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PALEONTOLOGY

The largest freshwater odontocete: A South Asian river dolphin relative from the proto-Amazonia

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Several dolphin lineages have independently invaded freshwater systems. Among these, the evolution of the South Asian river dolphin *Platanista* and its relatives (Platanistidae) remains virtually unknown as fossils are scarce. Here, we describe *Pebanista yacuruna* gen. et sp. nov., a dolphin from the Miocene proto-Amazonia of Peru, recovered in phylogenies as the closest relative of *Platanista*. Morphological characters such as an elongated rostrum and large supraorbital crests, along with ecological interpretations, indicate that this odontocete was fully adapted to fresh waters. *Pebanista* constitutes the largest freshwater odontocete known, with an estimated body length of 3 meters, highlighting the ample resource availability and biotic diversity in the region, during the Early to Middle Miocene. The finding of *Pebanista* in proto-Amazonian layers attests that platanistids ventured into freshwater ecosystems not only in South Asia but also in South America, before the modern Amazon River dolphin, during a crucial moment for the Amazonian evolution.

INTRODUCTION

Cetacean freshwater transitions occurred in several areas asynchronously during the Neogene. Modern "river dolphins" arose from such events, as the similar morphology of these only distantly related taxa is the result of a clear convergent evolution (*1*, *2*). Among odontocetes (toothed cetaceans), four clades of river dolphins are recognized (Fig. 1A): Iniidae, Lipotidae, Platanistidae, and Pontoporiidae (*2*, *3*). The Yangtze river dolphin *Lipotes vexillifer* (Lipotidae) had fully riverine habits but was declared extinct a couple decades ago (*4*, *5*). Among the extant taxa, only *Platanista* (Platanistidae) and *Inia* (Iniidae) are strictly freshwater inhabitants (*6*), as the La Plata dolphin *Pontoporia blainvillei* (Pontoporiidae) roams shallow coastal waters.

Platanista from the South Asian river systems (Fig. 1) is one of the most enigmatic toothed cetaceans and unique by bearing enlarged, thin and pneumatic supraorbital crests that enclose the melon, a fatty structure integral to the echolocation system, which the animal uses to locate and capture prey in muddy waters. Echolocation in *Platanista* is so dominant that the animal is almost blind (*7*). The evolutionary history of *Platanista* (*8*) and kin remains elusive because fossil data of close relatives are restricted to marine forms such as *Araeodelphis*, *Pomatodelphis*, *Prepomatodelphis*, and *Zarhachis* (*2*, *3*). Contrarily, distant Platanistoidea relatives are one of the most diverse and frequently fossilized cetaceans, with records ranging from the Late Oligocene until the Middle Miocene. A similar situation pertains to the South American river dolphin *Inia* (Iniidae), whose fossil relatives have mostly been found in marine environments (*9*–*11*), with the exception of *Ischyrorhynchus* from the Late Miocene of Argentina (*12*). The overall fossil record of river dolphins is of limited value because the factors that led to repeated freshwater lifestyles from marine ancestors in Cetacea would preferably require fossils of freshwater forms (*13*, *14*).

Here, we describe a previously unknown platanistid dolphin found in Early to Middle Miocene layers of Peruvian Amazonia. Its holotype skull is characterized by a robust and long rostrum with enlarged teeth, well-developed supraorbital crests, a large temporal fossa, and a deep circumnarial basin. A series of phylogenetic analyses place the new taxon as a sister group to extant *Platanista*, thus demonstrating that at least two clades of odontocetes (Platanistidae and Iniidae) transitioned into freshwater environments in South America. Size estimations based on cranial measurements of the holotype of the new species and specimens referred to the same genus indicate that the new dolphin likely is the largest known freshwater odontocete, at 2.8 to 3.5 m at a minimum, surpassing the 2.5-m maximum size of modern "river" dolphins. Such a large body size, also recorded in other proto-Amazonia inhabitants (i.e. fishes and crocodilians), might be attributed to the large resource availability in proto-Amazonian ecosystems (*15*–*18*). Additional factors that may have contributed to the great body size of this new taxon include the lack of direct predators and competitors in the Pebas mega-wetland system. This finding confirms not only an independent marine-freshwater transition of cetaceans in South America but also that this diversity in the vast Pebas mega-wetland system might have greatly benefited from the warmer Middle Miocene climatic conditions in the area.

RESULTS

Systematic paleontology

Odontoceti

Platanistidae

Pebanista yacuruna sp. nov.

(Fig. 2).

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Etymology

The generic name *Pebanista* stresses the relationship between this taxon from the Pebas Fm. (section S1) and the extant Ganges and Indus river dolphins *Platanista* (*Platanista gangetica* and *Platanista minor*). The specific Kichua (northern Quechua) name honors the "yacuruna," a mythical water creature in the Peruvian Amazonia.

Holotype

MUSM 4017, an isolated skull from an adult individual that preserves the posterior part of the rostrum, facial region including part of the right supraorbital crest, the temporal and occipital regions (Fig. 2, section S2, and figs. S3 to S5). The specimen is permanently stored at the vertebrate palaeontology collection of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM).

Locality, age and horizon

MUSM 4017 was collected in 2018 in stratigraphic levels that correspond to the upper Pebas Fm. exposed along the Rio Napo, Loreto, Peru (latitude, −3.012468°; longitude, −73.404855°). The palynological assemblage indicates freshwater environments, assignable to palynological Zones T-13 to Zone T-15 of Jaramillo *et al.* (*19*), ranging from the late Early Miocene to the Middle Miocene [circa 17 to 14 million years

