



Research

Cite this article: Ferreira GS, Nascimento ER, Cadena EA, Cozzuol MA, Farina BM, Pacheco MIAF, Rizzutto MA, Langer MC. 2024 The latest freshwater giants: a new *Peltocephalus* (Pleurodira: Podocnemididae) turtle from the Late Pleistocene of the Brazilian Amazon. *Biol. Lett.* **20**: 20240010.
<https://doi.org/10.1098/rsbl.2024.0010>

Received: 8 January 2024

Accepted: 15 February 2024

Subject Category:

Palaeontology

Subject Areas:

palaeontology, taxonomy and systematics

Keywords:

giant reptiles, vertebrate palaeontology, Testudines, body size, Amazon basin, megafauna

Author for correspondence:

G. S. Ferreira

e-mail: gabriel.ferreira@senckenberg.de

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.7095346>.

The latest freshwater giants: a new *Peltocephalus* (Pleurodira: Podocnemididae) turtle from the Late Pleistocene of the Brazilian Amazon

G. S. Ferreira^{1,2}, E. R. Nascimento³, E. A. Cadena^{4,5}, M. A. Cozzuol⁶,
B. M. Farina^{7,8}, M. L. A. F. Pacheco⁹, M. A. Rizzutto¹⁰ and M. C. Langer¹¹

¹Senckenberg Centre for Human Evolution and Palaeoenvironment at the Eberhard Karls Universität Tübingen, Tübingen, Germany

²Geowissenschaften Fachbereich, Eberhard Karls Universität Tübingen, Tübingen, Germany

³Centro de Biologia Experimental (CIBEBI), Programa de Mestrado e Doutorado em Geografia, Universidade Federal de Rondônia (UNIR), Porto Velho, Brazil

⁴Facultad de Ciencias Naturales, Grupo de Investigación Paleontología Neotropical Tradicional y Molecular (PaleoNeo), Universidad del Rosario, Bogotá, Colombia

⁵Smithsonian Tropical Research Institute, Panamá, Panama

⁶Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

⁷Department of Biology, University of Fribourg, Fribourg, Switzerland

⁸Swiss Institute of Bioinformatics, Fribourg, Switzerland

⁹Laboratório de Paleobiologia e Astrobiologia, Universidade Federal de São Carlos, Sorocaba, Brazil

¹⁰Instituto de Física, Universidade de São Paulo, São Paulo, Brazil

¹¹Departamento de Biologia, Universidade de São Paulo, Ribeirão Preto, Brazil

GSF, 0000-0003-1554-8346; BMF, 0000-0001-6506-3801; MIAFP, 0000-0002-8810-2321

Overkill of large mammals is recognized as a key driver of Pleistocene megafaunal extinctions in the Americas and Australia. While this phenomenon primarily affected mega-mammals, its impact on large Quaternary reptiles has been debated. Freshwater turtles, due to the scarcity of giant forms in the Quaternary record, have been largely neglected in such discussions. Here we present a new giant podocnemidid turtle, *Peltocephalus maturin* sp. nov., from the Late Pleistocene Rio Madeira Formation in the Brazilian Amazon, that challenges this assumption. Morphological and phylogenetic analyses of the holotype, a massive partial lower jaw, reveal close affinities to extant Amazonian species and suggest an omnivorous diet. Body size regressions indicate *Pe. maturin* possibly reached about 180 cm in carapace length and is among the largest freshwater turtles ever found. This finding presents the latest known occurrence of giant freshwater turtles, hinting at coexistence with early human inhabitants in the Amazon.

1. Introduction

Overkill of large mammals is considered one of the main factors driving the extinction of the Pleistocene megafauna in the Americas and Australia [1], but it was not limited to mega-mammals. Although the Amazonian Miocene is famous for its gigantic reptiles [2], large Quaternary species are also known and might have been affected by anthropogenic action. Human predation for giant turtles, for example, has been linked to body size decline in tortoises (Testudinidae) over the Late Neogene and Quaternary, and the over-exploitation of island species leading to their extinction is well documented [3]. Freshwater turtles are usually overlooked, as giant species (straight carapace length >150 cm [3]) are absent from the Quaternary record. The largest freshwater turtles nowadays, *Chitra chitra* (Trionychidae) and *Podocnemis*

expansa (Podocnemididae), reach no more than 140 and 110 cm, respectively [4], and only a handful of them have crossed the 150 cm threshold in the past [5], most recently and prominently during the Miocene [6]. Unlike their terrestrial and marine relatives, size disparity of freshwater turtles is less variable over time [5] and gigantic forms are rare. Here, we challenge this idea by presenting a new giant podocnemidid from the Late Pleistocene Rio Madeira Formation, Brazilian Amazon. The holotype of *Peltocephalus maturin* sp. nov. is composed of a partial lower jaw, which enabled us to establish its close affinities to the extant Amazonian *Peltocephalus dumerilianus* and infer an omnivorous diet. Age inferences pinpoint *Peltocephalus maturin* as the latest giant freshwater turtle, inhabiting the Amazonian rainforest on the fringe of human arrival.

