

Research



Cite this article: Pujos F, Salas-Gismondi R. 2020 Predation of the giant Miocene caiman *Purussaurus* on a mylodontid ground sloth in the wetlands of proto-Amaozonia. *Biol. Lett.* **16**: 20200239.
<http://dx.doi.org/10.1098/rsbl.2020.0239>

Received: 10 April 2020

Accepted: 23 July 2020

Subject Areas:

palaeontology, ecology, evolution

Keywords:

bite marks, *Purussaurus*, ground sloth, Miocene, proto-Amaozonia

Author for correspondence:

Rodolfo Salas-Gismondi

e-mail: rodolfo.salas@upch.pe

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5082870>.

Palaeontology

Predation of the giant Miocene caiman *Purussaurus* on a mylodontid ground sloth in the wetlands of proto-Amaozonia

François Pujos¹ and Rodolfo Salas-Gismondi^{2,3}

¹Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín, 5500 Mendoza, Argentina

²BioGeoCiencias Lab, Facultad de Ciencias y Filosofía, Laboratorios de Investigación y Desarrollo (LID), Centro de Investigación para el Desarrollo Integral y Sostenible (CIDIS), Universidad Peruana Cayetano Heredia, Lima, Peru

³Departamento de Paleontología de Vertebrados, Museo de Historia Natural-Universidad Nacional Mayor de San Marcos, Avenida Arenales 1256, Lima 14, Peru

FP, 0000-0002-6267-3927; RS-G, 0000-0001-9990-8841

Thirteen million years ago in South America, the Pebas Mega-Wetland System sheltered multi-taxon crocodylian assemblages, with the giant caiman *Purussaurus* as the top predator. In these Miocene swamps where reptiles and mammals coexisted, evidence of their agonistic interactions is extremely rare. Here, we report a tibia of the mylodontid sloth *Pseudopreotherium* bearing 46 predation tooth marks. The combination of round and bisected, shallow pits and large punctures that collapsed extensive portions of cortical bone points to a young or sub-adult *Purussaurus* (approx. 4 m in total length) as the perpetrator. Other known crocodylians of the Pebas System were either too small at adulthood or had discordant feeding anatomy to be considered. The pattern of tooth marks suggests that the perpetrator attacked and captured the ground sloth from the lower hind limb, yet an attempt of dismembering cannot be ruled out. This discovery from the Peruvian Amazonia provides an unusual snapshot of the dietary preferences of *Purussaurus* and reveals that prior to reaching its giant size, young individuals might have fed upon terrestrial mammals of about the size of a capybara.

1. Background

Following the extinction of non-avian dinosaurs, the largest Cenozoic continental predator was neither a mammal nor a bird, but the giant caiman *Purussaurus* [1]. This animal exceeded 10 m long and inhabited South America during the middle and late Miocene (*ca* 13–6 Ma) [2–6], when a system of wetlands flourished in northwestern Amazonia (figure 1*a*) [7,8]. Several lignitic localities of the Pebas Formation near the Peruvian city of Iquitos have yielded geological and palaeontological data regarding the life within this vast complex of lakes and swamps, named the Pebas Mega-Wetland System [2,7–9]. The record includes a plethora of fossil evidence [10,11], among which crocodylians showed notable disparity and diversity [2,12].

In October 2004, a mission to the Napo River (figure 1*b*) discovered new lignitic Miocene bonebeds (*ca* 13 Ma), particularly near Iquitos City. The Na069 bonebed preserves dysoxic swamp deposits bearing a diverse aquatic and terrestrial vertebrate assemblage, particularly rich in fish, turtle, reptile and mammal remains [13]. Among them, a severely damaged tibia of a mammal was discovered and collected by one of us (F.P.). Preparation of the specimen revealed multiple bite marks that were inflicted prior to fossilization.

The aim of this study is to describe and interpret the origin of the bite marks preserved on a 13-million-years-old mammalian long bone. We point to the

