al.*, 1997, 2003) and Formentera (Luján *et al.*, 2017), the lattermost being particularly young, having been dated at around 195 kya (Filella-Subirà *et al.*, 1999).

The taxonomy of large and giant fossil tortoise species has been puzzling for decades, and only recently have we started to understand their true diversity and their relationships. Historically, all giant tortoise species were considered as members of *Testudo* Linnaeus, 1758 (a name now restricted to five extant species and their closely related, extinct taxa; TTWG, 2021), like the majority of other tortoises, and were later transferred into other 'wastebasket genera', in particular *Cheirogaster* Bergounioux, 1935 and *Geochelone* Fitzinger, 1835 (Bergounioux, 1935; Hummel, 1935; Kuhn, 1964; Auffenberg, 1974; de Broin, 1977; Fritz & Bininda-Emonds, 2007; Georgalis & Kear, 2013; Luján *et al.*, 2014; Vlachos *et al.*, 2014).

Recent investigations provided evidence that the extinct European giant tortoises were neither monophyletic nor belonged necessarily to one of these two genera. Some of them represented stem Testudinidae, e.g. *Fontainechelon* Pérez-García *et al.*, 2016, *Pelorochelon* Pérez-García *et al.*, 2016 and other probable stem Testudininae, for example

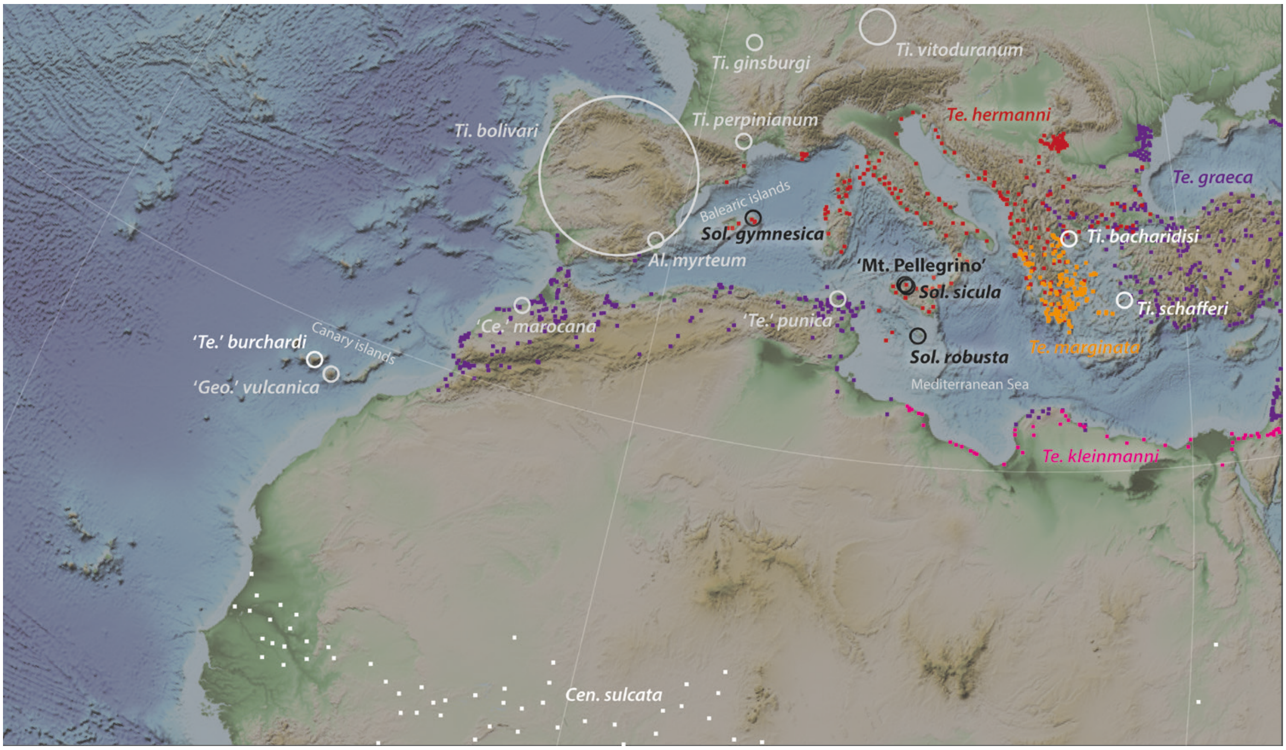

Figure 1. Map of the circum-Mediterranean area and northern Africa showing the distribution of extant species of tortoises (filled squares), based on the data of TTWG (2021): *Te. graeca*; *Te. hermanni*; *Te. marginata*; *Te. kleinmanni*; *Centrochelys sulcata*, and other large and giant tortoises from the Neogene-Quaternary either included in our analysis or mentioned in the text. Map generated in GPlates 2.2.0, using the 1 arc minute resolution topography of Amante *et al.* (2009).

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Cheirogaster s.s., *Taraschelon* Pérez-García, 2015 (Pérez-García & Vlachos, 2014; Pérez-García *et al.*, 2016, 2017), whereas some hold more derived positions in the Geochelonini crown group, for example *Alatochelon* Pérez-García, Vlachos & Murelaga, 2020 and *Titanochelon* Pérez-García & Vlachos, 2014 (Pérez-García & Vlachos, 2014; Vlachos & Rabi, 2018; Pérez-García *et al.*, 2020). Therefore, our current understanding emerging from a growing body of research suggests that these tortoises correspond to several distinct lineages that were once grouped together simply because of their large shell size. These lineages have a complicated and yet unclear palaeobiogeographical history, but at least some of the more derived lineages originated in Africa (Pérez-García *et al.*, 2020).