2. Material and methods

(a) Radiocarbon dating and geochemical analyses

Three bone samples were analysed at the Center for Applied Isotope Studies of the University of Georgia (USA) for radiocarbon dating using bioapatite protocols [7,8]. The samples were taken from the posterior portion of MERO.PV.H 007 by removing the superficial layers and digging into the fossilized bone. Micro-Raman spectroscopy and energy dispersive X-ray fluorescence (EDXRF) analyses of fossil fragments and sediments from the same locality were analysed to evaluate the reliability of the bioapatite dating [9]. Detailed descriptions of those analyses are presented in electronic supplementary material, file S1.

(b) Morphology, body size and phylogenetics

The holotype MERO.PV.H 007 was digitized using an Artec Spider portable scanner. We also scanned lower jaws of the extant podocnemidids *Erymnochelys madagascariensis* (SMF 7879), *Peltocephalus dumerilianus* (SMF 40168), and *Podocnemis unifilis* (SMF 55470) with a Nikon XT H 320 μ CT at the 3D Imaging Lab of the University of Tübingen, Germany. The dentaries were manually segmented, and surface models were saved as .stl files using Amira (v. 2020.2, ThermoFisher) and visualized on Blender (v. 3.4.1). Scanning parameters and Morphosource repository links to the datasets are shown in electronic supplementary material, file S1.

We modified a recent matrix of Pleurodira [10] by incorporating some characters from Evers *et al.* [11], as well as three new characters. We scored MERO.PV.H 007, excluded most non-Podocnemidoidae, using TNT v. 1.5 [12] (detailed descriptions on electronic supplementary material, file S1). We built a morphometric dataset comprising one angular (AJR) and seven linear measurements taken from the dentaries of 56 extant podocnemidids, two extant Pelomedusidae, and two extinct podocnemidids, MERO.PV.H 007 and VPPLT-979 (*Stupendemys geographica* [6]), to compare the new specimen within Podocnemididae. The linear measurements were divided by the maximal dentary lateral length (ML) to remove absolute size, log-transformed and plotted to characterize their distribution in the dataset (electronic supplementary material, figure S10). Principal component analysis (PCA) was applied to the morphometric dataset using the *prcomp* function in R [13], to visualize the main aspects of variation in the dentary of podocnemidids. We created a second dataset with dentary (MiL), lower jaw (JL), snout-to-mandibular condyle (SCm) and carapace (SCL) lengths for 354 specimens, sampling all the main Testudines lineages (electronic supplementary material, file S3) to estimate the body size of the new taxon. The four variables were analysed using two linear regression (*lm* function in R) approaches: predicting SCL from JL, which in turn was estimated from MiL (two regressions), and inferring SCm from the predicted JL, and then predicting SCL from SCm (three regressions). We obtained best fit, lower, and upper estimates using the *predict* function. Lower and upper bounds were then obtained using the bounds from previous regressions (full description in electronic supplementary material, file S1); this inflates error margins, but provides more realistic uncertainties, which inevitably result from using multiple regressions (R script for all analyses is presented in electronic supplementary material, file S7).

3. Results

(a) Systematic palaeontology

Testudines Batsch, 1788 [14]

Pleurodira Cope, 1864 [14]

Podocnemididae Cope, 1868 *sensu* [15]

Peltocephalus Dumeril and Bribon, 1835

Peltocephalus maturin sp. nov.

(b) Etymology

Maturin refers to the giant turtle that vomited out the universe in Stephen King's stories, which in turn was inspired by the character Stephen Maturin who, in the book *H.M.S. Surprise* of Patrick O'Brian's *Aubrey-Maturin* series, names a giant tortoise.

(c) Holotype

MERO.PV.H 007 (figure 1a–c; electronic supplementary material, figure S7), mostly complete, massive, and fused dentaries, part of the Museu da Memória Rondoniense (MERO) collection, Porto Velho, Brazil.

(d) Locality and horizon

MERO.PV.H 007 was collected by gold miners in the site known as Taquaras Quarry (electronic supplementary material, figure S1), in Porto Velho (Rondônia, Brazil), from unknown beds of the Rio Madeira Formation (Abunã Basin [16]), the only geological unit exposed in the quarry. That Late Pleistocene–Holocene unit was subdivided [17] into lower beds of locally laminated bioturbated claystones, with carbonized plant remains, and a greyish conglomeratic upper level, known as 'Mucururú' [18,19], the main auriferous and fossiliferous stratum [20]. Carbonized wood from the lower beds was dated between 46 310 and 21 310 years BP [16].