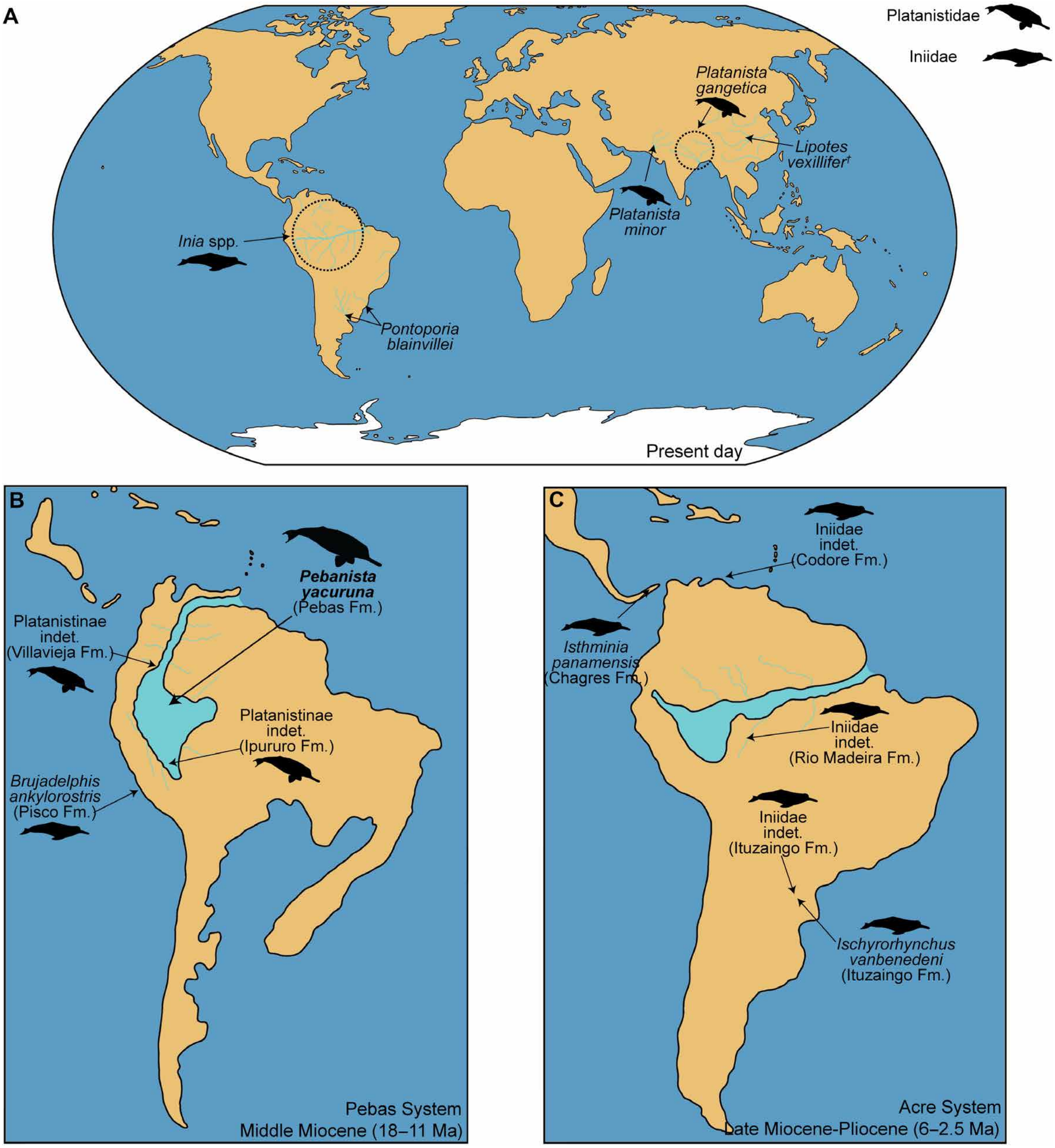

Fig. 1. Biogeographical and paleobiogeographic distribution of Iniidae and Platanistidae through the Neogene. Schematic representation of the region highlighting the presence of epicontinental waters in South America (pale blue). Extant geographical ranges of the Amazon river dolphin *Inia* and the South Asian river dolphins *Platanista* (**A**). Distribution of fossil Iniidae/Platanistidae records in the Early to Middle Miocene Pebas System (**B**) and Late Miocene Acre System (**C**). Modified from Benites-Palomino *et al.* (*14*).

