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RESEARCH

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Manouria morla sp. nov., the Ancient One: an Early Miocene large tortoise from the Swamps of Ahníkov, Czechia

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Abstract

Tortoises (*Testudinidae*) are a clade of turtles highly specialized to terrestrial environments, mainly living in semi-arid conditions. Herein, we present *Manouria morla* sp. nov., a new species of the genus *Manouria*, which is considered to be the most basal extant testudinid genus. The studied material comes from the Ahníkov I fossil site, formerly known as Merkur or Merkur-North, located in the Most Basin in NW Bohemia (Czechia), dated to the Early Miocene (Burdigalian, MN 3). *Manouria morla* sp. nov. is the oldest member of the *Manouria* lineage, which nowadays inhabits SE Asia only, and therefore its biogeography and plausible European origin are discussed. The specific type of multiplication of plastral scutes in the inguinal region is discussed as a new morphological character diagnostic for the genus. Based on zoological studies, specific environmental requirements of the genus *Manouria* allow us to use this taxon as a proxy for the paleoclimate reconstruction of the Ahníkov I fossil site which suggests a broadleaf evergreen tropical wet forest. The simplified use of fossil testudinids as a proxy for reconstructing semi-arid palaeoclimate is therefore disproven.

Introduction

Members of the clade *Testudinidae* larger than 35–75 cm in total carapace length are classified as medium to large tortoises, whereas species larger than 75 cm are considered to be giant-sized (Pérez-García et al., 2016; Valenti et al., 2022). The extant species of the *Testudinidae* are simply divided into three main different groups: the basal *Gopherus* Rafinesque, 1832 and *Manouria* Gray, 1854 (recovered either as a basal genera or as consecutive branches), as well as the *Geochelona* clade and the *Testudona* clade, the latter two constituting the subfamily *Testudininae* (Joyce et al., 2021; Le et al., 2006; Parham et al., 2006; Vlachos & Rabi, 2018). Differences between the clades *Geochelona* and *Testudona* are well summarized in Joyce et al. (2021) after Parham et al. (2006) and Vlachos and Rabi (2018). Apart from extant species, a large group of *Pan-Testudinidae* fossils are known from Europe, North America, Asia, and Africa (Vlachos & Rabi, 2018). The oldest stratigraphic record of large stem testudinid sensu Joyce et al. (2021) belongs to *Hadrianus majusculus* Hay, 1904 from the early Eocene of North America. However, a slightly younger *Fontainechelon cassouleti* (Claude & Tong, 2004) from the early Eocene of France seems to be the most basal member of the stem group (Carbot-Chanona et al., 2023; Pérez-García et al., 2016; Vlachos & Rabi, 2018).

The Paleogene American large stem testudinids reviewed by Vlachos (2018) are represented by the Eocene genera *Hadrianus* Cope, 1871a (*H. majusculus* and slightly younger *Hadrianus corsoni* [Leidy, 1871]) and *Cymatholcus schucherti* (Hay, 1899). Oligocene

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material is represented by aff. ‘*Stylemys*’ *gisellae* Carbot-Chanona et al., 2023 of uncertain generic identity, *Oligopherus laticuneus* (Cope, 1873), and the younger problematic ‘*Geochelone*’ *costaricensis* (Segura, 1944) with affinities to the extant genus *Indotestudo* Lindholm, 1929 (Carbot-Chanona et al., 2023; Vlachos, 2018; Vlachos & Rabi, 2018). According to Carbot-Chanona et al. (2023) and the references therein, the Late Miocene and younger material is attributed to the genera *Hesperotestudo* Williams, 1950 and extant *Gopherus*.

The Asiatic region has a very rich and unfortunately poorly studied fossil record. The species diversity is very high and further revisions are desirable. However, at least the summaries of fossils from the former Soviet Union, as compiled by Danilov et al. (2017), and those from China, as compiled by Brinkman et al. (2008), are available. The Eocene members of large stem *Testudinidae* from Kazakhstan and Kyrgyzstan belong to the genus *Hadrianus* divided into three different species: *Hadrianus vialovi* (Chkhikvadze, 1984) from the early Eocene of Kyrgyzstan; *Hadrianus davitashvili* Chkhikvadze & Amiranashvili, 1999 (middle Eocene, Kazakhstan) and *Hadrianus obailiensis* Chkhikvadze, 1970, (middle Eocene, Kazakhstan). However, according to Pérez-García et al. (2016), the genus *Hadrianus* is distributed only in North America and further investigation is needed to prove its Asian distribution. Chinese Eocene and younger material attributed to the genera *Testudo* Linnaeus, 1758 and *Kansuchelys* Yeh, 1963 need to be revised; however, their close relationship with the extant genus *Manouria* is assumed (Brinkman et al., 2008; Lapparent de Broin, 2002; Crumly, 1983). On the other hand, the only known fossil material of the genus *Manouria* is recorded from Japan, Pleistocene in age, and described as *Manouria oyamai* Takahashi et al., 2003 (see also Takahashi et al., 2018). Another stem testudinid genus with a record in the Paleogene and overlapping the Neogene is *Ergilemys* Chkhikvadze, 1972, currently including three dubious species: *Ergilemys insolitus* (Matthew & Granger, 1923) from the late Eocene of Mongolia; *Ergilemys saikanensis* Chkhikvadze, 1972 (early Oligocene, Kazakhstan); and *Ergilemys meschethica* (Gabunia & Chkhikvadze, 1960) from the Early Miocene of Georgia. Subsequently, Chkhikvadze (2002, 2007) considered *Ergilemys saikanensis* to be a member of the genus *Stylemys* Leidy, 1851. Also, Lapparent de Broin (2001) considered *Ergilemys meschethica* to be closely related to *Cheirogaster maurini* Bergounioux, 1935 or the genus *Titanochelon* Pérez-García & Vlachos, 2014. The last genus of large testudinids is the genus *Protestudo* Chkhivadze, 1970 with several species. Here we list only the large species, namely *Protestudo alba* Chkhikvadze, 1971 (Early Miocene, Kazakhstan) and *Protestudo darewskii* Chkhivadze, 1971 (Middle Miocene, Kazakhstan).

The Afro-Arabian record of testudinids is well summarized in Georgalis et al. (2021). The oldest African large testudinid is *Gigantochersina ammon* (Andrews, 1903) from the late Eocene/early Oligocene of Egypt (Holroyd & Parham, 2003). The Miocene fossil record of large testudinids is composed of *Impregnochelys pachytectis* Meylan & Auffenberg, 1986 and the genus *Namibchersus namaquensis* (Stromer, 1926). Also, some extant genera had their representatives in the Miocene: *Stigmochelys crassa* (Andrews, 1914), the genus *Kinixys* Bell, 1827 with specimens attributed to the recent species *Kinixys erosa* (Schweigger, 1812) by Meylan and Auffenberg (1986), and the genus *Centrochelys* Gray, 1872 with an uncertain attribution (see more in Georgalis et al., 2021). However, according to molecular data, the origin of the extant species is dated back to the Paleogene (Hofmeyr et al., 2017).

The Paleogene European large stem testudinids are well presented in Pérez-García et al., (2016) and they are grouped into two Eocene genera: *Fontainechelon* Pérez-García, Ortega & Fuentes 2016, which used to be placed in the American genus *Achilemys* Hay, 1908, respectively the dubious *Hadrianus allabiatus* Cope, 1871b (Claude & Tong, 2004; Pérez-García et al., 2016; Vlachos, 2018) and *Pelorochelon* Pérez-García, Ortega & Fuentes 2016, in the past synonymised with the record of the American genus *Hadrianus* (Broin, 1977; Pérez-García et al., 2016). The monophyly of the genus *Pelorochelon* Pérez-García et al., 2016—*Pelorochelon eocaenica* (Hummel, 1935) and *P. soriana* Pérez-García, Ortega & Fuentes (Pérez-García, et al., 2016)—is, however, disputed (Vlachos & Rabi, 2018). French Oligocene material is represented by *Taraschelon gigas* (Bravard, 1844) sensu Pérez-García (2016) and ‘*Ergilemys*’ *bruneti* Broin, 1977, a still problematic taxon with uncertain validity. After that, all Neogene large testudinids (crown *Testudininae*) from Europe belong to a single genus, i.e., *Titanochelon*, except *Alatochelon myrteum* Pérez-García et al., 2020 from the early Pliocene of Spain, probably closely related to African species *Centrochelys sulcata* (Miller, 1779).

The Central European material is represented by more taxa than the Neogene *Titanochelon vitodurana* (Biedermann, 1862) from Switzerland and *Titanochelon schleichi* Pappa, Vlachos & Moser, 2023 from Germany. Eocene material from Haunsberg near Salzburg, Austria, described by Vogeltanz et al. (1973) is nowadays attributed to the genus *Pelorochelon* (see Pérez-García et al., 2016). The same applies to the German ‘*Hadrianus*’ *eocaenica* (Hummel, 1935) from the famous late early to early middle Eocene of Geiseltal, recombined as *Pelorochelon eocaenica* (Pérez-García et al., 2016; Vlachos & Rabi, 2018). According to Sach (2025), the

Upper Freshwater Molasse reveals dozens of shell fragments attributed to the genus *Titanochelon*, all dated to the Middle Miocene, Mammal Neogene (MN) 5/6 units, with the one exception of the Early Miocene (MN 3) record from the locality of Stubersheim 3, attributed to *Geochelone* sensu lato (Böhme, 2003). Several large postcranial bones and shell fragments from the Middle Miocene fossil site Szurdokpüspöki from Hungary—initially described as *Testudo strandi* Szalai, 1936—also show affinities to the genus *Titanochelon*. Middle and Late Miocene material from Austria also represents large tortoises (see more in Gemel & Rauscher, 2000). Recently, a Middle Miocene shell from Czechia attributed to the genus *Titanochelon* was described by Březina et al. (2019) and dozens of undescribed or unreviewed specimens of large testudinids from the Miocene of Central Europe (in the meaning of the former Austro-Hungarian Empire) await their description in the light of new data.

The present paper aims to describe the fossil testudinid from the Early Miocene fossil site Ahníkov I, located in NW Bohemia, Czechia. Formerly, the locality is known as Merkur or Merkur-North (for explanation of the name change follow Ekrt et al., 2016). The material described here exhibits several characters allowing its taxonomic attribution to the extant genus *Manouria*. We present the description of the preserved material, together with new apomorphic features for the genus *Manouria* itself.

Geological setting

The Ahníkov I locality is a defunct fossil site close to the past municipality of Ahníkov between the cities Kadaň and Chomutov located in NW Bohemia (Fig. 1). The fossil site has been located in the NW protrusion of the Most Basin. The basement of the fossil site is developed by Proterozoic metamorphic rocks, subsequently covered by Carboniferous and Cretaceous sediments (Mach et al., 2014). The lowest part of the Most Basin is created by

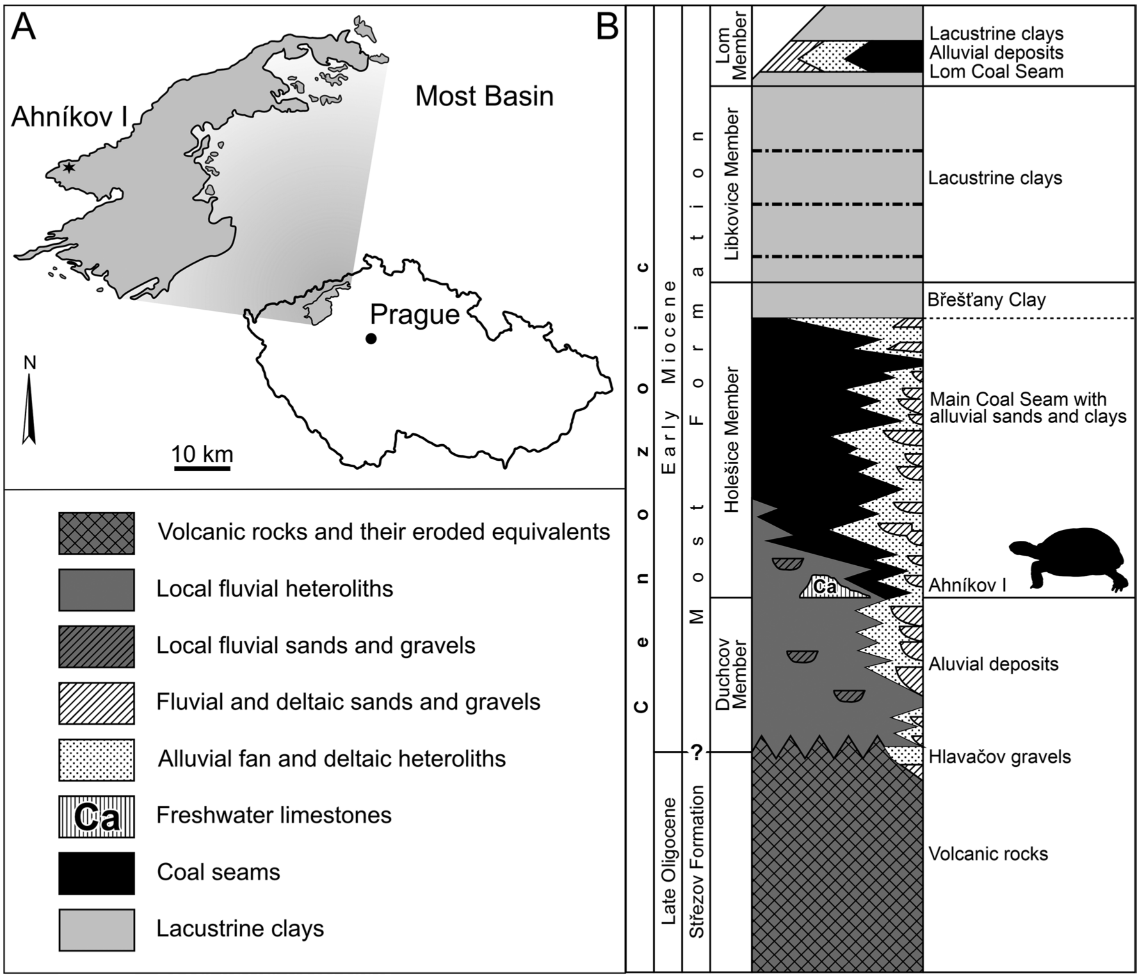

Fig. 1 Geographical position of the locality of Ahníkov I (formerly known as Merkur or Merkur-North). **A** Location map of Czechia within the Most Basin. **B** Stratigraphic column of the Most Basin. The tortoise drawing marks the level of the Ahníkov I fossil site. Modified from Mach et al. (2017)

volcanic rocks of the Střezov Formation developed during the late Oligocene by an intensive volcanic activity of the Ohře/Eger Graben (Rajchl et al., 2009). In the Early Miocene, the volcanic activity calmed, the whole area declined, and was later filled by fluvial sediments of the Central River (Mach et al., 2017; Pešek & Spudil, 1986). These fluvial sediments belong to the Duchcov Member, Most Formation. The Central River created alluvial fans which developed a swampy area (Holešice Member, Most Formation). According to Mach et al. (2017), several limestone deposits were developed as well. Lately, the swamps with the peat accumulation transformed into the Main Coal Seam of the Most Formation. The water level during the Early Miocene increased and the area changed from swamps to the lake and developed the lacustrine clays specific to the Břešťany Clay horizon and subsequently the Libkovice Member (see more in Chroust et al., 2023; Ekrt et al., 2022). Subsequently, a small regression event happened and recreated again a swampy area, which later transformed into the Lom Coal Seam of the Lom Member. Above the Lom Member, the Osek Member is composed of monotonous lacustrine clays and further sedimentation is eroded (Grygar et al., 2014; Mach et al., 2017; Ziegler & Dèzes, 2007).