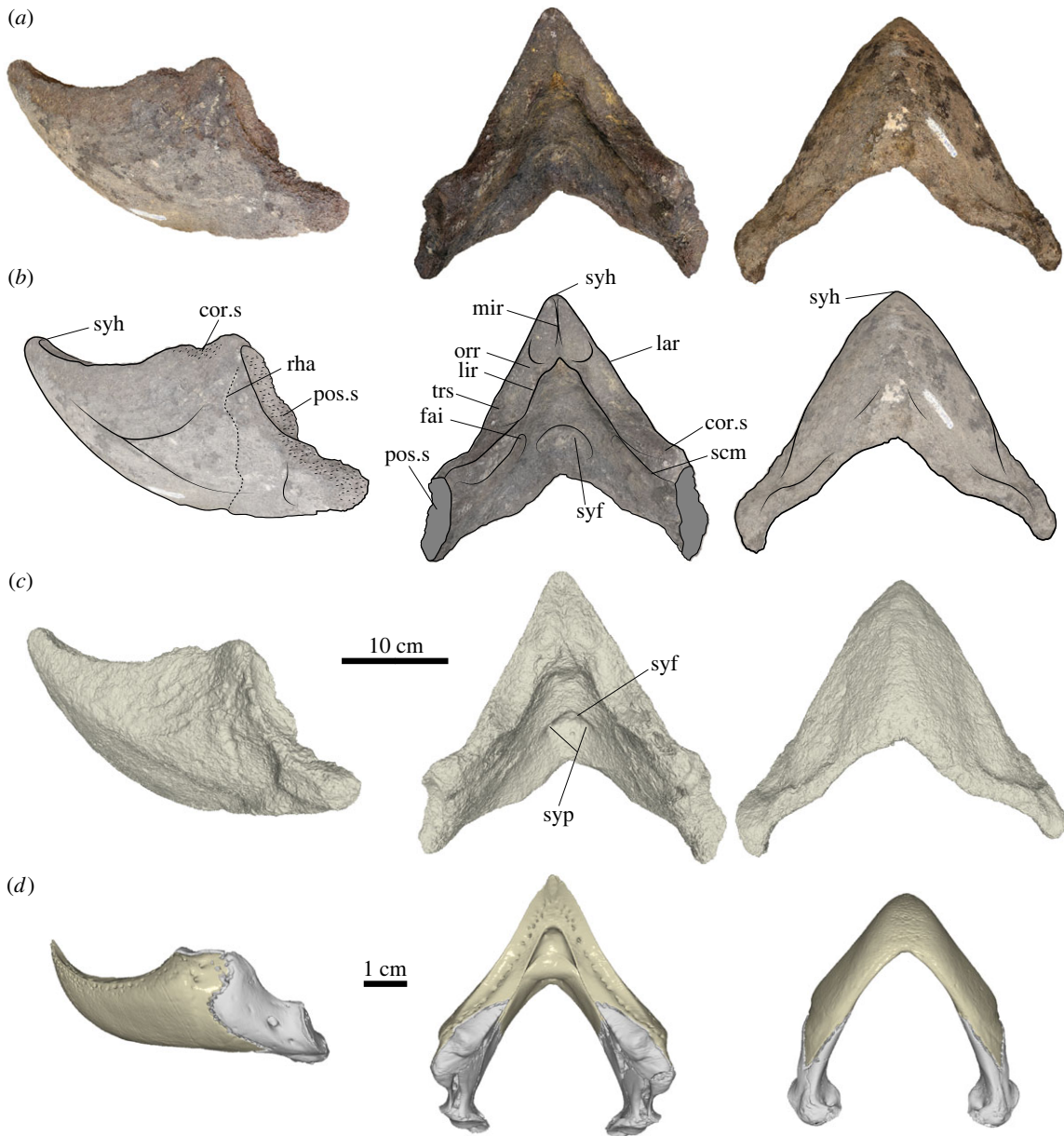


Figure 1. *Peltoccephalus maturin* sp. nov.: photographs (a), outlines (b) and 3D renderings (c) of the dentary MERO.PV.H 007, and 3D renderings of *Pe. dumerilianus* lower jaw (d) in left lateral (left), dorsal (centre) and ventral (right) views. Abbreviations: cor.s, suture to the coronoid; fai, foramen alveolare inferius; lar, labial ridge; lir, lingual ridge; mir, midline ridge; orr, orthogonal ridge; pos.s, suture with the posterior bone; trs, tritulating surface; rha, rhamphotheca posterior limit; scm, sulcus cartilagini meckeli; syf, symphyseal fossa; syh, symphyseal hook; syp, symphyseal pits.

(e) Diagnosis

Peltoccephalus maturin is assigned to Pelomedusoides based on its fused dentaries and to *Peltoccephalus* by the symphyseal hook higher than the coronoid process, the lingual platform and a small fossa with two pits on the posterior surface of the symphysis. It differs from *Podocnemis* spp. in its straight, instead of curved, labial and lingual ridges, U-shaped midline outline of the lingual ridges, well-developed symphyseal hook, transverse posterior (lingual) platform ventral to the tritulating surface and the symphyseal fossa; from *Erymnochelys madagascariensis* by two pits in the symphyseal fossa, instead of one; from both *Podocnemis* spp. and *E. madagascariensis* in its dorsoventrally—instead of posteroventrally—sloping posterior limit of the rhamphotheca. *Peltoccephalus maturin* can be distinguished from *Pe. dumerilianus* based on its much greater size, labial ridge higher than the lingual, symphyseal ridge separating left and right tritulating surfaces (all these shared with *Stupendemys geographica*), and secondary ridge orthogonal to the long axis of the tritulating surface, separating anterior and posterior tritulating areas (autapomorphy). *Peltoccephalus maturin* can be differentiated from *S. geographica* by narrow instead of expanded tritulating surfaces, upcurved pointed symphyseal hook and sharp but not protruding and anteriorly V-shaped lingual ridges, instead of protruding and U-shaped.

