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RESEARCH

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Testudinid turtle remains from the Late Miocene palaeo-island of Gargano, Italy, and an overview of Mediterranean insular tortoises

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Abstract
The Late Miocene Gargano "Terre Rosse" in southern Italy has yielded a diverse vertebrate fauna that comprises an array of endemic taxa, including forms characterized by extreme sizes and unique morphologies. We here document new testudinid fossil remains from this insular assemblage. The material comprises a mandible, abundant (though mostly fragmentary) shell remains, appendicular elements, and a few vertebrae, originating from different localities within the Gargano assemblage. Based on its femur morphology, we tentatively refer the Gargano form to *Solitudo*, a late Neogene and Quaternary insular genus, otherwise known from a few Mediterranean islands. Unfortunately, the incomplete preservation of the trochanters hinders observation of the main diagnostic character of *Solitudo*, however, the similarities in the femoral head and diaphysis allow an open identification of the Gargano material as cf. *Solitudo* sp. Still, the Gargano tortoise offers new anatomical information on the Mediterranean insular tortoises. An interesting feature of the few preserved plastral elements is the presence of sulci as distinct raised ridges, a character that has been reported in other insular extant and extinct tortoises as well. The preserved hyoplastron has a medially straight and laterally concave humeropectoral sulcus and a wide axillary scute, pointing to some resemblance to geochelonans. Moreover, the morphology of the mandible from Gargano, which has its lingual serration reaching towards the symphyseal area, is also indicative of geochelonan affinities. If our identification is correct, the Gargano form would correspond to the earliest occurrence of *Solitudo*, denoting that this insular testudinid already radiated during the Late Miocene. A thorough overview of the diversity and taxonomy of insular testudinids from the Mediterranean islands is provided.

Keywords Turtles, Testudinidae, Anatomy, Taxonomy, Palaeogeography, Insular faunas

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Introduction

Mediterranean islands are characterized by an astonishing array of endemic vertebrate taxa showing unique external morphologies and skeletal anatomies. Moreover, the fossil record attests to an even more fascinating diversity in these islands, encompassing a parade of unique, now extinct, forms, extralimital geographic occurrences for certain taxonomic groups, as well as extreme sizes, including multiple cases of both gigantism and dwarfism (Van der Geer et al., 2010). Accordingly, the numerous large and small Mediterranean islands offer valuable insights into the study of the evolution and biogeography of European and peri-European faunal assemblages (Van der Geer et al., 2010). Prominent examples of fossil Mediterranean endemics include a spectrum of iconic taxa, such as bizarre multi-horned ruminants, dwarf mammoths and hippopotami, giant hedgehogs, rabbits, and rodents, flightless birds, and large tortoises (Bate, 1914; Freudenthal, 1972, 1976, 1985; Freudenthal & Martín-Suárez, 2010; Freudenthal et al., 2013; Herridge & Lister, 2012; Leinders, 1984; Leith Adams, 1877; Mazza and Rustioni, 2011; Masini et al., 2013; Pavia et al., 2017; Quintana et al., 2011; Van der Geer et al., 2014; Van der Geer et al., 2010).

Although not as well studied as their sympatric mammalian counterparts, reptiles also possess a notable fossil record in the late Neogene and Quaternary of the Mediterranean Islands, including extralimital occurrences of continental taxa as well as endemic forms (Abbazzi et al., 2008; Bailon et al., 2002, 2014; Delfino, 2003; Delfino et al., 2008, 2011; Georgalis et al., 2019; Savorelli et al., 2025; Torres-Roig et al., 2021; Tschopp et al., 2018). Among them, tortoises (Testudinidae) have been important components, including records from islands where the group is now absent, such as Crete and Cyprus (Bachmayer et al., 1975; Bailon, 2023; Georgalis & Kear, 2013; Kotsakis, 1977; Vlachos, 2022b), but, most spectacularly, also comprising several now extinct, endemic, large-sized forms (Abbazzi et al., 2008; Bate, 1914; Bour, 1985b; Georgalis & Delfino, 2021; Leith Adams, 1877; Lydekker, 1889; Lapparent de Broin, 2002; Luján et al., 2017; Mercadal & Pretus Real, 1980; Szalai, 1938; Tagliafero, 1913; Valenti et al., 2022). The latter have been primarily found on the islands of Malta, Sicily, the Balearic Islands, Sardinia, and the Italian palaeo-island of Scontrone (Abbazzi et al., 2008; Bate, 1914; Bour, 1985b; Georgalis & Delfino, 2021; Lapparent de Broin, 2002; Leith Adams, 1877; Luján et al., 2017; Valenti et al., 2022; Zoboli et al., 2023). These large forms also span a considerable stratigraphic time, with their oldest record documented in the Late Miocene (Tortonian) of Scontrone (Georgalis & Delfino, 2021) and their youngest one in the latest Pleistocene of Sicily (Valenti et al., 2022). The affinities of these large insular endemic tortoises have long puzzled researchers and different taxonomic opinions have been proposed over the past 150 years (Auffenberg, 1974; Bate, 1914; Kuhn, 1964; Lapparent de Broin, 2002; Leith Adams, 1877; Lydekker, 1889; Pérez-García & Vlachos, 2014; Rhodin et al., 2015; Szalai, 1938; Tagliafero, 1913; Valenti et al., 2022). Recently though, Valenti et al. (2022) realized that at least some insular endemic testudinids are characterized by a rather distinctive femoral morphology (i.e., the so-called "insular" morphotype), which is different from that observed in geochelonans and testudonans. Based on this femoral morphology, Valenti et al. (2022) established a new genus, *Solitudo*, that encompasses forms from the Quaternary of Sicily and Malta, and the Pliocene of Minorca. Other large tortoises from the area, such as the oldest Mediterranean insular occurrence, i.e., the testudinid from the palaeoisland of Scontrone (Georgalis & Delfino, 2021), are not known from femur material and their potential assignment to *Solitudo* can therefore not be evaluated for the moment.

Here we describe testudinid material from another palaeo-island of the Central Mediterranean, the Late Miocene Gargano "Terre Rosse" in southern Italy. The material originates from different fissure fillings of slightly different ages. It is comprised of a single skull element (one well preserved mandible), multiple shell remains (both carapacial and plastral elements, isolated and in most cases incomplete), appendicular elements (partial or fragmentary remains of humeri, femora, ulnae, ilia, tibiae, one ungual phalanx, scapulae, ischium, pubis, and indeterminate pelvis elements), and a few vertebrae. With the exception of part of this material that was initially described in a PhD thesis (Delfino, 2002), the Gargano tortoise remains have been undocumented. We here provide thorough descriptions of this material, along with comparisons with other insular and continental testudinids, to provide a proper taxonomic referral for the Gargano tortoise specimens.

Material and methods

Part of the fossil material described herein is housed in the collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Torino (MGPT-PU), which is permanently curated at the Dipartimento di Scienze della Terra of the Università degli Studi di Torino, Italy. The remaining material here described is part of the collections of the Naturalis Biodiversity Center of Leiden (RGM), the Netherlands. The material was collected during different field campaigns organized by the Naturalis in the 1970s and 1980s and by the Dipartimento di Scienze della Terra of Torino since 2000 onwards.

The 3D surface scans of selected specimens were produced with an Artec Space Spider. The resulting 3D model files are available in the public online repository of Morphosource (https://www.morphosource.org/; for details, see the section "Availability of data and materials" below).

Anatomical terminology follows Gaffney (1996), Pérez-García and Vlachos (2014), Vlachos and Rabi (2018), Valenti et al. (2022), Evers et al. (2023), and Hermanson et al. (2024; based on their figs. 22–24 on testudinid humeri and the relevant descriptions).

Institutional abbreviations. **MDLCA**, Museo Sardo di Geologia e Paleontologia 'Domenico Lovisato', University of Cagliari, Cagliari, Italy; **MGPT-PU**, Museo di Geologia e Paleontologia Collections, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Turin, Italy; **MGPT-MDHC**, Massimo Delfino Herpetological Collection, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Turin, Italy; **RGM**, Naturalis Biodiversity Center of Leiden, The Netherlands; **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

The fossil tortoise remains here described were found in the red soil deposits (so called "Terre Rosse") that fill the extensive palaeokarst that affects the Mesozoic limestone in the Apricena-Poggio Imperiale quarry district (Foggia, Apulia, Southern Italy), on the northwestern slope of the Gargano promontory. The numerous fissures exposed in the quarries have yielded an extraordinary amount of fossil vertebrate remains of medium- to small-sized taxa, including mammals (mostly micromammals), amphibians, reptiles, and birds (Freudenthal, 1971, 1972, 1976, 1985; Masini et al., 2010, 2013; Masini and Fanfani, 2013; Pavia, 2013; Villier and Carnevale, 2013; Savorelli et al., 2025). The fossil association is highly unbalanced and exhibits all the characteristics of insular populations, including the presence of gigantic small mammals and birds, flightless birds and the absence of terrestrial carnivores as well as of urodeles (Pavia et al., 2017; Savorelli et al., 2025). The tortoise material described herein originates from the following localities in the Late Miocene Gargano "Terre Rosse": Biancone, Rinascita, Chirò 3, Chirò 4, Chirò 5A, Chirò 6, Chirò 7A, Chirò 10C, Chirò 12, Chirò 14A, Chirò 20A, Chirò 24, Chirò 25, Chirò 28A, Chirò 28B, Chirò 29, Chirò 30B, Chirò D1, Chirò D2, Fina 2, Fina 4, Fina A-N, Fina D, Fina E, Fina H, Fina K, Fina N, Gervasio, Nazario, Pepo N, Pirro 12, Pirro I 4, Pizzicoli 2, Pizzicoli 11, Pizzicoli 12, and San Giovannino. The age of the "Terre Rosse" fissure fillings has been recently discussed by Savorelli et al. (2025) who proposed a Messinian age, even if there is some uncertainty in the lower age limit of the assemblage that could even be Tortonian.

Systematic Palaeontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Testudinoidea Batsch, 1788

Testudinidae Batsch, 1788

Solitudo Valenti, Vlachos, Kehlmaier, Fritz, Georgalis, Luján, Miccichè, Sineo & Delfino, 2022

cf. *Solitudo* sp.

Figures 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, and 17.