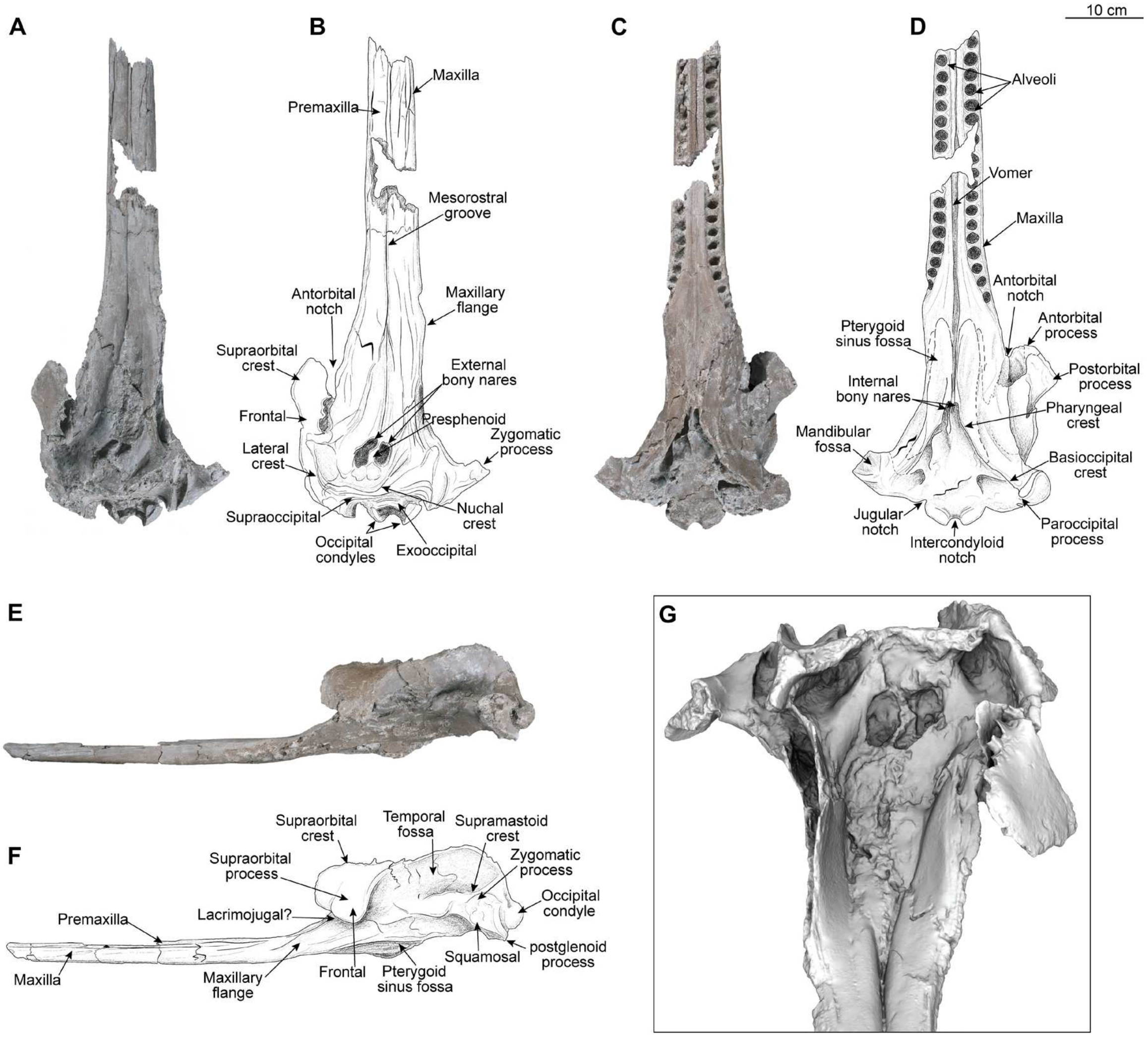

Fig. 2. *Pebanista yacuruna* gen. et sp. nov., MUSM 4017. Holotype skull in dorsal (**A** and **B**), ventral (**C** and **D**), left lateral (**E** and **F**), and anterodorsal views (F and **G**).

(Ma)]. Maximum likelihood analysis further constrains the age to the latest Early Miocene (circa 16.5 Ma.; section S1 and figs. S1 and S2).

Diagnosis and remarks

The holotype skull of *Pebanista yacuruna*, MUSM 4017, has a preserved condylobasal length of 698 mm and an estimated bizygomatic width of 281 mm. The sutures between the cranial bones (e.g., maxilla-premaxilla suture along the rostrum) are well closed or fused, indicating an adult stage. *Pebanista* is recognized as a member of Platanistidae by having the vertex of the skull deviated leftwards (Fig. 2, A and B); asymmetry of the premaxillae in the rostrum and facial areas of the skull; braincase anteroposteriorly shorter than wide; and lack of contact of the palatines, with both projecting dorsolaterally (figs. S3 and S4). The rostrum of the holotype specimen is dorsoventrally flattened and elongated, a condition shared with the extinct *Pomatodelphis*, *Prepomatodelphis*, and *Zarhachis*, in contrast to the transversely compressed rostrum of extant *Platanista*. On the preserved portion, the rostrum is formed by the premaxillae, maxillae, and vomer, being much more transversely robust than in other platanistids. The rostrum exhibits several well-preserved dental alveoli; these are proportionally larger than those of other platanistids (fig. S4). The facial region of the skull exhibits a well-developed circumnarial basin, delimited laterally by the supraorbital crests and posteriorly by the nuchal crest. The external bony nares are displaced to the left, creating an asymmetric array of the surrounding bones. *Pebanista* displays greatly developed lateral supraorbital crests, projecting dorsomedially over the level of the facial region of the skull. These crests are formed by the frontal bone, unlike in *Pomatodelphis* and *Zarhachis* in which they are formed by the frontal laterally and the maxilla medially, and unlike in *Platanista* in which the crests are only formed by the maxillae. The supraorbital crests in *Pebanista* are robust but transversely flattened as in *Platanista*. The dorsomedial edge of the crests presents several large vacuities, which could foreshadow the full excavation of the crest in *Platanista*, which receives the dorsal extension of the pterygoid sinus (*20*). Only the left orbit is preserved, which in lateral view is proportionally shorter than other platanistids, a condition solely shared with extant *Platanista*. The pterygoids in *Pebanista* cover most of the palatines ventrally, except for a narrow lateral stripe. *Pebanista* differs from

Pomatodelphis and *Zarhachis* by having transversely compressed walls of the supraorbital crests, partly resembling those of *Platanista*. The temporal fossa is anteroposteriorly longer than high and extends posteriorly into the occipital region (fig. S5). Posteriorly, the nuchal crest joins the supraorbital crest, giving the skull a squared posterior outline in dorsal view. The occipital shield projects slightly toward the anterior region of the skull, but it is not possible to assess whether this is its true shape, or a condition resulting from taphonomic compression.

Additional materials

cf. *Pebanista* MUSM 3593 an isolated rostral fragment and Platanistidae indet. MUSM 4759 an isolated tympanic bulla (section S2 and fig. S6).

Phylogenetic analyses

In all of our parsimony phylogenetic analyses, *Pebanista* was recovered within Platanistidae (Fig. 3 and fig. S7), with many of the other phylogenetic relationships being consistent with those of a prior work (*21*). All characters were equally weighted in a first analysis yielding phylogenies with poor intraclade resolution (low node support and high number of polytomies; section S2). Subsequent analyses were conducted with implied weighting of homoplasious characters (*22*, *23*), which resulted in improved support values for the two main Platanistoidea clades Platanistidae and Squalodelphinidae. Within Platanistidae, the two clades were supported with high bootstrap values (>70), one containing the fossil taxa *Zarhachis* and *Pomatodelphis* and the second uniting *Pebanista* and the extant *Platanista* (bootstrap value = 70). Following prior studies (*21*), and due to better resolution within Squalodephinidae, we opted for calculating the Adams consensus.