The Ahníkov I fossil site captures a horizon of the Holešice Member just before the development of the Main Coal Seam. The site is very rich in vertebrate fossils and besides the azonal assemblage including many aquatic and semi-aquatic organisms, dozens of zonal semi-arid habitat-preferring vertebrates are present as well. Fishes, frogs and salamanders are listed in Fejfar and Schleich (1994) and Kvaček et al. (2004). According to Ivanov (2002), snakes are attributed to constrictors, colubrines, natricids, elapids, and viperids. Lizards are identified as gekkotans, cordylids, lacertids, amphisbaenians, chamaeleonids, anguids, and shinisaurids (Čerňanský, 2012; Čerňanský & Bauer, 2010; Čerňanský & Joniak, 2009; Čerňanský & Venczel, 2011; Čerňanský et al., 2015; Klembara, 2008, 2012, 2015; Klembara & Rummel, 2018). Also, the locality witnesses one of the few known occurrences of a Neogene choristodere, represented by the species *Lazarussuchus dvoraki* Evans & Klembara, 2005. Apart from squamates, crocodylians are identified as members of the genus *Diplocynodon* Pomel, 1847 (Chroust et al., 2021). Thanks to the finds of micromammalian assemblages, the locality is dated to the Burdigalian, MN 3a Mammal Neogene unit (Fejfar, 1990; Fejfar et al., 2003; Fejfar & Kvaček, 1993; Ostende & Fejfar, 2006, 2015). For a list of fossil mammals, see table 1, p. 455 in Ostende & Fejfar (2015).

Turtle fragments from the Ahníkov I fossil site have been collected in hundreds (Dvořák et al., 2010). Some of them were arranged together to make almost complete shells. The turtle material was briefly listed in Fejfar and Schleich (1994) and partially published with figures in the popular science book compiled by Dvořák et al. (2010). Based on our initial overview, turtles are represented by chelydrids, geoemydids, testudinids, and trionychids, which we aim to describe in the upcoming contributions.

Materials and methods

Shell anatomical nomenclature follows Zangerl (1969). We use the phylogenetic nomenclature of PhyloCode (Cantino, and Queiroz, 2020), Art. 3.1 (Cantino & Queiroz, 2020) with the nomenclature for turtle clades defined by Joyce et al. (2021).

Photographs were captured with a Canon EOS M6 Mark II mirrorless digital camera and the specimens were digitised using a Shining 3D EinScan Pro 2X 3D surface scanner fixed on a tripod with Ein-Turntable (alignment based on features), and EXScan Pro 3.2.0.2–3.7.0.3 software. Larger specimens were digitized without the turntable, using individual expositions and manipulating the objects manually. Photogrammetry was conducted using Agisoft Metashape Professional 2.0.1, with photos aligned on High and meshes produced from depth maps on High or Ultra High. The models were automatically scaled using printed scale markers. Figures and illustrations were made using Corel PHOTO-PAINT and CorelDRAW software. Figures of 3D models are presented in orthographic view with the Radiance Scaling Lit Sphere shader (Vergne et al., 2010) enabled to enhance the epidermal scute sulci. The 3D models, the photogrammetric photograph series, and the virtual reconstruction of the shell of *Manouria morla* sp. nov. presented herein are uploaded to the MorphoSource project https://www.morphosource.org/projects/000722147. The list of studied elements including links is compiled in Table 1.

For comparative purposes, shells of *Manouria emys* (MNHN Rep 67, MNHN Rep 72 – *Manouria emys phayreyi*, MNHN Rep 75 – *Manouria emys emys*; NHMUK 1900.2.7.6 – *Manouria emys emys*) and *Manouria impressa* (NMP 6V 72733; MNHN Rep 63) were examined personally in the respective collections. Digitized shells of *Manouria emys emys* UMMZ Herps 227759 (juvenile; ark:/87602/m4/452477, ark:/87602/m4/452488) and *Manouria impressa* SMF 69446 (carapace, ark:/87602/m4/691236; plastron ark:/87602/m4/691240); FMNH 263045 (ark:/87602/m4/M116476; Dziomber et al., 2020) were examined through MorphoSource. For anatomical comparison, specimens of *Clemmydopsis* sp. NMP uncat.; *Cyclemys dentata* CAS Herp 248369 (ark:/87602/m4/451656); *Gopherus morafkai* MVZ Herp 43040 (ark:/87602/m4/451840); *Melanochelys trijuga* YPM Vz 014519 (ark:/87602/m4/

Table 1 List of shell elements of NMP Pv 12299 – *Manouria morla* sp. nov. (Ahníkov I, Early Miocene)

Anatomical description	Figure	MorphoSource link
Nuchal	Figure 2	https://doi.org/10.17602/M2/M722153
Peripheral 1 (left)	Figure 2	https://doi.org/10.17602/M2/M722173
Peripheral 2 + 3 (left)	Figure 3	https://doi.org/10.17602/M2/M722178
Peripheral 2 + 3 (right)	Figure 3	https://doi.org/10.17602/M2/M722183
Peripheral 5 (right)	Figure 3	https://doi.org/10.17602/M2/M722256
Peripheral 6 (right)	Figure 3	https://doi.org/10.17602/M2/M722262
Peripheral 7 + 8 (left)	Figure 4	https://doi.org/10.17602/M2/M722188
Peripheral 7 (right)	Figure 4	https://doi.org/10.17602/M2/M722198
Peripheral 9 (left)	Figure 4	https://doi.org/10.17602/M2/M722203
Peripheral 9 (right)	Figure 5	https://doi.org/10.17602/M2/M722208
Peripheral 10 (left)	Figure 5	https://doi.org/10.17602/M2/M722213
Posterior part of the carapace	Figure 5	https://doi.org/10.17602/M2/M722219
Costal 4 (left)	Figure 6	https://doi.org/10.17602/M2/M722229
Costal 5 (left)	Figure 6	https://doi.org/10.17602/M2/M722234
Costal indet	Figure 6	https://doi.org/10.17602/M2/M722239
Costal indet	Figure 6	https://doi.org/10.17602/M2/M722244
Anterior plastral lobe	Figure 7	https://doi.org/10.17602/M2/M722267
Hyoplastron (left)	Figure 7	https://doi.org/10.17602/M2/M722272
Posterior plastral lobe (left)	Figure 7	https://doi.org/10.17602/M2/M722288
Posterior plastral lobe (middle/right)	Figure 7	https://doi.org/10.17602/M2/M722280

452539); *Plesiobaena antiqua* SMNS 81603 and *Testudo graeca ibera* SMF 67588 (ark:/87602/m4/691222) were examined. The publication has been registered in the Zoobank under the code LSIDurn:lsid:zoobank.org:pub:BA16705B-89DC-4BFB-96D5-B424ED5AB9BC.

Institutional abbreviations

CAS—California Academy of Sciences, Herpetology Collection, San Francisco, USA; **FMNH**—Field Museum of Natural History (Zoology), Amphibian and Reptile Collection, Chicago, USA; **MNHN**—Muséum national d'Histoire naturelle, Paris, France; **MVZ**—Museum of Vertebrate Zoology, Herp Collection (Arctos), University of California, Berkeley, USA; **NHMUK**—Natural History Museum, London, United Kingdom; **NMP**—National Museum, Prague, Czechia; **SMF**—Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany; **SMNS**—State Museum of Natural History Stuttgart, Germany; **UMMZ**—University of Michigan, Museum of Zoology, Division of Reptiles & Amphibians, Ann Arbor, USA; **YPM**–Yale Peabody Museum, Vertebrate Zoology Division—Herpetology, New Haven, USA.

Phylogenetic analysis

To obtain the plausible phylogenetic relationships of the specimen NMP Pv 12299 with other turtles, a set of cladistic analyses was carried out using a morphological data set created by Vlachos and Rabi (2018), later modified by Pérez-García et al. (2021) and Carbot-Chanona et al. (2023). All references made in the text to the character numbers following the character numeration scheme of TNT, that is, the character list starting with 0. Character 124, angle formed by the gularo-humeral sulci, and character 130, the length of pectorals, were updated based on Pérez-García et al. (2021) and available literature. Compared to the modified matrix published by Carbot-Chanona et al. (2023), the scorings of *Pelorochelon eocaenica* and *Pelorochelon soriana* were updated based on the available literature (Hummel, 1935; Pérez-García et al., 2016). *Pelorochelon eocaenica*: 82(1) = nuchal notch present; 87(1&2) = neural 3 hexagonal, short-sided posteriorly or rectangular; 119(1) = gular protrusion well-developed. *Pelorochelon soriana*: 85(0&1) = neural 1 hexagonal, short-sided posteriorly or rectangular; 119(1) = gular protrusion well-developed, 122(0&1) = gulars and entoplastron not in contact or in contact with the anterior margin. *Hesperotestudo gilbertii* was excluded due to the lack of shell characters. Scorings of *Manouria emys* and *Manouria impressa* were updated based on personal observation. Scoring of *Manouria oyamai* is based on the available descriptions, figures, and supplemental materials (Takahashi et al., 2003, 2018). A review of selected characters was introduced in the analysis (see more in the discussion).

In total, the matrix consisted of 87 taxa and 173 characters. For the analysis, TNT 1.6 software was used

(Goloboff & Morales, 2023). We manually increased the memory to fit 1,000,000 trees (Memory > General RAM set to 999 MB; command "hold 1000000;"). The Parsimony model (ordering of characters) follows Vlachos and Rabi (2018) and a new character 129, which represents the mutual contact of pectorals in three states: 0 = present; 1 = present, pectorals only touch; 2 = absent, pectorals do not touch at the midline. Pleurodira was used as the Outgroup. We set several runs of Traditional Search (1000 replications, 100 trees to save per replication) and New Technology Search (Sect. Search, Ratchet, Drift, and Tree fusing; Init. addseqs = 500, Find min. length = 30) with either disabled or enabled Implied Weighting (K = 6, 10 or 15). Bootstrap and Jackknife GC frequencies (1000 replicates of traditional search, 100 replications each and 10 trees to save per replication, TBR) and Bremer supports were calculated using the topology from the strict consensus with Implied Weighting disabled. For more information, see the phylogenetic section and Supplemental files 1 and 2.

Systematic palaeontology

Testudinata Klein, 1760
  Cryptodira Cope, 1868
  Testudinoidea Fitzinger, 1826
  Pan-Testudinidae Joyce et al., 2004
  Testudinidae Gray, 1825
  Genus *Manouria* Gray, 1854
  Manouria morla sp. nov. (Figs. 2–7).

Holotype. NMP Pv 12299 (Figs. 2–7), partial, disarticulated shell consisting of anterior (Figs. 2–4) and posterior (Figs. 4–6) parts of the carapace and plastron (Fig. 7) and numerous indetermined shell fragments (unfigured). The estimated length of the shell is approximately 50 cm. The material is fragile, crumbled into several small fragments and glued together. Several elements were possible to put together and therefore are figured in an articulated state. Hypothetical reconstruction of the shell is included (Fig. 8).

Etymology. The species is named after Morla, a fantasy character from the book The Neverending Story (orig. Die unendliche Geschichte) written by Michael Ende (1929–1995), firstly published in 1979, later adapted as a movie in 1984. Morla, the Ancient One, is a giant tortoise who lives in the Swamps of Sadness. The new species described herein is the oldest known species of the genus from the Early Miocene of Czechia; therefore, the Ancient One. Its remains come from the swamp deposits of Ahníkov, a parallel to the Swamps of Sadness.

Type locality: Ahníkov I (formerly known as Merkur or Merkur-North), Ústí nad Labem Region, Czechia; MN 3, Burdigalian, Early Miocene (Fejfar, 1990; Fejfar et al., 2003; Fejfar & Kvaček, 1993; Ostende & Fejfar, 2006, 2015).

Diagnosis: The genus *Manouria* can be diagnosed by the following autapomorphies: prominent visceral rims associated with the body wall attachment, developed close to the sutures between the peripherals and costals (also on the nuchal and the pygal); thin carapacial elements (costals/neurals); axillary buttresses long and thin and just barely in contact with costal bones; the visceral surface of costal 5 shows the attachment for the inguinal buttress; the sinusoidal shape of the posterior carapacial edge; the presence of the pygal notch; the presence of 12 marginal pairs; coincidence between the costo-peripheral suture and the pleuro-marginal sulcus; significant serration of the posterior peripherals; posterior sulcus of the fifth vertebral coinciding with the suprapygal-pygal suture; overlap of the plastral scutes into the dorsal surface of the anterior and posterior plastral lobes; lateral portion of the humero-pectoral sulcus perpendicular to the axial plane and anteriorly deflected; pectorals medially short; contact between the inguinal and femoral scutes is present; the presence of the multiplication of inguinal scutes.

Manouria morla sp. nov. differs from *Manouria oyamai* in a thicker plastron and carapace, not flattened nuchal, no overlap of the first pleural at the nuchal, and a more posteriorly extended xiphiplastron with a deep anal sulcus.

Manouria morla sp. nov. differs from *Manouria emys phayrei* in its cervical being longer than wide and the post-gular region, which contains no overhanging epiplastral lip, the presence of paired concavities just anterior to the entoplastron, and anteroposteriorly longer pectoral scutes.

Manouria morla sp. nov. differs from *Manouria emys emys* in the length of the gulars, which are not in contact with the entoplastron, and the post-gular region, which contains no overhanging epiplastral lip and the presence of paired concavities just anteriorly to the entoplastron. Also, the pectorals seem to meet along the midline, whereas in *M. emys emys* they do not.

Manouria morla sp. nov. differs from *Manouria impressa* in larger size and domed carapace, shape of the cervical and nuchal, pleuro-marginal sulcus which follows the costo-peripheral suture, strong curvature of the posterior carapacial rim with more developed serration, absence of a gular spur, and short medial contact of scutes. Conversely, *M. morla* sp. nov. shares with *M. impressa* the shape of the gulars, which are located far from the entoplastron, and the presence of paired concavities in the post-gular area.

For more details and comparison with other taxa, see more in Taxonomic attributions and Supplemental materials.