(f) Radiocarbon dating and geochemical analyses

Radiocarbon analyses provided ages between $14\,290 \pm 45$ and 9060 ± 50 cal BP (detailed description in electronic supplementary material, file S1). However, high iron counts and the presence of haematite, gypsum and carbonates in the geochemical analyses indicate a poorly preserved and intensively weathered bone, and bioapatite dating has been shown to produce younger ages in warm and wet conditions [9,21]. We consider that this may be the case here, given that vertebrate fossils [17,20], palynology

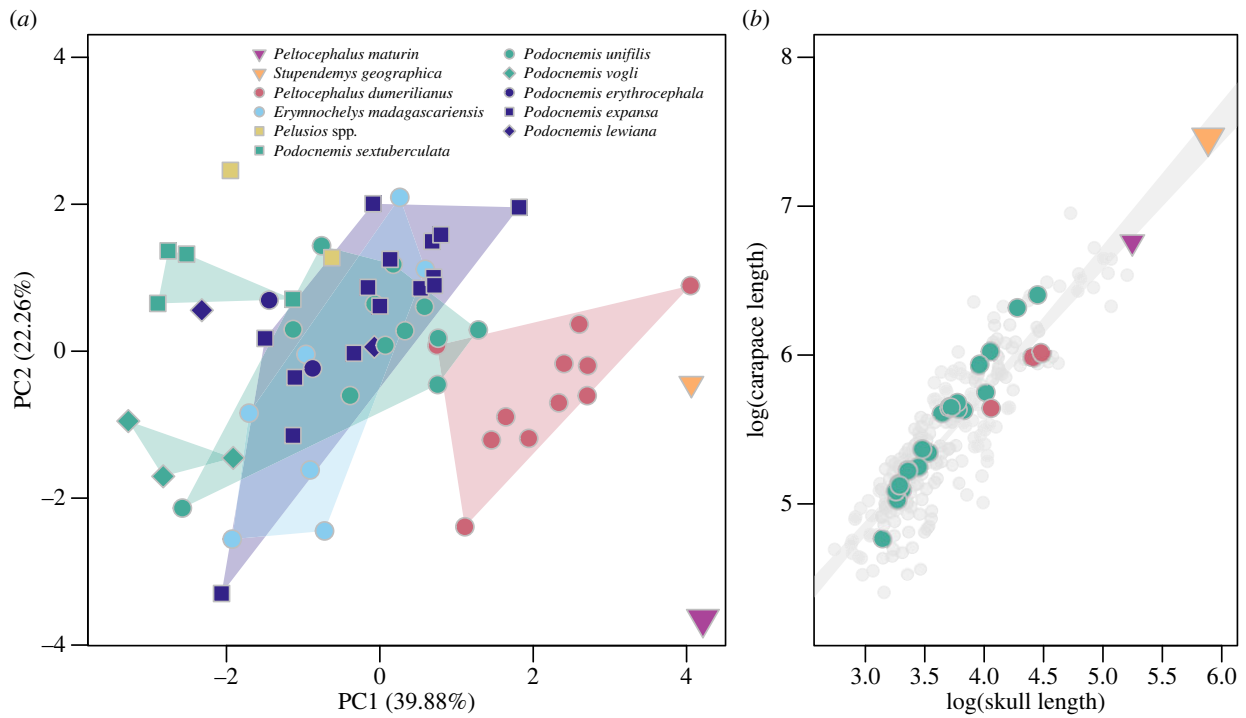


Figure 2. Results (a) of the principal component analysis of dentary linear and angular measurements and (b) linear regression between log-transformed skull length (SCm) and straight carapace length (SCL).

[19], and radiocarbon dating of sediments and carbonized trunks [16] from the Rio Madeira Formation all point to a Late Pleistocene age.

(g) Phylogenetic and morphospace analyses, and body size estimates

The phylogenetic analysis yielded 474 most parsimonious trees with 537 steps, the strict consensus of which shows *Peltocephalus maturin* and *Peltocephalus dumerilianus* within Erymnochelyinae as sister-taxa supported by two synapomorphies (electronic supplementary material, figure S9). Analyses of log-transformed measurements of the lower jaw (electronic supplementary material, figure S10) confirm that *Pe. maturin* differs morphologically from both *Pe. dumerilianus* and the giant Miocene podocnemidid *Stupendemys geographica*. In comparison to extant podocnemidids, the relative values of MiL, MW, TSW and TSML of *Pe. maturin* plot within the range observed for specimens of *Pe. dumerilianus*, but other metrics distinguish those species. Likewise, PCA results (PC1 = 39.88%, PC2 = 22.26%; figure 2a) show *Pe. maturin*, *Pe. dumerilianus*, and *S. geographica* closer on positive PC1 and the mid-range PC2, compared to *Podocnemis* spp. and *Erymnochelys madagascariensis*. These results reflect the narrow angle of the lower jaws in the group including *Pe. maturin*, as well as their smaller and broader (on the midline) triturating surfaces and higher symphyseal hook and coronoid process (electronic supplementary material, figure S7).

The linear regressions (figure 2b) show similar relations between the dentary and lower JL, and the latter with that of the skull (SCm) in different turtle groups ($R^2 = 0.9896$ and 0.9833 , respectively), whereas 78.4% and 78.6% of the SCL is explained by JL and SCm, respectively. Best fitted estimates of *Pe. maturin* SCL were 170.4 mm (Approach 1) and 173.7 cm (Approach 2) with cumulative lower and upper bounds between 140.74 and 216.98 cm (detailed description in electronic supplementary material, files S1).