Body size reconstruction

The estimated body size of the holotype specimen of *Pebanista yacuruna* is 280 cm, based solely on the bizygomatic width. The bizygomatic width of cf. *Pebanista* MUSM 3593 (estimated from the

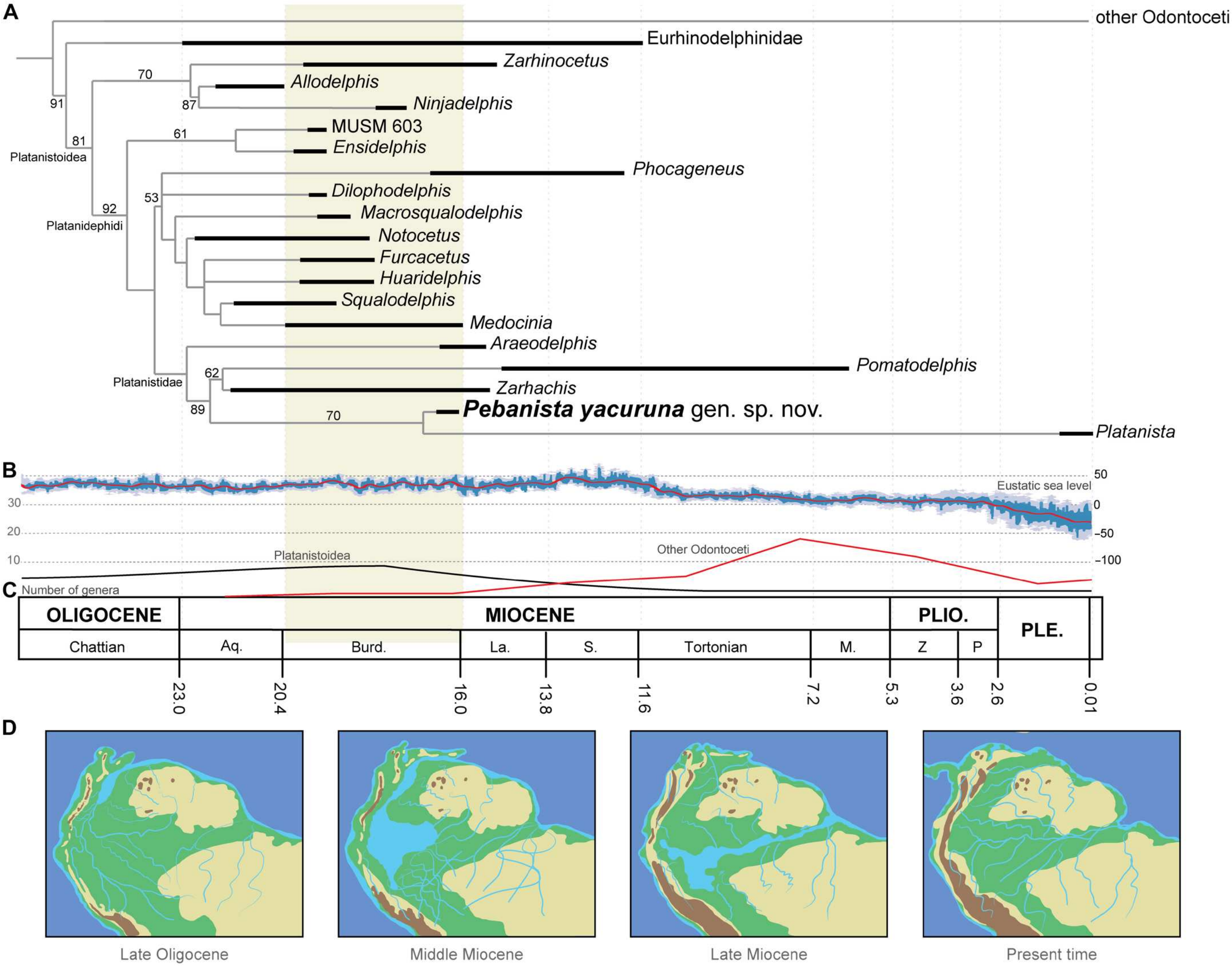

Fig. 3. Phylogenetic relationships of *Pebanista yacuruna* gen. et sp. nov. and the evolutionary context of Platanistoidea within proto-Amazonia. Adams consensus from three most parsimonious trees (**A**); eustatic sea level evolution (*63*) across the mid-Late Neogene (**B**); diversity of Platanistoidea (*28*) versus other Odontoceti clades (**C**); geographical evolution (*49*, *50*) of the Neotropical region (**D**).

holotype specimen proportions) resulted in an estimated body length of 347 cm. However, prior works have shown that regression equations using the bizygomatic width might underestimate body lengths, especially for hyperlongirostrine taxa such as *Zarhachis* (*21*), instead suggesting the use of the condylobasal length of the skull, a feature not preserved in the holotype skull of *Pebanista*. Thus, the estimated body sizes for *Pebanista* (range, 281 to 347 cm) should be considered minima for this fossil platanistid dolphin.

DISCUSSION

The South Asian river dolphins *Platanista gangetica* (Ganger river dolphin) and *P. minor* (Indus river dolphin) are the sole extant platanistids. Their fossil relatives, the marine Platanistoidea, were highly diverse between the Oligocene and the Early Miocene, reaching a cosmopolitan distribution. Their wide array of body sizes and skull morphologies indicates that they occupied different trophic levels and developed diverse predatory strategies (*21*, *24*, *25*). The fossil record indicates that the peak diversity of platanistoids was reached during the Early Miocene, a time of global cooling and increased subsidence in the Andean-Amazonian foreland basin system (*26*), including many records of squalodelphinids and allodelphinids (*27*), but began declining toward the Middle Miocene (*28*). Changes in sea level and other oceanic conditions related to the Middle Miocene Climatic Optimum, as well as the emergence of other toothed cetacean groups such as delphinoids (*29*, *30*), beaked whales (*31*), and physeteroids (*32*–*34*), may be related to the decline of platanistoids in marine environments (*35*). Such ecological displacement might have resulted in the surviving Platanistidae being restricted to freshwater environments.