Material. *Biancone*: one shell fragment (RGM.453532); *Rinascita*: one fragment of femur (RGM.454271) and one fragment of an ilium (RGM.454272); *Chirò 3*: one costal fragment (RGM.215166) and five shell fragments (RGM.451175–RGM.451179); *Chirò 4*: 10 shell fragments (RGM.261501–RGM.261503, RGM.261505, and RGM.451220–RGM.451226); *Chiro 5A*: five shell fragments (RGM.215088–RGM.215091 and RGM.443170); *Chirò 6*: two shell fragments (RGM.451270 and RGM.451271); *Chirò 7A*: one tibia (RGM.215002); *Chirò 10C*: two costal fragments (RGM.451419 and RGM.451420); *Chirò 12*: six shell fragments (RGM.451426–RGM.451431); *Chirò 14A*: one costal fragment (RGM.451591); *Chirò 20A*: one peripheral (RGM.215206); *Chirò 24*: three shell fragments (RGM.452337–RGM.452339); *Chirò 25*: one shell fragment (RGM.215019) and one ilium (RGM.215015); *Chirò 28A*: two costal fragments (RGM.261805 and RGM.261826), one peripheral (RGM.261848), one bridge peripheral (RGM.261841), three shell fragments (RGM.261819, RGM.261822, and RGM.261823), and one fragment of a humerus (RGM.261817); *Chirò 28B*: one costal fragment (RGM.261456) and three shell fragments (RGM.261187, RGM.261454, and RGM.261466); *Chirò 29*: two shell fragments (RGM.261423 and RGM.261436); *Chirò 30B*: three shell fragments (RGM.215121, RGM.215122, and RGM.215124); *Chirò D1*: three shell fragments (RGM.261179, RGM.261181, and RGM.261185), two fragment of pelvises (RGM.261183 and RGM.261209); *Chirò D2*: one bridge peripheral (and RGM.261956), four shell fragments (RGM.261957, RGM.261958, RGM.261963, and RGM.261966); *Fina 2*: two left humeri (MGPT-PU 139141 and MGPT-PU 139142) and one right ischium (MGPT-PU 139140); *Fina 4*: one costal (MGPT-PU 139139) and one fragment of a (probably) right xiphiplastron (MGPT-PU 139143); *Fina A-N*: one shell fragment (RGM.453779); *Fina D*: one costal fragment (RGM.453784); *Fina E*: one shell fragment (RGM.453931); *Fina H*: 21 shell fragments (RGM.453936–RGM.453956), one fragment of humerus (RGM.453958), one fragment of ?humerus (and RGM.453959), one tibia (RGM.453957), one fragment of ilium (RGM.453960), one fragment of a scapula (RGM.443165), and one fragment of vertebra (RGM.443205); *Fina K*: one partial left mandible (RGM.454048) and one right ulna (RGM.454049);

Fig. 1 Mandible. 3D images of left mandible (RGM.454048) in labial (**a**), dorsolabial **(b)**, ventrolabial (**c**), ventral (**d**), medial (**e**), dorsomedial (**f**, **g**), dorsal (**h**), anteromedial (**i**), posteromedial (**j**), anterodorsal (**k**), and posterolateral (**l**) views. Abbreviations: *fai* foramen alveolare inferius, *fdfm* foramen dentofaciale majus, *fM* fossa Meckelii, *imf* intermandibular foramen, *lab* labial ridge, *lin* lingual ridge

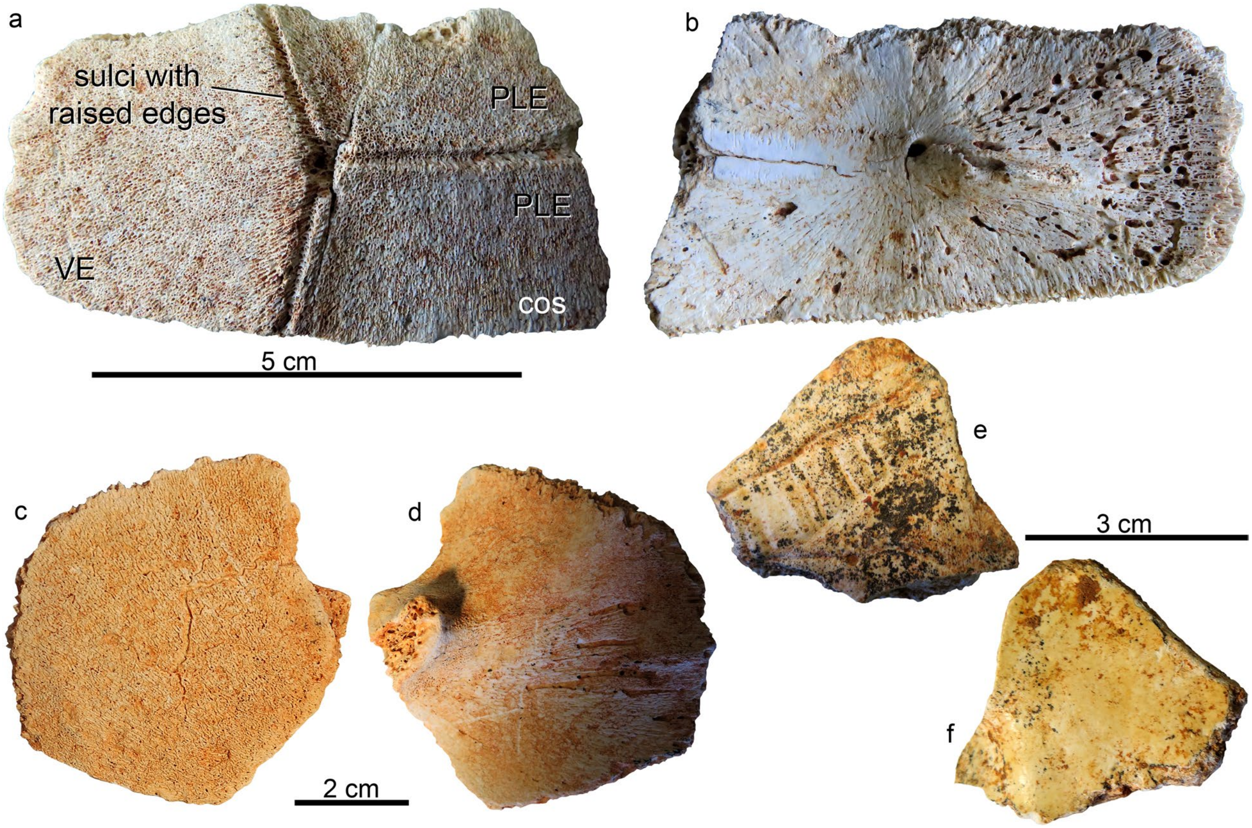

Fig. 2 Carapace elements. **a**, **b** Costal (MGPT-PU 139139) in dorsal (**a**) and visceral (**b**) views; **c**, **d** costal ?VII fragment (MGPT-PU 138991) in dorsal (**c**) and visceral (**d**) views; **e**, **f** costal fragment (MGPT-PU 138989) in dorsal (**e**) and visceral (**f**) views. Abbreviations: *cos* costal plate, *PLE* pleural scute, *VE* vertebral scute

Fina N: one shell fragment (RGM.454054); *Gervasio*: one fragment of a femur (RGM.443156) and one ulna (RGM.453473); *Nazario*: two shell fragments (RGM.454938 and RGM.454939); *Pepo N*: two shell fragments (RGM.455340 and RGM.455341); *Pirro 12*: one peripheral (RGM.455348), one plastron fragment (MGPT-PU 138988), and one right humerus fragment (MGPT-PU 138987); *Pirro I 4*: one costal ?VII fragment (MGPT-PU 138991), one bridge peripheral (MGPT-PU 138937), one left xiphiplastron (MGPT-PU 138992), four shell fragments (MGPT-PU 138993a–MGPT-PU 138993c, and RGM.215422) and one right femur (MGPT-PU 138990); *Pirro indeterminate*: one costal fragment (MGPT-PU 138989); *Pizzicoli 2*: one caudal vertebra (RGM.454281); *Pizzicoli 11*: one femur of a very young individual (RGM.454284); *Pizzicoli 12*: seven shell fragments (RGM.261357, RGM.261369, RGM.261388, and RGM.261775–RGM.261778), two fragments of humeri (RGM.261326, RGM.261365), one fragment of a ?humerus (RGM.261333), and one fragment of probably a pelvis (RGM.261773); *San Giovannino*: one peripheral (RGM.215399), one right hypoplastron (RGM.261507), 22 shell fragments (RGM.215400–RGM.215407, RGM.215425–RGM.215429, RGM.215438, RGM.454940–RGM.454945, RGM.455216, and RGM.215326), two partial humeri (RGM.215423 and RGM.455172), one ?ulna fragment (RGM.215368), two tibiae (RGM.455217 and RGM.455319), one ilium (RGM.215367), one fragment of scapula (RGM.443191), and one ungual phalanx (RGM.215013); *Gargano imprecise locality(ies)*: one peripheral (MGPT-PU 100011), two shell fragments (MGPT-PU 100009 and MGPT-PU 100012), one right hyoplastron (MGPT-PU 100008), one (probably) partial hypoplastron (MGPT-PU 100010), one shell fragment (RGM.261968), three fragments of humeri (RGM.424215, RGM.424219, and RGM.424220), four caudal vertebrae (MGPT-PU 100002, RGM.179021, RGM.179029, and RGM.261411).

Description

Mandible (Fig. 1)

A single, partial left mandible (RGM.454048) is available in our sample, preserving the entire dentary and coronoid (Fig. 1). This specimen, which is the only available turtle

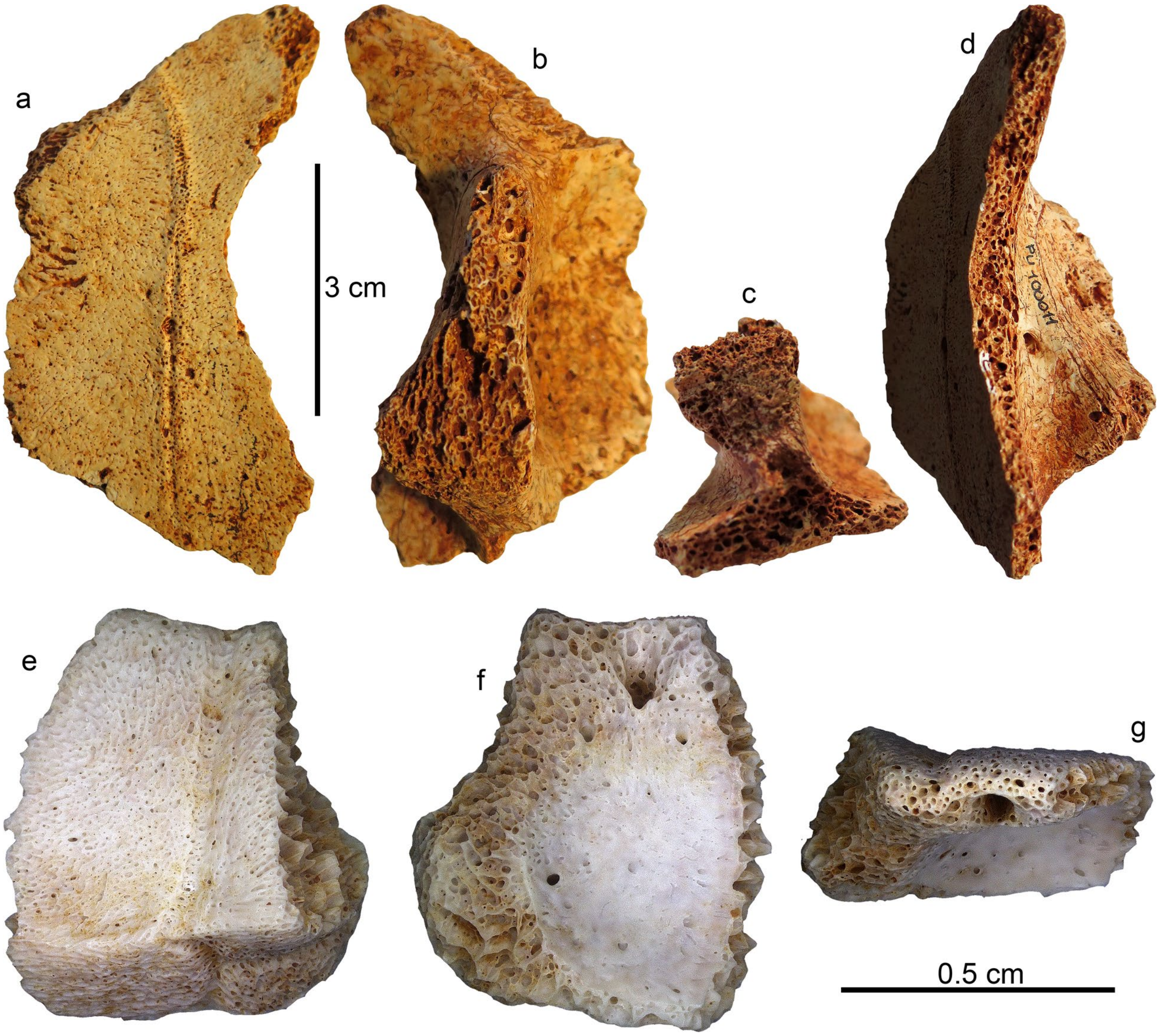

Fig. 3 Carapace elements. **a**–**d** Posterior peripheral (MGPT-PU 100011) in dorsal (**a**), visceral (**b**), cross-section (**c**), and lateral (**d**) views; **e**–**g** peripheral (MGPT-PU 138937) in lateral (**e**), visceral (**f**), and dorsal (**g**) views