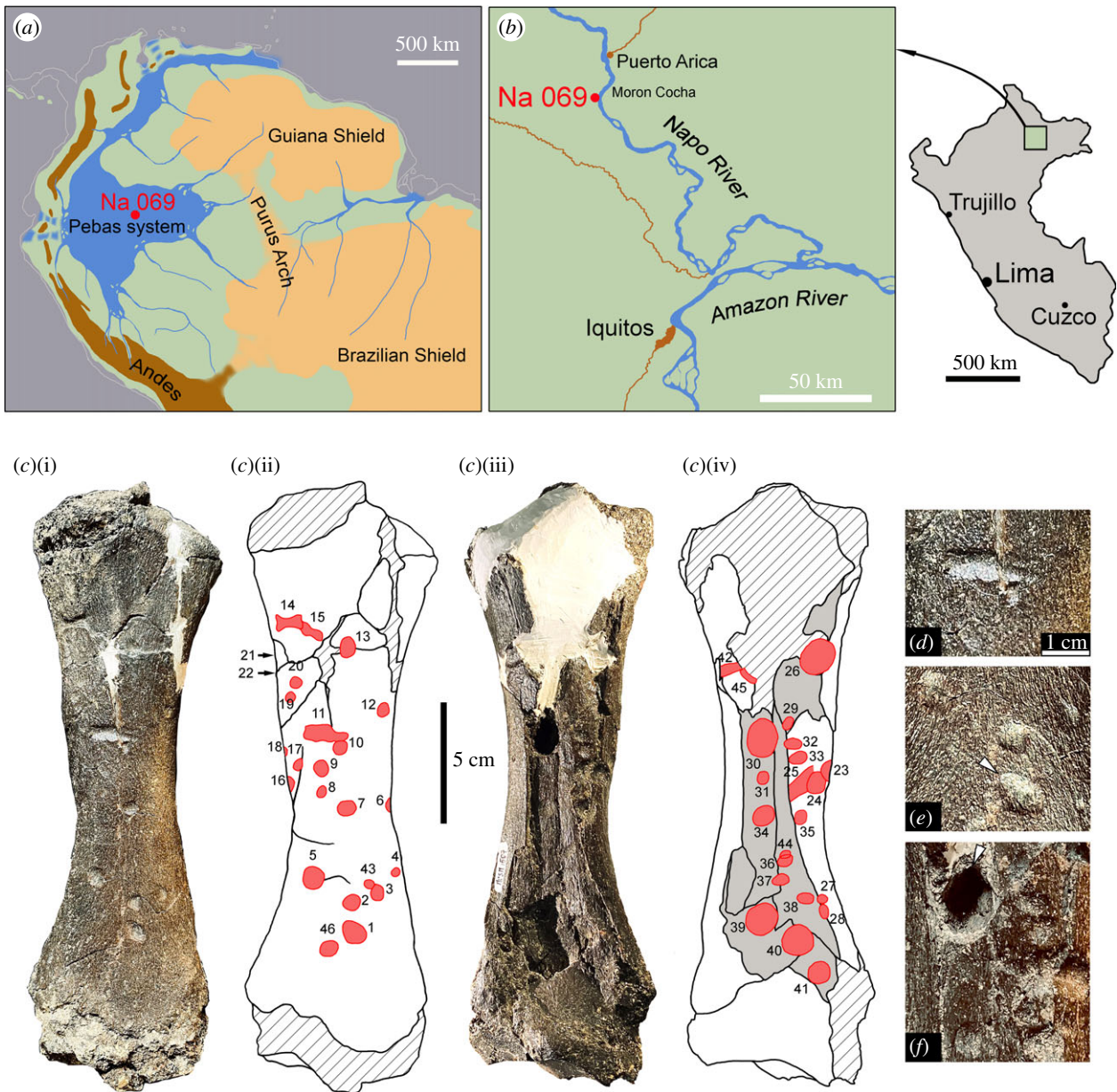


Figure 1. (a) The Pebas Mega-Wetland System (approx. 13 Ma) in northwestern South America (from [8]). Reprinted with permission from AAAS, showing the estimated position of locality Na069. (b) Location of Na069 on the Napo River, northeastern Peru. (c) Left tibia of *Pseudopreotherium* sp. (MUSM 1587) and mapping of the bite marks: photograph and schematic drawing in anterior (i,ii) and posterior (iii,iv) views. (d) Transversal, wide score (#11) of the anterior side. (e) Shallow, blunt pits (#1,2) of the anterior side. (f) Deep, large puncture (#30) of the posterior side. In (c)(iv), grey colour indicates collapsed areas of cortical bone. In (e) and (f), the white arrows indicate the bisecting.

putative perpetrator of the attack and its victim and discuss this uncommon evidence of predator–prey interaction from proto-Amazonian times.

2. Methods

We analysed bite marks and anatomy of the tibia MUSM (Museo de Historia Natural de San Marcos, Peru) 1587. To facilitate description, we numbered them and followed bite marks terminology of ([14–17]; electronic supplementary material). To identify the perpetrator and its *modus operandi*, we examined feeding anatomy of modern and Miocene crocodylian specimens from the literature and stored at MUSM, UCMP (University of California Museum of Paleontology, USA), DGM (División de Geología e Mineralogía, Brazil), IGM (Servicio Geológico Colombiano, Colombia) and MNHN (Muséum national d'Histoire naturelle, France).