Description

Carapacial bones

The nuchal (Fig. 2A–G) is damaged, only just over its anterior half is preserved, and therefore the evaluation of the general shape is not possible. However, it seems to be wider than long. It contacted the peripheral 1 anterolaterally. The anterior edge is concave, forming a shallow nuchal notch (Fig. 2B–D). The nuchal is slightly bent transversely and relatively thick (Fig. 2E–G). In ventral view, at the body wall attachment site, a prominent pattern of raised proximal (posterior) edges of the scute areas, a wide groove, and a rounded transverse ridge (Fig. 2D).

All preserved anterior peripherals (1–3) share a flared free edge upwards, an anterior protrusion (spike) just prior to the intermarginal sulcus, which indicates the anterior serration (not preserved in peripheral 1), and a prominent rim developed in ventral view (Figs. 2–3).

The left peripheral 1 (Fig. 2H–N) is slightly wider than long, trapezoidal-shaped, with the free edge the widest. Its anteromedial part is broken, therefore, we cannot evaluate if the spikes were present. The lateral left suture with the subsequent peripheral is geometrically simple and straight, whereas the right (medial) suture with the nuchal is more complex, forming a ventral lappet, following the shape of the nuchal. The pleuro-marginal sulcus approaches the costo-peripheral suture only at its edges (more developed on its left posterior corner), whereas the medial peak of the sulcus is located more anteriorly, reminding the shape of the tent (Fig. 2J–K). In posterior view, the proximal part of peripheral 1 is slightly concave ventrally (Fig. 2I).

The peripheral 2 (Fig. 3A–N) is vaguely trapezoidal, almost equidimensional, preserved in both counterparts. Its anterior edge is sinusoidal, with the anteromedial corner going anteriorly. Laterally to the protrusion, the second intermarginal sulcus is developed (Fig. 3A, I). The pleuro-marginal sulcus follows the posterior suture of the peripheral. Ventrally, the proximal edges of the marginals are incised further away from the proximal border of the element, indicating a somewhat smaller ventral than dorsal exposition of those scutes. Proximally, there is a gutter-like socket for the costal (Fig. 3M).

The peripheral 3 (Fig. 3A–N) is irregularly subtrapezoidal and longer than wide, with preserved right and left counterparts. The posterior (proximal) part of the peripheral is directed dorsomedially, showcasing the domed shape of the carapace (Fig. 3E, F). In the anterior part, the plate is relatively flat and simple. A short gutter for the costal is present anteroproximally, which opens into the shell cavity at the level of the anterior edge of the suture for the hyoplastron (Fig. 3E). More posteriorly, the ventral part of the element thickens, develops a strap-like, posteromedially directed and ventrolaterally elongated sutural contact for the hyoplastron, and subdivides into two distinct lappets – a dorsal one, towards the costals, and ventral one, towards the plastron. As a result, the plate is Y-shaped in posterolateral view (Fig. 3D, 3G), with a wide, cup-like concavity of the shell cavity viscerally. The suture for the axillary buttress seems to be fully contained within the area of the peripheral and ends far from the costo-peripheral suture, with no evidence suggesting its extension onto the costals. Lateroventrally, just ventral to the marginal (free) edge, the external surface is flattened into a distinct, triangular facet.

Two plate-like, sulci-bearing fragments are preserved, which we interpret as ventral lappets of the right peripherals 5 and 6 (Fig. 3O–R) based on the shape of the sulci, which resemble the fifth to the seventh marginals, medially followed by the pectoro-abdominal sulcus (Fig. 3P, R). Nevertheless, such interpretation must be taken with caution due to the fragmentary nature of those elements. Both fragments seem to partially preserve sutures for the

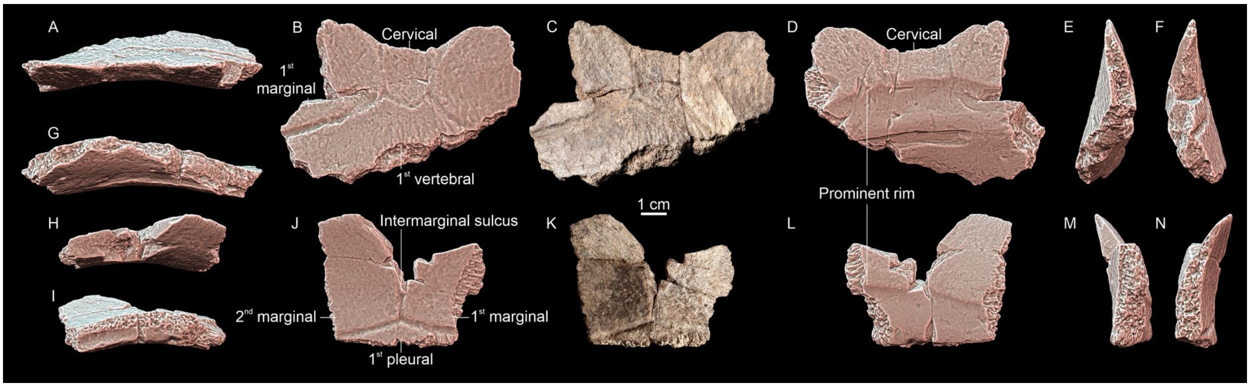

Fig. 2 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), isolated nuchal in **A** distal view, **B** dorsal view, **C** dorsal view (photograph), **D** ventral view, **E** right lateral view, **F** left lateral view, **G** proximal view. Isolated left peripheral 1 in **H** distal view, **I** proximal view, **J** dorsal view, **K** dorsal view (photograph), **L** ventral view, **M** right lateral view, **N** left lateral view

plastron and interperipheral sutures (both in peripheral 5 and the anterior one in peripheral 6). Their external surfaces are rough, while visceral surfaces are smooth. On the alleged peripheral 6, close to the sulcus, an ectoparasite pit or shell infection mark is preserved (Fig. 3R). No lateral or dorsal parts of those bones are preserved.

The peripheral 7 (Fig. 4A–J) is incomplete (the right counterpart is better preserved), longer than wide, and preserves the flattened lateral part, which is the edge of the bridge, followed by a flat surface dorsally and ventrally. Its anteromedial edge shows a thick, strap-like, almost vertical suture for the inguinal buttress of the hypoplastron. In dorsolateral view, a sinuous intermarginal sulcus is preserved (Fig. 4C, H), whereas anteriorly, the surface of it is slightly depressed. In ventral view, an obtusely angled sulcus between the inguinal scute and two marginals is imprinted (Fig. 4I, J). The visceral surface of the bone is concave, and forms posteriorly a triangular and narrowing pocket of the inner shell cavity (Fig. 4D–E).

All preserved, each of the posterior peripherals (8–11) shares a well-developed protrusion (spike), located just

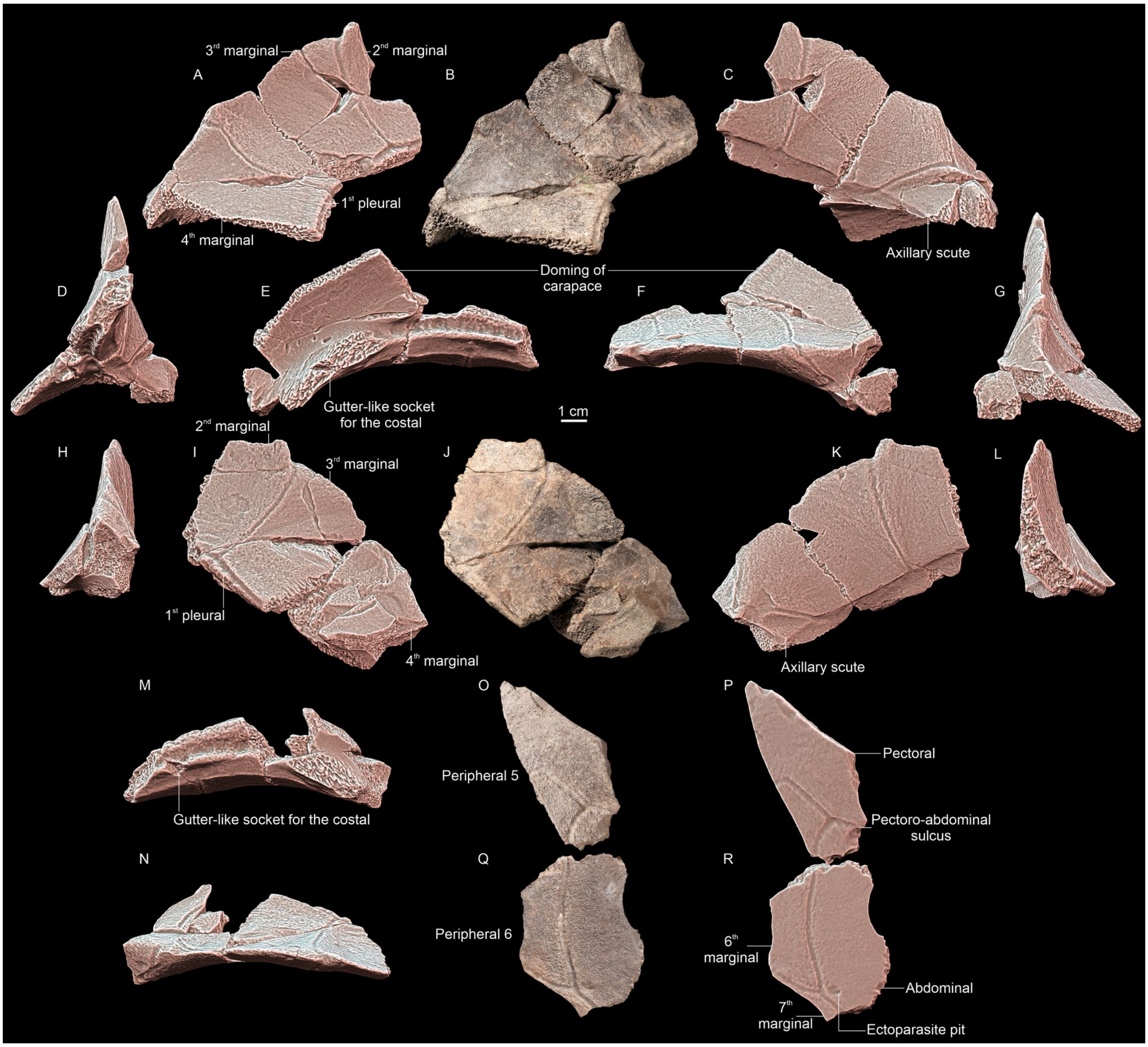

Fig. 3 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), articulated left peripheral 2 + 3 in **A** dorsal view, **B** dorsal view (photograph), **C** ventral view, **D** right lateral view, **E** proximal view, **F** distal view, **G** left lateral view. Articulated right peripheral 2 + 3 in **H** right lateral view, **I** dorsal view, **J** dorsal view (photograph), **K** ventral view, **L** left lateral view, **M** proximal view, **N** distal view. Peripheral 5 in **O** external view (photograph), **P** external view. Peripheral 6 in **Q** external view (photograph), **R** external view

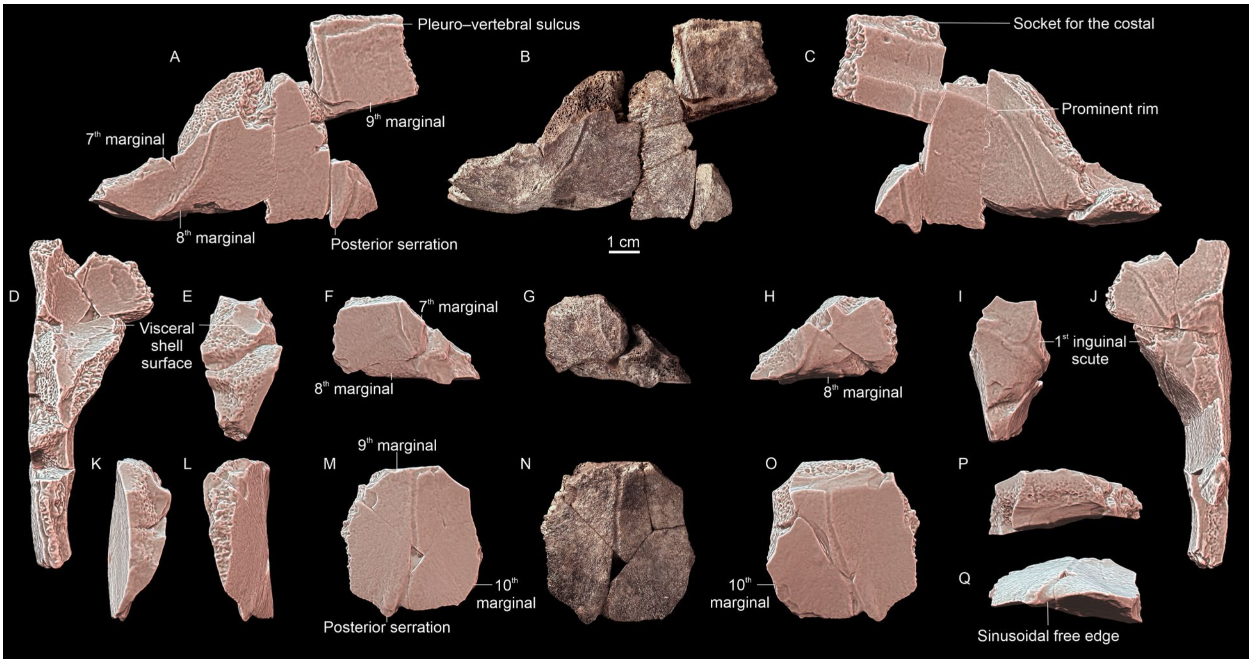

Fig. 4 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), articulated left peripheral 7 + 8 in **A** external view, **B** external view (photograph), **C** internal view, **D** dorsal view, **J** ventral view. Isolated right peripheral 7 in **E** dorsal view, **F** external view, **G** external view (photograph), **H** internal view, **I** ventral view. Isolated left peripheral 9 in **K** right lateral view, **L** left lateral view, **M** external view, **N** external view (photograph), **O** internal view, **P** proximal view, **Q** distal view

anteriorly to the intermarginal sulcus, indicative of; posterior serration; a pleuro-marginal sulcus following the costo-peripheral suture; a sinusoidal free edge; and (with the exception of the peripheral 11) a prominent proximal tubercle for the distal apex of the rib.

The left peripheral 8 (Fig. 4A–C) is damaged posteriorly, but roughly rectangular, with a scuffed anteromedial corner and a protrusion (spike). The intermarginal sulcus is imprinted just posteriorly to the spike. In marginal view, the edge is sinusoidal rather than straight and slightly deflected dorsally. In ventromedial view, a prominent rim at the proximal edge of the marginal scutes is developed as in the anterior part of the carapace (Fig. 4C). The proximal edge of the bone bears a gutter for the costal but, in contrast to the anterior peripherals, at the level of the intermarginal sulcus. The ventral edge of that gutter projects a short, knob-like process for the rib (Fig. 4C).