skull element from Gargano, is 37.8 mm long and 7.8 mm thick. Based on the preserved part, it is possible that some other bones of the lower jaw are present as well, but we are unable to discern any sutures. In dorsal view, the dentary is straight throughout its length. Its ventral border is curved in lateral view. There are two distinct ridges, a labial and lingual one, which are both moderately serrated and quite tall, creating a deep, trough-like, triturating surface. The lingual ridge is more serrated than the labial one, and reaches the symphyseal area, comparable to the condition seen in *Chelonoidis* Fitzinger, 1836, and without leaving a gap like the one reported for the members of Testudona (see Evers et al., 2023). In lateral view, the dorsal edge of the dentary is markedly convex and the ventral edge is markedly concave. Anteriorly, a tooth-like symphyseal end is noted. The surface of the top part of the coronoid bone in left lateral view is expanded and rugose, whereas the surface of the bottom part is much smoother. In their limit, a double opening of the small foramen dentofaciale majus is present, forming a groove. In lingual view, the foramen intermandibulare medius is clearly observed, leading towards the fossa Meckelii, preserving also the foramen alveolare inferius approximately at its middle part. The Meckelian groove is clearly observed in lingual view. Distally, a distinct foramen is also observed, however, and given the inability to observe the sutures of the mandible, we are unable to confirm if it is the intermandibular foramen or something else. The

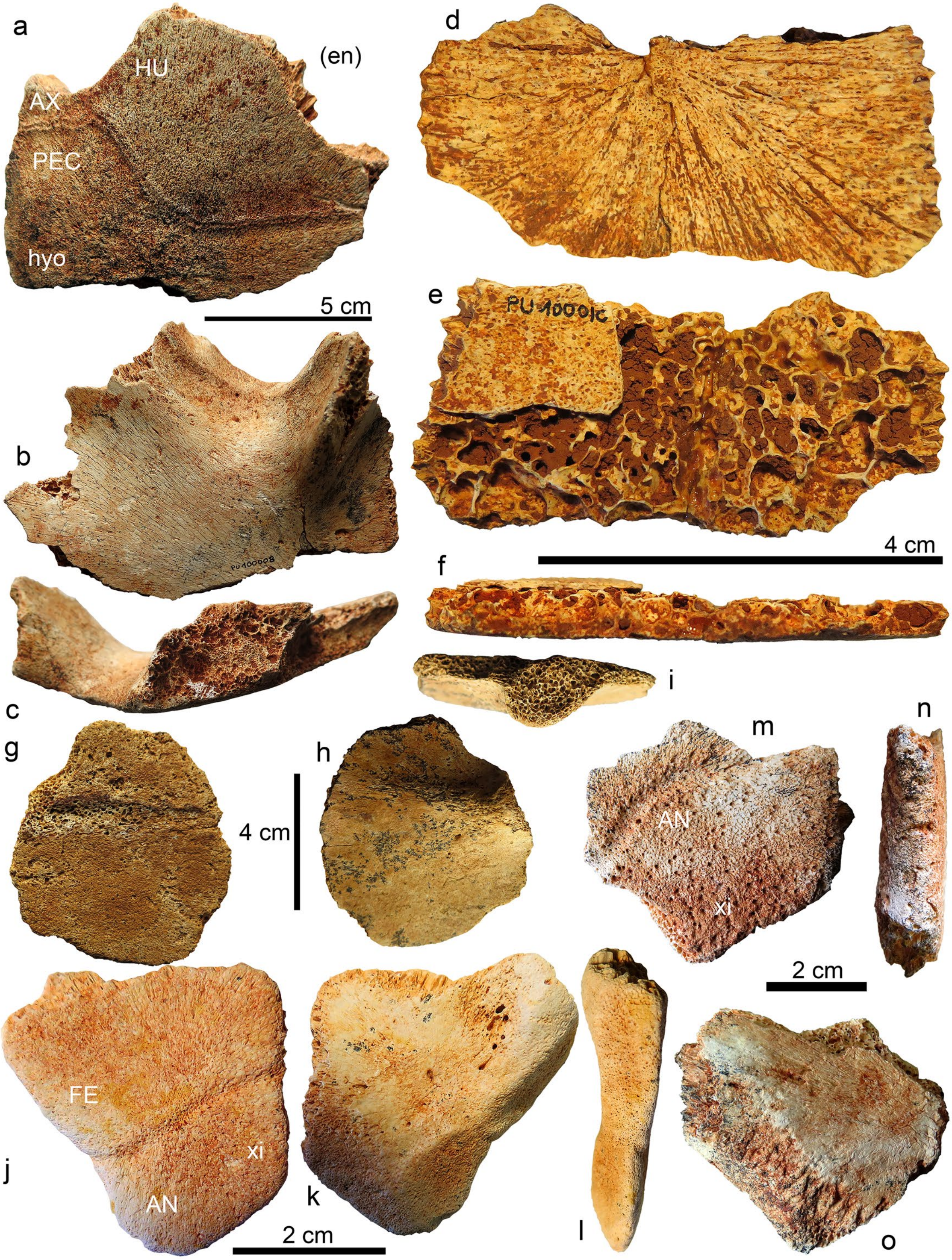

Fig. 4 Plastral elements. **a**–**c** Partial right hyoplastron (MGPT-PU 100008) in ventral (**a**), dorsal (**b**), and lateral (**c**) views; **d**–**f** shell fragment, probably partial hypoplastron (MGPT-PU 100010) in ventral (**d**), dorsal (**e**), and lateral (**f**) views; **g**–**i** indeterminate plastron fragment (MGPT-PU 138988) in ventral (**g**), dorsal (**h**), and lateral (**i**) views; **j**–**l** left xiphiplastron (MGPT-PU 138992) in ventral (**j**), dorsal (**k**), and lateral (**l**) views; **m**–**o** plastral fragment, probably partial xiphiplastron (MGPT-PU 139143), in ventral (**m**), lateral (**n**), and dorsal (**o**) views. Abbreviations: *AN* anal scute, *AX* axillary scute, *en* entoplastron plate, *FE* femoral scute, *HU* humeral scute, *hyo* hyoplastron plate, *PEC* pectoral scute, *xi* xiphiplastron plate

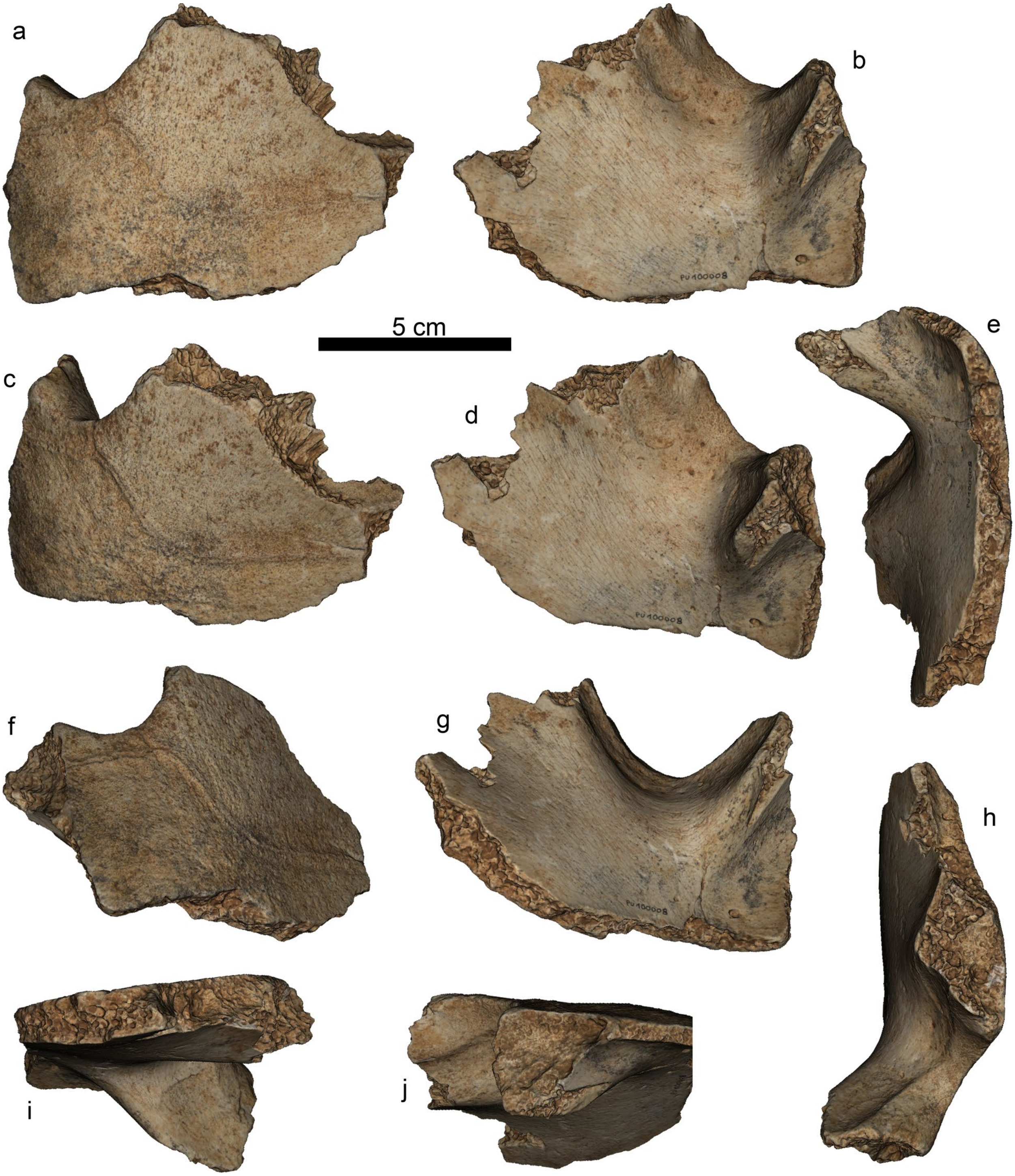

Fig. 5 3D images of right hyoplastron (MGPT-PU 100008) in ventral (**a**), dorsal (**b**), anteroventral (**c**), anterodorsal (**d**), posterior (**e**), posteroventral (**f**), posterodorsal (**g**), lateral (**h**–**i**), and anterior (**j**) views

dentary is slightly larger than that of an extant specimen (MGPT-MDHC 532) of *Centrochelys sulcata* (Miller, 1779), which has a straight shell length of 530 mm.

