



A new species of a bony spur-thighed tortoise from the Early Pliocene (MN15) of Jradzor site, Armenia, and the origin of the *Testudo graeca* (Testudines, Testudinidae) complex

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Abstract

The origin of the *Testudo graeca* complex has been suggested to be in the Caucasus. Poor fossil records and incomplete preservation of available fossils limit deep-time reconstructions of the paleobiogeographic history of the complex. The present work describes recently discovered tortoise species found from the Early Pliocene Jradzor site, Armenia. Apart from being one of the few well-preserved and complete species of the genus in the fossil record, the Jradzor species is the only well-dated (~4.16 and 3.98 Ma) form among fossil representatives of the genus. The tortoise material is numerous and comprises several complete and partial shells, including some rare cranial elements and numerous postcranial bones, including the presence of bony thigh spurs. The material clearly belongs to a testudinid taxon, based on the alternating neural plates, the coincidence between the costal/peripheral sutures and the pleural/marginal sulci, the presence of a well-developed epiplastral lip, and the complete fusion of the trochanters of the femur, reaching an average carapace length of 30 cm. Furthermore, the presence of a clear hypo-xiphiplastral hinge on the plastron indicates that the Jradzor tortoise is a member of the true *Testudo* (or *sensu stricto*) lineage. Our morphological and phylogenetic analysis placed the Jradzor tortoise within the context of the Eurasian Testudinini, showing that the recovered material should be described as a new species, that is phylogenetically placed as a sister group to the extant *Testudo graeca* complex. The new material allows an evaluation of the validity of previously known and relevant taxa and their inclusion in a new phylogenetic analysis like *Testudo eldarica* and *Testudo kuchurganica*, excluding *Testudo burtschaki* that should be considered as a nomen dubium. The new material presented herein sheds light on the origin and early evolution of the modern Mediterranean tortoises.

Keywords

Armenia, Early Pliocene, fossil calibration, South Caucasus, Testudinidae, *Testudo*, tortoises

Introduction

When Linnaeus named the first species of turtles and tortoises known at the time, they were all included in his new genus *Testudo*: tortoises, freshwater and marine turtles alike. As a result, *Testudo* is the first wastebasket taxon in turtles, with numerous extant and extinct species

originally described as members of *Testudo*, and a complicated nomenclatural history with names attributed to it at the family, family-group, and genus-group levels. Since then, the application and taxonomic extent of this genus have been modified and gradually restricted to its current usage (see Crumly 1988; Fritz and Bininda-Emonds 2007 and references therein). Subsequent

designations by Fitzinger (1843) and Lindholm (1929) made the Linnean species *Testudo graeca* Linnaeus, 1758 the type species of *Testudo* Linnaeus, 1758 (according to the TTWG 2025 and references therein), causing a multitude of taxonomic changes in different levels and in the fossil record, and a re-definition of the taxonomic concept of the genus. A robust framework supported by molecular data also emerged in recent decades, when Fritz and Bininda-Emonds (2007) resolved the application of both *Testudo* and *Geochelone* Fitzinger, 1835 to their proper clades, and shortly after Fritz et al. (2007, 2009) provided detailed resolution within *Testudo* and *Testudo graeca* complex as well. This solid framework allowed the revision of numerous extinct testudinid taxa as well and the incorporation of more fossils in cladistic analyses.

Currently, the genus or clade *Testudo* is restricted only to those derived tortoises that contain a true hypo-xiphiplastral hinge in the posterior lobe (Amiranashvili 2000; Lapparent de Broin 2001; Danilov 2005; Danilov et al. 2017; Vlachos and Rabi 2018; Pérez-García et al. 2022; and references therein), creating a movable posterior part of the plastron. Although similar mobilities can be seen in non-*Testudo* species as well (Gmira 1995; Lapparent de Broin et al. 2006a, 2006b, 2006c; Vlachos et al. 2018; and references therein), the true hinge is identified not only by the movable posterior lobe but also by the accompanying coincidence between the hypo-xiphiplastral suture and the abdomino-femoral sulcus, at least medially. Recent cladistic analyses reveal a single origin of this morphology in tortoises, being one of the few (or even the only) non-homoplastic character in the highly homoplastic group of tortoises or Testudinidae (Pérez-García et al. 2022).

Based on the scheme of Vlachos and Rabi (2018) and Pérez-García et al. (2022), numerous and diverse hingeless species are branching outside and along the stem leading to the derived clade *Testudo*, whose phylogenetic relationships remain, sometimes, unclear. The total clade of *Testudo* is sister to other extant genera with decent fossil records, such as *Chersine* Merrem, 1820 and *Agrionemys* Khosatzky & Mlynarski, 1966, all further related to the extant *Indotestudo*, forming together the clade *Testudona* Parham in Parham et al. 2006 or the tribe Testudinini Batsch, 1788. Testudinins have a rich fossil record in Eurasia and northern Africa (see Georgalis et al. 2021 and references therein for further information on the African fossil record) that requires an extensive and laborious revision, particularly in reconciling the relationships between hinged and hingeless taxa and their phylogenetic relationships.

The highest specific diversity of the true, hinged *Testudo* species is found in Greece, a country that hosts two extant (*Testudo graeca*, *Testudo marginata* Schoepff, 1793) species with an extensive fossil record in the country as well, and at least three extinct species (*Testudo marmorum* Gaudry, 1862; *Testudo brevittesta* Vlachos & Tsoukala, 2016; *Testudo hellenica* Garcia

et al., 2020) (see Vlachos 2021 and references therein). Fossil members of the true *Testudo* can also be found outside Greece. The best preserved and quite diverse species is the recently described *Testudo lohanica* Pérez-García et al. 2022 from the Late Miocene of Romania, including well-preserved skeletons along with the first complete cranial remains described for an extinct species of the genus. Other species attributed to *Testudo* originate from the Late Miocene of Crimea but are known only by shell remains, including *Testudo bosporica* Riabinin, 1945, *Testudo eldarica* Khosatzky & Alekperov in Alekperov 1978, from the Late Miocene of Azerbaijan (based on Danilov et al. 2017), *Testudo chernovi* Khosatzky, 1948 from the Early Pliocene of Moldova, Ukraine, Romania and Georgia; *Testudo kuchurganica* Khosatzky, 1948 from the Early Pliocene of Moldova and Ukraine, and possibly *Testudo pecorinii* Delfino in Abbazzi et al. 2008, from the Late Pliocene of Sardinia. Although these taxa are recovered in a monophyletic *Testudo*, their internal relationships remain unresolved (Vlachos and Rabi 2018; Pérez-García et al. 2022; and references therein). Furthermore, several occurrences, especially from paleoanthropological or archeological sites, are identified as *Te. graeca* in the entire circum-Mediterranean region, but they need a taxonomic revision in the proper historical context.

This paper deals with the description of a new species of *Testudo* from the late Early Pliocene site Jradzor in Armenia (Fig. 1), based on abundant and well-preserved fossils. The new species represents the earliest and one of the few records of the genus *Testudo* in Armenia, since so far, the only *Mauremys caspica gambariani* Chkhikvadze in Melik-Adamyan et al. 1988 from the Early Pliocene of Nurnus and *Testudo graeca ibera* from the Holocene of Verin Khatunarkh (Aknashen), Armenia reported by Bakradze and Chkhikvadze (1984). The tortoise material from Jradzor originates from eleven fossiliferous levels dated ~4.16–3.98 Ma (Lazarev et al. 2023) (Fig. 1B), thereby covering the time period of the calculated early divergence of the *Testudo graeca* complex in the southern part of the Armenian Lesser Caucasus. The findings include not only several carapace and plastron remains that allow the documentation of the morphology of the entire shell, but also some cranial and several appendicular remains, making the Jradzor tortoise one of the most complete fossil *Testudo* occurrences. Besides the tortoise material, several Jradzor levels contain some elements of a geoemydid species (see Suppl. material 1), which are going to be described elsewhere with detailed comparison with the slightly older *Mauremys* from Nurnus. Thus, this paper focuses only on the description of the new tortoise species.

At present, and based on molecular data, at least two different extant subspecies of *Testudo graeca* have been recorded from Armenia, all belonging to the *Testudo graeca* species complex: *Testudo graeca armeniaca* Chkhikvadze & Bakradze, 1991 (which includes also the synonymized taxa *Te. gr. pallasi* Chkhikvadze

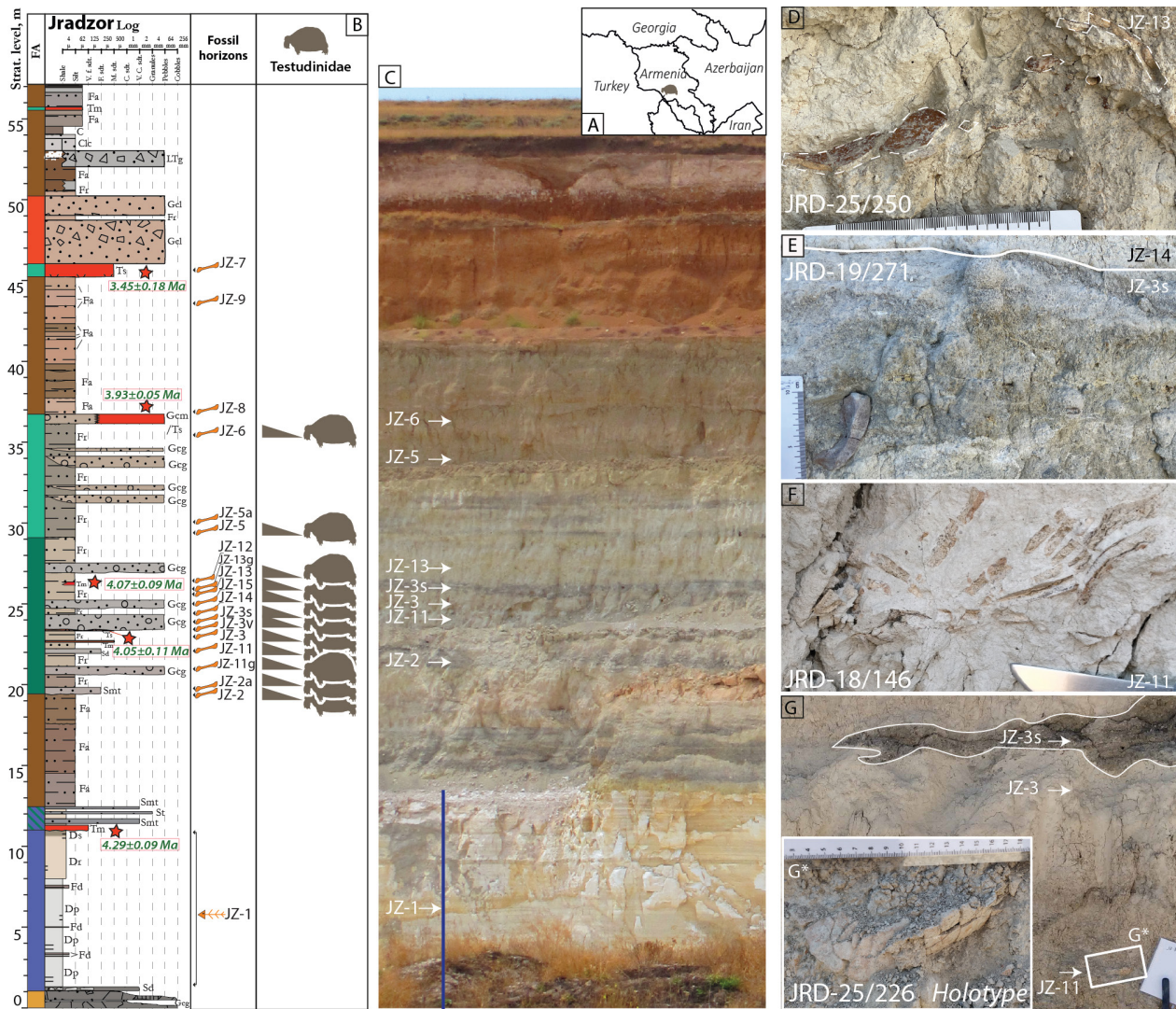


Figure 1. A. Geographic map of the Armenia and neighboring countries with the location (indicated by a turtle) of the Jradzor site; B. Log and C. Photograph of the Jradzor section with stratigraphic positions of horizons yielded tortoise remains; D–G*. Photographs of different specimens of tortoises as they have been found in the field.

& Bakradze, 2002 and *Te. dagestanica* Chkhivadze, Mazanaeva, Shammakov, 2011), and *Testudo graeca iberica* Pallas, 1814 (see TTWG 2025 and references therein) (Arakelyan et al. 2011). The Caucasian occurrences of these species belong mostly to the well-supported mtDNA Clade A of Fritz et al. (2007), although some occurrences of *Te. gr. iberica* are recovered in the Clade C as well, coming mainly from the Balkans and Türkiye. These findings led Fritz et al. (2007) to suggest a Caucasian origin for the *Testudo graeca* complex, followed by subsequent range expansions in various Mediterranean regions. The fossil record can help in calibrating these events based on phylogenies. Both Fritz et al. (2007, 2009) used some fossil taxa to calibrate their phylogenies (including *Testudo burtschaki* Chkhikvadze, 1975, *Testudo eldarica* Khosatzky & Alekperov in Alekperov 1978, *Testudo chernovi*, *Testudo kuchurganica*, *Testudo marmorum*, *Testudo* aff. *kenitrensis*), recovering minimum divergence times for the eastern *Testudo graeca* subspecies in

the Early Pliocene at about $4.10\text{--}4.20 \pm 0.61\text{--}0.71$ Ma. However, as discussed below, the generic attribution to the true *Testudo* clade of the fossil species used for these calibrations requires critical revision.

Material and Methods

Material

The studied material is stored at the Institute of the Geological Sciences (IGS) of the National Academy of Science of the Republic of Armenia, Yerevan, Armenia. The herein described tortoise material comes from the eleven fossiliferous levels (JZ-2, JZ-2a, JZ-11g, JZ-11, JZ-3, JZ-3V, JZ-3s, JZ-14, JZ-15, JZ-13, JZ-5, JZ-6) of Jradzor section (Fig. 1). They represent more than 1400 different specimens, one-third of which are identifiable and taxonomically informative. In this section, the description is presented from a taxonomic perspective,

and the specimens are illustrated in anatomical order, incorporating specimens from different levels. In the Suppl. material 1, however, the most informative specimens are also figured, divided by their discovery level.

The cranial and few postcranial remains have been CT scanned using the Bruker Skyscanner 2211 at the Université de Fribourg, Switzerland with the following settings: 18 µm resolution, 334 mA, 60 kV, 0.5 mm Al filter. The tomographic reconstructions were performed using the NRecon software in Fribourg, Switzerland. The consequent visualization and segmentation of the bone material were performed using the Amira 9.0 software in Porrentruy, Switzerland.