The peripheral 9 (Figs. 4K–O, 5A–G) is preserved completely on the right side of the carapace, whereas its left counterpart is preserved partially. This plate is rectangular, wider than long. The pleuro-marginal sulcus is developed slightly laterally to the costo-peripheral suture (Figs. 4M, 5C). In distal (marginal) view, a thin sinusoidal edge is developed, more convex in the posterior part, posteriorly to the spike (Figs. 4Q, 5G). The proximally directed knob for the rib is preserved as a very short, rugose, oval area (Fig. 5F).

The peripheral 10 (Fig. 5H–N) is rectangular, wider than long. The intermarginal sulcus is laterally convex, as in the preceding peripheral. Proximally, a gutter for the costal is formed (Fig. 5M). In distal (marginal) view (Fig. 5N), the edge is straighter than in the preceding peripherals, and much thicker along the spike and the intermarginal sulcus. In ventromedial view, at the level of the prominent rim, at least two pits are present (Fig. 5L), plausibly caused by ectoparasites or shell infection (Drumheller et al., 2023; Zonneveld & Bartels, 2022).

The peripheral 11 (Fig. 5O–R) is trapezoidal with a prolonged posterolateral edge, longer than wide. At the lateral edge, a protrusion (spike) is formed. Posteriorly to it, a straight intermarginal sulcus is imprinted. The distal (marginal) edge of the peripheral is flared outwards, i.e., posteriorly (Fig. 5Q). The margino-vertebral sulcus coincides with the suprapygalo-peripheral suture (Fig. 5S).

Only a small, left posteromedial fragment of the suprapygal 1 (Fig. 5R–U) is preserved, which is medially sutured to suprapygal 2. A short portion of the suture for the peripheral 10 is preserved. The preserved part of the element is longer than wide, with a smooth surface.

The suprapygal 2 (Fig. 5O–U) seems to have been a lenticular heptagon, wider than long in its posterior part, and subtly concave viscerally. This plate is sutured to the

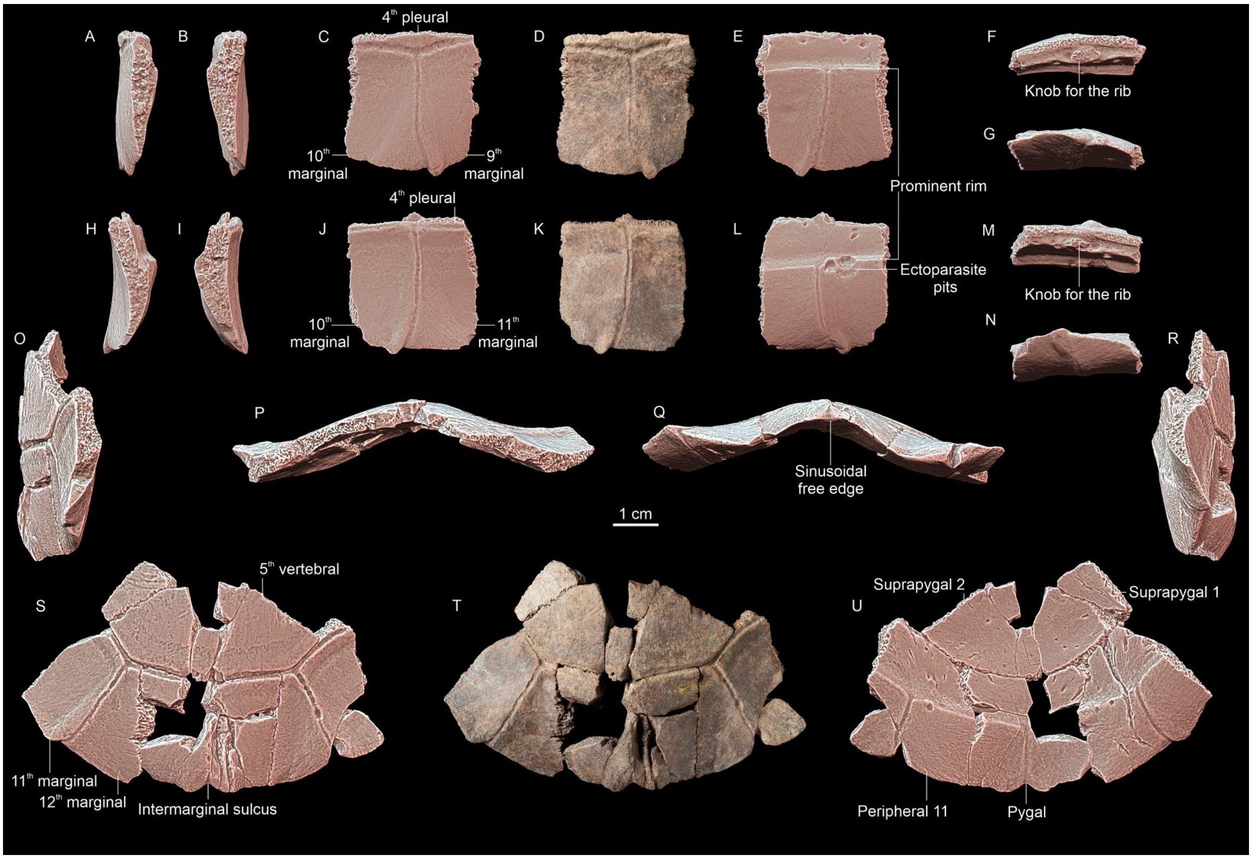

Fig. 5 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), isolated right peripheral 9 in **A** right lateral view, **B** left lateral view, **C** external view, **D** external view (photograph), **E** internal view, **F** proximal view, **G** distal view. Isolated left peripheral 10 in **H** right lateral view, **I** left lateral view, **J** external view, **K** external view (photograph), **L** internal view, **M** proximal view, **N** distal view. Articulated suprapygals 1 + 2, pygal and peripherals 11 in **O** right lateral view, **P** proximal view, **Q** distal view, **R** left lateral view, **S** external view, **T** external view (photograph), **U** internal view

suprapygal 1 anterolaterally, to the peripheral 11 posterolaterally, and to the pygal posteriorly. The posterior vertebral sulcus follows the suture between the suprapygal, pygal, and posterior peripherals (Fig. 5S). Both the dorsal and ventral surfaces are smooth.

The pygal (Fig. 5O–U) is rectangular, wider than long. It is split in half on both the posterodorsal and anteroventral (distal half) surface by the last intermarginal sulcus (i.e., there is no single supracaudal scute), and the free edge of the pygal forms a distinct pygal notch. In ventral view, a prominent rim is developed roughly at the mid-length of the pygal, indicating a smaller ventral than dorsal exposition of the last marginal pair (Fig. 5U). According to our reconstruction, in vivo, the pygal was likely positioned nearly vertically, with a slight anterodorsal inclination, and its free, marginal edge was curled ventrally.

The identification of two costal fragments as the costals 4 and 5 is based on their mutual articulation and the fact that the interpleural sulcus in the presumed costal 4 is straight, parallel to the long axis of the bone, and located along its middle, and the pleuro-peripheral sulcus is nearly straight, with no wedging of the peripheral between the pleurals. They are identified as left based on the position of the distally projecting end of the rib relative to the midline.

The left costal 4 (Fig. 6A–D) has its distal end preserved. The second interpleural sulcus divides the costal along the middle of its anteroposterior width. Anteriorly to the sulcus protrudes a short, dorsoventrally flattened distal apex of the rib. The distal suture of the costal is subdivided into two obliquely oriented faces, presumably contacting two neighbouring peripherals. The flexure point, probably corresponding to the interperipheral suture, is posterior to the interpleural sulcus.

The left costal 5 (Fig. 6E–H) has its distal part preserved. The external surface is featureless, with no sulci. The visceral surface shows the attachment for the inguinal buttress.

Two additional proximal fragments of costals (Fig. 6I–P) have only the costo-neural suture and short proximal portions of the intercostal sutures preserved. In visceral view (Fig. 6L, P), the costal rib necks are thin and elongated, located close to the suture with the neural. The external surfaces bear intervertebral sulci.

Carapacial scutes

The cervical was longer than wide, subpentagonal-shaped in dorsal view (Fig. 2B–D). The lateral edges gently converge posteriorly, whereas the posterolateral ones converge more abruptly, resulting in a short posterior process invading the anteromesial part of the first vertebral area (Fig. 2B–C). Ventrally, it was over twice as wide as long and nearly rectangular, with the lateral edges barely converging anteriorly (Fig. 2D).

The first vertebral (Fig. 2B–D) extended over the nuchal anteriorly, the costal 1 laterally, and the neural 1 posteriorly. The mesial part of the anterior edge of the first vertebral was concave and formed a socket receiving the short posterior process of the cervical. The anterolateral sulcus is straight and obtusely inclined in the posterolateral direction. The first pleuro-vertebral sulcus is unknown, but certainly it did not develop on the nuchal.

The posterior sulcus of the fifth vertebral coincides with the suprapygalo-pygal suture and laterally extends onto peripheral 11 and costal 8 (Fig. 5S–T).

The first to third marginals (Figs. 2J–L, 3A–N) showed anterior serration and their posteromedial edges coincided with the costo-peripheral sutures. The proximal and distal ends of the intermarginal sulci always slightly turn towards the preceding marginal.

The seventh marginal (Fig. 4A–J) overlain the edge of the bridge and was ventrally in contact with the first inguinal scute, whereas the inguinal series continued onto the plastron. The eighth to eleventh marginals (Fig. 4A–Q, 5A–S) displayed posterior serration and anteromedially coincided with the costo-peripheral sutures. As in the case of anterior marginal scutes, the posterior intermarginal sulci are slightly bent. The twelfth marginals were divided by an intermarginal sulcus, due to which a single supracaudal scute is not developed (Fig. 5S–U).

The axillary scute followed ventrally along the anterior facet of the axillary buttress and met with the pectoral scute at the axillary notch (Fig. 3C–L).

Plastral bones

Both epiplastra are preserved (Figs. 7A–G). The right one is missing the anterior tip and the left one is incomplete posteriorly, but combined fully representing the

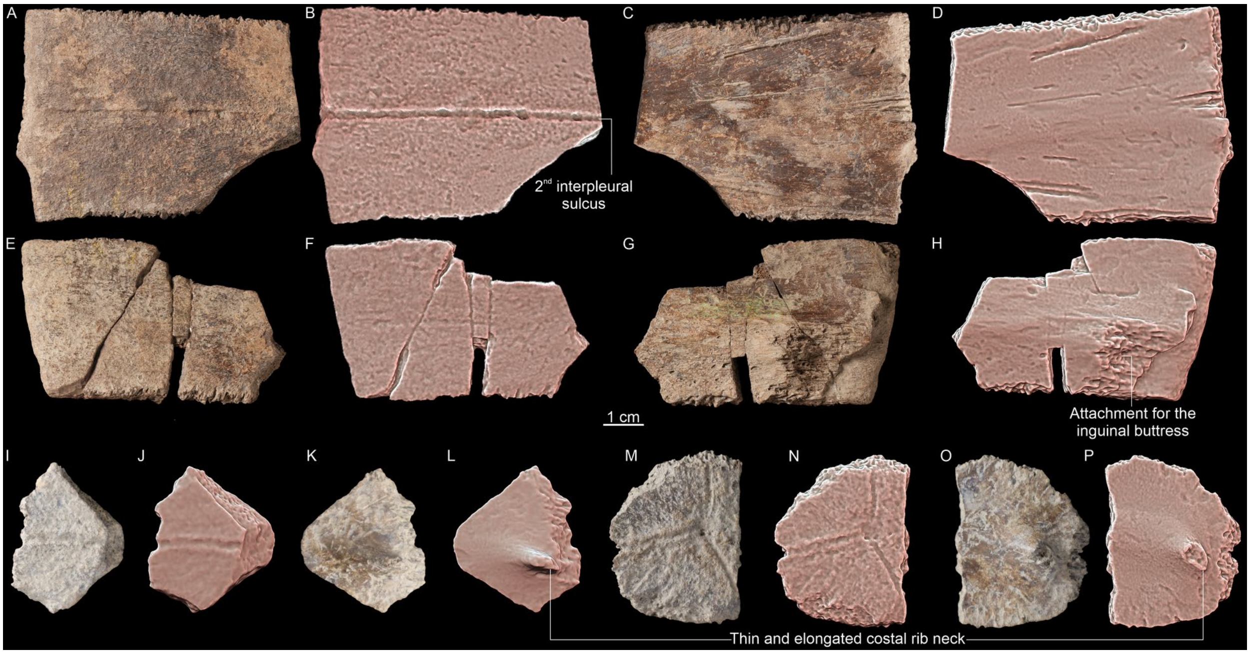

Fig. 6 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), fragment of costal 4 in **A** external view (photograph), **B** external view, **C** internal view (photograph), **D** internal view. Fragment of costal 5 in **E** external view (photograph), **F** external view, **G** internal view (photograph), **H** internal view. Indeterminate carapacial fragment in **I** external view (photograph), **J** external view, **K** internal view (photograph), **L** internal view. Indeterminate carapacial fragment in **M** external view (photograph), **N** external view, **O** internal view (photograph), **P** internal view

morphology of the most anterior plastral lobe. The epiplastron is almost as wide as long, flattened. Each epiplastron expands into a distinct anterior (gular) protrusion, which constitutes about a third of the bone's length. The anterior tip of this protrusion is uneven, divided into small projections, and medially deeply notched towards the intergular sulcus (Fig. 7A–D). The gular protrusion is subtly concave dorsally, but convex ventrally and gradually tapers towards the free edges. There is no spur-like projection ("ptychogasterid spike") in the lateral part of the gular protrusion, nor is it laterally thickened (Fig. 7A, C). Posteriorly to the gular protrusion, the dorsal gular platform is concave, facing dorsally. A minor epiplastral lip is formed along the proximodorsal edge of the gular scute area. The epiplastral lip forms no overhang, nor gular pocket (Fig. 7E). In anterior view, the gular platform shows no distinct U-shaped medial depression. Posteriorly to the gular platform, the epiplastron gradually descends before diverting posteriorly towards the hyoplastron, so in the lateromedial aspect, the epiplastron is distinctly S-shaped. Instead, the body wall margin is correlated with a gradual, rounded concavity on the visceral surface behind the bases of the gular sulci. This concavity is particularly clear medially, whereas laterally it is bordered by paired, posteromedially elongated depressions for the muscle or tendon attachment, which merge posteriorly and eventually continue onto the entoplastron (Fig. 7A). In addition, several nutritive foramina are recognized in that region. A prominent rim of the body wall is clear viscerally (Fig. 7A). The epiplastron suturally contacts the hyoplastron posterolaterally and the entoplastron posteromedially.

The entoplastron (Figs. 7A–G) is incomplete, missing a part of the right corner and nearly the whole left side, but it seems to have been subhexagonal, with the anterior angle less acute than the posterior. It sutures with the epiplastron anterolaterally and the hyoplastron posterolaterally. In visceral view, an anteromedial concavity is developed, being a continuation of the pits located on the epiplastra, demarcated posterolaterally by a raised, roughened, posteromedially inclined field. Laterally to that area, a shallow concavity is present, whereas the posterior part of the entoplastron is slightly convex. In lateral view, the anterior portion of the entoplastron is bent upwards and the external (ventral) surface in that part is gently convex. In ventral view, no sulci are present except for the sagittal (interhumeral) sulcus obscured by a break.