Carapace (Figs. 2, 3)

The carapace is represented by several fragmentary remains of costals and peripherals (including bridge peripherals). 10 partial or fragmentary costals are

Fig. 6 3D images of partial right hypoplastron (RGM.261507) in ventral (**a**), dorsal (**b**), anteroventral (**c**), anterodorsal (**d**), posteroventral (**e**), laterodorsal (**f**), posterolateroventral (**g, i**), and lateral (**h**) views. Abbreviations: *ABD* abdominal scute, *FE* femoral scute, *hypo* hypoplastron plate

available. The partial costal MGPT-PU 139139 clearly shows a shorter medial and a longer lateral side (Fig. 2a, b), typical of the alternating pattern seen in the costal plates of many testudinids. This partial costal is crossed by the sulci of one vertebral and two successive pleural scutes. The sulci are quite deep and present distinct raised ridges, creating remarkable furrows that are easily recognized on the plates. Viscerally, the basis of the costal ribs heads is observed, placed far away from the neural/costal suture. The free rib heads were likely relatively quite thin. Specimen MGPT-PU 138991 probably corresponds to a fragment of a costal plate, most likely the costal VII, judging by the thick rib head viscerally that might correspond to the posterior region and the sacral ribs (Fig. 2c, d). Specimen MGPT-PU 100011 is fragmented, but appears to have belonged to one of the

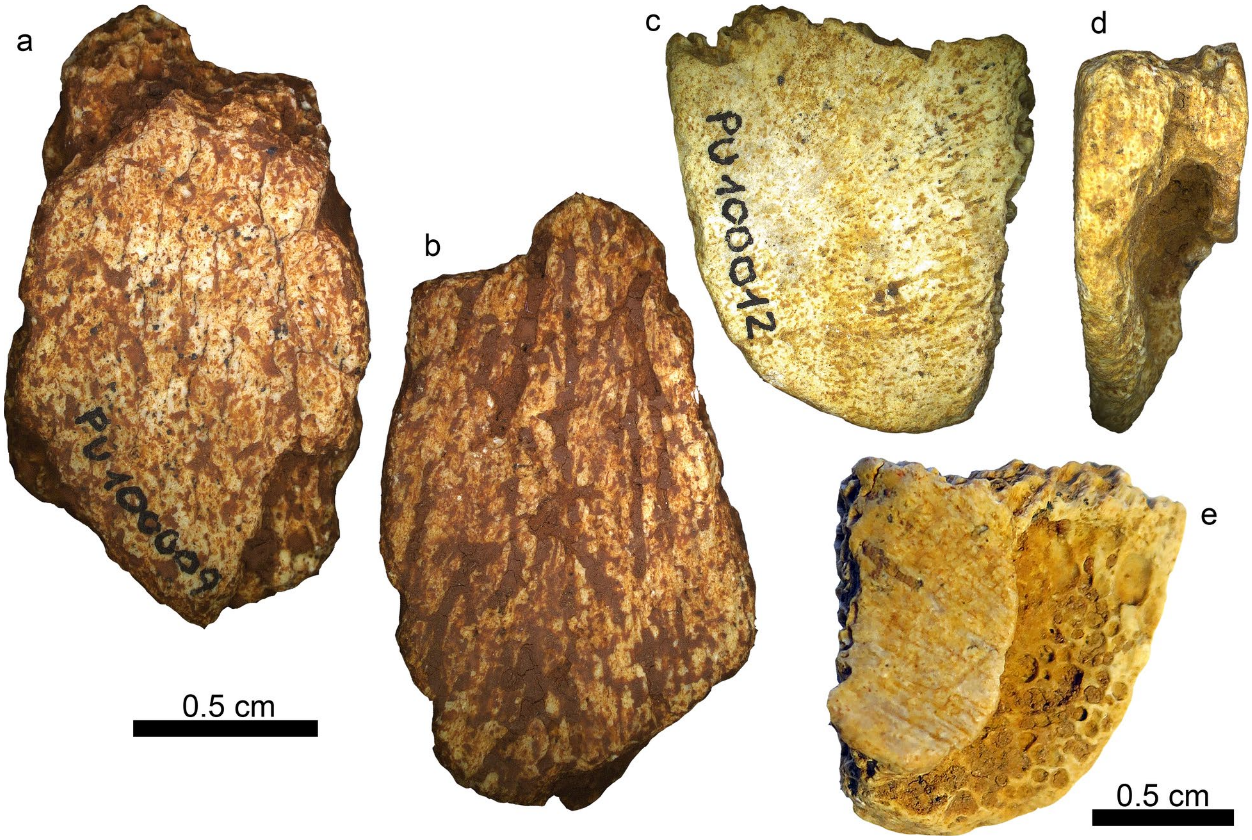

Fig. 7 Shell fragments. **a**, **b** MGPT-PU 100009 in external (**a**) and internal (**b**) views; **c**–**e** MGPT-PU 100012 in external (**c**), lateral (**d**), and internal (**e**) views

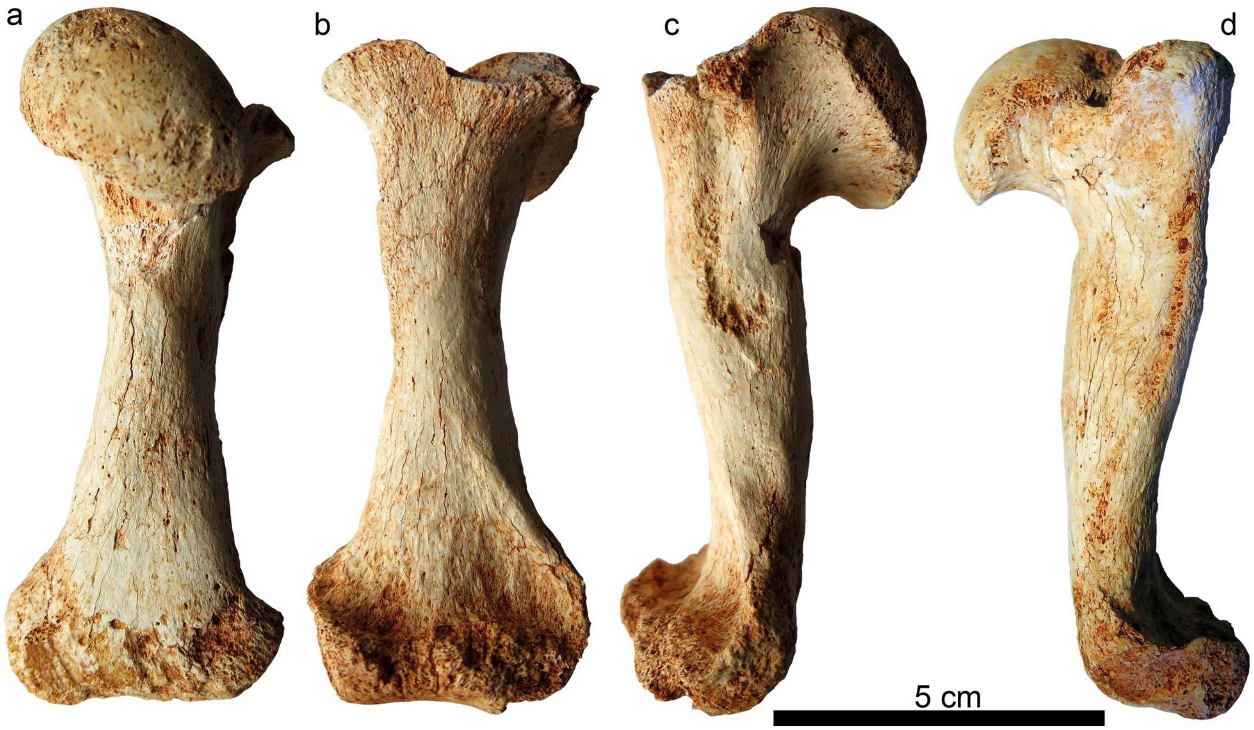

Fig. 8 Right femur (MGPT-PU 138990) in dorsal (**a**), ventral (**b**), posterior (**c**), and anterior (**d**) views

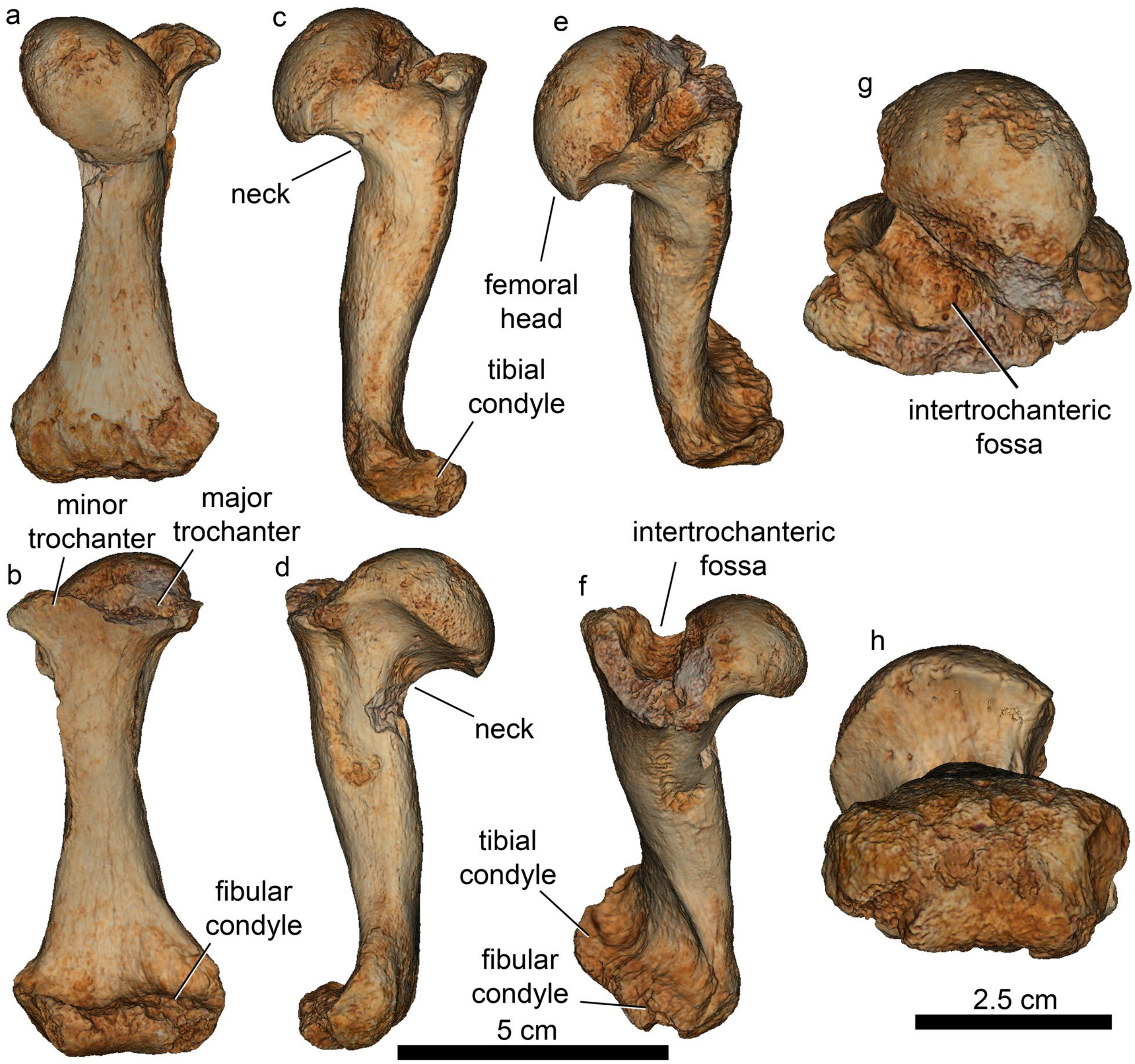

Fig. 9 3D images of right femur (MGPT-PU 138990) in dorsal (**a**), ventral (**b**), anterior (**c**), posterior (**d**), anteroproximal (**e**), posteroventroproximal (**f**), proximal (**g**), and distal (**h**) views. Scale bars: 5 cm for **a–f** and 2.5 cm for **g**, **h**

posterior peripherals that contribute to the formation of the inguinal buttress (Fig. 3a–d). A deep and straight sulcus is preserved externally.