The fossil record of Platanistidae is sparse. Some platanistoids from North America, such as *Araeodelphis* and *Dilophodelphis*, have been phylogenetically placed either within Platanistidae or Squalodelphinidae (*20*, *21*, *24*, *25*). Our phylogenetic analyses recovered *Araeodelphis*, a small taxon from the Early Miocene Calvert Fm. in Maryland (*36*), as the most basal stem member of the Platanistidae, in agreement with prior studies (*20*, *21*, *24*). Within Platanistidae, two clades are recognized: the first includes *Pomatodelphis* and *Zarhachis* (Fig. 3), both found in coastal marine environments from North America. These taxa are characterized by a long slender rostrum with small teeth, a minor development of the supraorbital crests, and a vertex mostly symmetrical when compared to *Platanista*. In addition, vertebrae found in Middle Miocene layers of Venezuela have been tentatively referred to *Zarhachis*, but the material is poorly diagnostic (*27*, *37*). Our phylogenetic analyses unambiguously recovered *Pebanista* as the sister taxon of *Platanista*, thus constituting the closest known relative of the extant South Asian river dolphins. *Pebanista* displays characters previously used to nest together *Pomatodelphis* and *Zarhachis*, such as the flattened rostrum and transverse expansion of the premaxilla (*38*, *39*). However, *Pebanista* also has numerous characters found in *Platanista*, including reduction of the orbit and strong asymmetry of the facial region, medially concave supraorbital crests, enlargement of the temporal fossae, and thickening of the zygomatic process of the squamosal (*40*). In addition, *Pebanista* also has enlarged teeth, which along with the robust rostrum and well-developed skeletal muscle insertions on the skull, it suggests an active raptorial feeding behavior (*41*). The supraorbital crests in *Pebanista* also are distinctive: These are more transversely robust than the thin plate-like crests of *Platanista* but not as robust as in *Zarhachis* or *Pomatodelphis*. Nevertheless, the inner structure of the crests indicates the presence of areas with higher bone density in the outer surface of the supraorbital crests and slightly lower densities medially. This might have facilitated focusing the sound waves of the biosonar system (*20*), also evidenced by the dorsomedial orientation of the supraorbital crests and their medially concave inner surface. Furthermore, the medial surface of the crests of *Pebanista* has a series of cavities or vacuities, resembling the condition observed in *Platanista*, which receives the dorsal extension of the pterygoid sinus (*38*, *39*).

Odontocetes invaded fresh waters several times independently during the Neogene (Fig. 1). Among the four extant clades of river dolphins, only *Inia*, *Platanista*, and the recently extinct *Lipotes* are restricted to freshwater environments, as *Pontoporia* also inhabits coastal environments of Brazil and Argentina. The marine-freshwater transition of Iniidae is better understood than that of Platanistidae because of new findings of the past decade. Two close relatives of *Inia* have been recovered in Late Miocene marine layers of Panama and Peru: *Brujadelphis* and *Isthminia*, respectively (*9*, *10*), indicating that iniids still inhabited coastal marine environments during those times. More recently a third iniid, *Kwanzacetus*, was recovered from rocks of the same age in Angola (*11*), further denoting the high diversity and broad geographic distribution of these cetaceans in marine environments. Marine iniids appear to have survived into the Pliocene, as evidenced by an isolated earbone from the Codore Fm. of Venezuela, which despite resembling that of extant *Inia*, still retained a cochlear morphology better suited for marine environments (*42*). There is little evidence of freshwater iniids in South America, but fossils from the Ituzaingo Fm. in Argentina, as the ones referred to the genus *Ischyrorhynchus*, already indicate the presence of iniids in fluvio-deltaic environments as early as the Late Miocene (*43*). The invasion of freshwater habitats thus must have occurred much earlier and independently in proto-Amazonia by *Pebanista* and in South Asia by *Platanista*. Previously described material from La Venta in Colombia and the Fitzcarrald Arch in Peru already provide evidence that platanistids invaded freshwater systems in South America during the Middle Miocene. Such findings comprise two isolated earbones respectively found in each locality. Both the La Venta and Fitzcarrald periotics display characters solely found in *Platanista* earbones, such as a great reduction of the posterior process and the reduced aperture for the cochlear aqueduct (*13*, *14*, *44*). Thus, the two morphotypes are much closer to *Platanista* than to *Zarhachis* or *Pomatodelphis* and as such might represent taxa closely related to the clade of *Pebanista* and *Platanista*.

The occurrence of *Pebanista* in Early to Middle Miocene layers of the Pebas Fm. in Peru (*45*, *46*) not only confirms the presence of platanistids in the South American continent but also indicates that these animals reached body lengths similar to those of their marine relatives (i.e., larger than extant freshwater dolphins). During the Early to Middle Miocene (23 to 10 Ma), most of the modern west Amazon rainforest area (i.e., in Colombia, Peru, and Brazil) was covered by continental-scale fresh water to brackish water foreland system (the Pebas System) parallel to the Andes (*47*, *48*), with at least two large-scale events of marine influx from the Caribbean (*49*–*53*). This basin formed by by flexural subsidence in response to the Andean tectonic loading since the earliest Miocene (*48*, *54*). The massive proto-Amazonian Pebas wetland system was established during the Early Miocene and reached its maximum extent during the Middle Miocene Climatic Optimum (*46*, *49*, *51*), creating a complex arrangement of terrestrial and aquatic environments rich in nutrients and prey types (*55*). Extraordinary faunal diversity inhabited this region, including a wide array of fishes, turtles, crocodylians (caimans and gharials), and small to large mammals (e.g., marsupials, sloths, rodents, primates, and ungulates), among others (*15*, *56*–*58*). The diverse aquatic environment of the Pebas System, with widely varied and abundant food resources, might have greatly benefited the evolution of large predators, such as *Pebanista* and gharials, the latter a group of longirostrine crocodylians with extant representatives in southeast Asia. *Pebanista* and South American gharials, such as *Gryposuchus*, display an analogous evolutionary pattern, in which marine ancestors invaded and diversified in freshwater environments during the Neogene (*58*). Furthermore, abundance of similar prey items suitable for longirostrine forms and favourable environmental conditions might have prompted the evolution of gigantism among platanistids and *Gryposuchus* (*58*, *59*), markedly exceeding the size of their modern relatives (Fig. 4). The evolution of such large sizes in *Pebanista* and coeval crocodilians (*60*) could be related to a red-queen pattern of size