The hyoplastron (Fig. 7A–G) is partially preserved, missing the posteriormost and lateralmost portions. The hyoplastron contacted the epiplastron anteriorly, the entoplastron anteromedially, the peripherals laterally, and (presumably) the hypoplastron posteriorly. The axillary notch and axillary buttress are developed. In visceral view, the lateral outline of the hyoplastron thickens towards the notch and further towards the axillary buttress. The axillary buttress meets the main plate of the plastron at an obtuse angle of about 155° and is externally separated from it by a shallow, ridge-like rugosity just posterior to the axillary notch.

The hypoplastron (Fig. 7H–K) preserves mostly posterolateral parts on both sides, whereas the anteromedial parts are broken into dozens of fragments. Therefore, the general shape is not possible to evaluate. However, it can be assumed that the hypoplastron formed sutures with the hyoplastron anteriorly and with the xiphiplastron posteriorly. The inguinal buttress forming the connection with peripheral 7 is partially preserved and located far anteriorly from the hypo-xiphiplastral suture. It forms a narrow but distinct, predominantly dorsally projecting, transverse structure with a feather-like sutural lateral edge for the peripheral. The lateral edge posterior to the inguinal buttress, along the body wall attachment, is distinctly thickened. The suture with the xiphiplastron is straight and inclined posterolaterally.

Both xiphiplastra (Fig. 7H–K) are preserved but both counterparts miss their anteromedial parts. The xiphiplastron is trapezoidal, slightly longer than wide, and flattened. It is relatively thick in the anterolateral part along the body wall attachment, continuing the thickening of the hypoplastron, but this thickening decreases posteriorly, medially, and posterolaterally, so the free edges of the xiphiplastron are sharpened. Posteriorly, the xiphiplastron extends into a well-developed, triangular anal protrusion separated from its contralateral counterpart by a distinct triangular anal notch. The protrusion is nearly flat (subtly convex) ventrally and its distal (posterior) tip is gently deflected dorsally. The xiphiplastron formed sutural connections with the hypoplastron anteriorly and its counterpart medially. There is a clear constriction at the level of the femoro-anal sulcus. Between the anal protrusions, where the interxiphiplastral suture is located, a small xiphiplastral tubercle is present (Fig. 7J).

Plastral scutes

The gular was an elongated scute, longer than wide, and developed into the gular (anterior) protrusion (Fig. 7A–G). It was in contact with the humeral posteriorly. In ventral view, the gular outline terminates clearly anteriorly to the entoplastron and does not reach it nor cover it (Fig. 7B, D). The gularo-humeral sulcus is gently sinusoidal and asymmetric. The angle formed by the gularo-humeral sulci in ventral view is very obtuse, more than 90°. In dorsal view, two isolated gular scute areas are well defined, with nearly parallel, gently anteriorly diverging

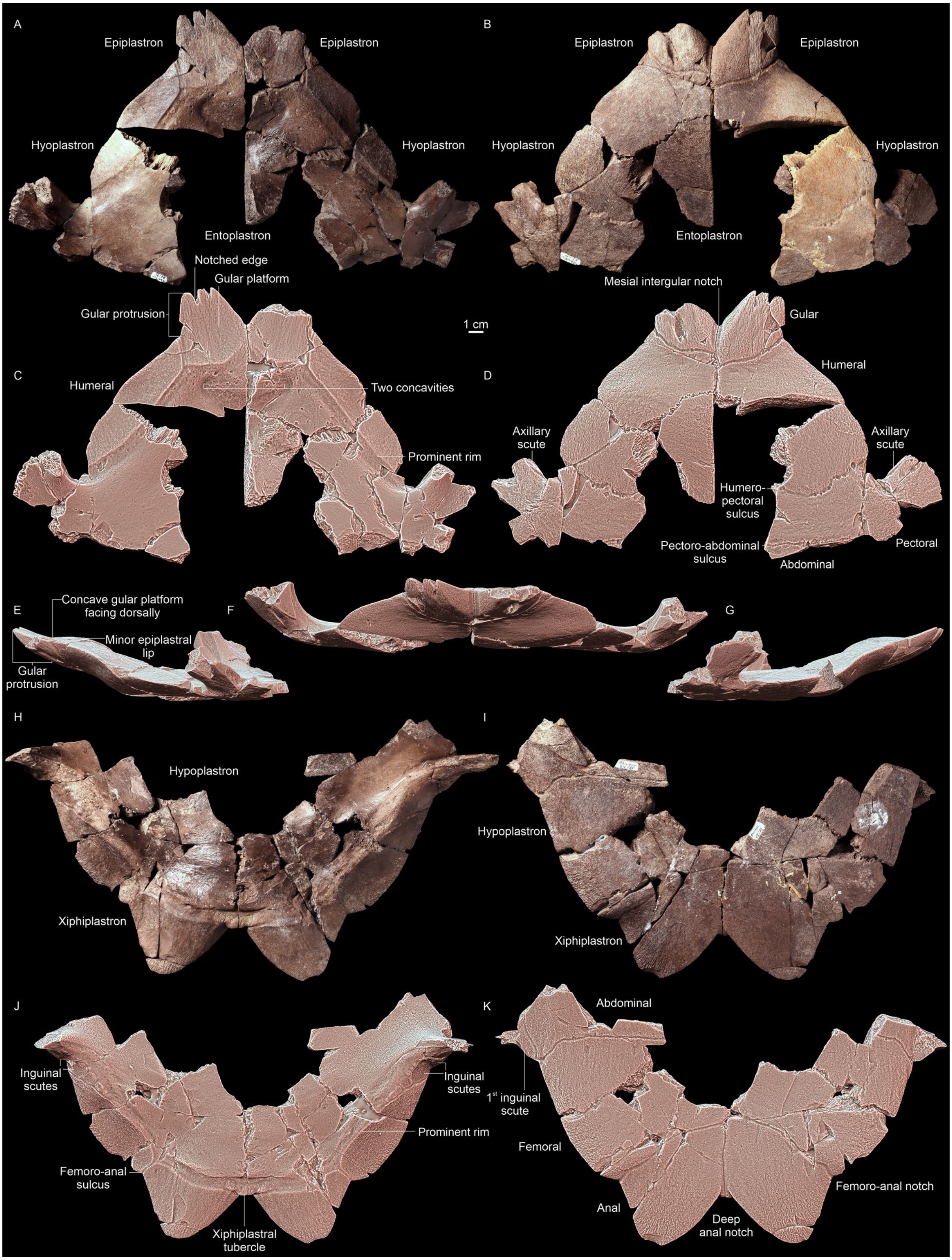

Fig. 7 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), anterior part of the plastron in **A** internal view (photograph), **B** external view (photograph), **C** internal view, **D** external view, **E** left lateral view, **F** anterior (epiplastral) view, **G** right lateral view. Posterior part of the plastron in **H** internal view (photograph), **I** external view (photograph), **J** internal view, **K** external view

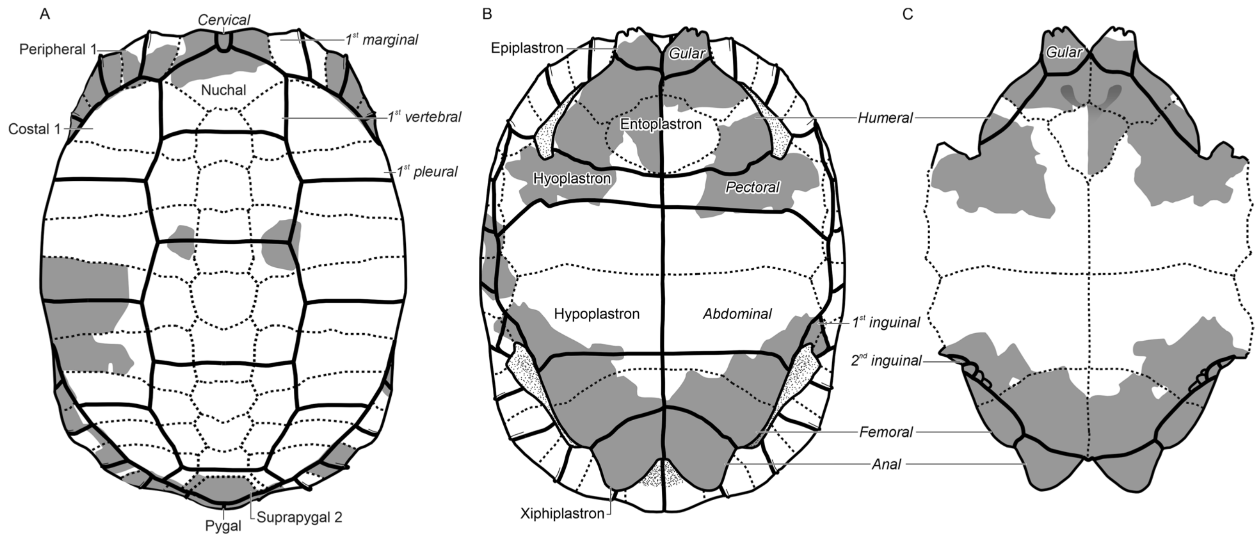

Fig. 8 Hypothetical reconstruction of the shell of *Manouria morla* sp. nov. (Ahníkov I, Early Miocene). **A** dorsal view of the carapace, **B** ventral view of the plastron, **C** dorsal view of the plastron. Preserved parts indicated in grey color

gularo-humeral sulci, transverse posterior edges, and anteromedially converging posteromedial edges. They extended approximately halfway along the epiplastral length.

The humeral was trapezoidal, longer than wide, and occupied the hyoplastron and the whole lateral half of the epiplastron (Fig. 7B, D). The scute was longer than the gular. It was located posteriorly to the gular and anteriorly to the pectoral. In ventral (external) view, the humero-pectoral sulcus seems to be mostly perpendicular to the axial plane. The medial part of the humero-pectoral sulcus is not preserved, but in contrast to most carapacial and plastral sulci, which have straight and clean edges, the humero-pectoral sulcus has a more punctuated, uneven appearance, as if it was composed of lined up pits. It did not cross the entoplastron and, based on extrapolation from the preserved parts of the hyoplastra, likely just posterior to the entoplastron (Fig. 7B, D). In dorsal view, the humeral extensively overlapped much of the lateral part of the epiplastron and hyoplastron, although that dorsal exposition did not reach the axillary notch.

The axillary scute is partially preserved in anterior view of the axillary buttress both on the peripheral 3 and the hyoplastra (Fig. 7A–G). The preserved portions amount to a lanceolate shape.

The pectoral was a short scute, wider than long, and covered part of the hyoplastron only (Fig. 7A–G). It was located posteriorly to the humeral, and anteriorly to the abdominal. The preserved portion of the pectoro-abdominal sulcus is linear, roughly perpendicular to the axial plane, but with a slight medial taper. It seems that both counterparts of the pectoral scute met along the midline (see Fig. 10).

The exact shape of the abdominal scute, due to the incompleteness of the plastron, is impossible to evaluate. However, as in the extant species of *Manouria*, it did not enter the posterior part of the bridge, but instead it was restricted laterally to the main plate of the plastron. Its lateral edge was sinuous and posterior nearly transverse with posterior deflection in the lateralmost part (Fig. 7B, D, I, K).

The first inguinal scute (Fig. 7H–K) was located ventrally to the seventh and eighth marginals and continued ventrally along the inguinal buttress to the abdominal scute, with no contact with the femoral on the right side of the body and possible minor contact on the left side (obscured by damage). As in the extant species of *Manouria*, the scute has two distinct facets, exposed ventrally and posteriorly and separated by a ridge-like edge (Fig. 10). Posteromedially to it, a series of inguinal scutes were present on the plastron. The second scute, followed by several post-inguinal scutes (at least three), ordered by size and several (about four) much smaller peri-inguinal scutes can be distinguished medially to the second inguinal scute (Fig. 9A). The femoral was wider than long and overlain the posterior part of the hypoplastron and the anterior part of the xiphiplastron (Fig. 7H–K). The abdomino-femoral sulcus is medially straight and transverse, predominantly positioned at the level of the inguinal notch, with a small posterior deflection of the lateral portion. The femoro-anal sulcus is directed posterolaterally (both sides set at an obtuse angle), slightly sinuous, resulting in gentle anterior convexity, and with a slightly more pronounced posterior deflection of the lateralmost part. Dorsally, the femoral had a substantial, teardrop-shaped exposition on the posterior part of the hyoplastron and anterior part of the xiphiplastron. The sulcus separating the dorsal exposition of the femoral and anal scutes is straight and directed posterolaterally.The anal was trapezoidal, fully located on the xiphiplastron and posterior to the femoral (Fig. 7H–K). The medial length of the anal scute was lesser than the medial length of the femoral. A deep, triangular anal notch is present.

The anal scutes were markedly overlapping onto the dorsal surface of the posterior part of the xiphiplastron, the anterior edge of that exposition is gently concave. However, medially, their dorsal exposition is still much smaller than the ventral exposition, particularly medially, where the contralateral anal scutes fail to meet due to the presence of a small mesial tubercle. This tubercle has a small, triangular exposition ventrally (Fig. 7J).

Taxonomic attribution of the remains

NMP Pv 12299 can be attributed to the *Testudinidae* based on the coincidence between the pleuro-marginal sulci and costo-peripheral sutures (Carbot-Chanona et al., 2023; Joyce et al., 2021; Vlachos & Rabi, 2018). The attribution to the genus *Pelorochelon* can be refuted based on the presence of anterior and posterior marginal serration with protrusions/spikes on the edges of peripherals associated with intermarginal sulci (Pérez-García et al., 2016). In addition, more differences were found: NMP Pv 12299 differs from *Pelorochelon* spp. in the presence of a pygal notch, the pleuro-marginal sulci variably contacting the costo-peripheral sutures, the posterior sulcus of the fifth vertebral coinciding with the suprapygal-pygal suture, small medial length of pectorals, and the presence of an increased number of inguinal scutes (Hummel, 1935; Pérez-García et al., 2016). For more details, see the Supplemental file 1.

The extant basal testudinids are divided into the genera *Gopherus* and *Manouria*. After the comparison, we can exclude the affinity of NMP Pv 12299 to the genus *Gopherus* by the absence of an anterior medial protrusion of the nuchal, the posterior sulcus of the fifth vertebral coinciding with the suprapygal-pygal suture, the presence of a well-developed twelfth marginal, the absence of an overhanging lip of the epiplastron, the absence of the contact between the gulars and the entoplastron, and a wider angle formed by the gularo-humeral sulcus (Vlachos, 2018). For more details, see the Supplemental file 1.