4. Discussion

Higher labial than lingual ridges and the presence of symphyseal and secondary transversal ridges support the distinctiveness of *Peltocephalus maturin* from the closely related *Peltocephalus dumerilianus*. A lingual platform, upcurved symphyseal hook, and a symphyseal fossa with two pits support the affinity of both *Peltocephalus*, as well as their distinctiveness from other podocnemidids, which is further supported by our phylogenetic and morphometric analyses. *Peltocephalus maturin* and *Pe. dumerilianus* are recovered as sister-taxa within Erymnochelyinae [15], supported by two synapomorphies (electronic supplementary material, figure S9). *Peltocephalus maturin* plots on the same quadrant as *Pe. dumerilianus* and *Stupendemys geographica* (figure 2a). The two latter species appear closely related in other phylogenetic analyses [10,15] and our results support this hypothesis. The PCA results also reflect less the diets of podocnemidids than their phylogenetic relations based on molecular data (e.g. [22–25]). For example, *Erymnochelys madagascariensis* clusters with the *Podocnemis* spp. albeit having a diet more like that of *Pe. dumerilianus* [26].

Considering that skull height and the proportions/complexity of the triturating surfaces adequately distinguish general feeding categories in turtles [27–30], the dentary morphology of *Pe. maturin* suggests a diet akin to that of *Pe. dumerilianus*. Although extant podocnemidids are all plant-biased omnivorous, *Pe. dumerilianus* has the highest percentage of animal items in its diet [26], commonly preying on apple snails [31]. Its simpler triturating surface reflects that habit, whereas the more herbivorous *Podocnemis*

spp. show more ridged surfaces (see electronic supplementary material, figure S7). The narrow triturating surface of *Pe. maturin* is not consistent with durophagy or predominant herbivory, but its midline orthogonal ridge (absent in *Pe. dumerilianus*; electronic supplementary material, figure S7) implies a less carnivorous diet.

Size difference has been proposed to explain the coexistence of the Miocene *Caninemys tridentata* and *S. geographica* [10] and could also prevent ecological competition among extant Amazon podocnemidids, which were likely living during the Late Pleistocene [24,25]. The 27.8 cm long dentaries of *Pe. maturin* are among the largest ever found for turtles, comparable to those of the marine *Archelon ischyros*, the carapace (SCL) of which is estimated to be 221 cm (specimen NHMW-Geo 1977/1902/0001; M. Rabi 2022, personal communication). We estimated *Pe. maturin* SCL at about 180 cm, smaller than the largest known turtles, like *A. ischyros*, *S. geographica* (max SCL = 286 cm [6]), and some Quaternary tortoises [32], but larger than any Quaternary freshwater turtle from the Amazon (*Podocnemis expansa*, the largest podocnemidid SCL = 109 cm) or elsewhere (*Chitra chitra*, the largest trionychid SCL = 140 cm [4]).

Previous evidence indicated that podocnemidids attained gigantic sizes (SCL > 150 cm [3]) at least twice: Late Palaeocene [33,34] and Miocene [6,35]. This is consistent with the periods in which extreme sizes evolved in other groups of turtles [5], as well as in other reptiles, e.g. the Palaeocene giant snake *Titanoboa cerrejonensis* [36] and the giant Miocene crocodiles, such as *Purussaurus brasiliensis* [37] and *Mourasuchus pattersoni* [38]. *Peltocephalus maturin* adds giant freshwater turtles to the Pleistocene record, which already includes large squamates (e.g. *Varanus priscus*, *Wonambi naracoortensis* and *Tupinambis uruguaiensis* [39–41]) and tortoises (e.g. *Titanochelon schaefferi* and *Megalochelys atlas* [32]). Furthermore, those giant reptiles seem to have disappeared after 50–40 kyr ago [40], with testudinids showing body size decrease by the end of the Pleistocene [3].

Although explicit analyses of body size evolution in freshwater turtles are lacking, until now, no gigantic representative of this ecological group was known after the Miocene [5]. The Late Pleistocene *Peltocephalus maturin* fills this gap, hinting at the possibility that it was coeval with the early peopling of South America [42]. It has been suggested that extinctions of giant tortoises in the Late Pleistocene to Early Holocene, particularly in Australia and South America, followed a similar pattern to those of herbivorous mammals and other megafauna, and were directly related to human overexploitation [32]. There is plenty of evidence for that in the case of tortoises from remote islands, e.g. testudinids in the Turks and Caicos Islands, ca 1.4 kyr BP [32], and meiolaniids in Vanuatu, ca 3 kyr BP [43] and New Caledonia, ca 1.7 kyr BP [44]. Large terrestrial turtles have been part of the hominin diet since the Palaeolithic and tend to be more exploited by humans [32] because they are easier to notice and capture than smaller and freshwater turtles [45,46]. In the Amazon, some of the earliest evidence of human occupation—ca 12.6–11.8 kyr in Serranía La Lindosa, Colombia and ca 11.7–9.88 kyr in Caverna da Pedra Pintada, Brazil—is found together with both testudinid and podocnemidid remains [47–49] and, even today, the largest species are usually preferred for human consumption [50,51]. The possibility that *Pe. maturin* was part of the South American megafauna extinct by the arrival of humans is fascinating, but more data from the Late Pleistocene and Early Holocene deposits of the Amazon basin are needed to evaluate this hypothesis. In any case, what we do know is that the holotype of *Peltocephalus maturin* is one of the largest turtle dentaries ever found, revealing that a gigantic and now extinct freshwater turtle inhabited the Amazon rainforest on the fringe of human occupation of the Americas.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Supporting data and code are freely available from the Dryad Repository Repository: <https://doi.org/10.5061/dryad.zpc866tg2> [52] and the μ CT datasets are available on Morphosource Repository Project ID: 000553087.