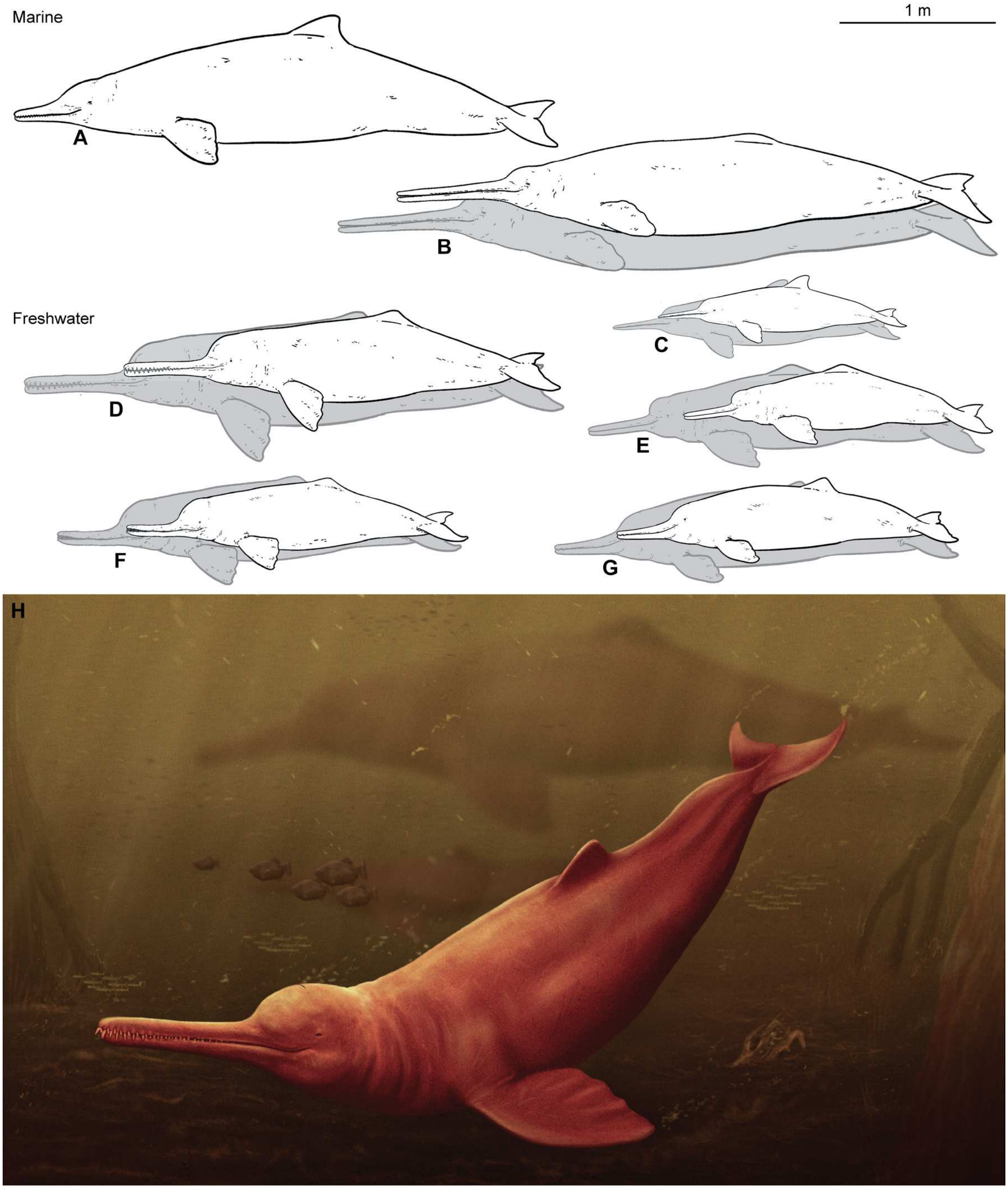

Fig. 4. Size comparison between "river dolphins" and marine platanistoids and river dolphins. White silhouettes indicate the minimum body length calculated or recorded; gray body outlines indicate the largest size recorded or estimated in: *Macrosqualodephis ukupachai*† (**A**), *Zarhachis flagellator*† (**B**), *P. blainvillei* (**C**), *Pebanista yacuruna*† gen. et sp. nov. (**D**), *Inia geoffrensis* (**E**), *Platanista gangetica* (**F**), and *Lipotex vexillifer* (**G**). Artistic reconstruction of *Pebanista yacuruna* gen. et sp. nov. by Jaime Bran (**H**).

increase, as a result of competitive interactions with other aquatic predators.

Pebanista is a new fossil taxon of platanistid dolphin from the Early to Middle Miocene (c. 16.5 Ma) Pebas Fm. in the Amazon Basin of Peru, the first freshwater representative of this clade in South America, characterized by an asymmetrical skull, large and robust rostrum, greatly developed supraorbital crests, and a circumnarial basin extending onto the whole facial region. *Pebanista* is recovered in our phylogenetic analyses as the closest known relative of extant *Platanista* from South Asia, sharing several synapomorphies with the latter, but also a combination of morphological characters that indicate a transitional stage between marine and freshwater habitats. The presence of this Early to Middle Miocene platanistid dolphin confirms the existence of this group in freshwater habitats of the Andean foreland basin system of the South American continent, long before the independent invasion of South American freshwater environments by the Amazon river dolphin lineage (Iniidae, *Inia*). After reaching the continental interior, *Pebanista* would have encountered the extraordinarily rich Pebas mega-wetland communities and vast freshwater environments of proto-Amazonia, thousands of kilometers, and oceans away from the range of extant *Platanista*, during a time in which the unusually broad diversity and great abundance of food resources also would have promoted its evolution toward a greater body size (Fig. 4).

MATERIALS AND METHODS

Phylogenetic analysis

To investigate the phylogenetic relationships of *Pebanista* within Platanistoidea, MUSM 4017 was coded in the morphological matrix of Bianucci *et al.* (*21*) using Mesquite 3.70 (*61*), resulting in a total of 24 operational taxonomic units and 48 morphological characters. Cladistic parsimony analyses were performed in PAUP 4.0a169 (*62*) via heuristic searches using the tree bisection-reconnection algorithm and treating all characters as unordered. Because of the high number of poorly supported nodes (less than 50% bootstrap support) and polytomies resulting from the first parsimony analysis, a series of analyses were performed by down-weighting of homoplastic characters with k values of 2, 3, 10, 20, and 40 (*22*, *23*). Because the topology remained unmodified, the lowest value was kept ($K = 2$). Both strict and Adams consensus trees were determined for each analysis, as was the statistical support for each, on the basis of 1000 bootstrap replicates.