Plastron (Figs. 4, 5, 6)

Only a few bones can be identified as plastral elements. The best-preserved plastron element corresponds to an almost complete right hyoplastron (MGPT-PU 100008; Figs. 4a–c, 5). As with the rest of the shell specimens, this plate is markedly thickened and robust compared to its entire size. Based on the entoplastral suture, which is preserved quite well, the presence of a wide entoplastron, probably rhomboidal with a slightly rounded posterior side, can be estimated. The humeropectoral sulcus is placed posterior to the entoplastron. It is straight medially and oriented perpendicular to the middle suture, but curved laterally. Laterally, it meets a large axillary scute, which covers a large part of the axillary notch and the axillary buttress.

The fragmentary right hypoplastron RGM.261507 clearly shows the presence of an inguinal scute (Fig. 6). The abdomino-femoral sulcus has edges markedly raised from the surrounding surface and is not parallel to the hypo-xiphiplastral suture but shows a modest but clear,

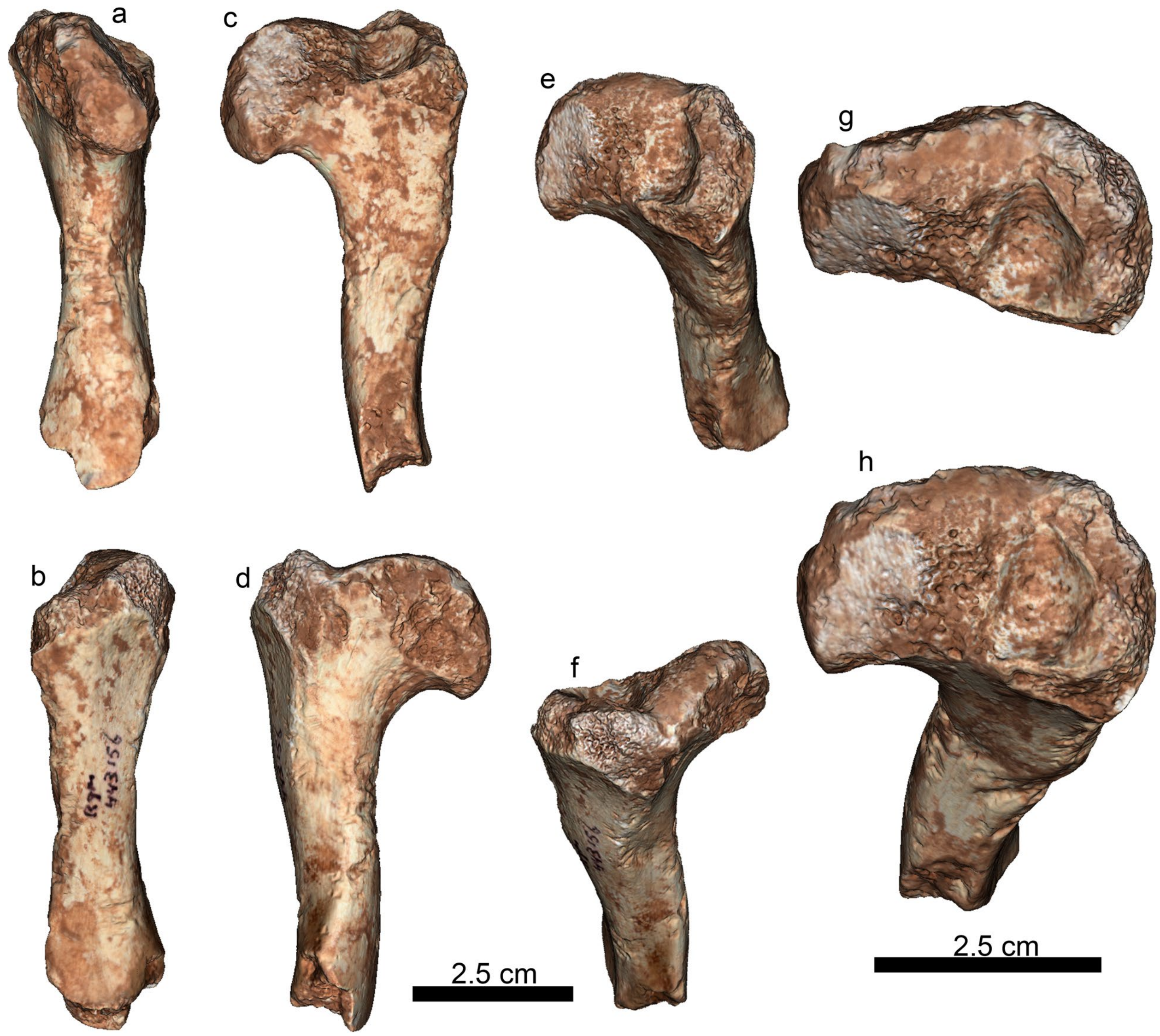

Fig. 10 3D images of proximal fragment of femur (RGM.443156) in dorsal (**a**), ventral (**b**), anterior (**c**), posterior (**d**), anteroproximal (**e**), posteroventroproximal (**f**), and proximal (**g**, **h**) views. Scale bars: 5 cm for **a**–**f** and 2.5 cm for **g**, **h**

anteriorly directed convexity in the abdomino-femoral sulcus.

MGPT-PU 138992 corresponds to a complete left xiphiplastron, with a wide and angular anal notch (Fig. 4j–l). The anals cover the posterior half of the xiphiplastron, with the femoroanal sulcus being relatively straight throughout its length. Another fragment (MGPT-PU 139143) appears to correspond to the plastron as well, probably a fragment of the posterior part of the right xiphiplastron (Fig. 4m–o). If our identification is correct, the anal notch is deep and angular, the femoroanal sulcus deep and rounded, and the anals are seemingly short. MGPT-PU 100010 is quite fragmentary, but it appears to be a thin plastral plate, probably part of the hypoplastron (Fig. 4d–f).

Indeterminate shell fragments (Fig. 7)

A large number (117) of shell remains is available, originating from almost all localities, but these are very fragmentary and cannot be more precisely recognized as carapace or plastral elements (Fig. 7).

Appendicular skeleton (Figs. 8, 9, 10, 11, 12, 13, 14, 15, 16, 17a–f)

The best-preserved element of the appendicular skeleton is an almost complete right femur (MGPT-PU 138990), with a total length of 92.1 mm (Figs. 8, 9). The femur shows a relatively slender and almost rectilinear diaphysis, thicker proximally and thinner distally, with a slight curvature on the distal part. The neck is well-defined, and

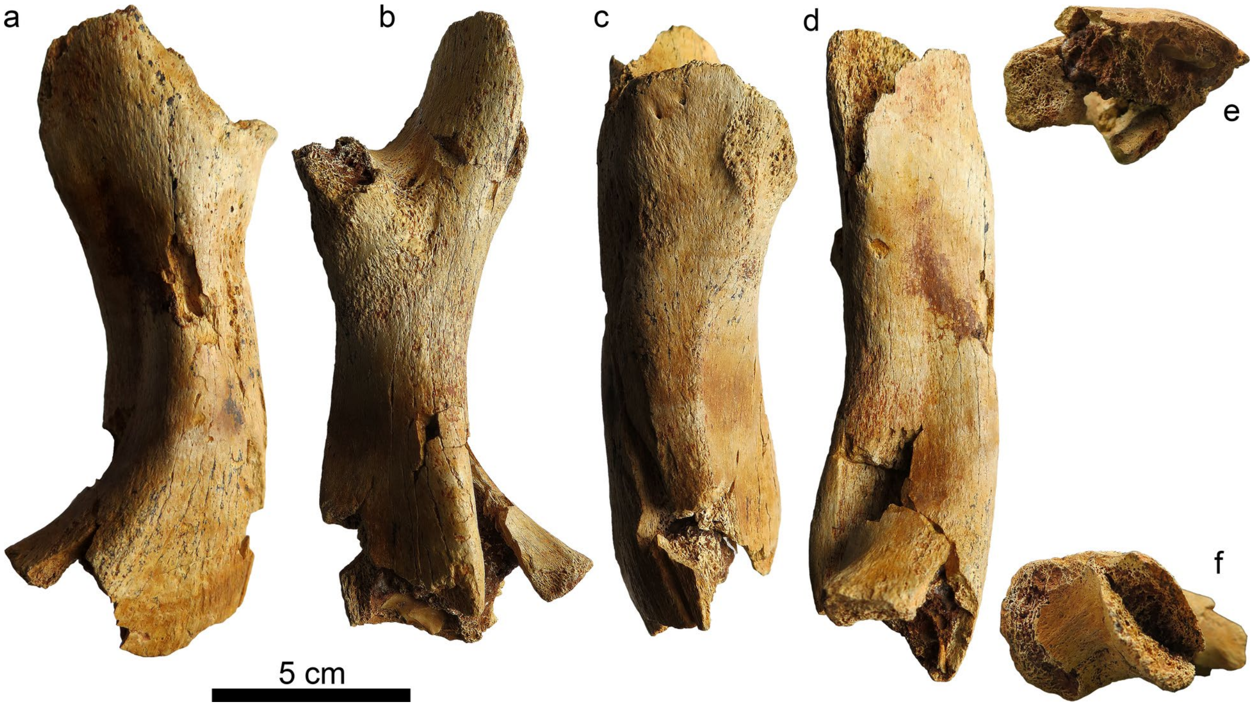

Fig. 11 Right humerus (MGPT-PU 138987) in capitular (**a**), intertubercular (**b**), radial (**c**), ulnar (**d**), proximal (**e**), and distal (**f**) views

the femoral head expands almost perpendicularly in lateral view. The intertrochanteric fossa is rather wide and deep, but it is not possible to observe its entire morphology because the part with the major trochanter is broken. The trochanters do not extend more proximally than the femoral head. The major trochanter is not completely preserved, but most certainly the two trochanters were fused ventrally. The minor trochanter is complete and clearly separated from the fossa and the femoral head. The area of muscular insertion on the small trochanter is triangular. The femoral head is narrow, narrower than the combined width of the trochanters, and oval, 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 and weakly developed. Three additional femoral specimens [RGM.443156 (Fig. 10), RGM.454271, and RGM.454284] are available from the Gargano Naturalis collection. RGM.443156 (Fig. 10) preserves the proximal and the middle parts, missing the distal end of the bone. The proximal part is incomplete, seemingly eroded or incompletely preserved, not permitting a clear observation of the proximal anatomy of the head and the trochanters. Based on the commonly preserved parts, femur RGM.443156 is similar to the MGPT-PU 138990 femur. Femur RGM.454284 is notable due to its extremely small size, apparently pertaining to an individual of a very young ontogenetic stage. The proximal and distal ends are incompletely ossified and preserved. Compared to the ontogenetically older specimens, the juvenile femur RGM.454284 is a bit straighter in diaphysis, has a slightly narrower middle shaft in diaphysis, and the surface of the bone is smooth, contrary to the rugose surface of the larger specimens.

Some partial humeri are preserved, showing the development of thin processes (or trochanters in terminology followed in previous publications) that are slightly diverging towards the proximal end (Figs. 11, 12, 13, 14). The largest among them is the right humerus MGPT-PU 138987, with a total length of 135.1 mm (Figs. 11, 12). This specimen is thicker (stouter) and longer than the humeri of a *Centrochelys sulcata* specimen (MGPT-MDHC 532) with a straight shell length of 530 mm. Another partial right humerus (MGPT-PU 139142) is quite eroded but preserves a sufficient part of the shaft, showing that it was quite straight throughout the entire middle part (Fig. 13a–d).