Supplementary material is available online [53].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.S.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing; E.R.N.: data curation, funding acquisition, writing—review and editing; E.A.C.: formal analysis, investigation, writing—review and editing; M.A.C.: investigation, methodology, writing—review and editing; B.M.F.: formal analysis, methodology, writing—review and editing; M.L.A.F.P.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; M.A.R.: formal analysis, methodology, writing—review and editing; M.C.L.: conceptualization, investigation, methodology, resources, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. G.S.F. received funding from Deutscher Akademischer Austauschdienst (DAAD) (grant no. 57598274) and Federal Ministry of Education and Research (BMBF) and the Baden-Württemberg Ministry of Science as part of the Excellence Strategy of the German Federal and State Governments (grant no. PRO-FERREI-2022-10). E.R.N. was funded by Scientia Consultoria Científica. B.M.F. received funding from the Swiss Government Excellence Scholarship (grant no. 2021.0350). M.C.L. received funding from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (grant no. 20/07997-4). M.L.A.F.P. received funding from FAPESP (grant no. 2022/11586-5) and CNPq (grant no. 420424/2023-7).

Acknowledgements. We thank MERO (Museu da Memória Rondoniense) for loaning the specimen studied here, Prof. Dr F. Rodrigues and E. Silva of Laboratório Quimiosfera, IQ/USP, for the micro-Raman analyses and C. Kyriakouli, from the 3D Imaging Lab of the University of Tübingen, for μ CT and surface scanning. We thank the reviewers A. Pérez-García and H. Smith, and editors S. Johar, D. Beerling and R. Honeycutt for comments and suggestions on the manuscript; V. Alberici, N. Salvador, R. Delcourt and M. Rabi for insightful discussions and constructive critiques; and W. Joyce, M. Rabi and J. Sterli for sharing photographs of specimens.

References

1. Sandom C, Faurby S, Sandel B, Svenning JC. 2014 Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. B* **281**, 20133254. (doi:10.1098/rspb.2013.3254)
2. Hoorn C *et al.* 2010 Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**, 927–931. (doi:10.1126/science.1194585)
3. Joos J, Pimiento C, Miles DB, Müller J. 2022 Quaternary megafauna extinctions altered body size distribution in tortoises. *Proc. R. Soc. B* **289**, 20221947. (doi:10.1098/rspb.2022.1947)