The taxonomy of the large-sized extinct species from the islands of Malta (Leith-Adams, 1877; Tagliaferro, 1913), the Balearic Islands (Eivissa, Formentera, Mallorca and Menorca) (Bate, 1914; Mercadal & Pretus Real, 1980; Bour, 1985; Luján *et al.*, 2017) and Sicily (Burgio & Cani, 1988; Bonfiglio *et al.*, 1999; Delfino, 2002; Chesi, 2008), as well as the Canary Islands [Gran Canaria (López-Jurado & Mateo, 1993) and Tenerife (Ahl, 1925; Bravo & Coello, 1975; Hutterer *et al.*, 1998)], is still in a state of flux (Luján *et al.*, 2014, 2017; Pérez-García & Vlachos, 2014; TEWG, 2015; Georgalis *et al.*, 2021). Many of these giant species were described as members of the genus *Testudo* (Leith-Adams, 1877; Tagliaferro, 1913; Bate, 1914; Ahl, 1925). However, a later discovered species from Gran Canaria was assigned to *Geochelone* (*Geochelone vulcanica* López-Jurado & Mateo, 1993). Recently these taxa have been either associated with *Titanochelon* Pérez-García & Vlachos, 2014 or with the African genus *Centrochelys* Gray, 1872, at least tentatively (TEWG, 2015; Georgalis *et al.*, 2021).

In the present study, we report new remains probably, but not demonstrably, belonging to a single specimen of a previously unknown large-sized tortoise from the latest Pleistocene of Zubbio di Cozzo San Pietro, a tectonic cave on the slopes of Monte Catalfano in Bagheria, Palermo, Sicily (Fig. 2) (Valenti *et al.*, 2017; Battaglia *et al.*, 2020), and discuss its relationships. Because our repeated efforts failed to obtain DNA sequences from the material, even though we applied sophisticated Next Generation Sequencing (NGS) approaches optimized for sequencing ancient DNA from subfossil material [Supporting Information (Appendix S1); see also Kehlmaier *et al.* (2017, 2019, 2021)], the following assessment is based exclusively on morphology.

The pubis ZCSP US.2-Q4 was Accelerator Mass Spectrometry (AMS) dated at the Center for Isotopic Research on Cultural and Environmental Heritage (CIRCE), Napoli, revealing an age of 12.5 ± 0.5 kyr BP and therefore providing evidence that the ZCSP specimen from Sicily represents the youngest record

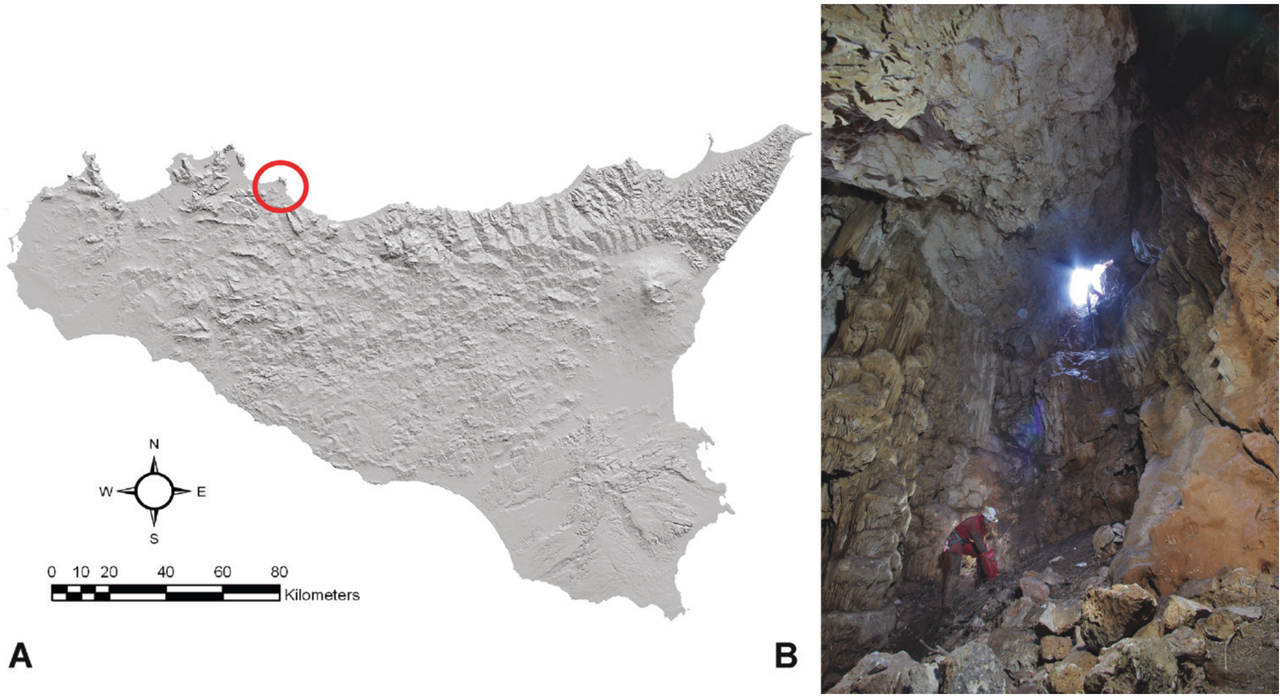

Figure 2. Map of Sicily, showing the location of the cave Zubbio di Cozzo San Pietro (A). Base of the pit-hole of the cave entrance (B).

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of a large-sized tortoise species in the Mediterranean area. This record bridges a gap of at least 300 kyr [the estimated age of the faunal complex that follows the one hosting the giant tortoises from Alcamo and the Ragusa area (Masini *et al.*, 2008)], from the previously known youngest findings of giant tortoises in the Sicilian-Maltese area, and provides firm evidence for the occurrence of large-sized tortoises in the western Mediterranean during the latest Pleistocene.

INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History, New York, USA; LGPUT: Laboratory of Geology and Palaeontology, University of Thessaloniki, Thessaloniki, Greece; MDHC: Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino, Torino, Italy; MEF: Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; MGUP: Museo Geologico Università Palermo, Palermo, Italy; MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain; MTD: Museum of Zoology, Senckenberg Dresden, Dresden, Germany; MUZSP: Zoological Museum of Sao Paolo, Sao Paolo, Brazil; NHMUK: Natural History Museum, London, United Kingdom; NHMW: Naturhistorisches Museum, Vienna, Austria; PPC: Peter Pritchard Collection Chelonian Research Institute, accessed in Oviedo, Florida, now in Ojai, California, USA; ZCSP: Zubbio di Cozzo San Pietro Cave, material deposited at Laboratorio di Antropologia, Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche, Università di Palermo, Palermo, Italy.