3. Results

(a) The prey

The left tibia (MUSM 1587; figure 1c, electronic supplementary material) belongs to a middle-sized ground sloth (*Xenarthra*, Folivora), as indicated by the femoral facets, the medial being concave and the lateral being convex. The epiphyses are completely fused to the diaphysis, indicating that this specimen belonged to an adult individual. This tibia is attributed to the mylodontid sloth *Pseudopreotherium* based on a robust diaphysis with concave lateral side and convex proximomedial side with a well-marked tuberosity; sharp intercondylar eminence; medial condyle anteroposteriorly extended; and odontoid and discoid facets strongly concave and subequal in size. *Pseudopreotherium* was previously recognized in the middle Miocene of Colombia and late Miocene of Brazil and Venezuela ([18]; electronic

supplementary material). The body weight of the sloth [19] is estimated in 78.5 kg, equivalent to a large capybara ([20]; electronic supplementary material).

(b) The tooth marks

Forty-six tooth marks are identified on the shaft of the tibia (figure 1c–f; electronic supplementary material). Highly tooth-marked bones probably represent grasping elements during capturing or dismembering [15]. Five are large punctures that reached the trabecular bone, 36 are shallow pits and four are wide scores. Pits and punctures vary in diameter from 3 (#44) to 15 mm (#30). Most often they are round, but some are clearly bisected (e.g. #1, 5 and 30). Bisected pits and punctures are produced by carinated crown teeth of crocodylians and are not recorded in bones modified by mammals [14,21]. Most of the tooth marks present on the anterior side of the tibia are relatively small and shallow pits. Large punctures are restricted to the posterior side. Some punctures (#30, 40 and ?45) and pits (#31, 34 and ?37) of the posterior surface comprise a serial marking (i.e. multiple marks inflicted by adjacent teeth in one bite [15]) along the shaft. The serial marking was produced by a violent, powerful bite that simultaneously fractured and depressed large areas of the surrounding cortical bone (figure 1c). On the anterior surface, at least two serial pits (#1 and 5) are identified. The four scores represent only 8.9% of the total number of bite marks. Scavenging usually produces abundant scores [15,17] and comparatively few scores are rare. They are flat-bottomed, roughly parallel between them and transverse to the main axis of the diaphysis. Parallel scores suggest grasping and dragging but also attempted disarticulation [15]. Hook scores (i.e. parabolic depressions, *sensu* [15,17]) are not observed. These particular marks are usually associated with dismemberment of the carcass by ‘death rolling’ or inertial feeding [15,22].

(c) The predator

Thirteen million years ago, South America was an island continent; placental carnivorans have not yet reached its shores, and borhyaenid marsupials occupied niches of large carnivores. The bisected pits and punctures observed in the tibia does not match with the heterodont dentition of borhyaenids [23]. Instead, they are typical in bones dispatched by crocodylians [15,21]. In the lignitic bone beds of the Pebas Formation, up to seven sympatric crocodylian taxa have been previously identified: the blunt-snouted caimanines *Gnatusuchus pebasensis*, *Kuttanacaiman iquitosensis* and *Caiman wannlangstoni*; the smooth-fronted caiman *Paleosuchus* sp.; the gavialoid *Gryposuchus pachakamue*; and two large caimanines, the ‘duck-faced’ *Mourasuchus atopus* and the giant *Purussaurus neivensis* [2,12]. The first three are characterized by a posterior crushing dentition suited to feeding on clams, with *Gnatusuchus* additionally bearing a highly modified mandible and anterior dentition attributed to head-burrowing [2]. Because the dentition of *Kuttanacaiman* and *C. wannlangstoni* is relatively close to that of living caimans, they might had been able to feed upon a wider range of prey than *Gnatusuchus*. However, these animals were far too small as adults (approx. 1.7–2.3 m) to inflict the large punctures documented in MUSM 1587. *Paleosuchus* sp. was also a caiman of similar small size, but with gracile, sharply pointed teeth that instead would have produced minute and narrow scores [24], shown to be absent. *G. pachakamue* [12], as typically in gavialoids, possesses a long

and slender snout with sharp teeth and probably fed upon small and rapid prey [25]. *M. atopus* had a long, flat and wide rostrum and bore multiple thin teeth that progressively decrease in size towards the back of the mouth [3,5]. *Mourasuchus* was a relatively large animal (approx. 4–5 m) but probably fed upon small organisms by any kind of filtering strategy [3]. Finally, the feeding anatomy of *P. neivensis*, the top predator of the Pebas System, is consistent with the bite marks observed in the tibia.