Other preserved limb bones include a few ulnae [RGM.453473, RGM.454049 (Fig. 15), and potentially also RGM.215368], tibiae [RGM.215002, RGM.453957, RGM.455217 (Fig. 16a–i), and RGM.455319 (Fig. 16j–q)], and an ungual phalanx (RGM.215013). The ulna (Fig. 15) is notably tall and quite robust, with a curved middle part. The proximal part is wide and expanded, with a triangular cross-section, a slightly concave proximal articular surface without any prominent olecranon. A well-marked

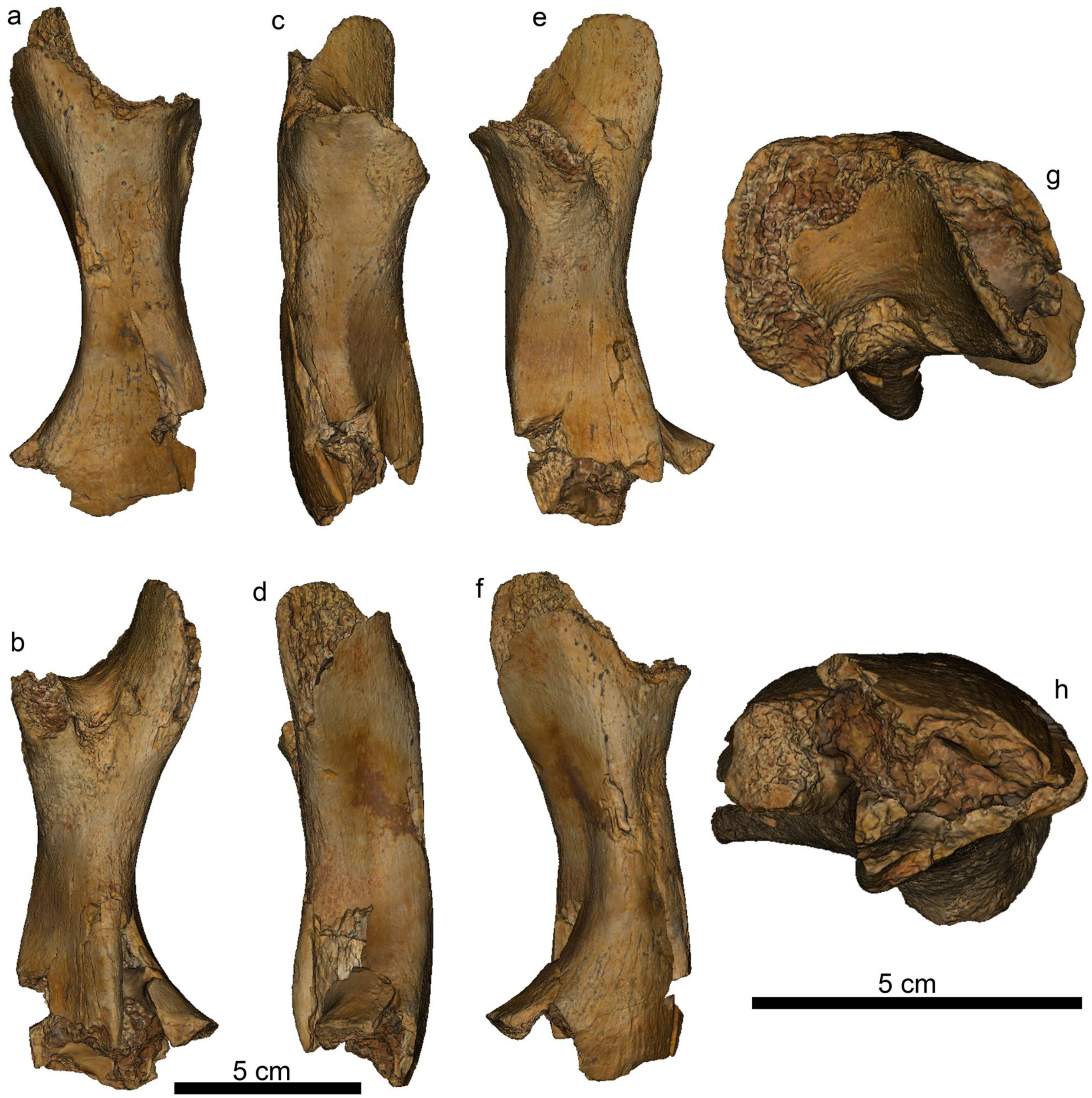

Fig. 12 3D images of right humerus (MGPT-PU 138987) in capitular (**a**), intertubercular (**b**), radial (**c**), ulnar (**d**), radio-intertubercular (**e**), ulno-capitular (**f**), proximal (**g**), and distal (**h**) views. Scale bars: 5 cm for **a**–**f** and 2.5 cm for **g**, **h**

concavity is present on the dorsal side of the ulna. The distal end is narrower than the proximal one, with a convex distal articular surface. The right tibia RGM.455217 is nearly complete and 94.1 mm long (Fig. 16a–i). It is thicker (stouter) and longer than the tibiae of a *Centrochelys sulcata* specimen (MGPT-MDHC 532; 73.5 mm) with a straight shell length of 530 mm. The proximal end is triangular and wide, with a concave proximal articular surface, showing dorsally a clearly marked cnemial crest with a wrinkled surface. The shaft is rather straight and robust. The distal part preserves a clearly marked and deep articular surface for the astragalocalcaneum.

The pectoral girdle is represented solely by two scapular fragments (RGM.443165 and RGM.443191; not figured), while the pelvic girdle is documented by ilial fragments [RGM.215015, RGM.215367, RGM.453960 (Fig. 17c–f), and RGM.454272], one right ischium (MGPT-PU 139140), and indeterminate pelvic fragments

Fig. 13 Partial humeri. **a**–**d** Partial right humerus (MGPT-PU 139142) in capitular (**a**), intertubercular (**b**), radial (**c**), and ulnar (**d**) views; **e**–**h** left humerus diaphysis fragment (MGPT-PU 139141) in capitular (**e**), intertubercular (**f**), radio-intertubercular (**g**), and ulnar (**h**) views

(RGM.261183, RGM.261209, and potentially also RGM.261773). MGPT-PU 139140 corresponds to the right ischium of a young individual (Fig. 17a, b), showing the typical triradiate structure of the bone, but not fused with the rest of the pelvis.

Vertebrae (Fig. 17g–k)

Five caudal vertebrae plus an indeterminate vertebral fragment are available in the sample from Gargano. The most complete caudal vertebra is MGPT-PU 100002 (Fig. 17g–k). It is procoelous, with a short centrum,

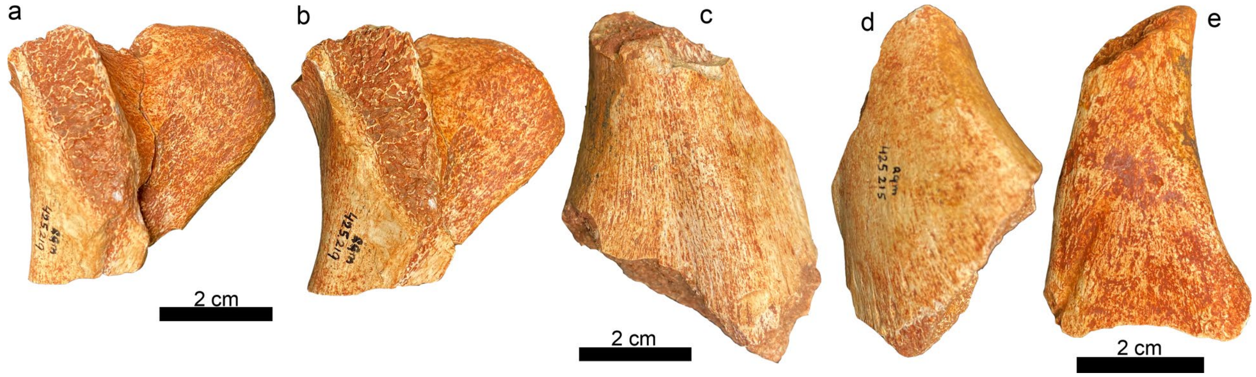

Fig. 14 Additional humeri. **a**–**d** proximal fragment of humerus (RGM.424219) in intertubercular (**a**), and radio-intertubercular (**b**) views; **c**, **d** distal fragment of humerus (RGM.424215) in capitular (**c**) and intertubercular (**d**) views; **e** distal fragment of humerus (RGM.453958) in capitular view

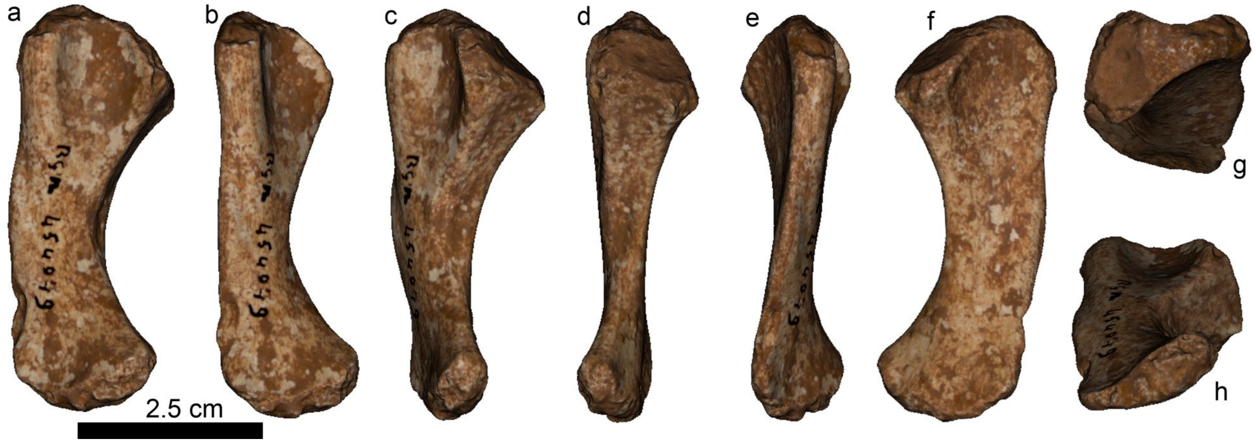

Fig. 15 Ulna. 3D images of right ulna (RGM.454049) in dorsal (**a**), laterodorsal (**b**), lateroventral (**c**), medial (**d**), lateral (**e**), ventral (**f**), proximal (**g**), and distal (**h**) views

dorsoventrally compressed condyle and cotyle, a wide anterior and a narrow posterior articular surface, and well-preserved, long transversal articular processes.