The shell diagnosis for the genus *Manouria* has not been sufficiently defined. For example, the diagnosis of the shell elements proposed by Lapparent de Broin et al. (2006) focused on the posterior carapace area, where the authors identified a trapezoid-shaped suprapygal 1, which is longer and narrower than the hexagonal suprapygal 2. The pygal is divided by the intermarginal sulcus, indicating the presence of the twelfth pair of marginals. Furthermore, the posterior sulcus of the fifth vertebral coincides with the suprapygalo-pygal suture. Also, a short gular, which does not reach the entoplastron, is mentioned as well (however, this character is apparently variable: the gular overlaps the entoplastron in *Manouria emys* (MNHN Rep 75) and may be at least closely approach it in *M. impressa* (see Takahashi et al., 2018; Fig. 4H). Apart from the cranial material, a thin carapace, the cervical scute wider than long (not in the fossil *M. oyamai* and the specimens of *M. emys* examined by us, so therefore this character is variable among the genus), the presence of the anal notch, the epiplastral protrusion, the femoral scute broadly contacting the inguinal on the plastral surface, the inguinal buttress contacting exclusively the costal 5, present in all members of the genus *Manouria*, also in *M. impressa* (SMF 69446; contra Takahashi et al., 2018)., the absence of a thickened overhanging epiplastral lip, a coincidence between the pleuro-marginal sulci and the costo-peripheral sutures, and the absence of a medial keel were proposed as well (Takahashi et al., 2003, 2018). The xiphiplastral tubercle is present in *Manouria impressa* (SMF 69446). The presence of a higher number of inguinal scutes is common in other tortoises, for example, in *Gopherus agassizii* (Cooper, 1861) or *Stigmochelys pardalis* (Bell, 1828), however, the pattern is different and incompatible with the genus *Manouria* (Crumly, 1984; Loveridge & Williams, 1957; Takahashi et al., 2003).

Therefore, *Manouria morla* sp. nov. is attributable to the genus *Manouria* based on thin carapacial elements (costals/neurals), inguinal butters in contact with the costal 5, intermarginal sulcus located on the pygal (presence of 12 marginal pairs), posterior sulcus of the fifth vertebral coinciding with the suprapygal-pygal suture, pronounced sinusoidal edge of the carapace in posterior view, epiplastral protrusion, absence of thickened overhanging epiplastral lip, short gular not reaching the entoplastron, presence of an anal notch, femoral scute broadly contacting the inguinal scute on the hypoplastral surface, and presence of an increased number of inguinal scutes (Crumly, 1984; Lapparent de Broin et al., 2006; Takahashi et al., 2003, 2018).

Manouria morla sp. nov. differs from *Manouria oyamai* in a thicker carapace (marginal parts) and a not flattened nuchal. It differs from *Manouria emys* and *Manouria impressa* in the anteriorly deflected (“anteriorly convex”) lateral part of the humero-pectoral sulcus and the last pair of marginal scutes reaching only across the marginal half of the pygal bone anteroventrally. It differs from *Manouria emys* in the absence of a pronounced-like

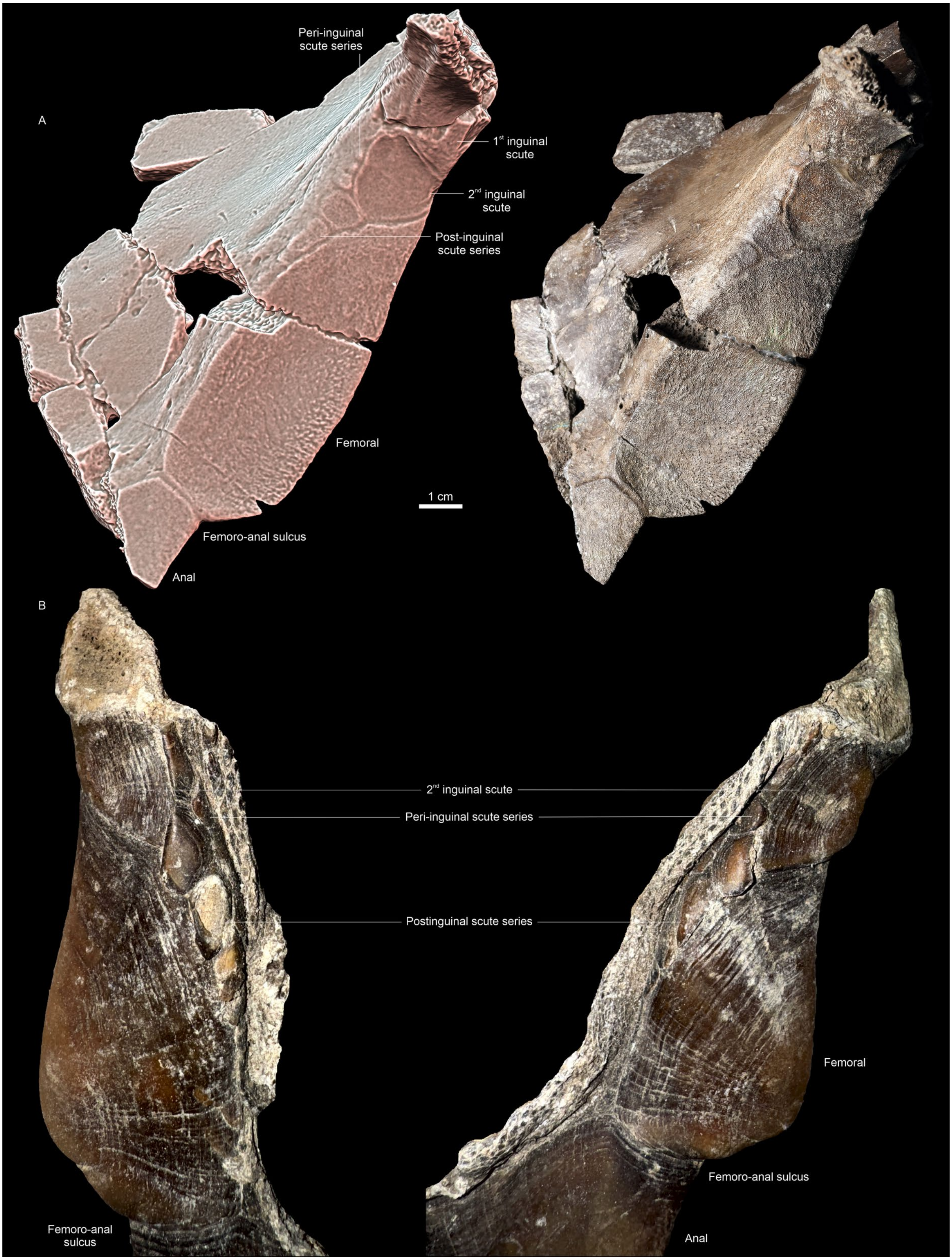

Fig. 9 *Manouria morla* sp. nov. (Ahníkov I, Early Miocene), inguinal scutes. **A** Detail of right hypoplastron and xiphiplastron with in posterodorsolateral view preserved first and second inguinal scutes, probably three to five post-inguinal scutes, and four small peri-inguinal scutes. **B** Detail of the right and left inguinal edges plastron of *Manouria emys* NHMUK 1900.2.7.6 in posterodorsal view with the determination of epidermal scutes. Not to scale

epiplastral lip, the presence of a medially thickened postgular region of the epiplastra and pectorals, which share longer mutual contact. It differs from *Manouria impressa* in the lack of pronounced dorsal depression in the middle part of the gular projection, cervical longer than wide, and the fifth vertebral not overlapping with the pygal. It differs from *Manouria impressa* and *Manouria oyamai* in more pronounced serration of the carapace.

Thanks to the above-mentioned combination of characters, we can identify the Ahníkov I material as a representative of the genus *Manouria*. For the genus *Manouria*, we notice more diagnostic morphological features, such as the sinusoidal shape of the posterior carapacial edge, and prominent visceral rims associated with the body wall attachment, developed close to the sutures between the peripherals and costals (also on the nuchal and the pygal) and in anterior and on the posterior plastral lobes, where the scutes from the external surface overlap the edges of the plastron and extend onto its dorsal surface.

In *Manouria morla* sp. nov., the midline and the central part of the plastron and the domed carapace are unknown. However, among the *Manouria* spp., these areas are very fragile and thin (e.g., mid-plastral fenestra, in some specimens of *Manouria emys* occupied by additional interplastral bones: MNHN Rep 72, MNHN Rep 75), and very variable among individuals. The fact that both areas are not preserved may be circumstantial evidence for the affinity with *Manouria*.

The genus *Manouria* contains two extant species, *Manouria impressa* (Günther, 1882) and *Manouria emys* (Schlegel & Müller, 1840) with two subspecies, *Manouria emys emys* (Schlegel & Müller, 1840) and *Manouria emys pharei* (Blyth, 1853). Besides the extant species, a Neolithic material of ?*Manouria emys* from Thailand (Claude et al., 2019) and one fossil species described as *Manouria oyamai* (Takahashi et al., 2003) from the Pleistocene of Japan are known. *Manouria impressa* is thought to be the most basal form (Lapparent de Broin 2003; Lapparent de Broin et al., 2006). Several Chinese fossil testudinids have been historically referred to the genus *Manouria*, but because this referral is not currently accepted, in some cases contradicted by our phylogenetic results, and due to the limited available information, they were not included in this study (e.g., Crumly, 1983; Li et al., 2008; Takahashi et al., 2003).

Manouria emys mainly differs from *Manouria impressa* in being about twice as large, having a more domed carapace instead of being relatively flat, less prominent posterior serration of the carapacial margin, and having different morphology of the epiplastral region (Lapparent de Broin et al., 2006; Moll, 1989). The pattern of the pectoral scutes also differs in *Manouria impressa* and *Manouria emys* subspecies. In *M. impressa* the pectorals meet in the midline of the plastron and their mutual contact is relatively long anteroposteriorly, in *M. emys phayrei* the pectorals only touch, and in *M. emys emys* the pectorals do not reach the midline of the plastron (Stanford et al., 2015).

The shape and the position of the femoro-anal sulcus can be divided into three different states (Fig. 10).

1) In *Manouria impressa*, the femoro-anal sulcus is typically straight along its whole length and positioned posteriorly to the inguinal notch. A less common variant (e.g., FMNH 263045, NMP6V 72733) involves formation of small, rounded, laterally placed anterior processes of the femoral invading the area of the abdominal, but the lateralmost end of the femoro-anal sulcus is typically anteroposteriorly level with its medial end.
2) In *Manouria emys emys*, the femoro-anal sulcus is typically positioned around the level of the inguinal notch. It may be straight but with lateral ends deflected posteriorly, inclined gently posterolaterally along its whole length, or the femoral may project small, rounded laterally placed anterior processes invading the area of the abdominal, but typically the lateral end of the sulcus is located posteriorly to its medial end.
3) In *Manouria morla* sp. nov. and *Manouria oyamai*, the femoro-anal sulcus is medially straight, positioned posteriorly to the level of the inguinal notch, with a posterior deflection of the lateral part, so the lateral end of the sulcus is located posteriorly to its medial part (note that the medialmost ends of the sulcus are not preserved in *M. morla* and *M. oyamai*, but to be level with the lateralmost ends, they would need to be deflected strongly posteriorly, which would constitute a unique morphology in itself; nonetheless, we consider it more likely that the medial part was straight, as in other *Manouria* spp.). Overall, the cervical was more similar to that in *Manouria emys* and probably *Manouria oyamai* than in *Manouria impressa* (MNHN Rep 63, MNHN Rep 75; Takahashi et al., 2003, 2018). The gular protrusion is more similar to that in *Manouria emys* (MNHN Rep 72, MNHN Rep 75) than in *Manouria impressa* (MNHN Rep 63; see Fig. 10). The morphology of the post-gular region is on the other side more resemblant of *Manouria impressa* (MNHN Rep 63), which also exhibits two distinct concavities anterior to the entoplastron, than of *Manouria emys* (MNHN Rep 72, MNHN Rep 75), which presents a more developed epiplastral lip and a flatter post-gular region (Fig. 10). It seems that both counterparts of the pec-

toral scute met along the midline, as in *Manouria impressa* (see Fig. 10). For closer comparison among *Manouria* spp., follow the Systematic palaeontology section.

Based on larger size, approximately 50 cm, domed carapace (as implied by the peripheral 3), shape and proportions of the cervical scute (as indicated by the circumcervical sulci), lack of spur-like ("ptychogasterid spike") epiplastral protrusions, pattern of the pleuro-marginal sulcus, which follows the costo-peripheral suture, and shape of the pectorals, a closer relation to the larger *M. emys phayrei* is supposed; however, this statement must be taken with caution. Two subspecies of *Manouria emys* have not been scored as separate taxonomical units in the used matrix and thus the polarity of their character evolution could not be rigorously tested. Conversely, the morphology of the gular region of the plastron appears intermediate, as it presents a combination of characters of both extant species.

For the comparison of *Manouria morla* sp. nov. with other members of the genus, see Table 2.

Discussion

Phylogenetic analysis and the position of *Manouria morla* sp. nov.

We ran eight phylogenetic analyses (Table 3) with all possible combinations of different search algorithms (Traditional Search and New Technology Search) and three different settings of Implied Weighting (off, K = 6, K = 10, and K = 15).