4. Rhodin AGJ, Iverson JB, Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP. 2021 Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. In *Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group* (eds AGJ Rhodin, JB Iverson, PP Van Dijk, CB Stanford, EV Goode, K Buhlmann), 9th edn. Chelonian Research Foundation and Turtle Conservancy. See <https://iucn-tfts.org/checklist/>.
5. Farina BM, Godoy PL, Benson RBJ, Langer MC, Ferreira GS. 2023 Turtle body size evolution is determined by lineage-specific specializations rather than global trends. *Ecol. Evol.* **13**, e10201. (doi:10.1002/ece3.10201)
6. Cadena EA, Scheyer TM, Carrillo-Briceño JD, Sánchez R, Aguilera-Socorro OA, Vanegas A, Pardo M, Hansen DM, Sánchez-Villagra MR. 2020 The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Sci. Adv.* **6**, eaay4593. (doi:10.1126/sciadv.aay4593)
7. Cherkinsky A. 2009 Can we get a good radiocarbon age from 'bad bone'? Determining the reliability of radiocarbon age from bioapatite. *Radiocarbon* **51**, 647–655. (doi:10.1017/S0033822200055995)
8. Cherkinsky A, Dantas MAT, Cozzuol MA. 2013 Bioapatite ¹⁴C age of giant mammals from Brazil. *Radiocarbon* **55**, 464–471. (doi:10.1017/S0033822200057593)
9. Zazzo A. 2014 Bone and enamel carbonate diagenesis: a radiocarbon prospective. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **416**, 168–178. (doi:10.1016/j.palaeo.2014.05.006)
10. Cadena EA, Link A, Cooke SB, Stroik LK, Vanegas AF, Tallman M. 2021 New insights on the anatomy and ontogeny of the largest extinct freshwater turtles. *Heliyon* **7**, e08591. (doi:10.1016/j.heliyon.2021.e08591)
11. Evers SW, Poinstein J, Jansen MA, Gray JA, Fröbisch J. 2023 A systematic compendium of turtle mandibular anatomy using digital dissections of soft tissue and osteology. *Anat. Rec.* **306**, 1228–1303. (doi:10.1002/ar.25037)
12. Goloboff PA, Catalano SA. 2016 TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**, 221–238. (doi:10.1111/cla.12160)
13. R Core Team. 2022 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
14. Joyce WG *et al.* 2021 A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss J. Palaeontol.* **140**, 5. (doi:10.1186/s13358-020-00211-x)
15. Ferreira GS, Bronzati M, Langer MC, Sterli J. 2018 Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira). *R. Soc. Open Sci.* **5**, 171773. (doi:10.1098/rsos.171773)
16. Rizzotto GJ, Cruz NM, Oliveira JG, Quadros MLES, Castro JM. 2006 *Paleoambiente e o registro fóssil pleistocênico dos sedimentos da formação Rio Madeira*. Belém, Brazil: Sociedade Brasileira de Geologia-Núcleo Norte.
17. Holanda EC, Ferigolo J, Ribeiro AM. 2011 New *Tapirus* species (Mammalia: Perissodactyla: Tapiridae) from the upper Pleistocene of Amazonia, Brazil. *J. Mammal.* **92**, 111–120. (doi:10.1644/10-MAMM-A-144.1)
18. Costa ML. 1991 Os Mucururus de Rondônia: considerações mineralógicas e geoquímicas. In *Anais do III simpósio de geologia da amazônia* (eds JBS Costa, JMG Fernandes, RL Bemerguy, IL Azevedo), pp. 464–478. Belém, Brazil: Sociedade Brasileira de Geologia.
19. Cozzuol MA, Latrubesse EM, da Silva SAF. 2004. *Estudo de viabilidade para implementação de usinas hidrelétricas no rio Madeira. Relatório parcial*. Paleontologia. Porto Velho, Brazil: UNIR/RIOMAR/FURNAS.
20. Holanda E, Cozzuol MA. 2006 New records of *Tapirus* from the late Pleistocene of southwestern Amazonia, Brazil. *Rev. Bras. Paleontol.* **9**, 193–200. (doi:10.4072/rbp.2006.2.03)
21. Wright DK. 2017 Accuracy vs. precision: understanding potential errors from radiocarbon dating on African landscapes. *Afr. Archaeol. Rev.* **34**, 303–319. (doi:10.1007/s10437-017-9257-z)
22. Vargas-Ramírez M, Castaño-Mora O, Fritz U. 2008 Molecular phylogeny and divergence times of ancient South American and Malagasy river turtles (Testudines: Pleurodira: Podocnemididae). *Org. Divers. Evol.* **8**, 388–398. (doi:10.1016/j.ode.2008.10.001)
23. Rodrigues JFM, Diniz-Filho JAF. 2016 Ecological opportunities, habitat, and past climatic fluctuations influenced the diversification of modern turtles. *Mol. Phylogenet. Evol.* **101**, 352–358. (doi:10.1016/j.ympev.2016.05.025)
24. Pereira AG, Sterli J, Moreira FRR, Schrago CG. 2017 Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Mol. Phylogenet. Evol.* **113**, 59–66. (doi:10.1016/j.ympev.2017.05.008)
25. Thomson RC, Spinks PQ, Shaffer HB. 2021 A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. *Proc. Natl Acad. Sci. USA* **118**, e2012215118. (doi:10.1073/pnas.2012215118)
26. Eisemberg CC, Reynolds SJ, Christian KA, Vogt RC. 2017 Diet of Amazon river turtles (Podocnemididae): a review of the effects of body size, phylogeny, season and habitat. *Zoology* **120**, 92–100. (doi:10.1016/j.zool.2016.07.003)
27. Claude J, Pritchard PCH, Tong H, Paradis E, Auffray JC. 2004 Ecological correlates and evolutionary divergence in the skull of turtles: a geometric morphometric assessment. *Syst. Biol.* **53**, 933–948. (doi:10.1080/10635150490889498)
28. Ferreira GS, Rincón AD, Solórzano A, Langer MC. 2015 The last marine pelomedusoids (Testudines: Pleurodira): a new species of *Bairdemys* and the paleoecology of Stereogenyina. *PeerJ.* **3**, e1063. (doi:10.7717/peerj.1063)
29. Hermanson G, Benson RBJ, Farina BM, Ferreira GS, Langer MC, Evers SW. 2022 Cranial ecomorphology of turtles and neck retraction as a possible trigger of ecological diversification. *Evolution* **76**, 2566–2586. (doi:10.1111/evo.14629)
30. Shippis BK, Peacock BR, Angielczyk KD. 2023 The topography of diet: orientation patch count predicts diet in turtles. *Anat. Rec.* **306**, 1214–1227. (doi:10.1002/ar.25125)
31. Vogt RC. 2001 Turtles of the Rio Negro. In *Conservation and management of ornamental fish resources of the Rio Negro basin, amazonia, brasil (project Piaba)* (ed. LN Chao), pp. 245–262. Manaus, Brazil: Editora da Universidade do Amazonas.
32. Rhodin AGJ *et al.* 2015 Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene Chelonians. In *Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group* (eds AGJ Rhodin, PCH Pritchard, PP Van Dijk, R Saumure, K Buhlmann, JB Iverson). *Chelonian Research Monographs* **5**, 000e.1–66. (doi:10.3854/crm.5.000e.fossil.checklist.v1.2015)
33. Cadena EA, Bloch JI, Jaramillo CA. 2010 New podocnemidid turtle (Testudines: Pleurodira) from the middle–upper Paleocene of South America. *J. Vertebr. Paleontol.* **30**, 367–382. (doi:10.1080/02724631003621946)
34. Cadena EA, Ksepka DT, Jaramillo CA, Bloch JI. 2012 New pelomedusoid turtles from the late Palaeocene Cerrejón Formation of Colombia and their implications for phylogeny and body size evolution. *J. Syst. Palaeontol.* **10**, 313–331. (doi:10.1080/14772019.2011.569031)
35. Wood RC. 1997 Turtles. In *Vertebrate paleontology in the neotropics. The Miocene fauna of La Venta, Colombia* (eds RF Kay, RH Madden, RL Cifelli, JJ Flynn), pp. 155–170. Washington, DC: Smithsonian Institution Press.
36. Head JJ, Bloch JI, Hastings AK, Bourque JR, Cadena EA, Herrera FA, Polly PD, Jaramillo CA. 2009 Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* **457**, 715–717. (doi:10.1038/nature07671)
37. Aureliano T, Ghilardi AM, Guilherme E, Souza-Filho JP, Cavalcanti M, Riff D. 2015 Morphometry, bite-force, and paleobiology of the Late Miocene caiman *Purussaurus brasiliensis*. *PLoS ONE* **10**, e0117944. (doi:10.1371/journal.pone.0117944)