LOCALITY INFORMATION

The Zubbio di Cozzo San Pietro Cave (ZCSP), is located in the Municipality of Bagheria, near Palermo, in north-western Sicily, Italy (Fig. 2). The cave opens at 298 m a.s.l. and has a tectonic origin, being set along a SE-NW oriented fracture. ZCSP has a drop of 17 m and a spatial development of 44 m; the entrance consists of a large inclined well about 13 m deep. A landslide cone occupies the entire area at the base of the well. A few metres below, a second room opens, characterized by a series of large stalagmites, formed under a discontinuity, also SE-NW oriented. This separates the entrance area from the vast dome-shaped room of over 200 m^2. The bottom of the ZCSP is completely filled with a thin layer of compact dark brown sediment and small rocky blocks coming from debris flows (Valenti *et al.*, 2017). During inspections, several points of the cave with a concentration of faunal, archaeological and human remains were identified (see Figure S1 in the Supporting Information). Among the archaeological finds on the surface there is a wide chronological range of potsherds ranging from recent prehistory to late antiquity. In some cases, the finds can be thought to have fallen in from the outside accidentally. As for point A (Supporting Information, Figs S1, S2), where the tortoise remains were found, it consists of a natural niche placed at a depth of 15.4 m, located in the south-east portion of the vast underground environment. The choice of this area for the excavation was also based on the type of finds and their association: human bones, ceramic fragments, lumps of red ochre and obsidian suggest the presence of a prehistoric burial area. The entire funerary area is characterized by disturbance caused by human and/or animal activity, which has strongly influenced the state of conservation of the findings and stratigraphy. Almost all of the osteological finds are fragmented.

The archaeological finds at point A, including five pottery fragments, constitute a limited but definitely interesting sample. Anthropological analyses covered 1838 human osteological findings, 70% of which were identified at an anatomical level. The archaeological and zoological survey was carried out on an osteological sample made up of 1089 remains, 629 of which (58%) were identified at the species level (Battaglia *et al.*, 2020). Repeated burial actions, although the contribution of animal activity cannot be ruled out, altered the original stratigraphy and account for the different layers of provenance of the four skeletal elements belonging presumably, but not demonstrably (see below), to the same tortoise individual and, therefore, required the numerical dating of one tortoise sample.

MATERIAL AND METHODS

FEMUR MORPHOTYPES AND CHARACTER CODING

In the absence of ancient DNA information, the preserved bone elements pose a challenging situation to reach a conclusion on the taxonomic affinities of the ZCSP tortoise. As such, the only element that provides some taxonomic insight is the femur. Luckily, femora are among the most common and best-preserved elements in the circum-Mediterranean fossil tortoise record. Therefore, it is necessary to describe the context in which we are analysing the new material from Sicily by providing a review of the Pleistocene large-sized to giant tortoises of the Mediterranean area and part of Macaronesia (see below).

Here, we compare the Sicilian femur using eight well-defined characters that are illustrated in Figure 3:

(1) The proximal fusion of the trochanters. Sampled insular species show an incomplete fusion (state 1) of the trochanters, which appear to be separated proximally, compared to other testudinids whose trochanters are fully fused proximally and connected by a ridge (state 2). Other, non-testudinid turtles show trochanters that are not fused (state 0).

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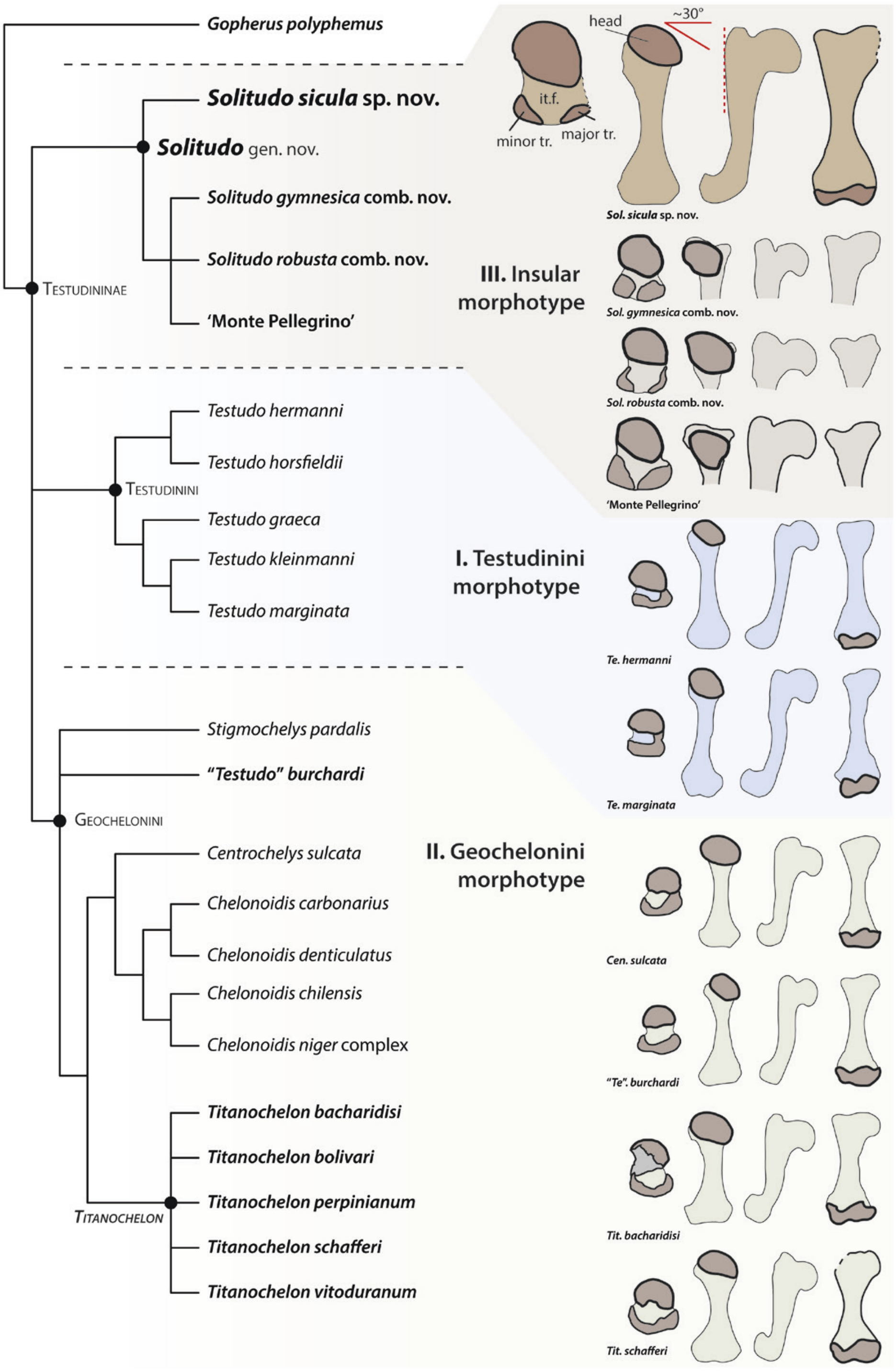