Anatomy

Mandible anatomy and terminology follow Evers et al. (2023). Humerus anatomy and terminology follow Hermanson et al. (2024). Femur anatomy and morphotypes follow Valenti et al. (2022). Cervical vertebrae anatomy follows mostly Williams (1950). Phylogenetic nomenclature follows Vlachos (2025).

Comparisons

The new tortoise species described herein is mainly compared with other extant and extinct true *Testudo* species, and with other species that have been traditionally associated with the *Testudo* clade but are not actually recovered within. The main extant taxa used for comparisons were *Testudo graeca* complex and *Testudo marginata*, based on personal data (partly published in Vlachos and Rabi 2018), with additional observations on 3D models available in Morphosource (e.g., *Testudo graeca iberica* SMF 67588 scanned by S. Evers and available at <https://www.morphosource.org/concern/media/000657126>; *Testudo marginata* FMNH 51672 in Evers et al. 2023 and available at <https://www.morphosource.org/concern/media/000409726>). For extinct taxa, a main comparison taxon was *Testudo lohanica* Pérez-García et al. 2022 from the Late Miocene of Romania, a species that also includes the only cranial material of an extinct *Testudo* known up to now. Additional comparisons of the shell morphology were made with other key *Testudo* spp., including *Testudo marmorum* from the Late Miocene (MN11–12) of Greece (based on Vlachos et al. 2019), *Testudo hellenica* from Late Miocene (MN10) of Greece, and *Testudo bosporica* from the Late Miocene of Crimea, Ukraine (based on Danilov et al. 2017). We also added further comparisons with *Testudo burtschaki* and *Testudo eldarica* both from the Late Miocene of Azerbaijan (based on Danilov et al. 2017), two taxa used by Fritz et al. (2009) for molecular clock estimates of the *Testudo graeca* complex. Finally, we also added comparisons with *Testudo kuchurganica* from the Early Pliocene of Ukraine (based on Danilov et al. 2017).

Phylogenetic analysis

To evaluate the phylogenetic relationships of the Jradzor tortoise, we performed a new phylogenetic analysis, which uses the matrix of *Testudo lohanica* from Pérez-García et al. (2022) as a basis that is also based on the modifications of Vlachos et al. (2019) of the original matrix of Vlachos and Rabi (2018). The new version herein contains several major modifications in both character and taxon sampling, as well as completion of scorings compared to previous versions.

Following the constructive criticism of Evers et al. (2023) on two of our mandible characters, we notice that the characters in question were mostly focused on a structure—the prearticular foramen—that is properly described and recognized in Evers et al. (2023), but was misnamed in Vlachos and Rabi (2018). As such, two original mandible characters 64 and 65 are removed, and a selection of Testudinidae-informative characters from Evers et al. (2023) are added to the matrix (characters 8, 10, 15, 30, 34, 40, and 48 of Evers et al. 2023). They will allow a broader documentation of phylogenetically informative characters in tortoises. We removed characters 170–172 (originally from the matrix of Joyce and Bell 2004) as they are uninformative for the ingroup. It is relevant to clarify that previously defined character 165 refers to the presence of dermal armor on posterior limbs, and not to the dermal armor present on the anterior limbs, like the features present in *Testudo lohanica*. Two new characters are added: Char. 167, “If thigh spurs are present, are they bony or keratinous? [0, bony; 1, keratinous; scored as inapplicable if no thigh spurs are present]”; Char. 168, “Shape of the entoplastron [0, rhomboidal; 1, pentagonal; 2, hexagonal]”. In terms of taxon sampling, and besides the Jradzor tortoise, we also added other relevant taxa like *Testudo eldarica* and *Testudo kuchurganica*, based on the descriptions and figures of Danilov et al. (2017). The character on the number of neural plates was left unscored in the Jradzor tortoise due to the lack of a complete neural series or at least a complete series of the posterior neurals and the suprapyrgals. The scorings of the extant taxa were corrected, improved, and completed using mainly the 3D models (available in Morphosource) reported in the table 1 of Evers et al. (2023; see there for specimen numbers and links). The matrix was constructed in Mesquite v. 3.70 (Maddison and Maddison 2021), and contains 41 taxa and 175 characters, with 29% of unscored characters mostly for the non-shell characters of extinct taxa (only 8% of the scorings of extant taxa remain unscored). The morphological matrix has been combined with the molecular data from Pereira et al. (2017) for the extant taxa, resulting in a total-evidence (morphology and DNA data) matrix of 41 taxa and 12529 characters. The matrix was analyzed in TNT v. 1.6 (Goloboff and Morales 2023; based on Goloboff et al. 2008; Goloboff and Catalano 2016), using a traditional TBR search (1000 replicates, 10 trees kept per replication), under implied (IW) weights (with a mild correction of homoplasy using

$k = 8$ for this matrix size, sensu Ezcurra 2024; see also Goloboff et al. 2018, and references therein for further information). Bremer supports and bootstrap/jackknife GC frequencies were also calculated in TNT. The evaluation of unstable taxa was performed using the IterPCR script of Pol and Escapa (2009) in the command version of TNT. Phylogenetic nomenclature (i.e., PhyloCode) is also provided in an address-like format, following Vlachos (2025). This paper, however, follows the traditional, Linnean scheme.

Systematic Paleontology

Testudines Batsch, 1788

Suborder Cryptodira Cope, 1868

Family Testudinidae Batsch, 1788

Subfamily Testudininae Batsch, 1788

Tribe Testudinini Batsch, 1788

Genus *Testudo* Linnaeus, 1758

Type species. *Testudo graeca* Linnaeus, 1758.

***Testudo sahakyanae* sp. nov.**

<https://zoobank.org/A90BF780-944D-4828-80C0-749F6B753F8C>

Figs 2–8

Vernacular name. The bony thigh spurred tortoise.

Phylogenetic nomenclature. *Testudines* Batsch, 1788 [Joyce et al. 2020a] / *Cryptodira* Cope, 1868b [Joyce et al. 2020b] / *Durocryptodira* Danilov & Parham, 2006 [Joyce et al. 2021] / *Testudinoidea* Fitzinger, 1826 [Joyce et al. 2021] / *Testuguria* Joyce et al. 2004 [Joyce et al. 2021] / *Testudinidae* Gray, 1825 [Joyce et al. 2021] / *Testudininae* Siebenrock, 1909 [Joyce et al. 2021] / *Testudona* Parham et al. 2006 [Joyce et al. 2021] / *Testudo* Linnaeus, 1758 / *Testudo sahakyanae* sp. nov. See Joyce et al. (2021) for further details.

Diagnosis. Member of Testudinidae based on the alternating pattern of neurals and costals, the coincidence between the costo-peripheral sutures and the pleuro-marginal sulci, the presence of an epiplastral lip, short pectoral scutes, and the fused trochanters of the femur. Member of Testudinini based on the ‘Testudinini morphotype’ femoral morphotype sensu Valenti et al. (2022), showing a clearly elliptical, oblique and narrow femoral head, a major trochanter that connects to the head, trochanters that are joined proximally but do not extend beyond the femoral head proximally, and on the lingual ridge of the mandible that weakens anteriorly, creating a symphyseal gap in the ridge of the symphyseal area, therefore, it is not continuous between the rami of the mandible (as in *Testudona* sensu Evers et al. 2023 = Testudinini herein). Member of the derived genus *Testudo* based on the presence of a movable hinge between the hypoplastra and the xiphiplastra.

Differential diagnosis. Close to *Testudo graeca* based on the presence of thigh spurs, differing from *Testudo graeca* in having 1–2 thigh spurs with a bony core, and the shorter supraoccipital process. Differs from *Te. graeca*, *Te. marginata*, and *Te. lohanica* in having a deep fossa Meckelii with a wider triangular dorsal opening between the surangular, the prearticular, and the articular. Closer to *Te. graeca*, *Te. marginata* and differing from *Te. lohanica* based on the less prominent coronoid. Similar to *Te. graeca* on the dorsal border of the ramus that is slightly concave, differing from the taller dentary of *Te. marginata* and the more straight dentary of *Te. lohanica*. The new species appears to have a reduced neural series with seven neural plates with narrow vertebrals, different from *Te. marmorum*, *Te. bosporica*, *Te. hellenica*, and *Te. lohanica* (one specimen has seven neurals) that have eight neurals, similar to *Te. graeca* and *Te. marginata* that mostly have a reduced neural series. Different from *Te. graeca* and *Te. marginata* in having a quite larger last neural, with hexagonal shape and short posterolateral sides. Further differences are found in the entoplastron, which is consistently much larger and wider than in extant *Te. graeca* and *Te. marginata*, as well as in *Te. marmorum*, *Te. bosporica*, *Te. eldarica*, *Te. kuchurganica*, *Te. hellenica*, and *Te. lohanica*. Further differs from *Te. eldarica* in having shorter pectorals medially and longer laterally, larger femoral covering on the hypoplastra laterally, and curved femoro-anal sulci. Further differs from *Te. kuchurganica* on the wider gulars, and the smaller and narrower posterior lobe. Based on the described differences, we described the tortoise remains from Jradzor as a new species *Testudo sahakyanae* sp. nov.

Holotype. JRD–25/226 (JZ–11), partial skeleton of a female tortoise individual, comprising most of the shell and associated appendicular elements (Figs 4, 7N–AA, Suppl. material 1).

Paratype. JRD–25/248 (JZ–13?), a partial skull with an associated mandible and hyoid remains (Fig. 2A–D).

Type locality and age. Different levels in the Jradzor diatomite mine, coordinates 40.029474°N, 44.814309°E, Ararat Province, Armenia. Based on both magnetostratigraphy and radioisotopic data, the fossiliferous layers have been dated between 4.16–3.98 Ma (Early Pliocene, MN15) (Fig. 1) (Lazarev et al. 2023).

Etymology. The species is named after our colleague Dr. Lilit Sahakyan, deputy director of the Institute of the Geological Sciences of the National Academy of Sciences of the Republic of Armenia, Yerevan, Armenia (used with her permission). This is in honor of our long-term collaboration, which made possible the excavations and study of the rich fossil record of the Jradzor site.

Referred material. More than 1460 specimens from at least 12 different levels in the Jradzor diatomite mine (JZ–2, JZ–2a, JZ–11g, JZ–11, JZ–3, JZ–3v, JZ–3s, JZ–14, JZ–15, JZ–13, JZ–5, JZ–6), belonging to at least 80 different tortoise individuals (Figs 2–8, Suppl. material 1).

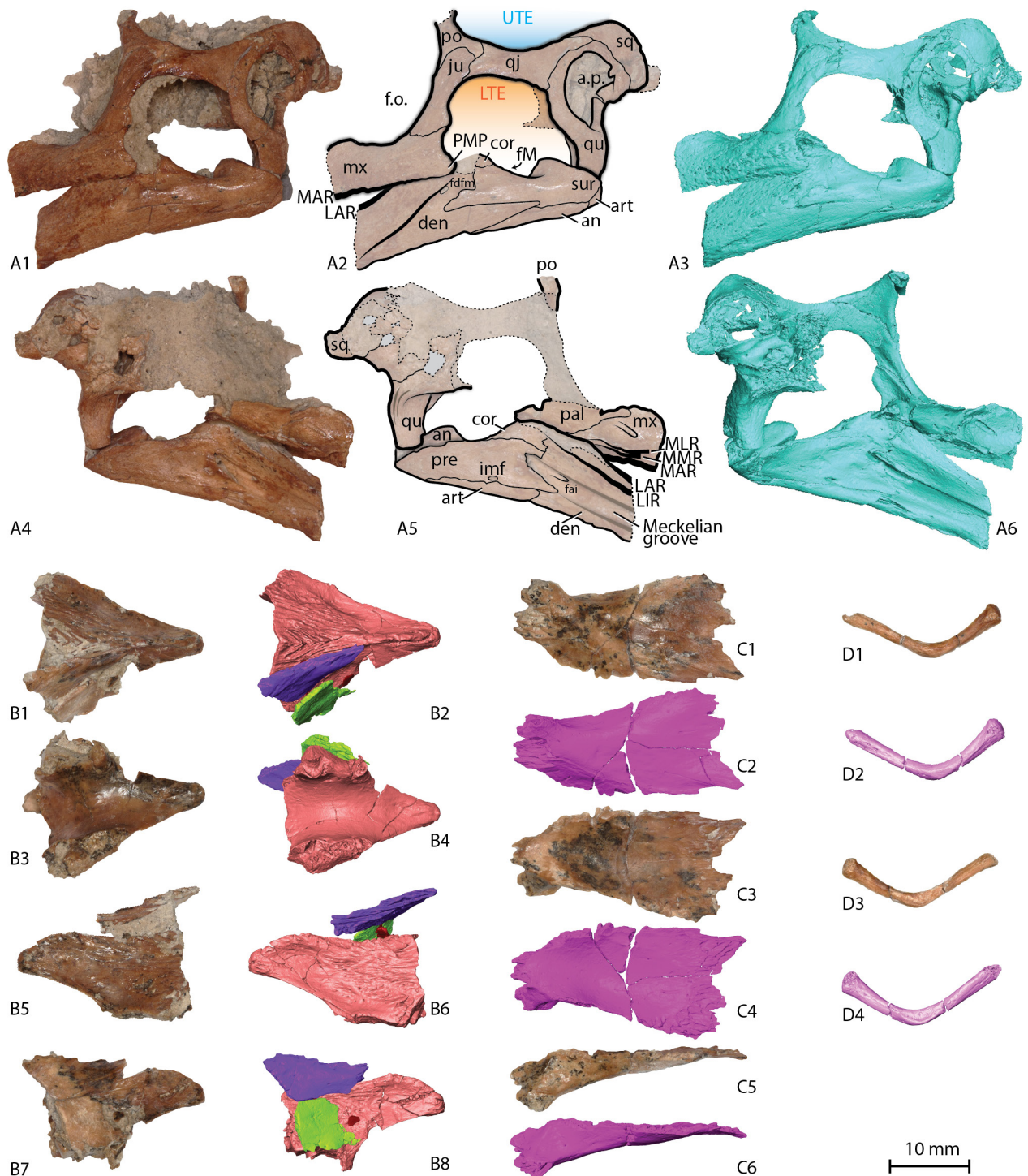


Figure 2. Cranial material of *Testudo sahyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. **A–D.** Cranial remains from JZ–13? level (JRD–25/248) corresponding to the paratype of *Testudo sahyanae* sp. nov. **A.** Partial left skull with a corresponding partial left mandible in articulation in **A1**. Lateral; **A2**. Drawing of the lateral; **A3**. Model of the lateral; **A4**. Lingual; **A5**. Drawing of the lingual; **A6**. Model of the lingual views; **B.** Supraoccipital fragment of the same skull in **B1**. Dorsal; **B2**. Model of the dorsal; **B3**. Ventral; **B4**. Model of the ventral; **B5**. Right lateral; **B6**. Model of the right lateral; **B7**. Left lateral, and **B8**. Model of the left lateral views; **C.** Almost complete right parietal of the same skull in **C1**. Right lateral; **C2**. Model of the right lateral; **C3**. Internal; **C4**. Model of the internal; **C5**. Dorsal, and **C6**. Model of the dorsal views; **D.** Almost complete ceratobranchial 1 from the hyoid apparatus corresponding to the same skull in **D1**. Dorsal; **D2**. Model of the dorsal; **D3**. Ventral and **D4**. Model of the ventral views. Scale bar: 10 mm, all specimens are in the same scale. Abbreviations: a.p., antrum postoticum; f.o., fossa orbitalis; ju, jugal; LTE, lower temporal emargination; MAR, maxillary ridge; MLR, lingual ridge of the maxilla; MMR, median maxillary ridge; mx, maxilla; pal, palatine; PMP, posterior maxillary process; po, postorbital; qj, quadratojugal; qu, quadrate; sq, squamosal; UTE, upper temporal emargination.