Body size

The body length of *Pebanista* was estimated on the basis of its bizygomatic width (BZW), using regression equations that reconstruct body size on the basis of this specific cranial measurement. However, prior studies (*21*) have suggested that body size reconstructions using the BZW underestimates the true body size in crown platanistoids. Therefore, the body size calculations presented in this study likely represent the minimum body sizes for this taxon. The BZW width of the specimen referred to cf. *Pebanista* MUSM 3593 was obtained using the proportion between the rostrum width at the base and the total BZW of the holotype specimen of *Pebanista yacuruna* MUSM 4017. Using this reconstructed BZW, the estimated body size of the referred specimen was calculated.

Supplementary Materials

This PDF file includes:

Supplementary Text
Sections S1 to S3
Figs. S1 to S7
Table S1
References

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Supplementary Text

S1: Extended geological context

The holotype specimen of *Pebanista yacuruna* gen. et sp. nov., MUSM 4017, was uncovered from sediments of the Miocene Pebas Formation exposed along the Napo River in Western Amazonia of Peru (lat: -3.012468°, long: -73.404855°, Amazon Basin). The unit is associated with a large-scale continental freshwater aquatic system (fluvio-lacustrine setting), which was at least twice affected by short-lasting regional marine floodings sourced from Caribbean marine waters(*54*, *64*). The Pebas Fm. has an estimated thickness of up to 1000 meters(*46*). However, individual sections outcropping along riverbanks in the Amazon Basin rarely exceed a few tens of meters, making it virtually impossible to determine robust regional correlations and precise ages. The *Pebanista* locality consists of an 8-meter-thick section, characterized by having massive to finely laminated blue to brown siltstones, interbedded with brown fine-grained sandstones, occasional black fossiliferous mudstones, and a massive indurated fossiliferous coquina level. The *Pebanista* remains and other fossils found at the locality, such as mollusc shells, and bony remains of a *Purussaurus* caimanine and a sloth, come from this coquina level.

Palynological Biostratigraphy and Biochronological Implications–During our 2018 fieldwork campaign that yielded the holotype specimen of *Pebanista yacuruna*, we collected four samples (at 1-meter intervals) for palynological analyses from the section bearing the holotype. Two samples were located below (RN39-02; RN39-04) and two above (RN38-02; RN38-03) the stratigraphic position of the fossil specimen. Samples were processed for palynological analysis following standard digestion procedures by using 10% HCl and 40% HF(*65*). Each sample was sieved using 10 µm and 100 µm meshes and permanent montages were prepared. Light microscopy was used to examine the palynological content, following morphological features, descriptions, and illustrations compiled in Jaramillo and Rueda(*66*). The section was dated using the palynological zonation proposed by Jaramillo et al.(*19*), which has been time-calibrated using carbon isotopes, radioisotopic dating, foraminiferal biozonations, and magnetostratigraphic data. A Maximum Likelihood (ML) analysis was then applied to statistically infer the most probable ages based on taxa abundances(*67*), while keeping the same zonation as the biostratigraphic reference. R code and reference datasets were from Ochoa et al(*68*).

Good pollen recovery was found in all samples, being characterized by high abundances of fern spores (e.g., *Polypodiisporites* and *Laevigatosporites*) and palms (e.g., Mauritiidites). We found no evidence of taxa reflecting marine or brackish environments in this section. The co-occurrence of key temporal indicator taxa, such as *Malvacipolloides maristellae* (First Occurrence Datum or First Appearance Datum [FAD] at 17.7 Ma), *Echitricolporites spinosus* (FAD at 17.1 Ma), with *Cyclusphaera scabrata* (Last Occurrence Datum or Last Appearance Datum [LAD] at 16.9 Ma), and *Crassoretitriletes vanraadshooveni* (FAD at 14.2 Ma), supports the presence of the Early Miocene zones T-13, T-14 and the lower part of zone T-15 (17.7 -14.2 Ma) in this section. Furthermore, according to the ML analysis, the studied samples have a high probability of belonging to the Early Miocene palynological zone T-13 *E. maristellae*, restricting the age of the *Pebanista* section to the upper Burdigalian Stage, circa 16.5 Ma (Supplementary Figure 2).

S2: Extended description of *Pebanista yacuruna* gen. et sp. nov., MUSM 4017

Phylogenetic position of *Pebanista*–Our series of phylogenetic have consistently recovered the relationships of *Pebanista yacuruna* within Platanistidae. In the first heuristic search, 72 trees were retained with a length of 105 step, a CI=0.600 and a RI of 0.817. *Pebanista* + *Platanista* were recovered as sister to *Zarhachis* + *Pomatodelphis*; however, *Araeodelphis* was recovered within a large polytomy that included other platanistoids. In the series of analyses with implied weighting the content of Platanistidae was consistent with previous workers (*21*). In these analyses with subsequent k values, 13 trees were retained with a length of 13 steps, a CI=0.600 and a RU=0.817. Platanistidae was recovered by the following combination of characters: articular rim on the lateral surface of the periotic forming a hook-like process {c. 20(2)}, separate ossicle at the apex of the anterior process of the periotic {c. 26(1)}, outer posterior prominence of the tympanic posteriorly longer than the inner posterior prominence {c. 29(1)} and mandibular symphysis reaching more than 65% of the mandibular length, including an angle between both mandibles broader than 50° {c. 47(1)}. *Araeodelphis* is recovered as the earliest branching platanistid due to a single character: absence of asymmetry in the rostrum {c. 4(0)}. The clade formed by the more crownward platanistids, without *Araeodelphis* is recovered by apex of the rostrum formed by both premaxillae and maxillae {c. 2(2)}, deeply grooved lateral rostral suture between the premaxilla and the maxilla {c. 3(1)}, presence of a distinct prominent dorsal crest in the antorbital-supraorbital region {c. 9(1)}, antorbital process of the frontal transversely thickened {c. 10(1)}, lack of accessory denticles on posterior teeth {c. 33(1)}. The monophyly of *Pebanista* and *Platanista* is recognised due to large and thin-edged aperture of the cochlear aqueduct of the periotic {c. 22(1)}, oval internal auditory meatus of the periotic with the dorsal opening for the facial canal lateral to the spiral cribriform tract {c. 25(1)}, tooth count between 25 and 33 {c. 34(1)}, vertex strongly pinched transversely with the posterior end of the maxillae converging posterior to the external bony nares {c. 41(1)}, transversely wide temporal fossa {c. 44(0)}. *Pebanista* differs from *Platanista* by possessing a transversely thickened antorbital process of the frontal, ventral exposition of the palatines and greatly enlarged alveoli {c. 46 (0)}.