Figure 3. Consensus tree of the seven most parsimonious trees of 5469 steps, resulting from the cladistic analysis of extant and extinct tortoises (22 taxa scored for 177 morphological characters). The femora of the circum-Mediterranean tortoises represent three morphotypes that are independent from body size. They belong mostly to two different morphotypes (I, II) that show a phylogenetic signal within Testudininae, i.e. Testudinini vs. Geochelonini, whereas insular tortoises from the Mediterranean show a different morphotype (III). The simplified drawings are not to scale. Abbreviations: major tr.: major trochanter; minor tr.: minor trochanter.

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(2) The extension of the trochanters relative to the femoral head. This is a difficult character as its interpretation might be affected by the orientation of the bone. Here, we place the flat ventral surface of the femur below the head in a vertical orientation and observe the extension of the trochanters relative to the highest point of the femoral head. In most tortoises the trochanters are at the same level or extending well beyond (state 0), whereas Testudinini have trochanters that do not extend beyond the femoral head (state 1).

(3) The orientation of the elongated axis of the femoral head compared to the anteroposterior plane. In most tortoises, the elongated axis of the femoral head is clearly oblique compared to the anteroposterior plane, between 25° and 45° (state 1). However, some Geochelonini show less oblique femoral heads, forming an angle that is less than 25° with the anteroposterior plane (state 2). Other turtles and some tortoises often show an oblique femoral head, developed at an angle equal to or greater than 45° compared to the anteroposterior plane (state 0).

(4) The presence of dorsoventral curvature in the distal part of the femur. Most tortoises have a distal part of the femur that is moderately curved (state 1), whereas some Geochelonini have distal parts that are almost straight (state 2). However, other turtles and some tortoises might have a curved distal part of the femur (state 0).

(5) The thickness of the diaphysis. Most tortoises have a slender diaphysis (state 0), but some Geochelonini have a diaphysis that is much thicker compared to their length (state 1).

(6) The extent of the ridge connecting the tibial and fibular condyles ventrally, which are developed but reduced in the insular species and Testudinini (state 1), and well-developed and extensive in Geochelonini (state 2). These character states contrast the condition seen usually in non-testudinid turtles that do not show such a ridge (state 0).

(7) The presence of a connection between the major trochanter and the femoral head, delimiting the intertrochanteric fossa posteriorly, in some tortoises (state 1), and the absence of such connection in others, including the insular species (state 0).

(8) The shape of the femoral head, which is clearly elliptical in most tortoises (state 1), whereas many insular species have a projection that creates an almost rounded triangular shape e.g. see '*Testudo*' *gymnesica* (state 2). Other outgroup turtles could also have spherical femoral heads (state 0).

These new characters have been added to those by Vlachos & Rabi (2018), in addition to modification of their character #157 (fusion of the trochanters of the femur). The various character states are given in the corresponding nexus file (see Supporting Information, Appendix S2). We selected testudinid taxa for which we have data on the femur, including extant taxa representative of all different testudinid clades, as well as relevant extinct tortoises. In particular, we scored the femur ZCSP US.0-Q2, femora of *Testudo graeca* Linnaeus, 1758 (MTD), *Testudo hermanni* Gmelin, 1789 (MDHC), *Testudo horsfieldii* Gray, 1844 (MDHC), *Testudo kleinmanni* Lortet, 1883 (MTD), *Testudo marginata* Schoepff, 1789 (MDHC), *Gopherus polyphemus* (Daudin, 1802) (outgroup, AMNH), *Stigmochelys pardalis* (Bell, 1828) (MNCN), *Chelonoidis carbonarius* (Spix, 1924), *Chelonoidis denticulatus* (Linnaeus, 1766) (MUZSP) and the *Chelonoidis niger* (Quoy & Gaimard, 1824) complex (PPC), two specimens of *Chelonoidis chilensis* (Gray, 1870) (MEF), the femora of '*Testudo*' *gymnesica* Bate, 1914 (NHMUK), '*Testudo*' *robusta* Leith-Adams, 1877 [NHMUK; see TEWG (2015) for the synonymy of names erected on the basis of Maltese remains], the unnamed taxon from Monte Pellegrino (MGUP), *Centrochelys sulcata* (Miller, 1779) (MNCN), *Titanochelon bacharidisi* (Vlachos *et al.*, 2014) (LGPUT) and *Titanochelon schafferi* (Szalai, 1931) (NHMW) based on personal observations, and the femur of '*Testudo*' *burchardi* Ahl, 1925 based on the figures of Ahl (1925).

The matrix for 177 characters and 22 taxa was constructed in MESQUITE 3.7 (Maddison & Maddison, 2019) and is given in the Supporting Information (Appendix S2). The taxon sampling aims to capture the femur morphotype of the possible candidate sister taxa of the ZCSP tortoise: extant small-sized testudinids e.g. *Te. hermanni* or both extant and extinct large-sized mainland and insular tortoises from the circum-Mediterranean area. The final matrix also contains a part of the total evidence matrix of Vlachos & Rabi (2018), including all the modifications in some scorings published since then (20 177 characters × 22 taxa). The total evidence matrix was analysed in TNT 1.5 (Goloboff & Catalano, 2015), under two rounds of Tree Bisection Reconnection (TBR; 1000 replicates).