Description of the Jradzor tortoise and comparative notes

Skull and mandible

Some skull remains are identified in the Jradzor material, including a partial skull and some isolated fragmented cranial bones (Figs 2, 3, Suppl. material 1), which allow documenting some of the cranial anatomy of the Jradzor tortoise.

The best-preserved specimen is JRD–25/248 (Fig. 2; paratype), which preserves several elements of a large adult tortoise individual. It includes a partial skull of a tortoise, preserving most of the left side. The posterior half of the lower jaw is preserved with its most left side (missing only the anteriormost part of the dentary) with still articulated in the mandibular condyle of the quadrate. From the dermal roof (Fig. 2A), the jugal, the postorbital, the quadratojugal, and the squamosal are preserved, all from the left side.

The jugal is thin and quite long, as high as the antrum postoticum developed almost vertically and contacts the maxilla ventrally, the postorbital anterodorsally, and the quadratojugal posterodorsally. Both dorsal and ventral sutures are rounded.

The postorbital is partly preserved, thin, and contacts the jugal anteroventrally with a rounded suture that sends a tip anteriorly that surrounds the dorsal part of the jugal on the rim of the fossa orbitalis. Posterodorsally, the postorbital contacts the quadratojugal, limiting the participation of the jugal on the upper temporal emargination.

The quadratojugal is thin, long, and tall, contacting the postorbital anterodorsally and the jugal anteroventrally, being taller posteriorly where it contacts the squamosal posterodorsally and the quadrate posteroventrally; there is no ventral extension of the quadratojugal.

The squamosal is placed posterodorsally. It is thin but quite large, and contacts the quadratojugal anteriorly and the quadrate ventrally.

In the preserved material, the maxilla contacts the jugal dorsally and the palatine medially. The border of the maxilla is straight with a maxillary ridge that is serrated. Posterolaterally, a moderate posterior maxillary process is noted, having a rounded tip. Ventrally, a part of the triturating surface of the maxilla is preserved, showing the presence of a distinct lingual ridge and another, median maxillary ridge developed in parallel with the maxillary and the lingual ridges. All triturating ridges are moderately serrated. Medially, the maxilla contacts the anterior part of the palatine, which is anteriorly concave, forming part of the floor of the fossa orbitalis together with the medial part of the maxilla. The palatine forms part of the posterior part of the lingual ridge.

The quadrate is large, contacting broadly the quadratojugal anterodorsally, the squamosal posterodorsally, and the prootic anteromedially; the remaining medial contacts are not visible. Ventrally, there is a long and thick extension of the squamosal that leads to the processus mandibularis, which is deep and concave, preserved with

the mandible in articulation. The quadrate forms a deep and elliptical cavum tympani, enclosing the incisura columella auris. Anterodorsally, it contacts the prootic, forming a relatively weak processus trochlearis oticum.

Some additional skull bones are preserved from this skull, including the supraoccipital (Fig. 2B) and the parietal (Fig. 2C), but no contact is preserved with the rest of the skull. The supraoccipital process is quite short, shorter than in the extant *Testudo graeca*. Viscerally, it is arched, forming the dorsal roof of a large foramen magnum, preserving the sutures with the opisthotic on both sides. The complete and well-preserved left parietal is thin, broad and long. Anteriorly and dorsally, there is a thickened part that extends horizontally to contact the postorbital and forms the rim of the fossa orbitalis.

Almost the entire left mandible in articulation with the processus mandibularis is preserved (Fig. 2A). The mandible is quite tall posteriorly at the suture with the coronoid, then gently diminishing its height towards the anterior part. All bones are preserved in good condition (the articular, the prearticular, most of the angular, the surangular, the coronoid, and the dentary). The articular is large, pyramidal in shape, the posterior part being articulated to the processus articularis (Fig. 2A5). The angular bone is long and represents part of the ventral border of the mandible, contacting the articular posteriorly, the surangular dorsally, and the dentary anteriorly.

The prearticular is large and does not form part of the articulation surface of the mandible, contacting the articular posterior, the coronoid dorsally, the dentary anteriorly, and the angular ventrally. Anterodorsally, on the contact with the coronoid, a large and circular prearticular foramen is visible (Fig. 3B4), as in *Te. graeca* and perhaps in *Te. lohanica*, but not in *Te. marginata*. At the base of the prearticular (Fig. 2A5), a single, medium-sized, elongated intermandibular foramen is present, similar to the condition seen in *Te. graeca*, *Te. marginata*, and *Te. lohanica*.

The surangular is preserved complete, showing the wide sutural surface with the dentary, covering the lateral and posterior parts of the mandible, contacting the articular posteriorly, the angular ventrally, the coronoid anterodorsally, and the dentary anteriorly (Fig. 2A2). The surface of the surangular is smooth, and no foramina are noted. In combination with the dentary, an anterior surangular process is present that does not extend beyond the level of the coronoid, as in *Te. graeca*, *Te. marginata*, and *Te. lohanica*. Between the surangular, the prearticular, and the articular, a deep fossa Meckelii is present with a triangular dorsal opening, much wider than in *Te. graeca*, *Te. marginata*, and *Te. lohanica*.

The coronoid is partly preserved, small and less prominent, as in *Te. graeca* and *Te. marginata*, but in *Te. lohanica* it is more prominent.

The dentary represents approximately half of each mandible ramus, and is quite tall posteriorly at the suture with the coronoid, then gently diminishing its height towards the symphysis. The dorsal border of the ramus

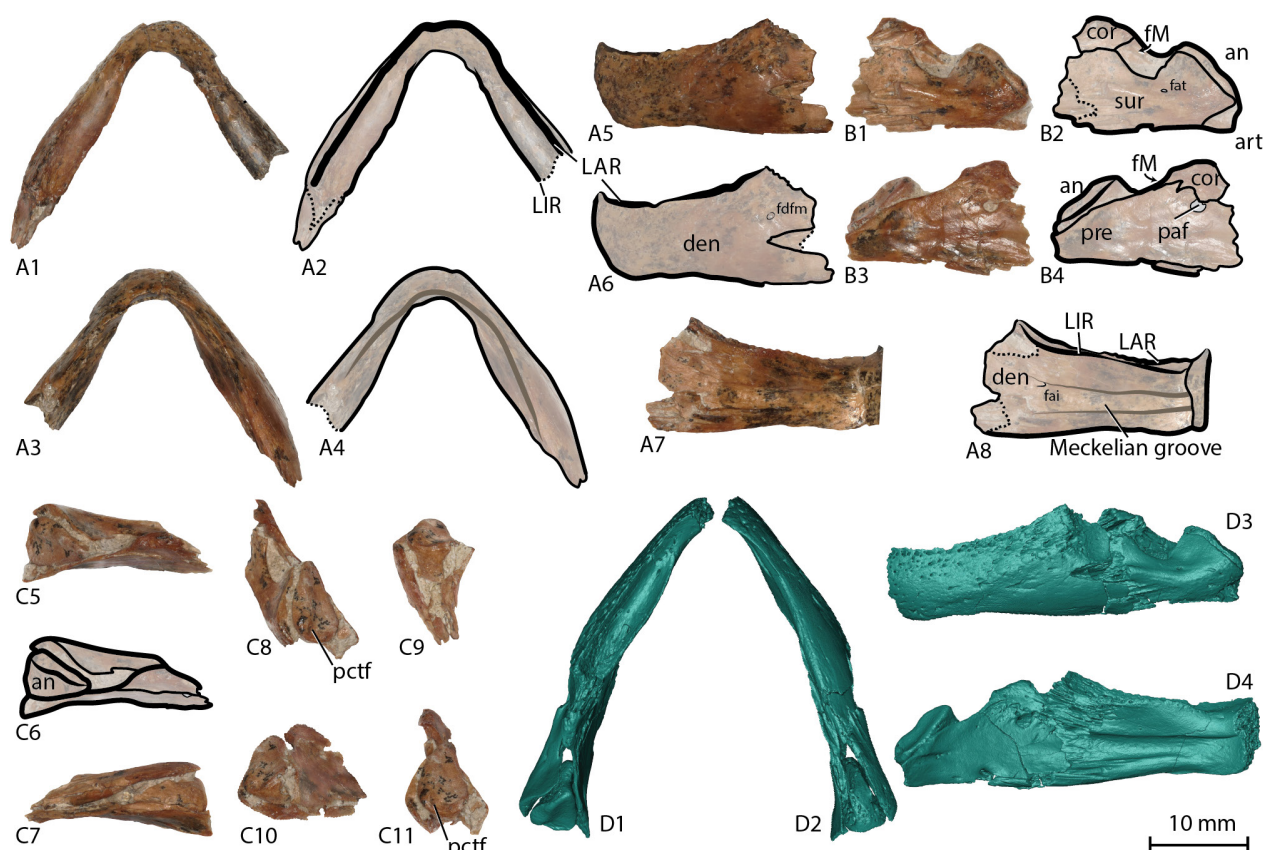


Figure 3. Mandible material of *Testudo sahakyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. **A–D.** Almost complete mandible from JZ–3? (JRD–25/210); **A.** Almost complete dentaries in **A1**. Dorsal; **A2**. Drawing of the dorsal; **A3**. Ventral; **A4**. Drawing of the ventral; **A5**. Left lateral views; **A6**. Drawing of the left lateral view of the mandible; **A7**. Left medial view; **A8**. Drawing of the left medial view; **B.** Left postdentary of the same mandible, found partly separated from the dentary but with a clear association with the mandible, in **B1**. Left lateral; **B2**. Drawing of the left lateral; **B3**. Left medial; **B4**. Drawing of the left medial; **B5**. Dorsal views; **B6**. Drawing of the dorsal; **B7**. Ventral; **B8**. Posterolateral views; **B9**. Anterodorsal view focusing on the angular; **B10**. Posteromedial view, and **B11**. Articular surface of the angular view; **D.** Model of the complete left ramus. **D1**. Dorsal; **D2**. Ventral. **D3**. Left lateral, and **D4**. Left medial views. Abbreviations: an, angular; art, articular; cor, coronoid; den, dentary; fai, foramen alveolare inferius; fat, foramen auriculotemporalis; fdfm, foramen dentofaciale majus; fM, fossa Meckelii; imf, intermandibular foramen; LAR, labial ridge of the dentary; LIR, lingual ridge of the dentary; paf, prearticular foramen; pctf, chorda tympani foramen; pre, prearticular; sur, surangular. Scale bar: 10 mm

is slightly concave, whereas the ventral border is straight throughout its width, similar to the morphology of *Te. graeca* and unlike the taller dentary of *Te. marginata* and the more straight dentary of *Te. lohanica*. The dorsal border of the symphyseal part is slightly elevated. The labial and lingual ridges are equally tall and moderately serrated, delimiting a transversely narrow and deeply excavated, trough-like triturating surface. A small foramen dentofaciale majus is observed in the limit between the rugose and the smooth surface of the lateral side of the dentary. Medially, a large Meckelian groove is observed, developed straight and parallel to the ventral straight border of the ramus. Inside the groove, an elongated foramen alveolare inferius is observed (Fig. 2A5, 3A8), inside the dentary, just in front of the tip of the prearticular extension.

From the same specimen, a part of the hyoid apparatus is also preserved, corresponding to a complete ceratobranchial I or cornu branchiale I, probably from the left side. It is long and robust, quite curved, preserving a

robust articulation with the corpus hyoidei (Fig. 2D). The dorsoposterior end towards the epibranchial is incomplete.

Another, more complete and better-preserved mandible is identified from level JZ–3? (JRD–25/210), which preserves an almost complete mandible including the entire left side (the articular, the prearticular, most of the angular, the surangular, the coronoid, and the dentary) and the right dentary (Fig. 3). The five postdentary bones (the articular, the prearticular, the angular, the surangular, and the coronoid) are recovered broken and separated from the dentary. The articular bone is complete, slightly “pressed” inside the mandible causing the opening of the surangular and the prearticular and fragmentation of the angular, like splitting a piece of wood. The right dentary is incomplete, missing the posterior part, and is broken posterior to the symphysis and slightly crushed on its ventral part.

The articular is large and pyramidal in shape. The dorsal surface of the articular is convex laterally and concave medially, showing a grooved articular notch

developed obliquely across the entire length of the dorsal surface of the element, matching the corresponding articular surface of the quadrate on the skull (Figs 2A2, A5, 3B2, B4). On the distal border of the crest and on the concave part just next to the crest, the posterior chorda tympani foramen is visible. It is quite similar to the specimen of *Testudo graeca iberica* (SMF 67588), but differs from the articular of *Testudo marginata* (FMNH 51672 in Evers et al. 2023), which is much smaller and more rounded. It is also larger than the articular bone of the mandible of *Stylomys nebrascensis* (in Evers and Al Iawati 2024), which is further differentiated by the presence of a retroarticular process not seen in the Jradzor material. It is much smaller than the elongated and pointed angular form of *Testudo lohanica* (Pérez-García et al. 2022). The angular bone is partly broken and misplaced; therefore, not much can be said about its morphology.

The prearticular is large and does not form part of the articulation surface of the mandible (Figs 2A, 3B), contacting the articular posteriorly, the coronoid dorsally, the dentary anteriorly, and the angular ventrally. Dorsoanteriorly, on the contact with the coronoid, a large and circular prearticular foramen is visible (Fig. 2F4), as in *Te. graeca* and perhaps in *Te. lohanica*, but not in *Te. marginata*. At the midpoint of the linguoventral margin, a single, medium-sized, elongated intermandibular foramen is present, similar to the condition seen in *Te. graeca*, *Te. marginata*, and *Te. lohanica*.