Discussion

Taxonomic identification and comparisons

The Gargano turtle clearly represents a member of Testudinidae based on the presence of an alternating pattern of the costal plates (and therefore the neural plates; Vlachos & Rabi, 2018), although the costal rib heads are notably placed far away from the costal / neural suture. The preserved material of the Gargano tortoises is fragmentary and disarticulated and originates from an array of different localities; the preserved humeri and femora attest to the presence of at least four different individuals of various sizes and of different ontogenetic stages. Based on the available information, the size overlap of some specimens, and the overall consistent and similar morphology, we prefer the conservative approach that they all belonged to the same taxon, pending the discovery of additional and more complete material from the Gargano localities. Even if the right femur MGPT-PU 138990 misses the major trochanter, which possesses diagnostic characters for the group (see Valenti et al., 2022 for detailed information), the rest of the bone is nearly identical in shape and size with the holotype right femur (ZCSP US.0-Q2) of *Solitudo sicula* Valenti et al., 2022, from the latest Pleistocene of Sicily (Valenti et al., 2022). The genus *Solitudo* is principally diagnosed by the presence of an incomplete fusion of the trochanters of the femur dorsally, in contrast to other testudinid genera in which the trochanters are connected proximally via a rounded ridge, while additional diagnostic characters include its femur being generally 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° and 45°, in contrast to other testudinid genera with relatively massive femora and broad and less oblique femoral heads, forming an angle that is less than 25° with the

Fig. 16 Tibiae. **a**–**i** 3D images of right tibia (RGM.455217) in dorsomedial (**a**), dorsal (**b**), ventrolateral (**c**), ventral (**d**), oblique proximal (**e**), proximal (**f**), distal (**g**), lateral (**h**), and medial (**i**) views; **j**–**q** 3D images of left tibia (RGM.455319) in ventral (**j**), lateral (**k**), dorsal (**l**), medial (**m**), proximal (**n**), distal (**o**), oblique proximal (**p**), and oblique distal (**q**) views

anteroposterior plane (see Valenti et al., 2022). The Gargano material matches the additional diagnostic characters of the genus, in particularly the slender diaphysis, the femoral head that is narrower than the combined anteroposterior width of the trochanters, and the oblique orientation compared to the anteroposterior plane (30°). Still, we are unable to confidently identify this material as belonging to *Solitudo*, as the major trochanter of the femur is missing. Thus, the Gargano tortoise material is left with open nomenclature, as cf. *Solitudo* sp.

Nevertheless, compared to the Sicilian taxon, the Gargano tortoise preserves additional elements of the shell that allow discussing some interesting characters. A striking feature is that the scute sulci are preserved as deep furrows with distinct raised ridges. Williams (1950) considered that this character was diagnostic for the insular extinct species *Chelonoidis cubensis* (Leidy, 1868). However, this character is observed in other members of the extant *Chelonoidis* as well and especially, in the Galapagos insular form *Chelonoidis nigra* (Quoy & Gaimard, 1824) complex (see Vlachos, 2018 for further information), as well as in other large tortoises such as the, also insular, *Aldabrachelys gigantea* (Schweiger, 1812), but also in an array of continental taxa, both extinct (e.g., Hay, 1908) and extant, such as *Manouria* Gray, 1854 (Walter Joyce, personal communication) and *Centrochelys* Gray, 1872 (MD, personal observation). The presence of this character in the Gargano tortoise further attests that this character is, taxonomically, much more widespread than previously thought. Additionally, the preserved hyoplastron has a medially straight and laterally concave humeropectoral sulcus, a character typically observed in Geochelona (or Geochelonini in alternative terminology), both extant and extinct (see Pérez-García & Vlachos, 2014; Vlachos & Rabi, 2018). If this is correct and the Gargano tortoise is indeed (close to) *Solitudo*, the morphology of the humeropectoral sulcus would suggest some geochelonan affinities for this taxon.

In addition, the Gargano tortoise preserves the dentary, an element that is so far poorly known and described in insular and continental extinct tortoises. Its morphology is comparable to the dentary of testudinids reported in Evers et al. (2023). The extent of the lingual ridge towards the symphyseal area is similar to the condition

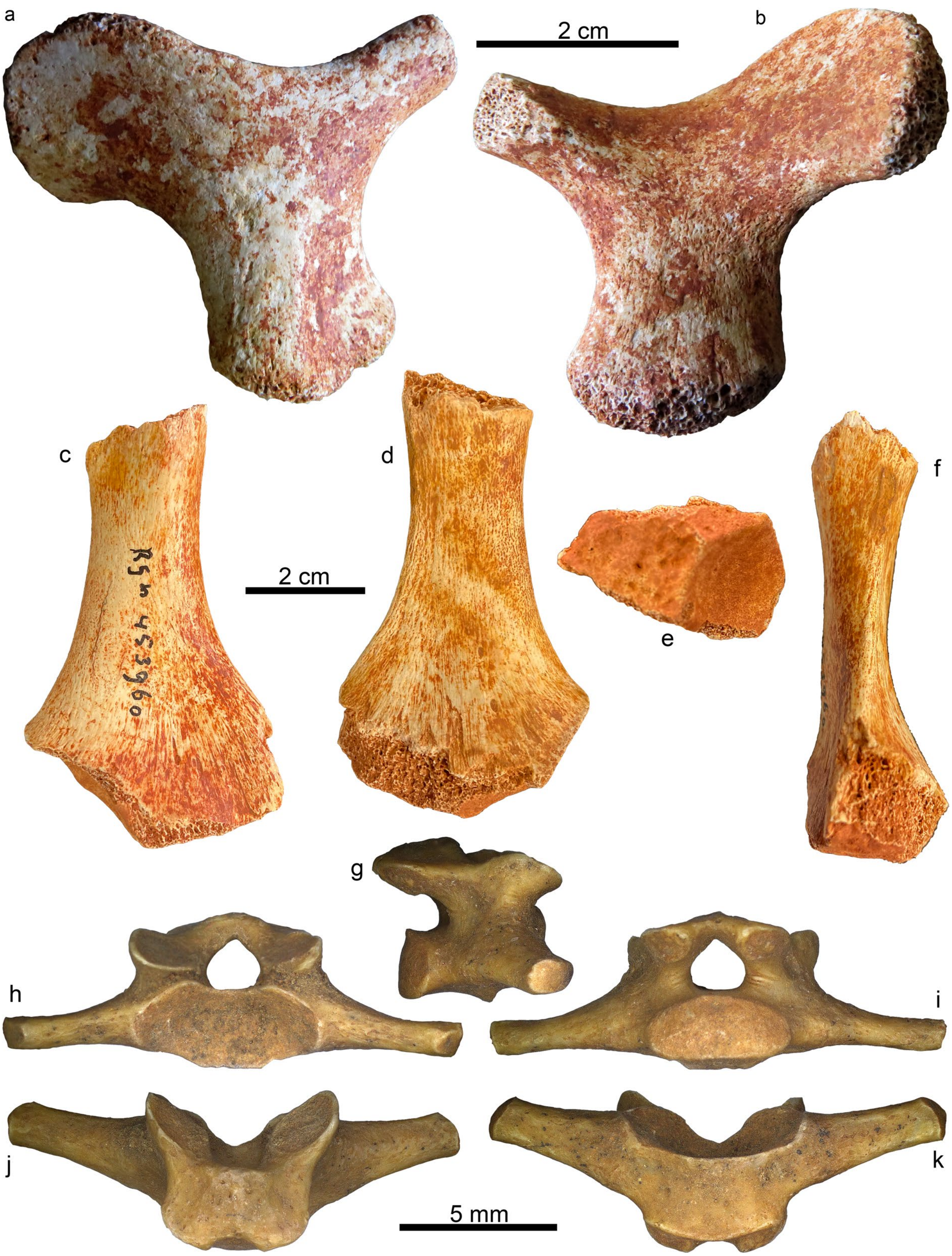

Fig. 17 Girdles and vertebra. **a**–**b** Right ischium (MGPT-PU 139140) in posterodorsal (**a**) and anteroventral (**b**) views; **c**–**f** fragment of right ilium (RGM.453960) in anterior (**c**), posterior (**d**), ventral (**e**), and medial (**f**) views; **g**–**k** caudal vertebra (MGPT-PU 100002) in right lateral (**g**), anterior (**h**), posterior (**i**), dorsal (**j**), and ventral (**k**) views

seen in members of Geochelona and not as in Testudona (or Testudinini in alternative terminology) based on the comprehensive compendium of Evers et al. (2023). Also, both ridges are clearly serrated and quite well developed. These might be further indications of closer relationships of *Solitudo* with Geochelona than Testudona, an unresolved question in Valenti et al. (2022). Nevertheless, additional specimens are needed for more detailed comparisons and any affirmative taxonomic conclusion.

Overview of the Mediterranean insular testudinids

Large-sized or even giant tortoises once achieved a diverse distribution across the Mediterranean islands. This is consistent with the pattern observed on other islands across the planet, where a number of extant (or recently extinct) large testudinid taxa dominate(d) their insular ecosystems, including islands of the Atlantic Ocean (Canary, Cabo Verde, and Caribbean Islands), the Indian Ocean (Madagascar, Seychelles, Aldabra, Mascarenes, and Indonesia), and the Pacific Ocean (Galapagos Islands) (Arnold, 1979; Bour, 1985a, 1994; Georgalis et al., 2021; Gerlach, 2004; Günther, 1877; Kehlmaier et al., 2019; Loveridge & Williams, 1957; Lapparent de Broin, 2002; Quoy & Gaimard, 1824; Rhodin et al., 2015; Rothschild, 1915; Scheyer et al., 2018; Turvey et al., 2017; Van Denburgh, 1914; Vlachos, 2018; Williams, 1950, 1952).

On the Mediterranean islands, such insular forms have so far mainly been documented from the Quaternary, but, nevertheless, their record goes further back in time, as some occurrences are known from the late Neogene. A number of these finds (i.e., those known by adequate femoral material) have been recently united into a single genus, *Solitudo*, that possesses a rather distinctive femoral morphology (Valenti et al., 2022). This rather distinctive morphology differentiated *Solitudo* from other continental testudonans and geochelonans and implied an endemic insular radiation of testudinids, confined to certain central and western Mediterranean islands, with different species distributed on different islands (Valenti et al., 2022).

The oldest occurrence of a large tortoise from the Mediterranean islands is the indeterminate large testudinid from the Late Miocene (Tortonian) palaeo-island of Scontrone in Italy (Georgalis & Delfino, 2021). The palaeo-islands of Scontrone and Gargano are considered to be parts of the same palaeobioprovince, the Apulo-Abruzzi area (Rook et al., 2008; Savorelli et al., 2025). The Scontrone form is solely known from rather incomplete remains, including plastral and indeterminate shell fragments plus a few remains of the appendicular skeleton (humerus, ilium, caudal vertebral, and probable pectoral girdle and pubis material), which unfortunately are insufficient to clarify its taxonomic affinities (Georgalis & Delfino, 2021). As such, it is unclear whether the Scontrone remains represent an early member or ancestor of *Solitudo* or whether it instead has closer affinities with continental large tortoises, such as *Titanochelon* or *Centrochelys*, which were thriving in the Neogene of neighboring continental Europe and Africa respectively (Georgalis et al., 2021; Lapparent de Broin, 2002; Pérez-García & Vlachos, 2014; Vlachos et al., 2020a, 2020b; Vlachos, 2025).

The next younger finds in the Mediterranean Islands are the Pliocene large-sized *Solitudo gymnesica* (Bate, 1914) and the much smaller *Testudo pecorinii* Delfino in Abbazzi et al., 2008. The former species was established (as *Testudo gymnesicus*) on the basis of appendicular remains, shell fragments, and osteoderms from the Early Pliocene of Minorca, in the Balearic Islands, Spain (Bate, 1914). While fragmentary, these specimens clearly attest to the presence of a large-sized tortoise on Minorca (Bate, 1914; Luján et al., 2017). The age of this testudinid was originally considered as Quaternary, but recent geological and palaeontological evidence concluded that the type locality is in fact Early Pliocene (Quintana et al., 2011). Additional coeval material from Minorca attributed to the same species has since been described (Mercadal & Pretus Real, 1980; Quintana et al., 2004). The taxonomic affinities and proper genus level placement of the Minorcan large tortoise have long been puzzling: it was originally described by Bate (1914) as a species of the wastebasket genus *Testudo* Linnaeus, 1758, subsequently placed in the Eocene French genus *Cheirogaster* Bergounioux, 1935 (e.g., Jiménez Fuentes & Martín de Jesús, 1991; Filella-Subirà et al., 1999; Quintana et al., 2004), but affinities with the giant European continental genus *Titanochelon* have been suggested more recently (Pérez-García & Vlachos, 2014; Rhodin et al., 2015). Nevertheless, the recent analysis of Valenti et al. (2022) demonstrated that the Minorca form shares distinct features in its femur, which they utilized to name a new genus, *Solitudo*. A similar, probably related form has been described from the Late Pliocene–Early Pleistocene of the nearby island of Ibiza by Bour (1985a, 1985b), which was originally (and rather exaggeratingly) referred to the Mascarene genus *Cylindraspis* Fitzinger, 1836. Furthermore, reports of a large-sized tortoise, probably also affiliated with *Solitudo gymnesica* exist from Pliocene localities on Mallorca as well, but these have never been figured (Bover et al., 2014). Finally, fossilized eggs attributable to a large testudinid have been described from the Late Pliocene / Early Pleistocene of Formentera Island, also in the Balearics (Filella-Subirà et al., 1999). This being said, the different Balearic islands were all inhabited by large tortoises, but whether all of these Balearic forms are conspecific or they represent distinct species cannot yet be answered on the basis of our current knowledge and the available fossil material.