RESULTS

Phylogenetic analysis

The cladistic analysis recovered seven most-parsimonious trees of 5469 steps (best score hit 1000/1000), whose consensus tree is given in Figure 3. According to our analysis, the femora of the circum-Mediterranean tortoises represent three morphotypes that are independent from body size and correspond well to the phylogeny of the most exclusive tribe-level clades: (I) a 'Testudinini morphotype', with femora that have clearly elliptical, oblique and narrow heads, slender diaphysis, narrow neck, a major trochanter that connects to the head, trochanters that are joined proximally but do not extend beyond the femoral

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head proximally, and less extended distal ridges; (II) a 'Geochelonini morphotype', with femora that have less oblique but still elliptical heads, thicker diaphysis, thicker neck and trochanters that are fully joined proximally; and (III) an 'insular morphotype', with slender femora, whose trochanters are separated proximally (note that the morphology of the distal part of these femora is mostly unknown) and femoral heads that are not elliptical in shape. Although these three morphotypes correspond to these three monophyletic clades, the position of the insular clade/morphotype remains unresolved because of the absence of other anatomical information from the shell, skull and skeleton. Based on the available information, the insular clade is supported by one synapomorphy (the incomplete fusion of the trochanters), whereas the most exclusive clade that contains the Maltese and Monte Pellegrino taxa is supported by one more synapomorphy (the elliptical shape of the head with a triangular projection). Albeit the support for the distinction of this clade is minimum, it is actually common to define clades including fossil taxa based on single synapomorphies. As we are unable to observe this femur morphology in any other extant or extinct species of tortoise available for observation and the notion that such a grouping would make sense from a palaeobiogeographical point of view, we have some confidence to formally recognize this clade at the generic level (see next section).

Our morphological analysis reveals that the ZCSP tortoise femur has a mixture of characteristics that define the recovered morphotypes I and III. On one hand, the trochanters of the ZCSP femur are clearly separated proximally as in the insular extinct tortoises '*Te.*' *gymnesica* and '*Te.*' *robusta*. On the other hand, and because these remaining insular taxa do not preserve the distal part of the femur, the ZCSP femur also shows some similarities with the morphotype I that defines extant small-sized tortoises from the Mediterranean and especially on the shape of the distal part and the femoral head that is clearly elliptical. Still, our analysis clearly places the ZCSP femur in the insular clade/morphotype. Finally, the ZCSP femur is clearly different from the morphotype II that defines the extant *Centrochelys* and extinct *Titanochelon*, both large-sized tortoises. Another outcome of the analysis is that not all insular tortoises share the same femur morphotype. While '*Te.*' *gymnesica*, '*Te.*' *robusta* and the Monte Pellegrino taxon show the morphotype III, the femur of '*Te.*' *burchardi* from the Pleistocene of Tenerife ['*Centrochelys*' *burchardi* in Georgalis *et al.* (2021)] is different from the known femora of the insular Mediterranean taxa [the large-sized testudinid from Scontrone is not represented by femora (Georgalis & Delfino, 2021)] and is much more similar to the femora of mainland large-sized tortoises (morphotype II). As such, this taxon is recovered in an unresolved position at the base of Geochelonini. Although not included in our analysis, to avoid unnecessary increase in taxon sampling given the limited character sampling, a similar situation is to be expected for '*Centrochelys*' *vulcanica*, the other Canarian taxon described by Lopez-Jurado & Mateo (1993) and recently commented on by Georgalis *et al.* (2021). Although that femur is not complete, the preserved morphology is much closer to '*Te.*' *burchardi* and to the morphotype II based also on personal observations of E. Vlachos.

In the absence of additional evidence from DNA and morphology, it is difficult to interpret the utility of these three morphotypes in terms of phylogenetic placement, but there is sufficient phylogenetic signal that permits to at least identify the Mediterranean femora at the generic or tribe level. How the insular morphotype fits in this scheme is an intriguing puzzle. Is it possible that this morphotype is the result of insular adaptation? On the one hand, the insular Gran Canarian species, '*Centrochelys*' *vulcanica*, does not show this morphotype and certainly preserves the morphotype of its, presumably geocheloninan, ancestral stock whether it is European or African. On other hand, other insular taxa, like the iconic Galápagos tortoise, also shows morphotype II, again in accordance to the morphology of its South American ancestral stock.

Consequently, the insular taxa from Malta, Menorca, Monte Pellegrino and ZCSP are proposed as members of a distinct and little-known lineage of large-bodied extinct tortoises of Mediterranean distribution. Based on the femur, the ZCSP tortoise is also distinct from the previously recognized Menorcan and Maltese species '*Te.*' *gymnesica* and '*Te.*' *robusta*, respectively, as well as from Early Pleistocene fossils from Monte Pellegrino, Sicily, of a large but not giant tortoise that appears to be similar to the Maltese taxon by having a femoral head that is clearly elliptical.

Whether this insular Mediterranean morphotype represents a distinct evolutionary path from a geocheloninan stock, developed in parallel to the Canarian lineage, or whether it is derived from another, perhaps testudininan, stock cannot be disentangled based on the available evidence. However, despite the phylogenetic uncertainty, the morphological distinctiveness of the insular Mediterranean tortoises is sufficient to recognize them formally as a distinct evolutionary lineage. We are confident that this will spur further studies that will resolve its placement among Testudinidae.

SYSTEMATIC PALAEONTOLOGY

Based on the morphotypes defined above (see section: Femur morphotypes and character coding), we describe

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the insular Mediterranean tortoises as a distinct taxon at the genus level and the ZCSP tortoise as a distinct species within this genus.

TESTUDINES BATSCH, 1788

TESTUDINIDAE GRAY, 1825

***SOLITUDO* GEN. NOV.**

Zoobank registration: urn:lsid:zoobank.org:act:08DE006C-E90B-4605-9711-952D72904E5F.

Type species: *Testudo robusta* Leith-Adams, 1877; Zubbo Cave = Zebbug Cave, Malta; Middle Pleistocene.

Etymology: From the Latin word *solitudo*, feminine, third declension, meaning solitude, loneliness, in allusion to the insular isolation of these tortoises. Also, the termination *-tudo* alludes to the name *Testudo* and the testudinid affinities of this new taxon.