The surangular (Figs 2A, 3B) is preserved completely, showing the wide sutural surface with the dentary, covering the lateroposterior surface of the mandible, contacting the articular posteriorly, the angular ventrally, the coronoid anterodorsally, and the dentary anteriorly. The lateral surface of the surangular is smooth without any foramina. At the articulation with the dentary (recovered slightly separated), an anterior process of surangular is present that does not extend anteriorly beyond the level of the coronoid, as in *Te. graeca*, *Te. marginata*, and *Te. lohanica*. Between the surangular, the prearticular, and the articular, a deep fossa Meckelii is present with a triangular dorsal opening (Fig. 2A5). It is much wider than in *Te. graeca*, *Te. marginata*, and *Te. lohanica*. The coronoid is partly preserved (Figs 2A, 3B), small and less-prominent as in *Te. graeca* and *Te. marginata*, but in *Te. lohanica* is more prominent.

The dentary represents approximately half of each mandible ramus. It is quite tall posteriorly at the articulation with the coronoid, then gently diminishing its height towards the symphysis, where it becomes taller again, but does not reach the level of the coronoid. The dorsal border of the ramus is slightly concave, whereas the ventral border is straight throughout its width, similar to the morphology of *Te. graeca* and unlike the taller dentary of *Te. marginata* and the more straight dentary of *Te. lohanica*. The dorsal border of the symphyseal region is slightly elevated. The labial and lingual ridges are equally tall and moderately serrated, delimiting a transversely narrow and deeply excavated, trough-like

tritulating surface. The lingual ridge weakens anteriorly, creating a symphyseal gap in the ridge at the symphyseal area. Thus, it is not continuous between the rami of the mandible, the gap being present in various species of *Testudona* (sensu Evers et al. 2023 = *Testudinini* herein). The lateral part of the labial ridge is rugose. A small foramen dentofaciale majus is observed in the limit between the rugose and the smooth surface of the lateral side of the dentary (Fig. 2A2). Medially, a large Meckelian groove is observed, developed straight and parallel to the ventral straight border of the ramus.

Carapace

The carapace of the Jradzor tortoise is well documented, including an almost complete shell (JRD–25/226, JZ–11; Fig. 4; holotype), and several well-preserved parts of the shell from different individuals (Fig. 5; Suppl. material 1). Only the neural series remains not well-documented due to the lack of complete neural series. Because of this a full documentation of the neural pattern and confirmation of some characters that are suggested from isolated specimens, including the reduced number of neurals, the possible presence of a pre-neural, and a large hexagonal last neural (see below), are impossible.

JRD–25/226 (Fig. 4) is the most complete tortoise individual preserved in the Jradzor material. Thus, we assign it as the holotype specimen of the new species. It comprises almost the entire shell and most of the appendicular skeleton. The preservation of the material is not good. The specimen is full of cracks and fractures; it has been flattened and compressed during active depositional processes, causing the fracture of the lateral parts and the bridge. Further, several parts of the carapace are moved and broken, and recovered as separated fragments around the specimen together with the bones of the appendicular skeleton. Most probably, this preservation results from the burial and taphonomic processes under the violent pyroclastic flows, corresponding to the medium tail of pyroclastic flow (Lazarev et al. 2023: table 2). In the case of the holotype, however, the depositional processes did not scatter significantly as in most of the available material, but remained, more or less, in close association. The state of preservation of the carapace is much worse compared to the plastron, which is better preserved, having its plates mostly in anatomical connection. Still, this specimen represents the most complete morphotype known in the Jradzor material. The total length of the shell is difficult to measure because of the crushing of the shell; however, it is estimated to have reached a total length of around 30 cm. Compared to other specimens found in Jradzor, this size fits well in the average size range of the Jradzor tortoise. The largest specimens (e.g., Fig. 5A) could reach a carapace length of up to 35 cm.

The carapace of JRD–25/226 (Fig. 4) preserves mostly the right side, missing most of the neurals and the left side and border. The nuchal is large, probably as wide as long, with a relatively straight border with no nuchal

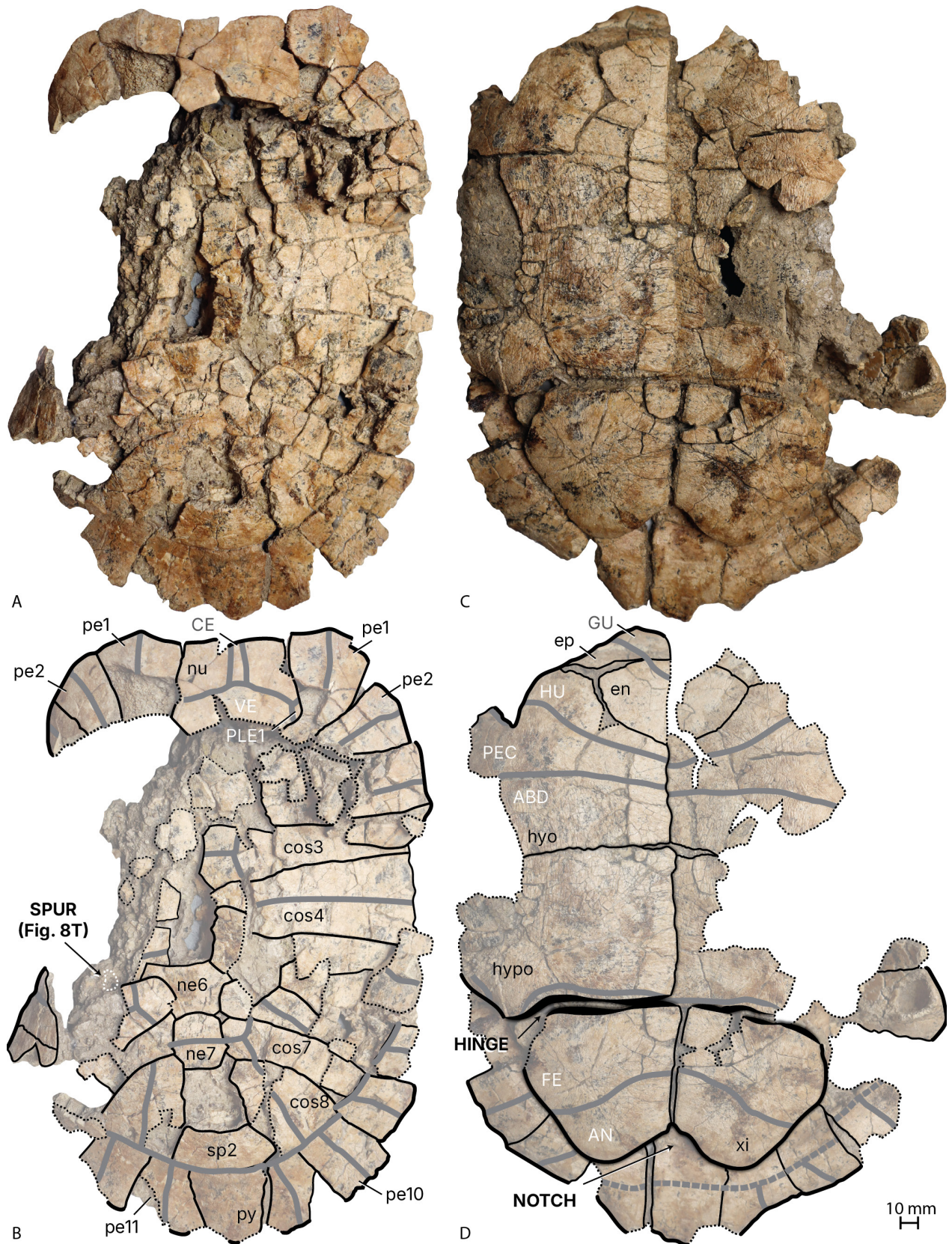


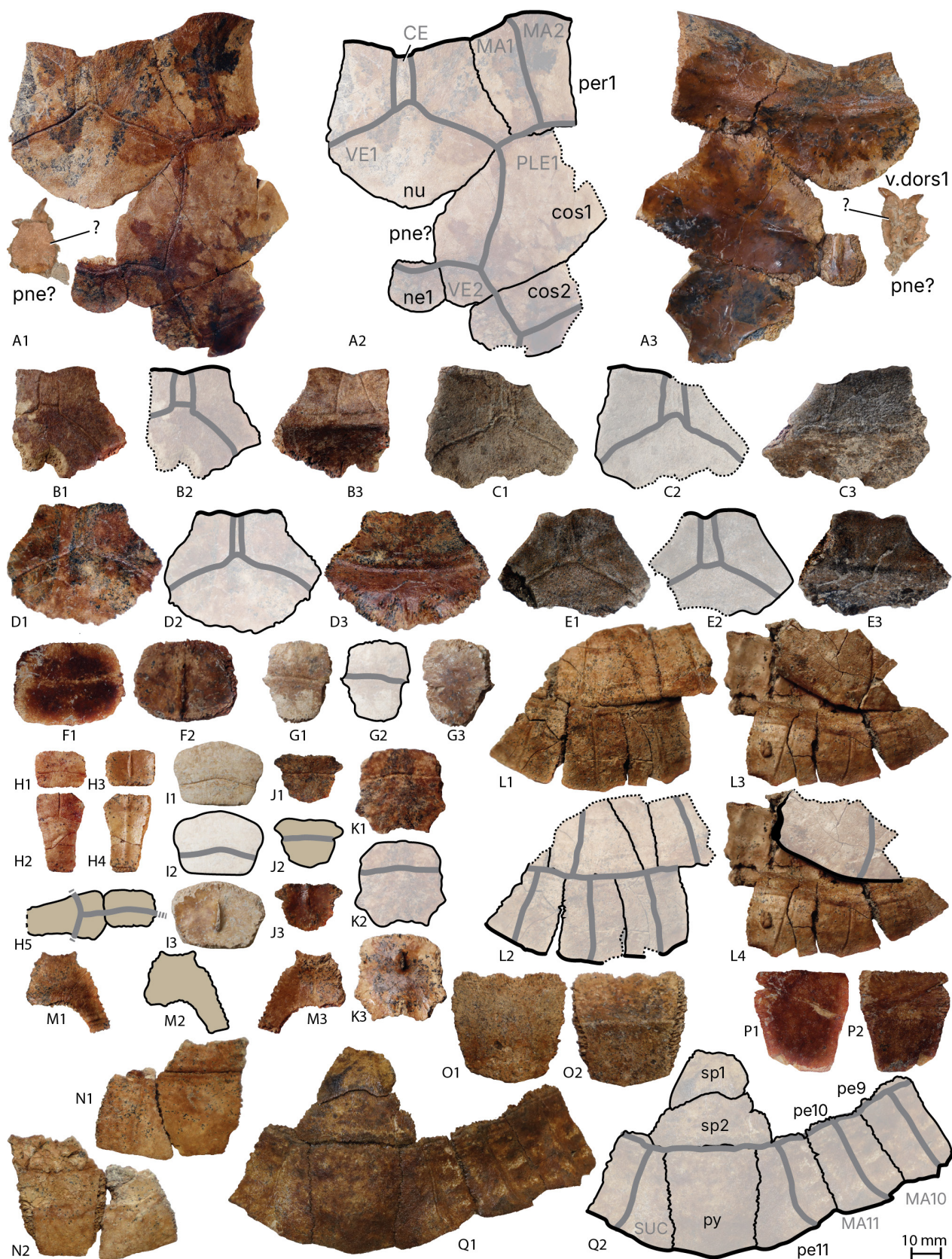
Figure 4. Photographs (A, C) and drawings (B, D) of almost complete shell of the holotype of *Testudo sahakyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site; Armenia (JRD–25/226, JZ–11) in dorsal (A–B) and ventral (C–D) views. Abbreviations (bony plates in small and horny scutes in capital letters): ABD, abdominal; AN, anal; CE, cervical; cos, costal; en, entoplastron; ep, epiplastron; FE, femoral; GU, gular; HU, humeral; hyo, hyoplastron; hypo, hypoplastron; ne, neural; nu, nuchal; pe, peripheral; PEC, pectoral; PLE, pleural; py, pygal; sp, suprapygale; VE, vertebral; xi, xiphoplastron. Scale bar: 10 mm.

notch. A long and narrow cervical is present, representing most certainly more than one-third of the nuchal length. Most of the neural series is not preserved. However, the last two neurals and the costals from the right side are preserved, allowing decent documentation of the neural anatomy. First of all, the specimen had a clear neural differentiation, as indicated by the shape of the costals that were alternatively long medially and short laterally (e.g., right costal 3) and short medially and long laterally (e.g., right costal 4). As such, we can expect the presence of a quite large and wider than long, octagonal neural 4, a wider than long, rectangular neural 5, followed by a large, octagonal neural 6 (present) and a large, hexagonal neural 7 with short posterolateral sides that contacts costal 7 and 8 laterally. This is probably the last neural, unless there was a quite small eighth one as well. The identified material does not allow a confident assessment of the number of neurals. However, similar large and hexagonal neurals 7 are found in extant *Testudo graeca* and *Testudo marginata* in direct contact with the suprapyg 1, indicative of a reduced neural series. Costals 4 and 6 are crossed by the pleural sulci. Costal 8 is large, contacting costal 7, neural 7, both suprapygs, the last three peripherals on each side, and being crossed diagonally by the vertebral 5 / pleural 4 sulcus (Fig. 4B). The sulcus between vertebral 5 and the supracaudal coincides with the suprapyg/pygal suture. Only the suprapyg 2 is preserved, being wider than long, with a straight anterior contact for the suprapyg 1, laterally contacting costal 8 on each side, posteriorly contacting peripheral 11 on each side of the pygal. The pygal is rectangular in shape, clearly longer than wide, with a wider anterior border, without a pygal notch, and without any evidence of flaring. The vertebral scutes are narrower than the pleural scutes in dorsal view. The anterior peripherals are long and narrow, moderately flared, and crossed by the marginal sulci. There are clear pointed protrusions at the border, near the placement of the marginal sulcus, especially on the first peripherals. The posterior peripherals are shorter than the anterior ones, similarly flared, but without any protrusions. All peripherals show a good coincidence between the costo-peripheral sutures and the pleuro-marginal sulci. The last two marginals are fused into a supracaudal (Figs 4B, 5Q1, Q2).