With disabled Implied Weighting, both the Traditional Search (200 most parsimonious trees, best score 889, CI 0.233, RI = 0.597) and the New Technology Search (47 most parsimonious trees, best score 889, CI 0.233, RI = 0.597) yielded the same poorly resolved topology, with most taxa crownward to *Stylemys capax* grouped in a large polytomy (Fig. 11). In this topology, only some clades were recovered, but that included a clade of *Gopherus brevisternus* (*Oligopherus laticuneus*

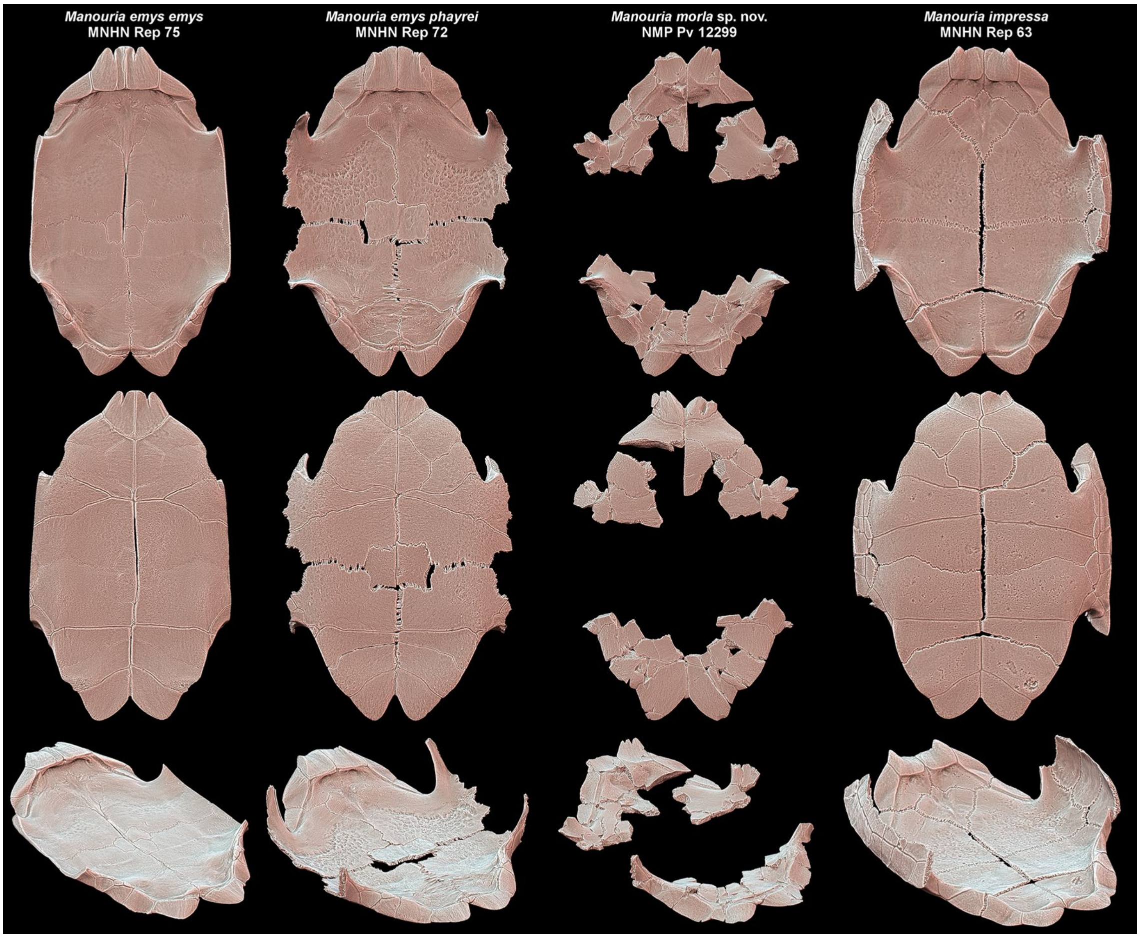

Fig. 10 Comparison of plastra of *Manouria* spp

(*Pelorochelon* spp. + *Manouria* spp.)). *Manouria morla* sp. nov. is a sister group to *Manouria emys*.

With Implied Weighting enabled (K = 6), the Traditional Search yielded 24 most parsimonious trees (best score 55.92914, CI 0.223, RI = 0.575), and the New Technology Search yielded 2 most parsimonious trees (best score 55.91607, CI 0.233, RI = 0.575). The topologies are significantly better resolved than with the Implied Weighting disabled but differ in details regarding the positions of taxa such as *Floridemys nana*, *Stylemys* spp., etc. However, in both cases *Pelorochelon* spp. and *Manouria* spp. are recovered as seperate grades along the stem of the trees, *Manouria morla* sp. nov. is found in a polytomy with *Manouria emys* and the clade of *Oligopherus laticuneus* and more derived taxa. This K value also results in paraphyletic or polyphyletic genera *Testudo, Indotestudo*, *Chelonoidis*, *Gopherus,* and (at least in New Technology Search) *Hesperotestudo.* For that reason, this topology is not considered preferred by us (data not shown).

With K = 10 the Traditional Search and the New Technology Search yielded significantly different topologies. The New Technology Search (a single most parsimonious tree, best score 41.48558, CI 0.228, RI = 0.587) shares many of the topological problems with K = 6 trees (e.g., non-monophyletic genera *Gopherus*, *Hesperotestudo*, *Indotestudo*, *Pelorochelon,* and *Testudo*) and the genus *Manouria* is still recovered as a grade, although *Manouria morla* sp. nov. and *Manouria emys* do form a clade. The Traditional Search topology (3 most parsimonious trees, best score 41.49576, CI 0.230, RI = 0.591) more consistently retains monophyletic genera: *Manouria* spp. is recovered as a clade (*Manouria oyamai* (*Manouria impressa* (*Manouria morla* sp. nov. + *Manouria emys*))) immediately stemward to the clade of monophyletic *Pelorochelon* spp. and more derived taxa), although individual species of the genera *Gopherus*, *Indotestudo*, and *Testudo* are still found distributed across various clades.

With K = 15 both the New Technology Search (best score 31.50763, CI 0.232, RI = 0.594) and the Traditional Search (best score 31.51069, CI 0.231, RI = 0.593) produced a single tree each with relatively similar topologies, differing in positions of several taxa, such as *Gigantochersina ammon*, aff. '*Stylemys*' *giselae* + *Testudo kaiseni*, *Gopherus mohavensis*, and arrangement of other *Gopherus* spp., and some derived *Testudinidae*. In both cases, however, a monophyletic clade of *Pelorochelon* spp. + (*Manouria oyamai* (*Manouria impressa* (*Manouria morla* sp. nov. + *Manouria emys*))) is recovered stemward to *Oligopherus laticuneus* and more derived taxa.In summary, all analyses recover *Manouria morla* sp. nov. and *Manouria emys* in either a close proximity (polytomy) or explicitly as sister taxa. Because of that and because *Manouria emys* is the type species of the genus, because its relationship with the other extant species, *Manouria impressa,* is widely accepted, and because there are no morphological characters suggesting otherwise, we are confident in our referral of the new species to the genus *Manouria*.

Monophyletic *Manouria* was recovered in 5/8 analyses (see Table 3 and Supplemental material 2) with a different number of synapomorphies. Traditional Search and New Technology Search with disabled Implied Weighting reveal four characters: presence of a significant posterior serration; wide vertebrals almost equal to the pleurals; lateral portion of the humero-pectoral sulcus perpendicular to the axial plane and anteriorly deflected; and contact between the inguinal and femoral scutes. Traditional Search with enabled Implied Weighting (K = 10) reveals also four characters, but including lack of contact between the gular and the entoplastron instead of the shape of the humero-pectoral sulcus. We note, however, that the overlap of the gular scutes onto the plastron can be variable among *Manouria* spp. (see *Manouria emys emys* MNHN Rep 75). Traditional Search and New Technology Search with enabled Implied Weighting (K = 15) reveal three characters supporting the monophyletic *Manouria*: presence of a significant posterior serration; wide vertebrals almost equal to the pleurals; and contact between inguinal and femoral scutes. The grouping of *Manouria oyamai* + (*Manouria emys* + *Manouria morla*) exclusive of *Manouria impressa* has one synapomorphy in the analyses with Implied Weighting disabled (cervical scute longer than wide) and in Traditional Search with K = 10 (first pleural not in contact with the nuchal). In all analyses in which the sister relationship of *Manouria morla* sp. nov. + *Manouria emys* is recovered, except of New Technology Search with K = 10, it is supported by the relatively flat dorsal epiplastral lip. The derived position of *Manouria morla* sp. nov. within the *Manouria* clade is interesting given that it is the oldest member of that clade. Also, *Manouria morla* sp. nov. is the only species within the genus lacking scored autapomorphic characters. Nevertheless, *Manouria morla* sp. nov. still exhibits a unique combination of characters within the genus, not all of the recognizable characters are scorable in the used matrix, and the material is incomplete (e.g., missing the cranium), opening the possibility of autapomorphic characters being discovered in the future.

Following Carbot-Chanona et al. (2023), *Manouria morla* sp. nov. can be referred to the *Pan-Testudinidae* based on its thin and elongated costal rib heads. Moreover, the gulars and the entoplastron are not in contact, the angle formed by gularo-humeral sulci exceeds 90°, the lateral portion of the humero-pectoral sulcus is

Table 2 Comparison of *Manouria* spp. using 13 characters. in dorsal (top), ventral (middle), and posterodorsolateral (bottom) view

	Character	***Manouria morla* sp. nov.**	***Manouria oyamai***	***Manouria emys phayrei***	***Manouria emys emys***	***Manouria impressa***
1	Cervical longer than wide	Yes	Yes	No	Both	No
2	Shallow nuchal notch	Yes	Yes	Yes	Yes	No
3	No anterior protrusion of cervical scute	Yes	Yes	Yes	Yes	No
4	Domed carapace	Yes	?	Yes	Yes	No
5	Pleuro-marginal sulcus along costo-peripheral suture	Yes	Yes	Yes	Yes	No
6	Pronounced sinusoidal edge of carapace in posterior view	Yes	?	Yes	Yes	No
7	Gulars far from entoplastron	Yes	Yes	Yes	No	Yes
8	Absence of gular spur	Yes	Yes	Partially	Yes	No
9	Absence of overhanging epiplastral lip	Yes	Yes	No	No	Yes
10	Presence of two concavities at post-gular region of epiplastra	Yes	Yes	No	No	Yes
11	Medial contact of pectorals	Longer	?	Shorter	No	Longer
12	Presence of xiphiplastral tubercle	Yes	?	Yes	No	Yes
13	Fifth vertebral overlapping pygal	No	?	No	No	Yes

Table 3 Comparison of results of different phylogenetic analyses

#	**Search**	**Implied weighting**	**Trees**	**Best score**	**Tree length**	**CI**	**RI**	***Manouria***	**Position of *M. morla* sp. nov.**
1	Traditional	Off	200	889	889	0.233	0.597	Clade	Sister to *M. emys*
2	New technology	Off	47	889	889	0.233	0.597	Clade	Sister to *M. emys*
3	Traditional	K=6	24	55.92914	927	0.233	0.575	Grade	In polytomy with *M. emys* and more derived taxa
4	New technology	K=6	2	55.91607	927	0.233	0.575	Grade	In polytomy with *M. emys* and more derived taxa
5	Traditional	K=10	3	41.49576	900	0.230	0.591	Clade	Sister to *M. emys*
6	New technology	K=10	1	41.48558	907	0.228	0.587	Grade	Sister to *M. emys*
7	Traditional	K=15	1	31.51069	896	0.231	0.593	Clade	Sister to *M. emys*
8	New technology	K=15	1	31.50763	894	0.232	0.594	Clade	Sister to *M. emys*

perpendicular to the axial plane with anteriorly deflected lateral parts, and there is a coincidence between the pleuro-marginal sulci and the costo-peripheral sutures. The attribution to the *Testudinidae* is confirmed by the first pleural, which is not in contact with the nuchal (reversed in *Manouria oyamai*), and the costal rib head near neural/costal suture (Carbot-Chanona et al., 2023; Vlachos & Rabi, 2018). A close phylogenetic position between the *Pelorochelon* and *Manouria* clades proposed by Carbot-Chanona et al. (2023) is confirmed by us. Investigation of other clades is beyond the scope of this paper, however, we note the very basal position of '*Testudo*' *sharanensis* as a sister taxon to *Hadrianus* spp. These taxa (and several more) were considered by Crumly (1983) to belong to '*Manouria*', which he considered at the time to lack apomorphic characters and suspected of being non-monophyletic. While their basal position in the testudinid phylogeny is confirmed by our analysis, we recognize a more exclusive, monophyletic *Manouria* clade and hypothesize that '*Testudo*' *sharanensis* may in fact belong to the genus *Hadrianus*. Additionally, the exclusion of *Titanochelon vitodurana* from the genus *Titanochelon*, and the *Geochelona* as a whole, and instead its far stemward, placement, as well as exclusion of several other fossil species from their presumed genera is striking. We believe such results are caused by a limited number of scorable characters in fossil taxa, lack of detailed and updated descriptions, or simply divergent and not comparable character of previous matrices featuring them. In the case of *Titanochelon vitodurana*, the previously used matrices of Vlachos and Rabi (2018) and Carbot-Chanona et al. (2023) are completely different, thus the placement of this taxon was thus far recovered based on incomplete and inaccurate data. Notably, extant representatives of most genera (with the exception of *Indotestudo* spp.) are generally grouped in the topology obtained here into monophyletic clades. As a result, these extinct cases of seeming polyphyletism deserve further investigation.

Fig. 11 Phylogenetic topologies obtained in four analyses using the complete dataset

The review of the current list of characters, terminology and new morphological characters

During the course of our work, we found a few discrepancies in the previous matrices, which deserve discussion. Moreover, we noted that the terminology referring to anterior structures of the plastra, mostly produced by the epiplastra and the gular scutes, lacks clear definitions, causing ambiguity and inconsistent usage by various researchers. In order to rectify that, we propose the following definitions (visualized in Fig. 12).

Gular protrusion: used for the gular scute-covered anterior protrusion of the epiplastra projecting beyond the margin of the anterior plastral lobe outlined by the outer (free) edges of the humeral scute areas, following Vlachos and Rabi's (2018) character 120. Note that there is a long-standing convention regarding the nomenclature of the anterior plastral structures in stem turtles, which involves the terms "process" and "projection" (e.g., Gaffney, 1990; Joyce, 2017; Szczygielski et al., 2018, 2024, 2025). We uphold this convention because it does not imply homology of the gular protrusion of the testudinids with the gular projections/processes of stem turtles. Nevertheless, the term "gular" does not necessitate homology of the scutes themselves, either (see Hutchison & Bramble, 1981 and Gaffney, 1990 for opinions regarding the usage of the terms "intergular", "gular", and "extragular")–it pertains to the throat area and thus may be used in a descriptive sense (analogically to the terms nuchal–applicable regardless of the presence or absence of the nuchal bone). Additionally, recently, Soares (2022) used the terms "gular protrusion" and "gular projection" referring to dorsally (viscerally) placed structures on the epiplastra of panchelonioids, which appear to be rudimentary homologues of the dorsal epiplastral processes of stem turtles (e.g., Gaffney, 1990, 1996; Jenkins et al., 1994; Joyce, 2007; Sterli et al., 2007; Sukhanov, 2006; Szczygielski & Sulej, 2019; Szczygielski et al., 2025). These are separate structures unrelated to the scute-induced processes discussed herein.

Gular spur: anterior extensions of the epiplastra, located within the lateral perimeter of the gular, medially to the gularo-humeral sulcus, and often thickened, are commonly known as a "ptychogasterid spike" (Hervet, 2004). Because this character has evolved multiple times among the *Testudinoidea* and is not synapomorphic for "ptychogasterids" (a group which is currently not universally accepted), it deserves new terminology. The simple use of the term "gular spike" may be misunderstood in the context of stem turtles, having variously developed spikes formed by the gulars and extragulars and typically involving whole scutes (Broin, 1984; Gaffney, 1990; Jenkins et al., 1994; Sterli et al., 2007; Li et al., 2008; Szczygielski & Sulej, 2016; Szczygielski et al., 2018, 2024, 2025). Therefore, we propose to use a new term, "gular spur", to avoid misleading conjecture with the genus *Ptychogaster* Pomel, 1847 and other convergent epiplastral structures.