Diagnosis: Members of *Solitudo* belong to Testudinidae because of the ventral fusion of the trochanters of the femur. However, *Solitudo* species show an incomplete fusion of the trochanters dorsally, in contrast to other testudinid genera in which the trochanters are connected proximally via a rounded ridge. Furthermore, members of *Solitudo* have femurs that are slender, with a femoral head that is narrower than the combined anteroposterior width of the trochanters and an oblique orientation compared to the anteroposterior plane between 25°–45°, in contrast to other genera with relatively massive femora and broad and less oblique femoral heads, forming an angle that is less than 25° with the anteroposterior plane.

Included taxa: *Solitudo robusta* (Leith-Adams, 1877) comb. nov., *Solitudo gymnesica* (Bate, 1914) comb. nov., *Solitudo sicula* sp. nov.

Remarks: The exact placement of *Solitudo* among Testudininae is unclear and should be examined when new material (skull, shell) is discovered. The femur alone, in its distinctiveness, does not allow firm assessment of the phylogenetic relationship with respect to any potentially related taxon (*Centrochelys*, *Stigmochelys*, *Testudo* and *Titanochelon*). It is noteworthy that the establishment of new fossil taxa on the basis of appendicular elements is not rare among testudinids, and has been used, besides most other insular taxa mentioned already, for the recently described species *Chelonoidis marcanoi* Turvey *et al.*, 2017 from the Quaternary of Hispaniola (Turvey *et al.*, 2017).

***SOLITUDO SICULA* SP. NOV.**

FIGS 4–5

Zoobank registration: urn:lsid:zoobank.org:act:F5011B57-E559-4F72-9131-D457D8B6B998.

Holotype: ZCSP US.0-Q2, an almost complete right femur, missing only part of the major trochanter (Fig. 4).

Figure 4. *Solitudo sicula* sp. nov. from the latest Pleistocene of Zubbio di Cozzo San Pietro Cave, Sicily, Italy. Holotype ZCSP US.0-Q2, right femur, in dorsal (A), anterior (B), ventral (C), posterior (D), proximal (E) and distal (F) view. The right femur of the extant *Te. marginata* (the largest Mediterranean extant tortoise) is included for comparison at the same scale. Scale bar = 10 cm.

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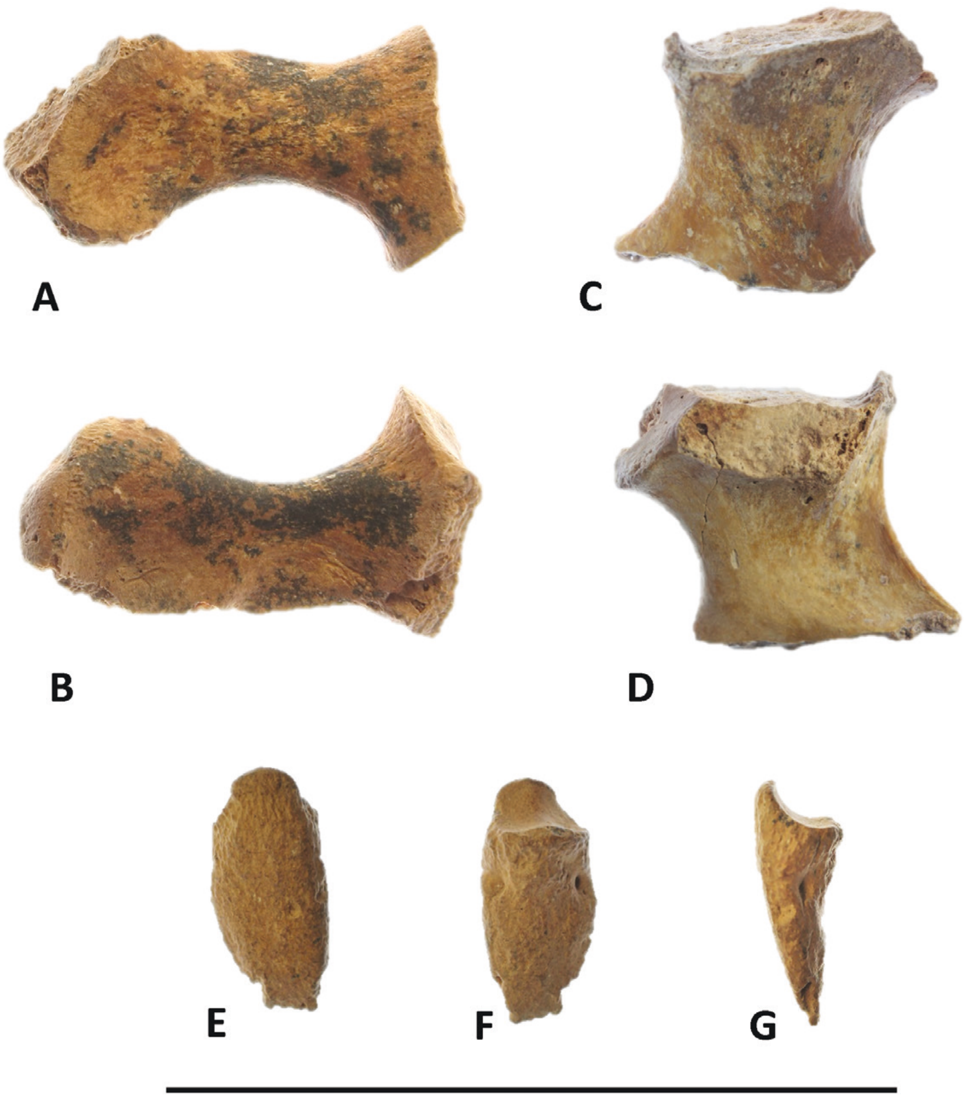

Figure 5. *Solitudo sicula* sp. nov. from the latest Pleistocene of Zubbio di Cozzo San Pietro Cave, Sicily, Italy. Right ischium ZCSP US.0-Q1 in dorsomedial (A) and ventrolateral (B) views. Left pubis ZCSP US.2-Q4 in ventromedial (C) and dorsolateral (D) views. Ungual phalanx ZCSP US.0-Q3 in dorsal (E), ventral (F) and lateral (G) views. Scale bar = 10 cm.