38. Cidade GM, Solórzano A, Rincón AD, Riff D, Hsiou AS. 2017 A new *Mourasuchus* (Alligatoroidea, Caimaninae) from the late Miocene of Venezuela, the phylogeny of Caimaninae and considerations on the feeding habits of *Mourasuchus*. *PeerJ*. **5**, e3056. (doi:10.7717/peerj.3056)
39. Molnar RE. 2004. *Dragons in the dust: the paleobiology of the giant monitor lizard* Megalania. Bloomington, IN: Indiana University Press.
40. Wroe S, Field J. 2006 A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation. *Quat. Sci. Rev.* **25**, 2692–2703. (doi:10.1016/j.quascirev.2006.03.005)
41. Hsiou AS. 2007 A new Teiidae species (Squamata, Scincomorpha) from the late pleistocene of Rio Grande do Sul State. *Brazil. Rev. Bras. Paleontol.* **10**, 181–194. (doi:10.4072/rbp.2007.3.05)
42. Pansani TR *et al.* 2023 Evidence of artefacts made of giant sloth bones in central Brazil around the last glacial maximum. *Proc. R. Soc. B* **290**, 20230316. (doi:10.1098/rspb.2023.0316)
43. White AW, Worthy TH, Hawkins S, Bedford S, Spriggs M. 2010 Megafaunal meiolaniid horned turtles survived until early human settlement in Vanuatu, Southwest Pacific. *Proc. Natl Acad. Sci. USA* **107**, 15512–6. (doi:10.1073/pnas.1005780107)
44. Gaffney ES, Balouet JC, de Broin F. 1984 New occurrences of extinct meiolaniid turtles in New Caledonia. *Am. Mus. Novit.* **2800**, 1–6.
45. Steele TE. 2010 A unique hominin menu dated to 1.95 million years ago. *Proc. Natl Acad. Sci. USA* **107**, 10771–10772. (doi:10.1073/pnas.1005992107)
46. Thompson JC, Henshilwood CS. 2014 Nutritional values of tortoises relative to ungulates from the Middle Stone Age levels at Blombos Cave, South Africa: implications for foraging and social behaviour. *J. Hum. Evol.* **67**, 33–47. (doi:10.1016/j.jhevol.2013.09.010)
47. Roosevelt AC *et al.* 1996 Paleoindian cave dwellers in the Amazon: the peopling of the Americas. *Science* **272**, 373–384. (doi:10.1126/science.272.5260.373)
48. Oliver JR. 2008 The archaeology of agriculture in ancient Amazonia. In *The handbook of South American archaeology* (eds H Silverman, WH Isbell), pp. 185–216. New York, NY: Springer New York.
49. Morcote-Ríos G, Aceituno FJ, Iriarte J, Robinson M, Chaparro-Cárdenas JL. 2021 Colonisation and early peopling of the Colombian Amazon during the Late Pleistocene and the Early Holocene: new evidence from La Serranía La Lindosa. *Quat. Int.* **578**, 5–19. (doi:10.1016/j.quaint.2020.04.026)
50. Smith NJH. 1979 Aquatic turtles of Amazonia: an endangered resource. *Biol. Conserv.* **16**, 165–176. (doi:10.1016/0006-3207(79)90019-3)
51. Miorando PS, Rebêlo GH, Pignati MT, Brito Pezzuti JC. 2013 Effects of community-based management on Amazon River Turtles: a case study of *Podocnemis sextuberculata* in the Lower Amazon Floodplain, Pará, Brazil. *Chelonian Conserv. Biol.* **12**, 143–150. (doi:10.2744/CCB-1011.1)
52. Ferreira GS, Nascimento ER, Cadena EA, Cozzuol MA, Farina BM, Pacheco MLAF, Rizzutto MA, Langer MC. 2024 The latest freshwater giants: a new *Peltocephalus* (Pleurodira: Podocnemididae) turtle from the Late Pleistocene of the Brazilian Amazon. Dryad Digital Repository. (doi:10.5061/dryad.zpc866tg2)
53. Ferreira GS, Nascimento ER, Cadena EA, Cozzuol MA, Farina BM, Pacheco MLAF, Rizzutto MA, Langer MC. 2024 The latest freshwater giants: a new *Peltocephalus* (Pleurodira: Podocnemididae) turtle from the Late Pleistocene of the Brazilian Amazon. Figshare. (doi:10.6084/m9.figshare.c.7095346)