Purussaurus possesses a broad, massive skull and robust jaws, typical in crocodylians of the macro-generalist ecomorph [26]. The dentition comprises large, conical anterior teeth particularly at the symphyseal jaw, and small, blunt to globular teeth posterior to the sixth alveoli in the dentaries and the maxillae [3,4]. Conical teeth are circular to oval in cross-section and the tip of the crown is blunt (figure 2d). Distinct mesial and distal carinae are present in all teeth but the carinae are attenuated at the tip [6]. In correspondence with the conical and blunt teeth of *Purussaurus*, pits in the tibia are round and relatively shallow. The attenuation of the carinae toward the crown apex is revealed by the absence of marks with sharp borders and the few bisected pits and punctures.

Based on the largest and deepest puncture (#30: 15 mm) and the distance between pits and punctures of the serial marking ([27–29]; 27–32 mm), we estimated the body length of the perpetrator. These tooth marks roughly match with the anterior dentition of individuals of approximately 50–60 cm of dorsal skull length (DSL), slightly larger than IGM DHL45, a skull of a young *P. neivensis* ([3]; figure 2b; electronic supplementary material). This individual is equivalent in size to an adult black caiman, *Melanosuchus niger* (e.g. MUSM CR; figure 2a). For the DSL of IGM DHL45, the estimated total body length [30] is approximately 3.86 m. A fully grown *P. neivensis* (e.g. UCMP 39704; figure 2c) provides much larger dentition measures and might have reached approximately 6.18 m of body length. Thus, the attack was most likely perpetrated by an approximately 4 m long young or sub-adult *Purussaurus*.

4. Discussion

Neontological and palaeontological data have shown that large to giant crocodyliforms (approx. 3–10 m) have a wide range of prey, such as invertebrates, fishes, mammals (including hominids) and even dinosaurs [14,31–33]. Regarding *Purussaurus*, previous evidence attributed to its feeding behaviour is based on a large shell of the aquatic turtle *Podocnemis* (late Miocene, Peruvian Amazonia) bearing a huge bite of approximately 60 cm [6,34] (figure 2e). As a result of this attack, the turtle lost several peripheral and pleural bones of the posterior left side of the carapace, and presumably, the corresponding hind limb was amputated. Bone regeneration lining the bite is testament that the victim survived and healed. The sinuosity observed along the healed margin suggests that the bite marks were inflicted by serial teeth. Both the carapace bone thickness at this region reaching approximately 15 mm and the size of the bite out imply a giant perpetrator, possibly as big as an adult size of *Purussaurus brasiliensis* (greater than 10 m in total length [6,35]). It seems to be that giant crocodylians with broad snouts and robust, blunt teeth, such as *Purussaurus* and the