Paratypes: ZCSP US.0-Q1, a fragment of a right ischium (Fig. 5A, B); ZCSP US.2-Q4, a left pubis (Fig. 5C, D); ZCSP US.0-Q3, an ungual phalanx (Fig. 5E-G). Due to the uncertainty of the attribution of the four skeletal remains to a single individual (see below), we do not group the ischium, the pubis and the phalanx along with the femur as a single holotype, but we keep them separated.

Type locality and age: Zubbio di Cozzo San Pietro Cave, Municipality of Bagheria, near Palermo, northwestern Sicily, Italy. Latest Late Pleistocene. For details about the locality, see Locality information above. The tortoise remains here described come from an archaeological funerary area (Battaglia *et al.*, 2020) placed at a depth of −15.4 m from the entrance and characterized by disturbance caused by human and/or animal activity that determined a complex stratigraphy. The remains of the pubis, ZCSP US.2-Q4, was AMS-dated revealing an age of 12.5 ± 0.5 kya BP (Supporting Information, Fig. S3). All the tortoise material is referred to the latest Late Pleistocene assuming that it belongs to the same, extremely rare taxon (large-sized tortoises have never been reported in the several Sicilian Late Pleistocene-Holocene archaeological and paleontological sites so far studied), even if not necessarily to a single specimen (considering the alteration of the stratigraphy, a non-demonstrable

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but likely option because of non-anatomical overlap of the preserved skeletal elements, as well as their congruent size and common testudinid morphology).

Etymology: Latin adjective in feminine gender, meaning 'Sicilian'.

Diagnosis: Member of *Solitudo* based on the generic characters mentioned above. Differing from other species of *Solitudo* in having trochanters that are at the same height with the femoral head, and a femoral head that is clearly elliptical, whereas in other species trochanters extend beyond the femoral head and the latter is not elliptical.

Description

Femur: ZCSP US.0-Q2 (Fig. 4; Supporting Information, Fig. S4) is a well-preserved right femur with a total length of 104 mm. The diaphysis is relatively slender and almost rectilinear, with a slight curvature on the distal part [more rectilinear than femora of *Te. hermanni* (adult and young individuals) and *Te. marginata*]. The dimensions of the narrowest point of the diaphysis are 13.1 × 12.9 mm. It is not possible to measure the original width of the femur at the level of the trochanters, as the trochanter major is laterally incomplete. The width of its preserved portion is 32 mm. The maximum width of the distal epiphysis is 37 mm. The neck is well defined, relatively long and contracted with respect to the maximum width of the head (not as in the Menorcan species which has a femoral head detached even more clearly from the neck). The minimum width of the neck is 22 mm; its minimum thickness is 16 mm. The intertrochanteric fossa is wide and occupies the entire surface between the trochanters; it is approximately 10 mm deep. The trochanters do not extend more proximally compared to the femoral head (see Supporting Information, Appendix S1 for comments on the orientation of the femur). The lateral surface of the head neck is nearly vertical, the head does not overhang the shaft as in *Te. hermanni* and *Te. marginata*. The two trochanters are joined ventrally (so that the intertrochanteric fossa does not open ventrally), but the muscular insertion surfaces are clearly separated, and in medial view, the space between these two surfaces becomes thinner until it forms a relatively thin crest. In ventral view, this crest is not rectilinear but forms a wide 'U' (above which much of the head of the femur is visible). These areas of muscular insertion are clear, as they are defined by a thin ridge. A similar ridge delimits the ventral margin of the muscular insertion surface of the head—the one that overlooks the intertrochanteric fossa; another similar crest delimits the insertion region of the distal condyles. The area of muscular insertion of the small trochanter is clearly triangular, and probably also that of the great trochanter, although the latter is partially incomplete. On the anterior surface of the diaphysis of the femur, at the small trochanter, there is a long ridge of muscular insertion of the femorotibialis (more than half of the diaphysis) evident but moderately developed (although not as much as in *Te. marginata*); it remains close to the edge between the anterior and ventral surface. On the posterior surface of the diaphysis, in connection with the great trochanter, there is an elongated area (depression with an irregular base) of muscular insertion of the adductor femoris, which expands distally by curving in a dorsal direction until it reaches the dorsal edge of the posterior surface at about the half of the diaphysis. The femoral head is narrow, narrower than the combined width of the trochanters (even more if we account for the missing part) and oval, clearly elliptical in outline, being oriented at an angle of approximately 30° compared to the anteroposterior plane. Distally, the tibial and fibular condyles are connected by a ridge ventrally, which is gently curved but only weakly developed.

Ischium: ZCSP US.0-Q1 (Fig. 5A, B; Supporting Information, Fig. S5) is an incomplete right ischium, missing the anteromedial area that contacts with the contralateral element and with the pubis. The anterior margin is laminar (it forms a sharp crest). On its ventral surface, at this anterior laminar margin there is a moderate depression medially bounded by an evident termination. The posterior margin is rounded and in dorsal view it forms a wide concavity. The dorsal surface near the medial margin is slightly concave. Posteromedially, the lateral ischial process forms a sort of low and broad tubercle with a rough surface (note that in *Te. hermanni* and *Te. marginata*, the morphology is completely different, taking the shape of a pointed process). Near the posteromedial margin, the ischium thickens ventrally as it is also indicated by the shape of the suture area with the left ischium. The posterior surface of this thickened area is characterized by an area of muscular insertion delimited by a small ridge similar to that of the trochanters of the femur.

Pubis: ZCSP US.2-Q4 (Fig. 5C, D) was an incomplete right pubis, preserving only its posterolateral portion. The three articular facets and the laminar region leading to the two other processes are preserved. This element has been destructively sampled for AMS-dating and no longer exists.

Ungual phalanx: ZCSP US.0-Q3 (Fig. 5E-G; Supporting Information, Fig. S6) is an ungual phalanx, with a length of 29 mm. The articular facet is divided into two concavities separated by a vertical convexity.

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The upper portion of the proximal epiphysis is clearly projecting. On its ventral surface, near the facet joint, there are two prominent foramina. The gross morphology of the phalanx is clearly different from that of *Testudo* spp.; it is wide and flat instead of being rounded in section.