Testudo pecorinii is known exclusively from a partial carapace and plastron from its type locality, the Late Pliocene–Early Pleistocene of Capo Mannu D4 Local Fauna, Sardinia (Abbazzi et al., 2008). Although based on limited material (solely the holotype shell MDLCA 23789), it is evident that this taxon is a member of the *Testudo* s.s. lineage, based on the likely presence of a hinge between the hypoplastra and xiphiplastra, and can be further differentiated from all other congeners by a combination of shell features (see Abbazzi et al., 2008). It seems that *T. pecorinii* represented a short-lived insular taxon of *Testudo* in the late Neogene and / or early Quaternary of the island of Sardinia that ultimately perished and left no descendants (Zoboli et al., 2023).

Nevertheless, it is the Quaternary that witnessed the most spectacular and well-known examples of large and giant tortoises in the Mediterranean islands.

Crete has currently no tortoises in its herpetofauna, but during the Pleistocene it was inhabited by the extant species *Testudo marginata* Schoepff, 1792. The Cretan form, a moderately large tortoise, was originally established by Bachmayer et al. (1975) as a supposedly distinct insular subspecies of this Greek mainland species, i.e., *Testudo marginata cretensis* Bachmayer et al., 1975. Subsequently, more shell remains were referred to the same taxon from other Pleistocene Cretan caves (Kotsakis, 1977). Recent works though, have casted some doubt on the subspecies level distinction of the Cretan form (e.g., Georgalis & Kear, 2013; Rhodin et al., 2015). Indeed, Vlachos (2022a) formally synonymized the Cretan subspecies with the mainland nominal form and attributed the differences proposed by Bachmayer et al. (1975) to erroneous observations of the original material or individual variation. This suggestion was supported in another publication by the same author the same year (Vlachos, 2022b), where he described multiple additional specimens of the Cretan tortoise from several caves in the island.

It should be noted here that large to giant fossil tortoise material has been also found in Neogene and Quaternary localities on other islands of the Aegean Sea, however, these are not taken into further consideration here, as during these times, these Greek islands were most probably interconnected to the (now nearby) Anatolian Peninsula (Georgalis & Kear, 2013; Vlachos, 2022a). These include fossil material from the Plio-Pleistocene of Lesbos (Lapparent de Broin, 2002) and Rhodes (Mueller-Töwe et al., 2011) Islands, as well as from the Late Miocene of Samos Island (Szalai, 1931; Vlachos et al., 2020b).

Similarly to Crete, testudinids also do not form part of the modern herpetofauna of Cyprus, but fossil material from Late Pleistocene and Early Holocene sites of the island demonstrated the presence of this group of turtles (see Bailon, 2023). The precise taxonomic affinities of the Cypriot tortoise are not clear and it has been referred to either as *Testudo* sp. or *Testudo* (s.s.) sp. (see Bailon, 2023). Moreover, it is not clear whether these tortoises were native to the island or they were simply introduced / transported by the first humans that arrived in Cyprus (see Bailon, 2023). Definitely, more fossil remains, eventually also from older localities, are required in order to address these questions.

Sardinia presents only very tentative hints of the presence of large tortoise remains in the Quaternary, confined so far exclusively to a single large phalanx from the Middle–Late Pleistocene of Monte San Giovanni (Zoboli et al., 2023). Only more complete large testudinid finds from Sardinia will eventually shed some light on whether the large Sardinian tortoise represented a further member of *Solitudo* or whether the finds correspond to a large member of *Testudo*.

Sicily has also yielded fossil remains of large tortoises, however, besides *Solitudo sicula* discussed above, these have mostly appeared in preliminary faunal lists or, at best, partially described or illustrated in the unpublished thesis of Delfino (2002). These preliminary descriptions of large tortoises include fossil remains from three Middle Pleistocene localities: Contrada Annunziata, Alcamo, and Contrada Castellazzo (Delfino, 2002). Nevertheless, this number of described remains is certainly much lower than the real amount of already recovered remains, at least judging from several mentions of so far unpublished material of large to giant tortoises from different Pleistocene localities across Sicily (e.g., Burgio & Cani, 1988; Burgio & Fiore, 1988). To all these occurrences, the younger taxon *Solitudo sicula* was recently added, known exclusively from the latest Pleistocene (approximately 12,500 years ago) cave of Zubbio di Cozzo San Pietro (Valenti et al., 2022). With a shell length of 50–60 cm, *Solitudo sicula* was larger than the extant *Testudo hermanni* Gmelin, 1789, that inhabits the island, while it possessed a rather distinctive femur morphology that was substantially different than that of other tortoises (Valenti et al., 2022). In fact, it was the discovery of *Solitudo sicula* that "triggered" the taxonomic idea that insular tortoises from the Plio-Pleistocene of certain Mediterranean islands were members of an insular endemic monophyletic lineage, the genus *Solitudo*, that was united by this kind of distinctive femur morphology, which differentiated it from other testudinids (Valenti et al., 2022). Furthermore, *Solitudo sicula* represents the youngest occurrence of large-sized tortoises from the Mediterranean islands.

Malta has by far the richest and most abundant fossil record of large testudinids, spanning also a considerably long history of discoveries, as the first remains were described already in the nineteenth century (Leith Adams, 1877; Lydekker, 1889). Amazingly for such a small geographic area, five different species have been named, all from Pleistocene caves: *Testudo robusta* Leith Adams, 1877, *Testudo spratti* Leith Adams, 1877, *Testudo robustissima* Tagliaferro, 1913, *Testudo despotti* Szalai, 1938, and *Testudo gaudense* Lanfranco, 1955. Frustratingly, all these taxa are only based on appendicular remains, vertebrae, and few carapace and plastron fragments (Lanfranco, 1955; Leith Adams, 1877; Szalai, 1938; Tagliaferro, 1913). *Testudo robusta* is currently considered to be the sole valid species. This species was recently referred to the African genus *Centrochelys* by Rhodin et al. (2015) and such generic placement has been subsequently followed by others (Luján et al., 2017). The establishment of the insular endemic genus *Solitudo* characterized by unique femoral morphology, however, shed more light on the affinities of the Maltese large tortoise (Valenti et al., 2022). Accordingly, *Testudo robusta* was designated by Valenti et al. (2022) as the type species of their new genus, as *Solitudo robusta*, as it shared the diagnostic characters of the slender femur with incomplete fusion of the trochanters dorsally, the femoral head that is narrower than the combined anteroposterior width of the trochanters, and an oblique orientation compared to the anteroposterior plane between 25° and 45°. That being said, however, it should be noted that the status of the other four named species of large tortoises from Malta (*T. spratti*, *T. robustissima*, *T. despotti*, and *T. gaudense*) was not further investigated by Valenti et al. (2022), and in fact, these species were not even mentioned in that work.

The tortoise remains from the Late Miocene of Gargano fill a gap between older insular testudinid remains from the palaeo-island of Scontrone (Georgalis & Delfino, 2021) and those from younger, Pliocene and Quaternary, localities in Sicily, Malta, and the Balearics (and potentially also from Sardinia). As clarified above, remains from the Plio-Pleistocene of Sicily, Malta, and Minorca, have been recently recombined as different insular endemic species of a single genus, *Solitudo*, principally united by a highly distinctive femur morphology (see Valenti et al., 2022). Remains from other Balearic Islands, as well as from Sardinia could potentially also belong to *Solitudo* but they are too incomplete and do not preserve femoral material in order to allow a confident genus level identification. This is also the case for the Scontrone testudinid, which represents the oldest insular testudinid from the Mediterranean Islands (Georgalis & Delfino, 2021). If the Gargano tortoise represents indeed a member of *Solitudo*, then it offers an unprecedented opportunity to glimpse into the plastral and mandibular morphology of this, principally femur-based, genus; interestingly, such plastral and mandibular morphology tentatively imply geochelonan affinities for *Solitudo*, though apparently more complete remains are necessary in order to decipher such taxonomic assumptions. Finally, the Gargano tortoise remains add to our knowledge of the peculiar insular endemic faunas of the two palaeoislands Gargano and Scontrone, a unique window into adaptive insular radiation and high diversity in the late Neogene of the Mediterranean Sea.

The taxonomy and distribution of the tortoises from the Mediterranean islands and palaeo-islands is a quite complex story, further complicated by the uneven and poorly preserved fossil record. This situation has not allowed the formulation of robust and well-supported taxonomic and phylogenetic hypotheses. The recently proposed *Solitudo* hypothesis is a first attempt to study and compare these occurrences with the mainland taxa from surrounding European, African and Asian localities in the emerging modern scheme of the circum-Mediterranean testudinid systematics. Although far from ideal and complete, the *Solitudo* scheme shows some evidence that tortoises with at least a similar femur morphology were distributed in several islands and palaeo-islands of the Mediterranean; whether this is enough to support the distinction of the clade remains to be tested in future analyses. Additional efforts are required in the future to revise previously known materials and describe new fossils (even if fragmentary) from insular localities of the area and even from surrounding coastal regions. The present work is placed in this context and will hopefully contribute to a better understanding of the evolution of tortoises in the Mediterranean.

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Author contributions

GLG, EV, and MD studied the material; GLG, EV, MD, and MP wrote the manuscript text; GLG, FC, and MD took the photographs; FC conducted the 3D scanning and Morphosource uploads; GLG prepared the Figures; MP collected part of the specimens in field campaigns in Gargano; MD and MP selected the material; MP and LVHO curated the material. All authors read, edited, and approved the final manuscript.

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Data availability

All fossil specimens described herein are permanently curated at the collections of MGPT-PU and RGM. 3D model files of selected specimens are available in the public online repository of Morphosource (https://www.morphosource.org/): right hyoplastron (MGPT-PU 100008 [Morphosource.org: Media 000721992, ark:/87602/m4/721992]); right humerus (MGPT-PU 138987 [Morphosource.org: Media 000722361, ark:/87602/m4/722361]); right femur (MGPT-PU 138990 [Morphosource.org: Media 000722432, ark:/87602/m4/722432]); right tibia (RGM.455217 [Morphosource.org: Media 000727945, ark:/87602/m4/727945]); left tibia (RGM.455319 [Morphosource.org: Media 000727950, ark:/87602/m4/727950]); right hypoplastron (RGM.261507 [Morphosource.org: Media 000727955, ark:/87602/m4/727955]); left mandible (RGM.454048 [Morphosource.org: Media 000731092, ark:/87602/m4/731092]); right ulna (RGM.454049 [Morphosource.org: Media 000736121, ark:/87602/m4/736121]); fragment of femur (RGM.443156 Morphosource.org: Media 000769221, ark:/87602/m4/769221).

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

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