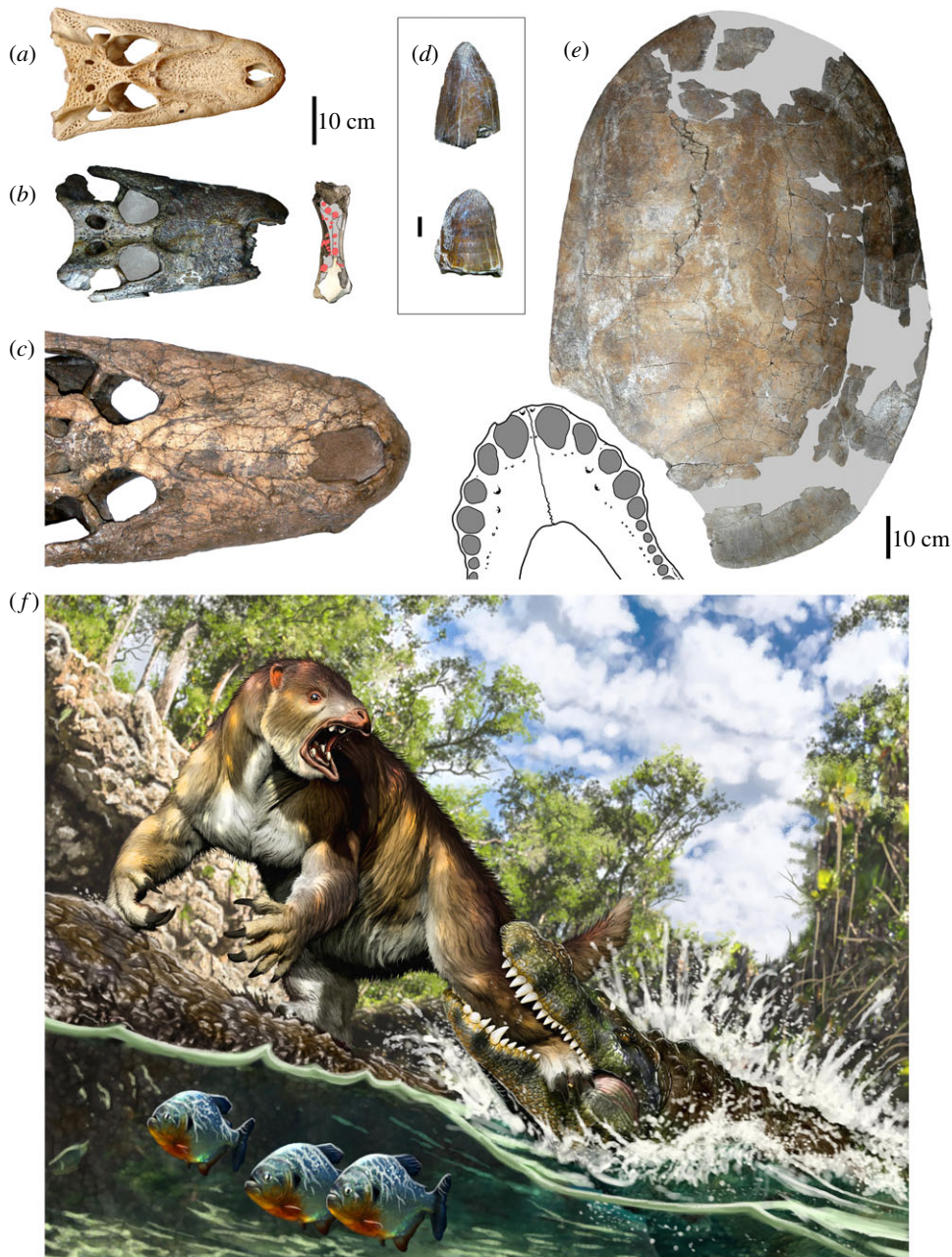


Figure 2. Skulls in dorsal view of (a) an adult size black caiman *Melanosuchus niger* (MUSM CR); (b) a juvenile *Purussaurus neivensis* (IGM DHL45). La Venta (Colombia), facing the bite-marked tibia; (c) a fully grown *P. neivensis* (UCMP 39704), La Venta (Colombia). (d) Teeth of *P. neivensis* (MNHN n/n) from La Venta (Colombia), scale bar is 10 mm. (e) Shell of *Podocnemis* (MUSM 919) in dorsal view from the late Miocene of Iñapari, Peruvian Amazonia. The carapace bearing a bite out of approximately 60 cm is faced with DGM 527-R, a huge jaw of *Purussaurus brasiliensis* from the late Miocene of Acre, Brazil [35]. (f) Life reconstruction of the putative attack of a young to sub-adult *Purussaurus* on the ground sloth *Pseudopreotherium* in a swamp of proto-Amaozonia. Art: Jorge A. González.

North American Cretaceous alligatoroid *Deinosuchus* [32,36], commonly prey on large turtles at adulthood.

The toothed-marked tibia of the ground sloth reveals that *Purussaurus* also fed upon terrestrial mammals within the proto-Amaozonian swamps. In 2004, lignite and coquina localities at Napo River yielded numerous fish and aquatic turtle remains along with teeth and bones of rodents and ground sloths [13]. These lignite deposits depict dysoxic and shallow wetlands [2,7], where lurking crocodylians were abundant and terrestrial mammals were ambushed or scavenged. Beside ground sloths and rodents, a wide array of native ungulates (i.e. astrapotheres, notoungulates, litopterns) documented with *Purussaurus* species in Miocene localities [6,37–41] might have represented prey items for large to giant individuals.

If living crocodylian species show substantial changes in bite force and diet throughout their ontogeny [42,43], it is reasonable to think that the notable increase in the bite force during the development of giant, extinct species have driven extreme shifts in feeding behaviour [6]. Bite forces recorded from the developmental series of *Alligator mississippiensis* range from 12 to 9452 N (about 1 ton-force), almost 800-fold increase from hatchling to a total body length of 3.71 m [44]. This increase in bite force is accompanied by other anatomical changes and reflects the transition from eating insects, spiders and small vertebrates to large mammals and turtles [45]. Because bite force does not differ significantly across same-sized brevirostrine taxa (alligatoroids and crocodyloids) [45], *Purussaurus*, *Alligator* and *Crocodylus* individuals of similar

size might be capable of chasing comparable prey items. Thus, a young *Purussaurus*, of about 3.5–4 m of body length, feeding upon ground sloths (around the size of a capybara) might have been predicted by this conservative bite-force scaling hypothesis.