The dorsal/anterodorsal epiplastral surface, delineated by the free (outer) edge and the circumgular sulci, has not been united in terminology. The terms used in the literature include the dorsal epiplastral pad (e.g., Luján et al., 2016, 2021) and the (dorsal) epiplastral lip (e.g., Lapparent de Broin et al., 2006; Luján et al., 2014; Vlachos & Rabi, 2018, character 122). The lip is a common term in anatomy but in the anterior plastral lobe it may variably be correlated with or developed separately from the gular scutes. The word "pad" has linguistic connotations with a convex, thickened structure, which is consistent with the morphology observed in most testudinids but less so with some other turtle taxa. Because the surface of the gular scute-bearing areas exhibits complexity beyond the formation of the lip, and because these features can be independent from one another. To properly describe the dorsal surface of the epiplastron, we propose the following terms:

Gular platform: dorsal or anterodorsal surface of the epiplastron exclusively covered by gular scutes and outlined by the gular sulci. The platform may be horizontal or anteroposteriorly slanted (e.g., facing anterodorsally). Regardless of inclination, it may be concave, roughly flat, or convex, creating the epiplastral pad. For determination of the gular platform geometry and inclination, we recommend excluding structures such as the gular spur, if present, because they can occur independently and, by definition, they are associated with a local thickening and a change to the surface geometry. In that context, we also disregard the mediolateral features of the cross section of the gulars, such as formation of mesial U-shaped concavities (e.g., in many geoemydids, see Fig. 12), because they are independent from the anteroposterior shape and inclination of the surface.

Epiplastral lip: a step-like increase in thickness of the anterior or anterolateral edge of the epiplastra, which may occur at the proximodorsal edge of the gular scutes or posteriorly to the gular scutes. It may be rounded off, have a well-defined, ridged posterodorsal edge, or form a posteriorly directed overhang (overhanging lip). We note for clarity that the presence of the overhang should be defined based on an in vivo orientation, with the plane of the main plate of the plastron parallel to the ground, and not in a vertical or subvertical position with the anterior edge pointing upwards.

Another issue is the scoring of characters regarding the shape of the humero-pectoral sulcus (characters 126 and 127; Vlachos & Rabi, 2018). Based on our investigation, the previous wording of these character definitions was imprecise, rendering their original meaning virtually irreproducible, and therefore causing different authors to understand and score the characters variably, causing inconsistencies. The original definitions of the two out of three states of characters 126 and 127, the concave or convex shapes of the sulcus, lack the direction for an unequivocal statement. Logically, the sulcus, as a linear imprint, cannot be really concave or convex in the sense conceived by the original authors, because its anterior convexity causes posterior concavity, and vice versa; the edge of a scute can be either convex or concave, but that requires a clear determination which of the scutes separated by the sulci should be considered. We consider the term "deflection", i.e., change of direction towards the given side, to be more unambiguous. Therefore, we recommend rephrasing the states, as follows:

126, Shape of the medial portion of the humero-pectoral sulcus: 0 = perpendicular to the axial plane, relatively straight throughout its width; 1 = perpendicular to the axial plane and posteriorly deflected; 2 = perpendicular to the axial plane and anteriorly deflected.

127, Shape of the lateral portion of the humero-pectoral sulcus: 0 = perpendicular to the axial plane, relatively straight throughout its width; 1 = perpendicular to the axial plane and posteriorly deflected; 2 = perpendicular to the axial plane and anteriorly deflected.

Moreover, we are not sure about Vlachos and Rabi's (2018) comment to character 127: scored as N/A in taxa having state 0 or 2 for character 126 (see below). In the case of *Manouria emys phayrei*, the humero-pectoral sulcus is medially wavy (126:2) and laterally anteriorly deflected (127:2). Both characters appear to be independent, non-contradictory, and seem to be scored as such for some taxa in the subsequent iterations of the matrix. In conclusion, we propose to exclude the dependence between characters 126 and 127, and describe the medial and lateral ends of the sulcus separately.

We propose to include a new character regarding the mutual contact of pectorals, which is very important for distinguishing *Manouria* subspecies, in three states: 0 = present; 1 = present, pectorals only touch; 2 = absent, pectorals do not touch at the midline. *Manouria impressa* and *Manouria morla* sp. nov. are scored as 0, *Manouria emys phayrei* is scored as 1 and *Manouria emys emys* is scored as 2. This character we considered to be ordered, with the absence of a mutual contact of pectorals being a derived character.

In the genus *Manouria*, the inguinal scute complex consists of two or sometimes three separate scutes. In most other tortoises, the inguinal is a single scute that can be either enlarged or reduced. Sometimes, there are small accessory scales, which are considered to be remnants of the larger multiple inguinal scutes (Crumly, 1984). However, to avoid misunderstandings, we here propose a nomenclature for these accessory scutes.

In NMP Pv 12299, two large scutes, the first (anterior) and the second (posterior) inguinal scutes, are followed by several post-inguinal scutes (at least three to five or

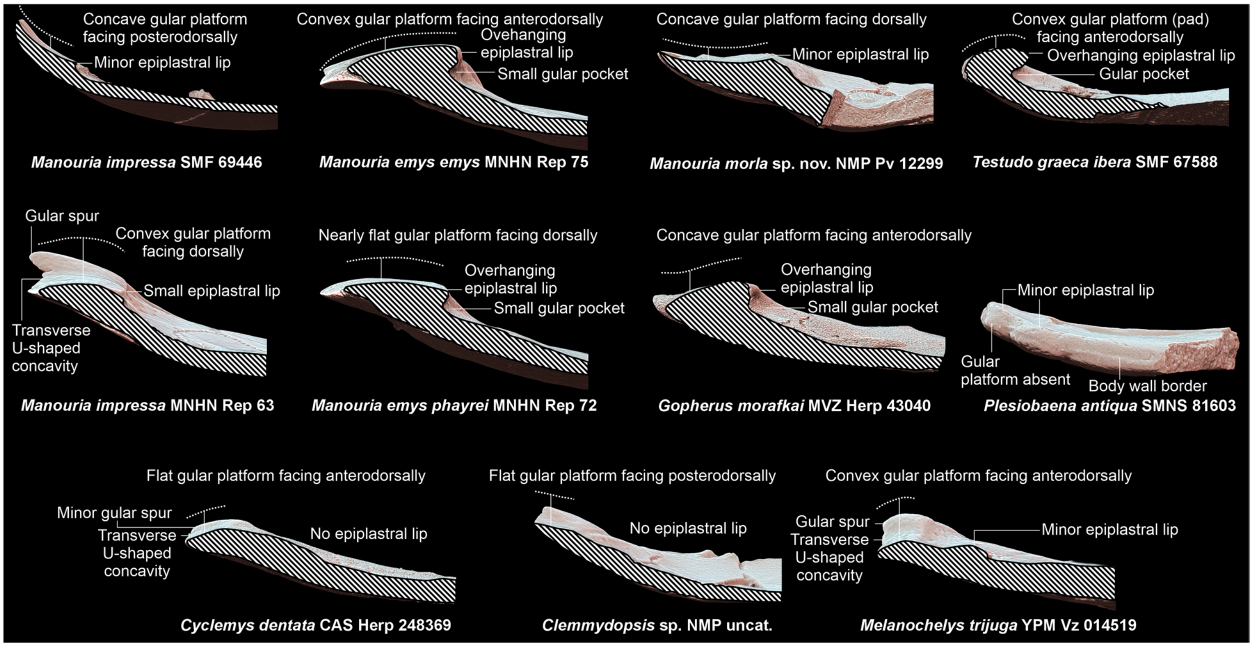

Fig. 12 Comparison of the gular region in various taxa showing varied morphologies of newly defined structures. Hatching indicates areas cut along the sagittal plane. Not to scale

more) ordered by size, and several (about four) much smaller peri-inguinal scutes, which are located along the medial edge of the second inguinal scute (Fig. 12). In *Malacochersus tornieri* (Siebenrock, 1903), *Homopus areolatus* (Thunberg, 1787) and *Homopus femoralis* (Boulenger, 1888), *Testudo graeca* Linnaeus, 1758 and *Testudo kleinmanni* Lortet, 1883, *Psammobates tentorius* (Bell, 1828), *Centrochelys sulcata*, *Gopherus agassizii*, and *Stigmochelys pardalis*, the inguinal scute is divided (Crumly, 1984; Takahashi et al., 2003). However, a condition similar as in the genus *Manouria* was observed only in *Stigmochelys pardalis* (ISEZ R/380, NMP6V 76145.2), in which the multiplication of scutes in the inguinal region is associated with an increased number of peri-inguinal scutes. Crumly (1984) stated that only in the genus *Manouria* the inguinal scute is composed of two or three elements, with the perimeter of the composite scute leaving a sulcus. We disagree with this statement, based on a clear system of sulci encircling numerous scute area in *Manouria morla* sp. nov. and the same pattern observed in *Mamouria emys* (NHMUK 1900.2.7.6), in which the presence of post-inguinal and peri-inguinal scutes is evident (Fig. 9).

Such a unique arrangement of inguinal scutes is apomorphic for *Manouria* spp. Even when the exact number of the inguinal scutes is uncertain in incomplete or poorly preserved specimens, the multiplication of the inguinal scutes is usually clear, and the sulci are well defined, therefore the character can be considered easily diagnostic.

For that reason, we redesigned the original Crumly's (1984) character regarding the multiplication of inguinal scutes (more than one or two) to include three states: 0 = absent (only a single inguinal scute is present); 1 = present (two inguinal scutes are present); 2 = present (more than two inguinal scutes are present). We consider this character to be ordered. All members of the genus *Manouria* and *Stigmochelys pardalis* are scored as 2, *Malacochersus tornieri*, *Homopus areolatus* and *Ho. femoralis*, *Testudo graeca* and *T. kleinmanni*, *Psammobates tentorius*, *Centrochelys sulcata*, and *Gopherus agassizii* should be scored as 1 and all other extant tortoises as 0.

A review of fossil species, especially members of the non-testudinid *Pan-Testudinidae* and early-diverging *Testudinidae*, is needed to provide a closer affinity to the basalmost extant genus *Manouria*. Nevertheless, the genus is here considered monophyletic and located at the base of the *Testudinidae.*

The evolutionary history of the genus *Manouria*

The oldest true testudinids are known from the beginning of the Neogene. The fossil record of the genus *Gopherus*, the second most basal extant testudinid, is known from the Early Miocene (Aquitanian) of North America (Vlachos, 2018). Therefore, the fossil record of the genus *Gopherus* is older than *Manouria*, even despite the significantly more derived phylogenetic position of the former, considering an extensive record of fossil forms separating both genera. According to molecular data, the extant species of the genus *Manouria* probably split between the Oligocene and the Early Miocene (Kehlmaier et al., 2023; Le et al., 2006; Pereira et al., 2017; Selvatti et al., 2023; Thomson et al., 2021). *Manouria morla* sp. nov. exactly fits within this gap, however, the phylogenetic results show its advanced position in the *Manouria* branch, closely related to *M. emys*, so therefore the split of the *Manouria* species must have happened even earlier.

Another issue is the biogeographic implications of *Manouria morla* sp. nov., extending the palaeobiogeographic distribution of the genus much farther to the west, from Asia to the heart of Europe. Thanks to that, we can propose at least three scenarios of the evolution of this turtle lineage. In the first scenario, the genus *Manouria* evolved in Europe, plausibly from ancestors related to *Pelorochelon* spp., and then spread to Asia during the Middle Miocene Climatic Optimum (MMCO), when the climatic conditions were favourable for dispersal. Later, due to cooling events (for instance, the Middle Miocene Climate Transition: MMCT), the genus went extinct in Europe. Therefore, the extant fauna represents only the relic occurrences which survived in climatically stable conditions. This scenario seems to be consistent with the palaeoclimatic data and with the European distribution of the closest relatives of *Manouria* spp. (*Pelorochelon* spp.), and therefore is considered here the most parsimonious. According to the second scenario, the opposite direction of dispersal is possible: *Manouria* evolved in Asia and later spread to Europe. However, the Ahníkov I locality is dated before the MMCO, which would require the ancestor of *Manouria morla* to reach the area prior to the supposedly optimal conditions, Moreover, it would necessitate either an earlier immigration of the ancestor of *Manouria* spp. to Asia, or an independent immigration of *Hadrianus* spp. or their ancestor to Europe, depending on what area the common ancestor of both genera inhabited. The third scenario would require the genus to diverge somewhere between Ahníkov I and the current area inhabited by *Manouria* spp., and from that point to reach both regions independently. This scenario currently has no fossil record support.

The genus *Manouria* as an environmental indicator

The locality of Ahníkov I was known for decades as recording a swampy area with flooding rivers and shallow lakes (Ekrt et al., 2016; Kvaček et al., 2004; Mach et al., 2017). Thanks to the high number of juvenile

Fig. 13 Life restoration of *Manouria morla* sp. nov. Digital painting by Rudolf Hima

crocodylians, and perhaps by the presence of choristoderes, a near-shore wetlands habitat was identified as well (Chroust et al., 2021; Evans & Klembara, 2005).

However, based on the findings of the genus *Manouria*, a broadleaf evergreen wet forest in the proximity of water, with a rainy season and a drier cool season, similar to the extant Kaeng Krachan National Park in Thailand, can be implied (Moll, 1989; Stanford et al., 2015). The mean annual temperature in the areas inhabited by the representatives of the genus *Manouria* is 27 °C, with the maximal mean annual temperature of 35 °C and the minimum mean annual temperature of 20 °C, humidity per year in the range of 73–85% and more than 2400 sunny days, which all fit a tropical evergreen rainforest or a semi-deciduous transitional forest (Haller-Probst, 1997). The same or similar conditions have already been proposed, however, always compared with an Everglades-like environment (Kvaček et al., 2004). This record is coherent with the findings of the fossil bee *Apis* sp. from the Most Basin, the extant relatives of which are also nowadays distributed in SE Asia (Kvaček et al., 2004). With that in mind, we want to strongly warn against the simplified use of fossil testudinids (generally identified as *Geochelone* sp.) as a proxy for reconstructing semi-arid conditions (Fig. 13).

Conclusion

We describe *Manouria morla* sp. nov., the oldest member of the extant genus *Manouria,* from the Ahníkov I (formerly known as Merkur or Merkur-North) fossil site from Czechia (MN 3, Early Miocene). To aid the description, *Manouria morla* sp. nov. was scored and included in a phylogenetic analysis. According to our results, it seems that the genus *Manouria* originated in Europe just before the MMCO and later spread to Asia, where it persists until now. In the end, the use of the genus *Manouria* as an environmental indicator is coherent with the knowledge of the swamp ecosystem of the Most Basin.

Supplementary Information

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Supplementary material 1.

Supplementary material 2.

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Author contributions

M. C. and T. S. wrote the main manuscript text, digitised and photographed specimens, prepared figures, performed the phylogenetic analyses and analysed the results. À.H.L. prepared the drawing of the shell. All authors studied the material and reviewed the manuscript.

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Data availability

The 3D models, the photogrammetric photograph series, and the virtual reconstruction of the shell of *Manouria morla* sp. nov. presented herein are uploaded to the MorphoSource project https://www.morphosource.org/projects/000722147.

Declarations

Competing interests

The authors declare no competing interests.

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