Several additional elements from the carapace are preserved in the Jradzor material (Fig. 5, Suppl. material 1), allowing the documentation of some morphological variability that is interpreted herein as intraspecific variability of the new species. Most of the variability in the carapace is seen in the nuchal plate (Fig. 5A–E). Most nuchals are as long as wide; however, some are slightly wider than long (e.g., Fig. 5C). There is significant variability in the shape of the anterior border, with some nuchals showing some moderate notches (e.g., Fig. 5A, E). The most significant variation is found in the shape and size of the cervical scute, which can be quite long (e.g., Figs 4, 5A, C–E) or short (e.g., Fig. 5B), quite narrow (e.g., Figs 4, 5A, D, E) or wider (e.g., Fig. 5B, C). The isolated

nuchals also permit observation of the visceral side, like in JRD–18/44 (Fig. 5B), showing that the cervical scute visceraally is usually longer and wider than dorsally, with varying widths across other nuchals. Although the nuchal of the holotype appears to be covered laterally by pleural 1 (Fig. 4), all other nuchals do not show this character state. Based on the partial anterior part of JRD–25/248 (JZ–13?; Fig. 5A), the sulcus between vertebral 1 and pleural 1 coincides with the nuchal/costal suture. Several parts of the carapace and plastron are preserved from this tortoise individual. Posterior to the nuchal of JRD–25/248 (Fig. 5A), a short neural is preserved, being rectangular and slightly longer than wide, crossed transversely by the intervertebral sulcus. The connection of this neural is certain and indicated by the sulcus. Thus, a space is left anteriorly for the formation of another neural plate. Most probably, this space was occupied by an additional preneural that is found isolated, being hexagonal with short posterolateral sides and without any sulcus dorsally. Ventrally, the remains of the first dorsal vertebra with the characteristic enlarged apophyses for the neck are noted, proving that it indeed occupied this space (Fig. 5A). There is no other costal 1/nuchal/neural association in the material to confirm this character further. The peripheral 1 is long, moderately flared, and contacts the nuchal, costal 1, and peripheral 2 (Fig. 5A). It is crossed by the marginal sulcus, with a small tip on the rim where the marginal is placed. There is a good coincidence of the costo-peripheral suture and the pleuro-marginal sulcus. The costal 1 is large, missing only the lateral part, firmly sutured to the peripheral, nuchal, two neurals, and costal 2. It is covered by the postero-lateral part of vertebral 1, the antero-lateral part of vertebral 2, and the antero-medial part of pleural 1 (Fig. 5A). Medially, the costal 1 is sutured to a small preneural anteriorly, a small neural 1 medially and the anterolateral sides of the octagonal neural 2. Visceraally, the costal ribs are clearly distinguished, being thin and long but placed away from the neural/costal suture. Costal 2 is large, missing the lateral part as well, but clearly being narrower medially and longer laterally, corresponding to the alternating pattern of the testudinids.

From the neural series, several isolated plates are identified (Fig. 5F–K; Suppl. material 1). Individual JRD–18/121 (JZ–13; Fig. 5F) preserves a large rectangular neural, being wider than long and crossed horizontally by a relatively straight sulcus; thus, it could correspond to the neural 5. Individual JRD–19/254 (JZ–13; Fig. 5G) preserves a complete neural, slightly asymmetrical, longer than wide, crossed horizontally by a sulcus, mostly rectangular but with some notches laterally that make it appear hexagonal. Individual JRD–25/228 (JZ–3 or JZ–13; Fig. 5H) preserves an association of a rectangular neural with its adjacent costal. The quadrangular neural is wider than long and crossed by the intervertebral sulcus towards the posterior part. An almost complete costal is also preserved, probably one that was in contact with the preserved neural, being longer medially and shorter laterally, indicating the presence of an alternating costal pattern seen in Testudinidae



(Vlachos and Rabi 2018). The medial side shows only two sutural sides, the larger one for the preserved neural, and a smaller one for the successive neural. Medially, the neural is crossed by the intervertebral sulcus, whereas laterally by the interpleural sulcus. Individual JRD–19/254 (JZ–13; Fig. 5I) preserves a complete rectangular neural, wider than long, crossed horizontally by the vertebral sulcus; it could correspond to the third or fifth neural. Individual JRD–25/242 (JZ–3; Fig. 5J) preserves a complete neural that is hexagonal with short anterolateral sides of a young individual, the anterior part being wider than the posterior part, and crossed horizontally by the intervertebral sulcus, which is constricted at the level of the sulcus. This corresponds probably to the last, neural 7 of a reduced neural series. The neural of the adult individual JRD–25/232 (JZ–3 or JZ–13; Fig. 5K) resembles a similar morphology, being a complete hexagonal neural with shorter anterolateral sides, and a wider posterior part. Its anterior portion is crossed horizontally by the intervertebral sulcus, and corresponds well to the morphology of the last neural of the holotype. Although disarticulated and isolated, these neurals are consistent with the morphology observed in the holotype and allow to confirm three observations: first, the presence of the alternating pattern characteristic to Testudinidae (Vlachos & Rabi, 2018); second, the presence of a characteristic hexagonal, crossed neural with short posterolateral sides; third, that most probably this species had indeed a reduced neural series with probably seven neural plates, which, however, has to be confirmed with more complete specimens.

Additional specimens allow us to document better the morphology of the posterior part of the carapace. Individual JRD–19/260 (JZ–11; Fig. 5L) comprises a partial left posterior part of the shell, with the portions of the carapace and plastron retained in the anatomical position. The preserved costals show the typical alternating pattern, whereas the peripherals are long and moderately flared, with good coincidence between the costo-peripheral sutures and the pleuro-marginal sulci. Individual

JRD–25/216 (JZ–3 or JZ–13; Fig. 5M) contains suprapygal 1 that is irregular in shape, as in the “mixed” morphotype of Lapparent de Broin et al. (2006a: fig. 5c) in some extant *Te. graeca* specimens: on its left side, it is short and trapezoid-shaped, whereas, on the right one, it has a ventral extension that embraces one side of suprapygal 2, like in the typical boomerang-shaped suprapygals, reaching to contact the peripheral. The collection JRD–19/256 (JZ–11; Fig. 5N, O) contains the remains of two well-preserved pygal specimens from different individuals. One is larger and isolated, whereas the second is preserved in a sutural contact with the posterior part of suprapygal 2 and in association with the left peripheral 11. Both are quadrangular, the posterior border being straight and narrower than the anterior one. There is a coincidence between the suture and sulci on its border, and it is not crossed by any marginal sulci, indicating the fusion of marginals 12 into a supracaudal. The visceral covering of the scutes on the pygal covers almost half of its visceral surface. Individual JRD–18/121 (JZ–13; Fig. 5P) contains an almost complete pygal that is comparatively narrower than other known pygals in the collection. One of the best specimens of the posterior shell border is seen in the individual JRD–25/263 (JZ–3 or JZ–13; Fig. 5Q), preserving both suprapygals, the left peripheral 11, the pygal, and the right peripherals 9–11. The suprapygal configuration is similar to the individual JRD–25/216 (JZ–3 or JZ–13; Fig. 5M), showing clearly the same “mixed” morphotype with the significant difference that the expanded side of the irregular suprapygal 1 is shorter and does not reach the left peripheral 11. Further, the last peripherals contact suprapygal 2, whose posterior border is symmetrical. The pygal is quadrangular, anteriorly slightly wider and not flared with a pointed end. In contrast, the posterior peripherals are moderately flared and show protrusions at the border near the marginal sulci. There is a good coincidence around the border, including the vertebral 5 / supracaudal sulcus that coincides well with the suprapygal 2 / pygal suture.

Figure 5. The most complete carapacial remains of *Testudo sahakyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. **A.** Partial anterior carapace (JRD–25/248, JZ–13?) in **A1.** Dorsal; **A2.** Drawing of the dorsal, and **A3.** Visceral views; **B.** Almost complete nuchal (JRD–18/44, JZ–13) in **B1.** Dorsal; **B2.** Drawing of the dorsal, and **B3.** Visceral views; **C.** Almost complete nuchal (JRD–18/43, JZ–3s) in **C1.** Dorsal; **C2.** Drawing of the dorsal, and **C3.** Visceral views; **D.** Complete nuchal (JRD–25/212, JZ–3) in **D1.** Dorsal; **D2.** Drawing of the dorsal, and **D3.** visceral views; **E.** Almost complete nuchal (JRD–25/244, JZ–3) in **E1.** Dorsal; **E2.** Drawing of the dorsal, and **E3.** Visceral views; **F.** Complete rectangular neural (JRD–18/121, JZ–13) in **F1.** Dorsal and **F2.** Visceral views; **G.** Complete hexagonal neural (JRD–19/254, JZ–13) in **G1.** Dorsal; **G2.** Drawing of the dorsal, and **G3.** Visceral views; **H.** Rectangular neural / costal association (JRD–25/228, JZ–3 or JZ–13) in **H1–2.** dorsal; **H3–4.** visceral, and **H5.** Drawing of the dorsal views; **I.** Complete rectangular neural (JRD–19/254, JZ–13) in **I1.** Dorsal; **I2.** Drawing of the dorsal, and **I3.** visceral views; **J.** Complete hexagonal neural (JRD–25/242, JZ–3) in **J1.** Dorsal; **J2.** Drawing of the dorsal, and **J3.** visceral views; **K.** Complete hexagonal neural (JRD–25/232, JZ–3 or JZ–13) in **K1.** Dorsal; **K2.** Drawing of the dorsal, and **K3.** Visceral views; **L.** Partial posterior left shell (JRD–19/260, JZ–11) in **L1.** Dorsal; **L2.** Drawing of the dorsal; **L3.** Ventral, and **L4.** Drawing of ventral views; **M.** Suprapygal 1 with “mixed” morphotype (JRD–25/216, JZ–3 or JZ–13) in **M1.** Dorsal; **M2.** Drawing of the dorsal, and **M3.** Ventral views; **N.** Left peripheral 11 / pygal association (JRD–19/256, JZ–11) in **N1.** Dorsal and **N2.** Visceral views; **O.** Complete pygal (JRD–19/256, JZ–11) in **O1.** Dorsal and **O2.** Visceral views; **P.** Almost complete pygal (JRD–18/121, JZ–13) in **P1.** Dorsal and **P2.** Visceral views; **Q.** Posterior shell border (JRD–25/263, JZ–3 or JZ–13) in **Q1.** Dorsal and **Q2.** Drawing of the dorsal views. Scale bar: 10 mm. All specimens are at the same scale. Abbreviations (bony plates in small and horny scutes in capital letters): CE. Cervical; cos. costal; MA. Marginal; ne. neural; nu. nuchal; pe. peripheral; PLE. Pleural; pne?. preneural?; py. pygal; sp. suprapygal; SUC. Supracaudal; VE. Vertebral; v.dors. dorsal vertebra.

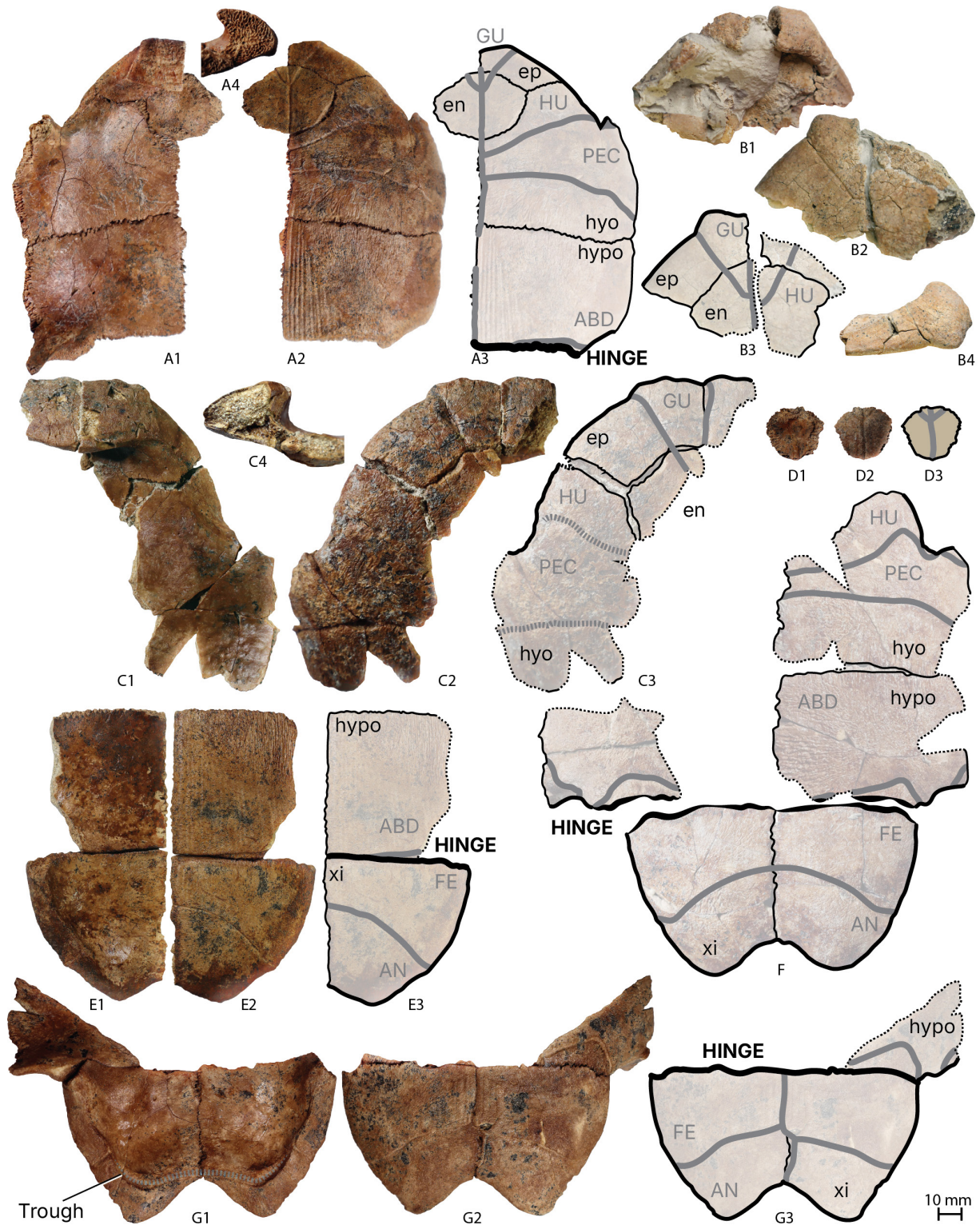


Figure 6. The most complete plastral remains of *Testudo sahyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. **A.** Left anterior plastron (JRD–25/228, JZ–3 or JZ–13) in **A1**. Visceral; **A2**. Ventral; **A3**. Drawing of the ventral, and **A4**. Medial views; **B.** Anterior lobe of a plastron (JRD–25/243, JZ–3) in **B1**. Visceral; **B2**. Ventral; **B3**. Drawing of the ventral, and **B4**. Right lateral views; **C.** Right anterior plastron (JRD–19/246, JZ–13) in **C1**. Visceral; **C2**. Ventral; **C3**. Drawing of the ventral, and **C4**. Medial views; **D.** Entoplastron of a young individual (JRD–18/118, JZ–11) in **D1**. Visceral; **D2**. Ventral, and **D3**. Drawing of the ventral views; **E.** Left posterior plastron (JRD–25/214, JZ–3) in **E1**. Visceral; **E2**. Ventral, and **E3**. Drawing of the ventral views; **F.** Posterior half of an almost complete plastron (JRD–25/250, JZ–13) in drawing of the ventral view; complete photographs of visceral and ventral views in the Suppl. material 1; **G.** Posterior lobe of a plastron with a fragment of the left hypoplastron (JRD–25/212, JZ–3) in **G1**. Visceral; **G2**. Ventral, and **G3**. Drawing of the ventral views. Abbreviations (bony plates in small and horny scutes in capital letters): ABD, abdominal; AN, anal; en, entoplastron; ep, epiplastron; FE, femoral; GU, gular; HU, humeral; hyo, hyoplastron; hypo, hypoplastron; PEC, pectoral; xi, xiphiplastron. Scale bar: 10 mm.