Instead, adult size *Purussaurus* species have no ecological analogues in the living world. The bite force of a giant individual of *P. brasiliensis* have been estimated in 69 039.2 N (approx. 7 tons-force) [6], a value that largely exceeds that of the strongest bite ever measured in the animal kingdom (i.e. 16 143 N in *Crocodylus porosus* [45]). With this powerful bite and a macro-generalist morphotype [26], giant individuals were able to incorporate into their diet larger and solidly shielded prey items (e.g. giant mammals and large turtles [46]).

P. neivensis was the only caiman of high trophic level found in the rich bonebeds of the Pebas Formation. Bite marks in the tibia are consistent with the blunt-tipped, carinated and robust crown teeth of a juvenile to sub-adult *Purussaurus*. The tibia of the *Pseudopreotherium* was trapped by the anterior upper and lower teeth during a powerful bite that fractured and depressed large portions of cortical bone. The presence of few scores is unusual in bones altered during scavenging [15,17], yet our understanding on scavenging versus predation mark patterning is still insufficient or controversial to distinguish between these sources of tooth-marking [47,48]. Predation is here favoured because the ground sloth is largely within the expected prey size of the

macro-generalist ecomorph of *Purussaurus* [26]. In present day Africa when a large Nile crocodile attacks a wildebeest or a zebra from the river, it tends to direct its attack to the neck or the hind limbs before dragging its prey into the water [43]. In Miocene proto-Amazonian wetlands, whereas giant individuals fed upon massive mammals and turtles, an immature *Purussaurus* gripped a capybara-sized ground sloth from the lower hind limb (figure 2f).

Data accessibility. All data are included herein or in the electronic supplementary material.

Authors' contributions. F.P. and R.S.-G. designed and performed research and wrote the manuscript. All authors discussed the results, edited the manuscript, approved the final version and agree to be held accountable for the content.

Competing interests. We declare we have no competing interests.

Funding. R.S.-G. acknowledges support from CONCYTEC, Peru (Incorporación de Investigadores, grant no. E038-2019-02-FONDECYT-BM), (grant no. E041-2018-01-FONDECYT).

Acknowledgements. We thank participants of the mission to Napo River (2004), especially P. Baby and J.-L. Guyot. We are indebted to the IGM (Colombia), T.J. Gaudin, L. Marivaux, R.D.E. MacPhee, P. Janvier and N. Pyenson; W. Aguirre for preparation of the tibia; the INAMHI (Ecuador), the SENAMHI (Peru) and the IRD (Ecuador, Peru and France) for their help during the Napo Mission. The authors thank S. Jouve and an anonymous reviewer for their constructive critical comments; P.-O. Antoine for inviting them to participate in the Eclipse Program, CNRS; J. Flynn for his continuous support to RS-G in proto-Amazonian studies.