Size: The femur is much larger than that of *Te. marginata*, which is the largest extant tortoise species in Europe (Ernst & Barbour, 1989; Bringsøe *et al.*, 2001). For example, the *Te. marginata* femur MDHC 370 has a length of 51 mm, while the straight carapace length of the same specimen is 300 mm. On the basis of the length difference of the femora (ZCSP US.0-Q2 is 104 mm long), we estimate the straight carapace length of the extinct Sicilian tortoise as exceeding 50 cm and maybe up to 60 cm, i.e. significantly larger than that of extant *Te. hermanni* [up to 37.5 cm in the Balkans and up to 22 cm in the western Mediterranean (Cheylan, 2001)], or any other *Testudo* species. The size record for *Te. marginata*, the largest species of the genus, is 40 cm, but most specimens are significantly smaller (Bringsøe *et al.*, 2001).

DISCUSSION

The funerary deposits from Zubbio di Cozzo San Pietro Cave in north-western Sicily, Italy, provided four skeletal remains likely belonging to a single specimen of a large-sized tortoise, dating back to the latest Late Pleistocene (12 500 BP), when Sicily was certainly separated from the mainland (Bonfiglio *et al.*, 1999). Its shell probably exceeded 50 cm in length and was therefore much larger than any of the contemporary and extant taxa that inhabit the Mediterranean area. These isolated finds are important from a biogeographic and stratigraphic point of view, being the youngest record of a large-sized/giant tortoise species in the Mediterranean area and one of the few known from Sicily. However, these specimens have also allowed us to discuss issues that concern the evolution of insular tortoises in the area during the past.

The identification of a new tortoise species in the latest Late Pleistocene of Sicily requires a discussion and a review of the taxonomic context that surrounded it geographically and chronologically. Tortoise fossils have been so far only scarcely described from Sicily, but testify for a continuous presence of *Te. hermanni* from the Middle Pleistocene to the present day. This species, which is currently the sole testudinid in the extant native herpetofauna of the island (Sindaco *et al.*, 2006), has been reported from the early Middle Pleistocene of Spinagallo (Kotsakis, 1977) and Grotta Marasà (Delfino, 2002), the late Middle to early Late Pleistocene of Contrada Pianetti (Bonfiglio *et al.*, 1997) and K 22 at San Vito Lo Capo (Delfino, 2002). *Testudo hermanni* has also been reported from several Holocene Sicilian localities such as Calathamet, Castello di Fiumedinisi, Grotta della Cannita, Grotta dell'Uzzo, Grotta di San Calogero and Castello di Brucato [see Chesi (2008) and literature therein]. Interestingly, giant testudinids are also known from Sicily, even if so far only briefly documented; remains of giant tortoises have been described and figured by Burgio & Cani (1988), Delfino (2002) and Chesi (2008) from the Middle Pleistocene localities of Alcamo (between Trapani and Palermo, north-western Sicily) and Contrada Annunziata, Contrada Castellazzo and Stazione ferroviaria in Comiso (all three near Ragusa, south-eastern Sicily), all of them pertaining to the '*Elephas falconeri* Faunal Complex' (Bonfiglio *et al.*, 2003; Masini *et al.*, 2008). Additionally, as yet undescribed remains from the older Sicilian Faunal Complex, the Early Pleistocene of Monte Pellegrino—the so-called Monte Pellegrino Faunal Complex—have been recovered, pertaining to an animal comparable in size to the ones described herein from Zubbio di Cozzo San Pietro [see also Delfino (2002)]. The available giant tortoise material from Alcamo and the Ragusa area does not include femora, whereas the remains of the large-sized tortoises from Monte Pellegrino contain two femora (Delfino, 2002) that have never been described in detail and that will be the subject, along with all the tortoise remains from this locality, of a future study. The inclusion of this sample in the analysis herein suggests that the Monte Pellegrino tortoise is a member of *Solitudo* gen. nov., but a different species compared to *Solitudo sicula* sp. nov. based on the different shape of the femoral head. Instead, the Monte Pellegrino tortoise is similar to *Solitudo gymnesica* from Menorca, differing only in small details on the size of the femoral neck and the development and size of the trochanters proximally. Therefore, *Solitudo* apparently inhabited Sicily from the Early to the latest Late Pleistocene.

CONCLUSION

The detailed morphological analysis of the tortoise remains from the Zubbio di Cozzo San Pietro Cave in north-western Sicily revealed the presence of an informative character: the incomplete fusion of the femur trochanters dorsally, which appear separated, as opposed to other testudinids in which they are connected via a rounded ridge. The same character occurs in other Sicilian tortoise fossils, as well as in all other extinct large-sized-taxa from the Mediterranean islands, which are curiously known almost exclusively by femora. However, other tortoises—extinct, extant, mainland and insular species from a broad

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taxonomic spectrum—do not share this morphology. This conclusion led to the hypothesis that extinct Mediterranean tortoises form part of a distinct evolutionary lineage that can be defined by this femur morphotype, formally defined here by the new genus-group name *Solitudo*. This genus includes the Maltese *Solitudo robusta*, the Menorcan *Solitudo gymnesica*, the unnamed taxon from Monte Pellegrino, Sicily, and the material from Zubbio di Cozzo San Pietro Cave described here as the new species *Solitudo sicula*. The broader testudinid relationships of this new lineage of 'lonely tortoises' of the Mediterranean islands are still unclear, and more skeletal elements and the possibility of recovering ancient DNA from some of the most recent specimens could shed more light on this problem.

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DATA AVAILABILITY

The authors confirm that the data supporting the findings of this study are available within the article and its Supporting Information.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Comments on the orientation of the femur, molecular work and bioinformatics.
Appendix S2. Character matrix.
Figure S1. Zubbio di Cozzo San Pietro, relief planimetry and transverse section indicating point A, where the tortoise remains come from, and all the points of the concentration of faunal (F), archaeological (RA) and human (H) remains modified from Battaglia *et al.* (2020).
Figure S2. The holotype ZCSP US.0-Q2 of *Solitudo sicula* sp. nov. *in situ* in the cave.
Figure S3. The results of the radiometric dating of the pubis ZSP US.2-Q4.
Figure S4. 3D model of the right femur ZCSP US.0-Q2 of *Solitudo sicula* sp. nov.
Figure S5. 3D model of the right ischium ZCSP US.0-Q1 of *Solitudo sicula* sp. nov.
Figure S6. 3D model of the ungual phalanx ZCSP US.0-Q3 of *Solitudo sicula* sp. nov.

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