Plastron

The plastron of the new species is known completely, based on the almost complete plastron of the holotype (Fig. 4) and several additional well-preserved plastra from other individuals (Fig. 6; Suppl. material 1), which also help document some morphological variation, attributed herein to the intraspecific variation.

The plastron of the holotype JRD–25/226 (JZ–11; Fig. 4C, D) is almost complete, preserving practically the entire left side (missing only the lateral parts of the hyoplastra and the hypoplastra that were connected to the bridge), the medial parts of the right side, and the entire posterior lobe that is recovered slightly separated from the hypoplastra. The epiplastra are short and wide, forming a thick epiplastral lip with a clearly convex dorsal surface with an overhanging lip over the entoplastron, creating a deep gular pocket. The epiplastra form part of the anteriormost portion of the anterior lobe, which is clearly elevated. The entoplastron is quite large, clearly wider than long, and rhomboidal in shape with nicely rounded sides; it is the largest element of the anterior lobe. The hyoplastra are large, with a medial border that is shorter than that of the hypoplastra, but, overall, are slightly longer than wide. The hypoplastra are also large, but slightly wider than long. The combined surface of the hypoplastra and the hyoplastra represents more than half of the plastron and is relatively flat medially, indicating that it was probably from a female individual; however, post-mortem deformation of the plastron could affect this observation. The posterior border of the hypoplastra is thickened and separated from the xiphiplastra, with the indentations of the sutures clearly visible, at the same level as the inguinal notch and the posterior end of the bridge. The posterior lobe is entirely formed by the xiphiplastra, which are large, wider than long. The anterior border of the xiphiplastra is thickened, the lateral borders are strongly converging posteriorly, and there is a deep angular notch at the posteriormost part. The xiphiplastral tips are rounded. The separation of the xiphiplastral from the hypoplastra and the morphology of their borders indicate the clear presence of a hypo-xiphiplastral movable hinge. The gulars are narrow and long, covering the anterior part of the entoplastron. The humero-pectoral sulcus is strongly convex laterally and gently curved, almost straight medially, and placed posterior to the entoplastron. There is a narrow axillary scute laterally on the axillary notch, visible in ventral view. The pectoro-abdominal sulcus is almost straight, crossing the middle part of the hyoplastron. The pectoral scutes are short, the shortest in the plastron, representing approximately one-quarter of the medial length of the hyoplastron. The abdominals are the largest scutes of the plastron, covering the posterior half of the hyoplastra and almost the entire hypoplastra. There is a small and narrow inguinal scute laterally, visible in ventral view, but it is not in contact with the femorals. The imprint of the abdomino-femoral sulcus is visible posteriorly, developed quite close and almost parallel to the hypo-xiphiplastral hinge. The femorals cover the anterior

half of the xiphiplastra and are slightly longer than the anal scutes. The femoro-anal sulcus is wide, omega-shaped, with a convex anteriorly medial part and a concave posteriorly lateral part (Figs 4D, 6F, 6G3).

Further plastron elements are noted in the Jradzor levels (Fig. 6; Suppl. material 1). The collected material from specimen JRD–25/228 (from JZ–3 or JZ–13; Fig. 6A) contains the remains of an adult tortoise known by a well-preserved partial plastron that preserves the left epiplastron, hyoplastron, hypoplastron, and the entoplastron. The hyo-hypoplastral area is completely flat throughout its medial surface, indicating that it belonged to a female individual. The epiplastron is short and narrow, thickened, with a clear epiplastral lip of a clearly convex dorsal surface, forming a deep gular pocket that overhangs the entoplastron. There is a faint constriction at the gularo-humeral sulcus. The entoplastron is hexagonal with slightly rounded posterior sides, wider than long, the anterior part being twice as long as the posterior one (divided horizontally by the epi-hyoplastral suture); compared to other specimens, this entoplastron is markedly smaller. The hyoplastra and hypoplastra are flat medially and curved laterally to form the bridge. The medial length of the hyoplastron is shorter than the medial length of the hypoplastron. The posterior part of the hypoplastron is thickened and straight, preserving a rugose posterior suture that indicates the presence of a hinge. The gulars are long, as long as the humerals medially, but narrow, covering the anterior part of the entoplastron. The humero-pectoral sulcus is strongly curved, starting laterally at the level of the axillary notch and then gently curved towards the middle, placed clearly behind the entoplastron. There is a small axillary scute. The pectoro-abdominal sulcus is convex anteriorly, starting laterally from the posteriormost part of the hyoplastron and gently curved until the middle of the medial border of the hyoplastron. The pectorals are quite short medially and measure approximately one-fourth of the medial length of the hyoplastron. The abdomino-femoral sulcus is only partly visible posterolaterally at the hypoplastron, coinciding mostly with the hypo-xiphiplastral suture, another indication of the presence of a movable hinge at the posterior lobe.

Individual JRD–25/243 (JZ–3; Fig. 6B) comprises the anterior lobe of a plastron that is quite similar to the holotype plastron, with a large, hexagonal entoplastron and long gulars that cover its anterior part. The epiplastral lip is thick with a convex dorsal surface, but only developed anteriorly without a significant overhanging over the entoplastron and just a small gular pocket. Individual JRD–19/246 (JZ–13; Fig. 6C) comprises a partial plastron of a quite large and robust tortoise individual, preserving the anterior part of the anterior lobe and most of the right side of the anterior half of the plastron. The epiplastra are quite wide and short, forming a well-developed but short epiplastral lip with a relatively straight dorsal surface, which is overhanging the entoplastron. The anterior border of the epiplastra is slightly trilobed with two faint tips on each side, one at the level of the gularo-humeral

sulcus and another next to it at the middle of each gular. The entoplastron is partially preserved, but based on the preserved part it was probably hexagonal in shape. The hyoplastra are quite long. The gulars are long and narrow, covering the anterior part of the entoplastron. The gularo-humeral sulcus is developed at a narrow angle with the midline. The remaining sulci are not well-preserved and visible. However, they indicate that the pectorals were probably longer medially than in other specimens but still measure less than the half of the medial hyoplastral length. Individual JRD-18/118 (JZ-11; Fig. 6D) comprises a complete entoplastron and several other fragments. The entoplastron measures 21 mm (therefore estimated to belong to a small-sized individual). It is longer than wide, hexagonal in shape with shorter anterior and longer posterior parts. It is crossed by the medial sulcus along its length and covered anteriorly by the gular scutes. Individual JRD-25/214 (JZ-3; Fig. 6E; Suppl. material 1) comprises the partial plastra of two individuals, including a partial entoplastron that is hexagonal in shape, wider than long and crossed medially by the medial sulcus. A partial hyoplastron with a curved humero-pectoral sulcus that is placed posterior to the entoplastron, a posterior lobe with a hypo-xiphiplastral hinge, a narrow and short angular anal notch, and a femoro-anal sulcus that is gently rounded and convex anteriorly with anals that are medially much longer than the femorals. Individual JRD-25/250 (JZ-13; Fig. 6F; Suppl. material 1) comprises a large part of a plastron, including most of the left hyoplastron, left hypoplastron, and part of the right hypoplastron, and the posterior lobe. The hyoplastra are large, with a medial border that is shorter than the medial border of the hypoplastra, but, overall, are slightly longer than wide. The hypoplastra are also large, but slightly wider than long. The posterior border of the hypoplastra is thickened and separated from the xiphiplastra, with the indentations of the sutures clearly visible, at the same level as the inguinal notch and the posterior end of the bridge. The posterior lobe is entirely formed by the xiphiplastra, which are large, wider than long. The xiphiplastral tips are rounded. The separation of the xiphiplastral from the hypoplastra and the morphology of their borders indicate the clear presence of a hypo-xiphiplastral movable hinge. The overall morphology of this specimen is quite similar to the morphology of the holotype. The humero-pectoral sulcus is strongly convex laterally and gently curved, almost straight medially, and gently placed posterior to the entoplastron. There is a narrow axillary scute laterally on the axillary notch, visible in ventral view. The pectoro-abdominal sulcus is almost straight, crossing the middle part of the hyoplastron. The pectoral scutes are short, the shortest in the plastron, representing approximately one-quarter of the medial length of the hyoplastron. The abdominals are the largest scutes of the plastron, covering the posterior half of the hyoplastra and almost the entire hypoplastra. There is a small and narrow inguinal scute laterally, visible in ventral view but not in contact with the femorals in ventral view. The

imprint of the abdomino-femoral sulcus is visible posteriorly, developed quite close and almost parallel to the hypo-xiphiplastral hinge. The femorals cover the anterior half of the xiphiplastra, being slightly longer than the anal scutes. The femoro-anal sulcus is wide, gently omega-shaped, with a convex anteriorly medial part and a concave posteriorly lateral part. Individual JRD-25/212 (JZ-3; Fig. 6G; Suppl. material 1) comprises the remains of an adult tortoise individual, including the posterior lobe of a plastron with a fragment of the left hypoplastron. The hypoplastron shows a weak inguinal buttress, and the presence of the lateral parts of the femorals with an anteriorly convex abdomino-femoral sulcus that reaches near the hypo-xiphiplastral suture medially in the preserved part. Laterally, a triangular inguinal scute is visible in ventral view. The entire posterior lobe is composed by the xiphiplastral, that are large, and the suture with the hypoplastra is wide and rugose—characters that indicate the presence of a movable hinge. The lateral borders of the xiphiplastral converge posteriorly and a deep but angular anal notch is present. The femoro-anal sulcus is gently rounded and convex anteriorly. The anals are medially almost as long as the femorals. Viscerally, the scutes cover a part of the border of the lobe, but not the posteriormost part at the middle. At the posterior border, right in front of the free edge of the anal scutes a deep trough is noted, and then the posterior and medial parts of the plastron are elevated.

There is important morphological variation in the plastron of this species, including polymorphisms in the degree of development of the epiplastral lip, the size of the entoplastron, the medial length of the pectorals, the shape of the femoro-anal sulcus, and the shape and size of the anal notch, most of which can be confidently attributed to sexual dimorphism. However, it is important to note that despite this variability, all preserved hypoplastra and xiphiplastra, from both sexes and different ontogenetic sizes as well as from all Jradzor levels, consistently present a clear movable hinge between the hypoplastra and the xiphiplastra, a clear diagnostic character of the genus *Testudo*.

Appendicular skeleton

Numerous appendicular elements are recovered in the Jradzor levels, allowing the documentation of most of the appendicular anatomy of this species (Figs 7–8; Suppl. material 1). In several cases, a significant number of appendicular elements is associated with shell remains: the tortoise individual JRD-25/250 (JZ-13) whose appendicular elements (Figs 7B, C, 8A–J) correspond to an almost complete plastron and additional elements (Fig. 6F; Suppl. material 1) and the appendicular elements of the holotype individual JRD-25/226 (JZ-11; Fig. 8K–X; see Fig. 4 and Suppl. material 1 for additional shell and appendicular remains from the same individual).

From the neck region, only some isolated vertebrae are preserved. A complete, perfectly preserved cervical vertebra 8 is identified from individual JRD-25/248 (JZ-13?; Fig. 7A; see Fig. 2A–D for associated cranial remains and Suppl.

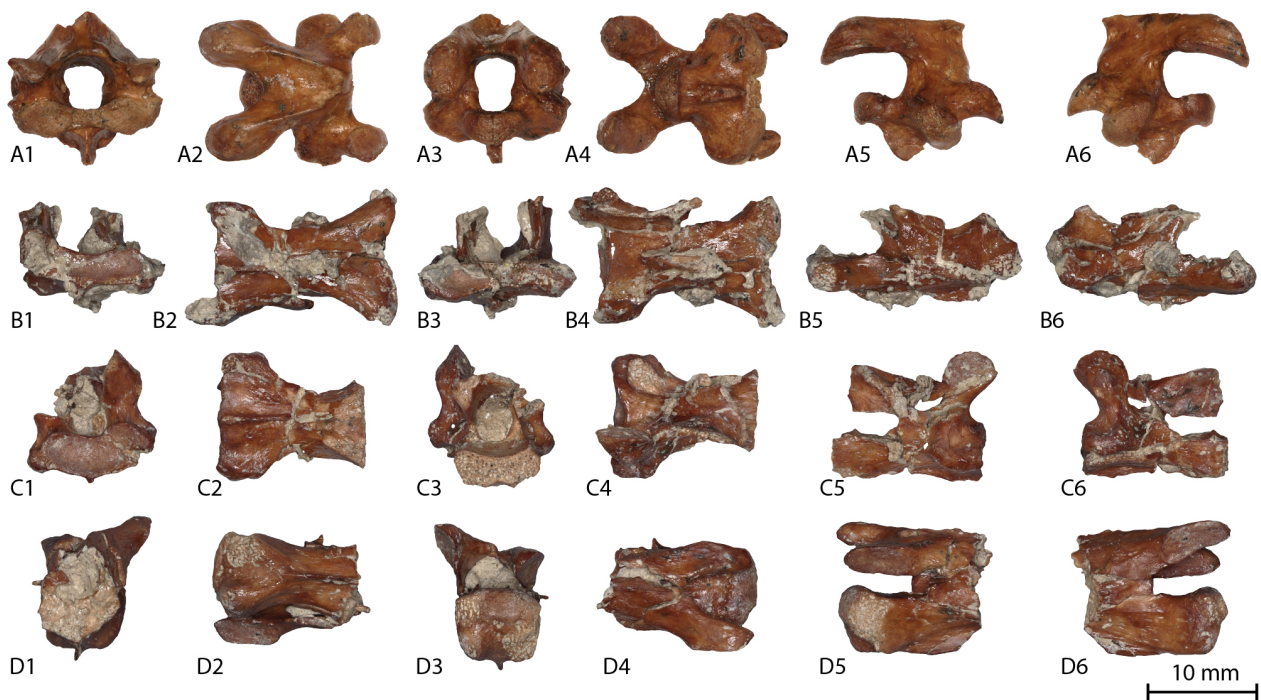


Figure 7. Selected cervical vertebrae of *Testudo sahyanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. **A.** Cervical vertebra 8 of individual JRD–25/248 (JZ–13?; see Fig. 2A–D for associated cranial remains and Suppl. material 1) in **A1.** Anterior; **A2.** Dorsal; **A3.** Posterior; **A4.** Ventral; **A5.** Right lateral, and **A6.** Left lateral views; **B–D.** Cervical vertebrae of individual JRD–25/250 (JZ–13; see Fig. 6F and Suppl. material 1 for additional shell and appendicular remains from the same individual); **B.** Cervical vertebra 7 in **B1.** Anterior; **B2.** Dorsal; **B3.** Posterior; **B4.** Ventral; **B5.** Right lateral, and **B6.** Left lateral views; **C.** Cervical vertebra 6 in **C1.** Anterior; **C2.** Dorsal; **C3.** Posterior; **C4.** Ventral; **C5.** Right lateral, and **C6.** Left lateral views; **D.** Cervical vertebra 5 in **D1.** Anterior; **D2.** Dorsal; **D3.** Posterior; **D4.** Ventral; **D5.** Right lateral, and **D6.** Left lateral views. Scale bar: 10 mm.

material 1). Its centrum is rather short and flattened, clearly biconvex with a double and wide convex anterior articulation and a single and convex posterior articulation. A ventral keel is present in the centrum, isolated in the middle. The prezygapophyses are small, developed above, and extend beyond each of the double convex anterior articulations. The arch is strong and tall, with strongly developed, nearly straight postzygapophyses. In dorsal view, from each postzygapophysis, a prominent keel is projecting anteriorly. They join at the level of the anterior margin of the neural arch and form a V-shaped morphology.