References

- Mook CC. 1941 A new fossil from Colombia. *Proc. U.S. Nat. Mus.* **91**, 55–61. (doi:10.5479/si.00963801.91-3122.55)
- Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara JV, Wesselingh FP, Antoine P-O. 2015 A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proc. R. Soc. B* **282**, 20142490. (doi:10.1098/rspb.2014.2490)
- Langston Jr W. 1965 Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. *Univ. Calif. Publ. Geol. Sci.* **52**, 1–157.
- Bocquentin VJ, Filho JPS, Buffetaut E, Negri FR. 1989 Nova interpretação do gênero *Purussaurus* (Crocodylia, Alligatoridae). *Anais do XI Congresso Brasileiro de Paleontologia* **1**, 427–433.
- Scheyer TM, Delfino M. 2016 The late Miocene caimanine fauna (Crocodylia: Alligatoroidea) of the Urumaco Formation, Venezuela. *Palaeontol. Electron.* **19.3.48a**, 1–57. (doi:10.26879/657)
- Aureliano T, Ghilardi AM, Guilherme E, Souza-Philo 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)
- Wesselingh FP, Räsänen ME, Irion G, Vonhof HB, Kaandorp R, Renema W, Romero Pittman L, Gingras M. 2002 Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainoz. Res.* **1**, 35–81.
- 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)
- Wesselingh FP, Hoorn MC, Guerrero J, Räsänen ME, Romero Pittman L, Salo J. 2006 The stratigraphy and regional structure of Miocene deposits in western Amazonia (Peru, Colombia and Brazil), with implications for late Neogene landscape evolution. *Scr. Geol.* **133**, 291–322.
- Nuttall CP. 1990 A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bull. Br. Mus. Nat. Hist. Geol.* **45**, 165–371.
- Monsch KA. 1998 Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **143**, 31–50. (doi:10.1016/S0031-0182(98)00064-9)
- Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara JV, Claude J, Antoine P-O. 2016 A new 13 million year old gavialoid crocodylian from proto-Amazonian mega-wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLoS ONE* **11**, e0152453. (doi:10.1371/journal.pone.0152453)
- Pujos F, Albino AM, Baby P, Guyot JL. 2009 Presence of the extinct lizard *Paradracaena* (Teiidae) in the Middle Miocene of the Peruvian Amazon. *J. Vertebr. Paleontol.* **29**, 594–598. (doi:10.1671/039.029.0227)
- Binford LR. 1981 *Bones: ancient men and modern myths*. New York, NY: Academic Press.
- Njau JK, Blumenschine RJ. 2006 A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. *J. Human. Evol.* **50**, 142–162. (doi:10.1016/j.jhevol.2005.08.008)
- Njau J, Gilbert H. 2016 Standardizing terms for crocodile-induced bite marks on bone surfaces in light of the frequent bone modification equifinality found to result from crocodile feeding behavior, stone tool modification, and trampling. *Forost* **3**, 1–13. (doi:10.13140/RG.2.2.15139.66087)
- Drumheller SK, Brochu CA. 2014 A diagnosis of *Alligator mississippiensis* bite marks with comparisons to existing crocodylian dataset. *Ichnos* **21**, 131–146. (doi:10.1080/10420940.2014.909353)
- Hirschfeld SE. 1985 Ground sloths from the Friasian La Venta fauna, with additions to the pre-Friasian Coyaima fauna of Colombia, South America. *Univ. Calif. Pub. Geol. Sci.* **128**, 1–91.
- Toledo N, Cassini GH, Vizcaíno SF, Bargo MS. 2014 Mass estimation of Santacrucian sloths from the Early Miocene Santa Cruz Formation of Patagonia, Argentina. *Acta Palaeontol. Pol.* **59**, 267–280. (doi:10.4202/app.2012.0009)
- Mones A, Ojasti J. 1986 *Hydrochoerus hydrochaeris*. *Mamm. Species* **264**, 1–7. (doi:10.2307/3503784)

21. Drumheller SK, Brochu CA. 2016 Phylogenetic taphonomy: a statistical and phylogenetic approach for exploring taphonomic patterns in the fossil record using crocodylians. *Palaio* **31**, 463–478. (doi:10.2110/palo.2016.030)
22. D'Amore DC, Blumenschine RJ. 2009 Komodo monitor (*Varanus komodoensis*) feeding behaviour and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology. *Paleobiology* **35**, 525–552. (doi:10.1666/0094-8373-35.4.525)
23. Prevosti FJ, Forasiepi A. 2018 *Evolution of South American mammalian predators during the Cenozoic: paleobiogeographic and paleoenvironmental contingencies*. Cham, Switzerland: Springer International Publishing AG.
24. Milàn J, Kofoed J, Bromley RG. 2010 Crocodylian-chelonian carnivory: bite traces of dwarf caiman, *Paleosuchus palpebrosus*, in red-eared slider, *Trachemys scripta*, carapaces. In *Crocodyle tracks and traces. New Mexico Museum of Natural History and Science, Bulletin 51* (eds J Milàn, SG Lucas, MG Lockley, JA Spielmann), pp. 195–200. Albuquerque, NM: New Mexico Museum of Natural History and Science.
25. Salas-Gismondi R, Moreno-Bernal JW, Scheyer TM, Sánchez-Villagra MR, Jaramillo C. 2018 New Miocene Caribbean gavialoids and patterns of longirostry in crocodylians. *J. Syst. Palaeontol.* **17**, 1049–1075. (doi:10.1080/14772019.2018.1495275)
26. Drumheller SK, Wilberg EW. 2020 A synthetic approach for assessing the interplay of form and function in the crocodyliform snout. *Zool. J. Linnean Soc.* **188**, 507–521. (doi:10.1093/zoolinnean/zlz081)
27. Buffetaut E. 1983 Wounds on the jaw of an Eocene mesosuchian crocodylian as possible evidence for the antiquity of crocodylian intraspecific fighting behaviour. *Palaontol. Z.* **57**, 143–145. (doi:10.1007/BF03031756)
28. Erickson BR. 1984 Chelonivorous habits of the Paleocene crocodile *Leidyosuchus formidabilis*. *Sci. Pub. Sci. Mus. Minnesota* **5**, 1–9.
29. Noto CR, Main DJ, Drumheller SK. 2012 Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: example from the Woodbine Formation of Texas. *Palaio* **27**, 105–115. (doi:10.2110/palo.2011.p11-052r)
30. Albarracín M, Madera R. 2011 Estudios bioecológicos del caimán negro (*Melanosuchus niger*) en la laguna de Limoncocha, Ecuador. *Anu. Univ. Int. SEK* **12**, 71–77.
31. Magnunsson WE, Viera da Silva E, Lima AP. 1987 Diet of Amazonian crocodylians. *J. Herpetol.* **21**, 85–95. (doi:10.2307/1564468)
32. Scheyer TM, Delfino M, Klein N, Bunbury N, Fleischer-Dogley F, Hansen DM. 2018 Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene. *R. Soc. Open Sci.* **5**, 171800. (doi:10.1098/rsos.171800)
33. Schwimmer DR. 2010 Bite marks of the giant crocodylian *Deinosuchus* on Late Cretaceous (Campanian) bones. In *Crocodyle tracks and traces. New Mexico Museum of Natural History and Science, Bulletin 51* (eds J Milàn, SG Lucas, MG Lockley, JA Spielmann), pp. 183–190. Albuquerque, NM: New Mexico Museum of Natural History and Science.
34. Salas-Gismondi R, Flynn J, Baby P, Tejada-Lara J, Antoine P-O. 2014 Sobre el origen de la diversidad amazónica. In *Iquitos* (eds R Varón Gabai, C Maza), pp. 84–91. Lima, Peru: Telefónica del Perú.
35. Price LI. 1967 Sobre a mandíbula de um gigantesco crocodilo extinto do alto Rio Juruá, Estado do Acre. *Atlas do simpósio sobre a biota amazônica* **1**, 359–371.
36. Schwimmer DR. 2002 *King of the crocodylians: the paleobiology of deinosuchus*. Bloomington, IN: Indiana University Press.
37. Tejada-Lara JV *et al.* 2015 Life in protoamazonia: middle Miocene mammals from the Fitzcarrald arch (Peruvian Amazonia). *Palaentology* **58**, 341–378. (doi:10.1111/pala.12147)
38. Antoine P-O *et al.* 2016 A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Res.* **31**, 30–59. (doi:10.1016/j.gr.2015.11.001)
39. Kay RF, Madden RH. 1997 Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). *J. Hum. Evol.* **32**, 161–199. (doi:10.1016/j.jgr.2015.11.001)
40. Negri FR, Bocquentin-Villanueva J, Ferigolo J, Antoine P-O. 2010 A review of Tertiary mammal faunas and birds from western Amazonia. In *Amazonia, landscape and species evolution: a look into the past* (eds C Hoorn, FP Wesselingh), pp. 245–258. Oxford UK: Blackwell Publishing.
41. Sánchez-Villagra MR, Aguilera AO. 2006 Neogene vertebrates from Urumaco, Falcón State, Venezuela: diversity and significance. *J. Syst. Palaeontol.* **4**, 213–220. (doi:10.1017/S1477201906001829)
42. Pooley AC. 1989 Food and feeding habits. In *Crocodyles and alligators* (ed. CA Ross), pp. 76–91. New York, NY: Facts on File.
43. Grigg G, Kishner D. 2015 *Biology and evolution of crocodylians*. Ithaca, NJ: Cornell University Press.
44. Erickson GM, Lappin AK, Vliet KA. 2003 The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *J. Zool.* **260**, 317–327. (doi:10.1017/S0952836903003819)
45. Erickson GM, Gignac PM, Lappin AK, Vliet KA, Brueggen JD, Webb GJW. 2014 A comparative analysis of ontogenetic bite-force scaling among Crocodylia. *J. Zool.* **292**, 48–55. (doi:10.1111/jzo.12081)
46. Cadena E-A, Scheyer TM, Carrillo-Briceño JD, Sánchez R, Aguilera-Socorro AO, 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)
47. Delaney-Rivera C, Plummer TW, Hodgson JA, Forrest F, Hertel F, Oliver JS. 2009 Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. *J. Archaeol. Sci.* **36**, 2597–2608. (doi:10.1016/j.jas.2009.08.001)
48. Njau JK. 2006 The relevance of crocodiles to Oldowan hominin paleoecology at Olduvai Gorge, Tanzania. PhD thesis, Rutgers University.