From the JRD–25/250 individual (JZ–13; Fig. 7B–D), three almost complete cervical vertebrae are identified from the same neck of a tortoise individual. They are quite fragmented and not well-preserved. Most of the neural arches are broken or incomplete. Based on the available remains, they are identified as successive cervical vertebrae 7–5. The body of the cervical vertebra 7 (Fig. 7B) is long and flattened with amphicoelous joints. The posterior articulation is double and concave, corresponding to the double convex articulation of the cervical vertebra 8. A ventral keel is present, being quite low, placed at the middle of the body. The neural arch is broken. The cervical vertebra 6 (Fig. 7C) is better preserved, with both the posterior part of the body and the postzygapophyses missing. Its body is also long and flattened. The anterior joint is clearly concave and wide. The prezygapophyses are quite tall and almost vertically

developed. The cervical 5 (Fig. 7D) has also a long and flattened body, with a posterior convex articulation that is quite robust, with an additional vertical expansion on each side. The postzygapophyses are present, projecting slightly posterodorsally.

Some elements of the shoulder girdle are present (Fig. 8A, K; Suppl. material 1), showing the typical morphology of the testudinid shoulder girdle (e.g., Auffenberg 1974). The scapula is developed almost vertically. The acromion is thicker but shorter than the scapula, developed at approximately 120°. The articular surface is quite concave and relatively rounded and short. Some elements of the pelvic girdle are preserved (Fig. 8B, C, Suppl. material 1). The ilium is quite thick, elongated, and vertically developed.

From the appendicular elements, the humerus is perhaps the best-preserved with numerous specimens from different individuals (Fig. 8D, E, M, Y, Z, Suppl. material 1). Its shaft is strongly arched, S-shaped, especially towards the distal end. The proximal end shows a prominent, almost spherical head that is clearly separated from the shaft by a well-developed neck, with an overhanging distal rim. Proximally, two processes are noted: the medial process (or major trochanter) that is quite robust and large, extending well beyond the height of the humeral head, connected to it with a thin proximal ridge. Towards the distal end, a faint extepicondylar groove is noted in radial view. The distal end is slightly asymmetrical, the



radial and ulnar epicondyles are similar in size. They are slightly separated by a shallow intercondylar groove. In intertubercular view, the capitellum and trochlea surfaces are quite distinct, the trochlea being slightly larger.

The radius (Fig. 8F, O, P, AA, Suppl. material 1) and ulna (Fig. 8Q, AB, Suppl. material 1) are also well-documented in the material. The radius is comparatively shorter than its corresponding ulna. Their articular contacts are quite short, both proximally and distally, leaving a quite long and quite narrow, pointed oval-shaped fenestra in between. The distal end of the zeugopodium, where the radius and ulna articulate, is wide and triangular in shape, leaving a small space for the intermedium (not identified in the available material).

The femur is well-represented in the Jradzor material, identified by many or almost complete elements from different individuals (Fig. 8G, H, N, AJ, Suppl. material 1). The femur of the Jradzor tortoise clearly shows the Testudinini morphotype (sensu Valenti et al. 2022), which includes: the shaft is almost straight with a small change of curvature distally; the proximal end is more robust, with a distinct and robust, elliptical head, separated by the shaft with a distinct neck and developed at an angle of 30–40° from the horizontal plane; the trochanters are clearly fused and joined proximally, the major being connected proximally to the head by a wide ridge that delimits the intertrochanteric fossa; the fused trochanters do not extend beyond the level of the femoral head; the distal end is narrow, the articular surface being weakly developed.

Several elements of the tibia (Fig. 8I, R, S; Suppl. material 1) and fibula (Fig. 8J; Suppl. material 1) are

preserved and have almost the same height. The tibia is much more robust than the fibula, especially proximally with a well-developed and robust, triangular in shape, articular surface. The distal end of the tibia is also well-developed with a double and expanded articular surface for the astragalocalcaneum. The distal surface of the fibula is more robust than the proximal one, with a convex articular surface for the astragalus. There are some elements of the astragalus and the calcaneum (e.g., Fig. 8X; Suppl. material 1), recovered mostly separately and unfused. The astragalus is much more robust than the calcaneum, being a thick and rounded tarsal element without clearly defined articular surfaces. Some additional carpal and tarsal elements, including some metatarsals, are recovered (e.g., Fig. 8AK, AL). They are highly asymmetrical with a shorter medial and taller lateral sides, a wide and expanded proximal end with a clearly concave articular surface, and a distal end with a double convex and modified joint. Several phalanges and unguals are identified (Suppl. material 1), being the typical unguals of testudinids based on the comparative material at our disposal, the anterior ones being comparatively shorter and wider than the posterior ones that are generally longer and more pointed.

Osteoderms

The recovered material of the Jradzor tortoise includes the presence of elements of dermal armor, in particular the presence of conical thigh spurs (Fig. 8T–V) and isolated osteoderms (e.g., Fig. 8W, AC–AI; Suppl. material 1). The presence of large and conical thigh spurs is

Figure 8. Selected appendicular elements of *Testudo sahayanae* sp. nov. from the Early Pliocene (MN15) of Jradzor site, Armenia. A–J. Appendicular elements of individual JRD–25/250 (JZ–13; see Fig. 5F and Suppl. material 1 for additional shell and appendicular remains from the same individual); **A.** Right scapula in **A1.** Anterior; **A2.** Ventrolateral, and **A3.** Posterior views; **B.** Left ilium in **B1.** Anterior; **B2.** Lateral, and **B3.** Posterior views; **C.** Left ischium in **C1.** Lateroventral and **C2.** Dorsomedial views; **D.** Left humerus in **D1.** Radial; **D2.** Capitular; **D3.** Ulnar; **D4.** Intertubercular; **D5.** Proximal, and **D6.** Distal views; **E.** Left humerus in **E1.** Radial; **E2.** Capitular; **E3.** Ulnar; **E4.** Intertubercular; **E5.** Proximal, and **E6.** Distal views; **F.** Left radius in **F1.** Dorsal; **F2.** Medial; **F3.** Ventral; **F4.** Lateral; **F5.** Proximal, and **F6.** Distal views; **G.** Left femur in **G1.** Dorsal; **G2.** Anterior; **G3.** Ventral, and **G4.** Posterior views; **H.** Right femur in **H1.** Dorsal; **H2.** Anterior; **H3.** Ventral, and **H4.** Posterior views; **I.** Left tibia in **I1.** Dorsal; **I2.** Anterior; **I3.** Ventral, and **I4.** Posterior views; **J.** Left fibula in **J1.** Dorsal; **J2.** Anterior; **J3.** Ventral, and **J4.** Posterior views; **K–X.** Appendicular elements of the holotype individual JRD–25/226 (JZ–11; see Fig. 3 and Suppl. material 1 for additional shell and appendicular remains from the same individual); **K.** Right scapula in **K1.** Anterior; **K2.** Medial; **K3.** Posterior; **K4.** Lateral, and **K5.** Ventrolateral views; **L.** Right pubis in **L1.** Anterior; **L2.** Medial; **L3.** Posterior; **L4.** Lateral; **L5.** Dorsal, and **L6.** Ventral views; **M.** Left humerus in **M1.** Radial; **M2.** Capitular; **M3.** Ulnar; **M4.** Intertubercular, and **M5.** Proximal views; **N.** Right femur in **N1.** Dorsal; **N2.** Anterior; **N3.** Ventral; **N4.** Posterior, and **N5.** Distal views; **O.** Left radius in **O1.** Dorsal; **O2.** Medial; **O3.** Medial; **O4.** Lateral; **O5.** Proximal, and **O6.** Distal views; **P.** Right radius in **P1.** Dorsal; **P2.** Medial; **P3.** Ventral; **P4.** Lateral; **P5.** Proximal, and **P6.** Distal views; **Q.** Left ulna in **Q1.** Dorsal; **Q2.** Medial; **Q3.** Ventral; **Q4.** Lateral, and **Q5.** Distal views; **R.** Right tibia in **R1.** Dorsal; **R2.** Posterior; **R3.** Ventral; **R4.** Anterior, and **R5.** Proximal views; **S.** Left tibia in **S1.** Ventral; **S2.** Anterior; **S3.** Dorsal, and **S4.** Distal views; **T–V.** Bony thigh spurs in different views; **W.** Osteoderm in different views; **X.** Right astragalus in **X1.** Posterior; **X2.** Distal; **X3.** Proximal; **X4.** Anterior; **X5.** Medial, and **X6.** Lateral views; **Y–AI.** Appendicular elements of individual JRD–19/251 (JZ–3); **Y.** Left humerus in **Y1.** Radial; **Y2.** Capitular; **Y3.** Ulnar, and **Y4.** Intertubercular views; **Z.** Right humerus in **Z1.** Radial; **Z2.** Capitular; **Z3.** Ulnar, and **Z4.** Intertubercular views; **AA.** Right radius in **AA1.** Dorsal; **AA2.** Medial; **AA3.** Ventral, and **AA4.** Lateral views; **AB.** Right ulna in **AB1.** Dorsal; **AB2.** Medial; **AB3.** Ventral, and **AB4.** Lateral views; **AC–AI.** Various osteoderms in dorsal and ventral views; **AJ.** Right femur of individual JRD–25/245 (JZ–3) in **AJ1.** Dorsal; **AJ2.** Anterior; **AJ3.** Ventral; **AJ4.** Posterior, and **AJ5.** Proximal views; **AK–AL.** Metatarsals of individual JRD–25/250 (JZ–13; see Figs 5F, 6B, C, 7A–J and Suppl. material 1 for additional shell and appendicular remains from the same individual); **AK.** Left metatarsal in **AK1.** Anterior; **AK2.** Lateral; **AK3.** Posterior; **AK4.** Medial; **AK5.** Proximal, and **AK6.** Distal views; **AL.** Right metatarsal in **AL1.** Anterior; **AL2.** Lateral; **AL3.** Posterior; **AL4.** Medial; **AL5.** Proximal, and **AL6.** Distal views. Scale bars: 10 mm. All specimens are placed at different scales.

a striking feature, recovered from the holotype, one of them (Fig. 8T) in association with the shell in the right posterior side of the shell (see arrow in Fig. 4B) and the other (Fig. 8U, V) isolated but in association with the appendicular elements of the holotype individual. The thigh spurs are robust and conical, with a rounded and convex distal surface and a pointed and slightly curved tip. CT scans of the thigh spurs indicated that they are completely ossified internally. One of them (Fig. 8V) is smaller and more curved than the other two, with a flattened to slightly concave internal surface, indicating that it could have been in contact with adjacent, larger thigh spurs. These thigh spurs were probably in association of at least 1–2 elements in close contact posterior to the femur of the animal, similar to the condition seen in extant Mediterranean Spurred Tortoise *Testudo graeca*. However, the extant *Te. graeca* has only one conical thigh spur on each side of the tail posterior to the femur without a bony core but made only by keratin. *Testudo sahyanae* sp. nov. had more than one bony thigh spurs, as in extant and extinct Geochelonini (e.g., the African Spurred Tortoise, *Centrochelys sulcata* (Miller, 1779), or in the extinct *Titanochelon bacharidisi* Vlachos, Tsoukala & Corsini, 2014), and members of *Hesperotestudo* spp. (see Auffenberg 1963 and references therein).

All osteoderms are found isolated, and the only evidence of some kind of osteoderm association comes from a couple of isolated half-pointed osteoderms that appear to have had some contact edges (e.g., Fig. 8AC–AE). So, there is some evidence of some minimal heavier dermal armor of some osteoderms sutured together, but nothing close or similar to the condition seen in *Testudo lohanica* (Pérez-García et al. 2021). The material from several individuals preserves isolated osteoderms or even collections of 7, 10, or even 17 osteoderms, with a size ranging from 2 to 13 mm, being mostly half-pointed, quite rounded and clearly separated from each-other; except in the exceptions mentioned above.

Phylogenetic analysis

The first run of TBR resulted in hitting the minimum score 96 out of 1000 times with overflow. The second run of TBR from RAM resulted in 45 most parsimonious trees of 4523 steps (fit: 203.30992; Consistency Index: 0.493; Retention Index: 0.414). The topology is mostly well-resolved, and most of the extinct taxa are recovered in stable positions (Fig. 9A). However, three main polytomies are noted (Fig. 9B). These polytomies are caused by the unstable positions of three taxa, which were further analyzed using the IterPCR script in TNT. *Paleotestudo antiqua* jumps in different basal positions of various Testudinini clades: branching along the stem of Testudinini but always more derived than the “*Te.*” *kenitrensis* + “*Te.*” *oughlamensis* clade; outside the *Testudo* + *Chersine* clade; basal to the *Chersine* clade; basal to

the *Testudo* clade. This instability is interpreted by the IterPCR due to missing information, and especially due to the lack of skull, mandible, and appendicular material. Therefore, the shell of *Paleotestudo antiqua* could support its placement in a branching positions of most main clades of Testudinini, and cranial information is needed to resolve this instability. The extant *Testudo marginata* is always recovered close to the extant *Testudo kleinmanni*. However, its position relative to some extinct taxa recovered there (e.g., *Testudo hellenica*, *Testudo bosporica*, *Testudo eldarica*) remains unclear. The IterPCR interprets this result as the scored character state for the general shape of the nuchal, which could support different positions within that derived clade. Similarly, the extinct *Testudo marmorum* adds further instability, jumping in all possible positions of the clade, including the *Testudo graeca* complex, based on its shell morphology. The IterPCR interprets this result as due to the lack of information from the skull and mandible, information that is scored for the other taxa belonging to the same clade, namely *Testudo sahyanae* sp. nov., *Testudo lohanica*, and the *Testudo graeca* complex. The missing information from the cranium could help in resolving the position of *Testudo marmorum*.

The new tortoise species described herein, *Testudo sahyanae* sp. nov., is consistently recovered within the derived clade of *Testudo*, based on the presence of a movable hinge between the hypoplastra and the xiphiplastra. Furthermore, it is consistently recovered as a member of the clade of the *Testudo graeca* complex (not the *Testudo marginata* + *Testudo kleinmanni* clade) based on the presence of a prearticular foramen in the mandible and the deep anal notch. It is always recovered in a more derived position than *Testudo lohanica* based on the “mixed” morphotype of the suprapygals, the low ventral keel on the cervical vertebra 7, the major trochanter of the humerus extending beyond the humeral head, and the presence of thigh spurs.

The positions of the added extinct taxa in this version of the matrix, *Testudo eldarica* and *Testudo kuchurganica*, scored only based on plastral characters and second-hand observations, provide mixed results. On one hand, *Testudo eldarica* is clearly recovered as a member of a true *Testudo*, consistently with the presence of a movable hinge. However, *Testudo kuchurganica* is surprisingly recovered outside *Testudo* and associated with the *Chersine* clade. This position is supported by the narrow gulars, the coincidence of the humeropectoral sulcus with the posterior end of the entoplastron, and the shape of the femoro-anal sulcus. Based on this topology, the plastral hinge would stop being the only non-homoplastic character in Testudinidae and would have been independently developed at least twice. However, this result should be interpreted with caution given the extremely low support that this placement has (Bremer support of 1 and minimal Bootstrap/Jackknife frequencies). It demonstrates that this position is quite fragile and could easily

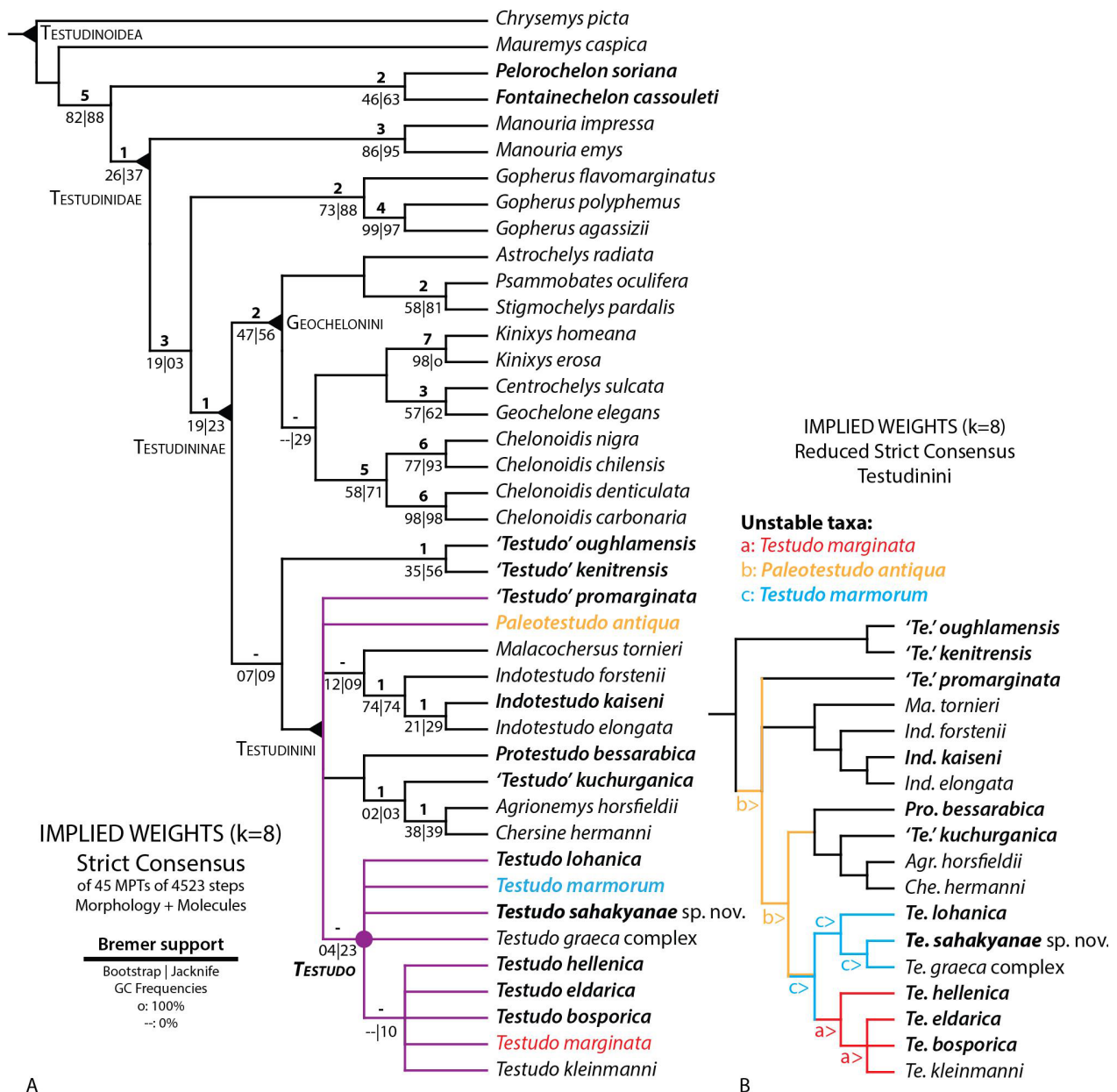


Figure 9. Phylogenetic analysis of *Testudo sahyanae* sp. nov. within the context of the total clade of Testudinidae. **A.** Strict consensus of 45 most parsimonious trees of 4523, coming from the combined analysis of a morphological and molecular matrix under implied weights (k=8). Bremer supports and Bootstrap/Jackknife GC frequencies are indicated. Three main polytomies are noted in purple; **B.** A reduced strict consensus of the Testudinini clade, showing the unstable positions of three taxa: *Testudo marginata* (a, in red) jumping in two positions within *Testudo*; *Paleotestudo antiqua* (b, in orange) jumping in basal positions within Testudinini; *Testudo marmorum* (c, in blue) jumping in various positions within *Testudo*.

change even with minimum changes in the matrix. The revision of both taxa (*Te. eldarica* and *Te. kuchurganica*) and the description of at least carapacial remains would be an important step forward. Relative to other taxa used in calibrations of Fritz et al. (2007, 2009) for *Testudo*, *Testudo burtschaki* and *Testudo cernovi* (found also with the unjustified emendation of *Testudo chernovi*), we recommend avoiding using them as calibration points for several reasons. First, *Testudo burtschaki* is known only by some isolated specimens, including a partial epiplastron with a thick epiplastral lip and gulars that cover the

entoplastron (figured in Danilov et al. 2017: fig. 88), lacking specimens that preserve characters that place it inside the true *Testudo* like the presence of a hypo-xiphiplastral hinge (Danilov et al. 2017). It is doubtful whether the available material is enough to diagnose the specimens beyond the level of Testudininae and probably *Testudo burtschaki* should be considered as a nomen dubium. On the other hand, *Testudo cernovi* is known by more complete material that would allow the description of diagnostic characters; however it is clear that the plastron of this taxon does not have any hypo-xiphiplastral

hinge, given that there is no coincidence between the femoro-anal sulcus and the hypoplastra contribute to the formation of the posterior lobe. Therefore, this taxon needs to be revised in the context of non-*Testudo* clades, as well as in relation to its coeval, sympatric and simultaneously published *Testudo kuchurganica*, recovered here outside *Testudo* as well (see above). Given the recovered position of *Testudo kuchurganica* herein and the overall similarities between *Testudo kuchurganica* and *Testudo chernovi* on the narrow gulars and the hexagonal entoplastron whose posterior end coincides medially with the humero-pectoral sulcus, it is likely that the two species represent the same, non-*Testudo* taxon and therefore not suitable for calibrating the *Testudo* clade; further revision is necessary. Compared to the recently published phylogeny of Gnetneva et al. (2018) that focuses on Testudinini, our results of the stable topology show a good general agreement in the relationships and placement of extinct taxa. *Testudo marmorum* and *Testudo eldarica* are clearly associated with the *Testudo graeca* complex, and *Protestudo bessarabica* is clearly associated with *Agrionemys*. However, the phylogeny of Gnetneva et al. (2018) is more extensive in terms of extinct taxon sampling than ours for Testudinini, especially for taxa placement outside the true *Testudo* or *Testudo* s.s., i.e., more closely associated with the extant *Agrionemys* or *Chersine*.

Concluding remarks

The new species described herein, *Testudo sahyanae* sp. nov., proves the presence of true *Testudo* populations in the Southern Caucasus region since at least the Early Pliocene, a clade that continues there to the present day. The recovery of tortoise specimens in recurring pyroclastic flows and different, successive stratigraphic levels suggests the persistence of *Testudo sahyanae* sp. nov. in challenging environments with continuous volcanic eruptions and pyroclastic flows. The tortoise remains are confined to eleven fossiliferous horizons (JZ-2, JZ-2a, JZ-11g, JZ-11, JZ-3, JZ-3V, JZ-3s, JZ-14, JZ-15, JZ-13, JZ-5, JZ-6), with ages ranging between ~4.16 and 3.98 Ma. Other fossiliferous layers (JZ-1, JZ-13g, JZ-12, JZ-5, JZ-5a, JZ-8, JZ-9, JZ-7) did not yield any tortoise remains (Fig. 1A). Only JZ-1 (lacustrine settings) provides a geoemydid remain. Even more interesting is the fact that the JZ-7 layer, which provided the richest mammalian assemblage, did not contain either tortoise or turtle remains. We assume that the depositional environment was not favorable for the preservation/fossilization of tortoise remains, rather than this species was absent in the assemblage.

The description of *Testudo sahyanae* sp. nov. brings new information on the evolution of *Testudo* in the broader Mediterranean region. The new species is known by some well-preserved and diverse shell remains and several appendicular elements, as well as some skull and

mandible remains. These are only the second findings of cranial remains of an extinct *Testudo*, after the much more complete cranial remains of the recently described *Testudo lohanica* from the Late Miocene of Romania (see Pérez-García et al. 2022). The new fossils reported herein are the first remains of an extinct tortoise and the first extinct tortoise species described from Armenia.

Based on our results, the clade leading to the modern *Testudo* is populated by several extinct species that help document the evolution of the genus since the Late Miocene. The subclade of the modern *Testudo graeca* complex is further populated by two recently described species, *Testudo lohanica* from the Late Miocene of Romania and the new species from the Early Pliocene of Armenia, as well as *Testudo marmorum* from the Late Miocene of Greece, a taxon known from the last century and recently revised (Vlachos et al. 2019). An interesting emerging picture is that the Romanian and Armenian extinct tortoises appear to have had different types of dermal armor on the anterior and posterior limbs, respectively. The presence or absence of the armor is not verifiable in *Testudo marmorum*. *Testudo lohanica* had forelimbs heavily covered with ossified osteoderms, forming a continuous protective shield of sutured polygonal elements. On the other hand, the new Armenian tortoise described herein probably had forelimbs free of such coverings (since in *Testudo lohanica* such covered limbs are recovered with their cover, and the taphonomical conditions in Jradzor allow detailed preservation of limbs in close association). Only a few of the recovered osteoderms show possible sutural sides, but it is unclear which limb they belonged to. Although the limbs are well-preserved in partly articulated specimens, we cannot find similar features to those of *Testudo lohanica*. The new Armenian tortoise described herein, instead, showed at least 1–2 bony thigh spurs posterior to the femur. This is somehow similar to the condition seen in the extant spur-thighed Mediterranean tortoise *Testudo graeca*, with the important difference that in the extant species, there is only one spur on each side that is apparently only keratinous without a bony core. Likely, the evolution of the clade leading to the modern *Testudo graeca* experimented with different adaptations of dermal armor and coverings, which needs to be further investigated and evaluated.

Testudo sahyanae sp. nov. comes from a well-defined, time-constrained framework within stratigraphic levels dated between 4.16–3.98 Ma. These occurrences could yield findings of great importance, as they belong to a tortoise that is morphologically and phylogenetically quite close to but still distinct from the extant *Testudo graeca* complex. Fritz et al. (2007, 2009) analyzed the mtDNA of extant members of this complex, suggesting a Caucasian origin for the *Testudo graeca* complex, followed by subsequent range expansions in various Mediterranean regions, calibrated with other fossil occurrences to the Early Pliocene at about 4.10–4.20 ± 0.61–0.71 Ma. The results presented herein testify that at that point, *graeca*-like tortoise populations were

present and diverse in the region. Because of the robust chronostratigraphic framework and the clear shared anatomical features, we suggest that *Testudo sahakyanae* sp. nov. should be considered as an ideal candidate for molecular calibrations of the origin and early divergence of the *Testudo graeca* complex.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

DV led the excavations of the fossil material and coordinated the preparation and curation of the fossil specimens. DV wrote the main draft of the geological information, EV wrote the main draft of the systematic paleontology and descriptions, all authors wrote the introduction, material and methods, and concluding remarks. DV designed the Figure 1 and the 3D models used in Figs 2, 3, EV designed Figs 2–9. DV performed the CT scans and created the 3D models of the specimens. EV performed the phylogenetic analysis. All authors edited and approved the final version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

List of referred specimens to *Testudo sahyanae* sp. nov. per level

Authors: Evangelos Vlachos, Davit Vasilyan

Data type: pdf

Explanation note: This file contains a detailed list of all referred specimens to *Testudo sahyanae* sp. nov. per level, including photographs and anatomical drawings of the most important specimens.

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Link: <https://doi.org/10.3897/sjp.145.182210.suppl1>

Supplementary material 2

Nexus file of the morphological matrix

Authors: Evangelos Vlachos

Data type: nex

Explanation note: Nexus file of the morphological matrix used for the phylogenetic analysis.

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Link: <https://doi.org/10.3897/sjp.145.182210.suppl2>

Supplementary material 3

TNT file of the total evidence matrix

Authors: Evangelos Vlachos

Data type: tnt

Explanation note: TNT file of the total evidence matrix, combining morphological and molecular information, used in the phylogenetic analysis.

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Link: <https://doi.org/10.3897/sjp.145.182210.suppl3>

Supplementary material 4

IterPCR results

Authors: Evangelos Vlachos

Data type: txt

Explanation note: Results of the analysis of the unstable taxa, using the iterPCR script of Pol and Escapa (2009), see text for more details.

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