General description of the skull–The holotype skull of *Pebanista yacuruna* gen. et sp. nov., MUSM 4017, has a preserved condylobasal length of 698 mm and an estimated bizygomatic width of 281 mm. The preserved skull dimensions are proportionally larger than other Platanistidae including extant *Platanista*, and the fossil taxa Araeodelphis, *Pomatodelphis, Prepomatodelphis* and *Zarhachis*. The sutures between the cranial bones are well-closed or fused (e.g., maxilla-premaxilla suture along the rostrum) indicating that it belonged to a fully mature specimen. The rostrum is dorsoventrally flattened and elongated, a condition shared with *Pomatodelphis, Prepomatodelphis* and *Zarhachis*, thus contrasting with the transversely compressed rostrum of *Platanista* (*38*, *39*). On the preserved portion, the rostrum is formed by the premaxillae, maxillae, and vomer, being much more transversely robust than in other platanistids. The rostrum exhibits several well-preserved dental alveoli which are well-developed, much larger, and deeper than in other platanistids. The facial region of the skull exhibits a well-developed circumnarial basin, delimited laterally by the supraorbital crest, and posteriorly by the nuchal crest. The external bony nares are displaced to the left, creating an asymmetric arrangement of the surrounding bones. Only the left supraorbital crest is preserved, projecting substantially over the level of the base of the rostrum and being transversely flattened as in *Platanista*, but more robust. This crest is not as stout as in *Pomatodelphis* and *Zarhachis*. The medial aspect of the crest is excavated by various vacuities, a condition also present in *Platanista*, but to a lesser extent in the new fossil taxon. No excavation of the supraorbital crest is observed in *Zarhachis* and *Pomatodelphis*. The temporal fossa is transversely longer than high and extends posteriorly, projecting the temporal crest well into the occipital region. Over the temporal fossa, the nuchal crest continues anteriorly, forming supraorbital crests and giving the skull a boxy outline in dorsal view. The occipital shield is perpendicular to the longitudinal axis of the skull, except for its dorsal end, which deflects anteriorly. However, it is not possible to assess whether this is the true shape of the crest, or a condition enhanced by taphonomic compression.

Premaxilla–Along the rostrum, the dorsal surface of the premaxillae is flat to slightly convex until the level of the antorbital notch, where the medial part of these deepens forming the circumnarial basin. Posteriorly, across the facial region of the skull, the premaxillae become slightly concave medially forming the premaxillary sac fossae. In dorsal view, the premaxillae are greatly exposed along the rostrum, limiting the dorsal exposure of the maxillae to a narrow strip along most of the rostrum. Both premaxillae retain a similar transverse width along the rostrum, without any narrowing or lateral expansion. The maxillary-premaxillary suture is well-closed and partly fused, being located within a narrow, shallow groove, much thinner than the condition observed in other platanistids such as *Pomatodelphis*, *Zarhachis* or *Platanista,* which exhibit a deep lateral groove. The mesorostral groove is closed along most of the rostrum, opening posteriorly at the level of the last maxillary tooth. The anteromedial sulcus is well-developed on the left premaxilla, being narrower on the right premaxilla due to the transverse compression of the bone, a condition shared with other platanistids and squalodephinids. The single premaxillary foramen is located on the left premaxilla, 21mm anterior to the level of the external bony nares, being longer (15mm) than wide (6mm). As in *Platanista*, this single premaxillary foramen is located at the level of the antorbital notch, and not anterior to it. The posteromedial sulcus is slightly narrower than its anteromedial counterpart, being mostly rectilinear on the left premaxilla and slightly curved on the right. On the facial region both premaxillae are strongly deflected to the left side of the skull, thus making the left external bony naris longer than wide and the right naris wider than long. Both premaxillae reach their highest elevation posterior to the external bony nares at the level of their respective nasal processes. The premaxillary sac fossa is well-developed on the left premaxilla, having a kidney-like shape. Because of the transverse compression, the premaxillary sac fossa on the right exhibits an oval outline.

Maxilla–The maxillae are mostly restricted to the lateral sides of the rostrum, being flat across the rostral surface. Anterior to the rostral base, the maxillae slightly project laterally and flatten, creating a blade-like ending of the maxillary flange, as in other platanistids. Ventrally, the maxillary surface is flat, and both maxillae contact each other until the level of the 13th dental alveolus (counting from the back), where the vomer is exposed ventrally as a narrow strip. The widest alveolus has an anteroposterior length of 16mm and a transverse width of 18mm. Posterior to the maxillary flange, the antorbital notch displays an acute V-shaped outline. A single dorsal infraorbital foramen is preserved on the left maxilla, displaying a sub-elliptical outline, reaching an anterodorsal length of 11mm and a transverse width of 4mm. No additional foramina can be identified within the maxillary surface. In the facial region, both maxillae are highly asymmetric, due to the deviation of the external bony nares, following the pattern of their respective premaxilla.

The lateral region of the ascending process of the maxilla projects dorsolaterally, forming the U-shaped circumnarial basin along with the premaxillae. Such development of the circumnarial basin is a condition unique to *Pebanista*, being a more-derived condition than the one observed in *Platanista*, and because of the overall contribution of the premaxillae and maxillae to the structure it resembles the supracranial basin observed in other odontocetes(*32*, *33*, *69*). Laterally, the circumnarial basin is surrounded by the greatly enlarged supraorbital crests, which are mostly formed by the frontals. The maxillae only contribute to a minor part of the medial wall of the supraorbital crests, at the level of the temporal fossa. Posteriorly, and within the circumnarial basin there are two posterolateral depressions located on the floor of the basin, each of which display a somewhat symmetrical outline.

Frontal + lacrimal–Most of the left frontal is preserved, except for the dorsal edge of the supraorbital crest. The right frontal has been lost during the taphonomic process, except for a small bony strip. The suture between the maxilla and the frontal is mostly fused until the level of the temporal fossa, where the suture between both bones can be identified posteriorly. Because of the shape and the overall development of the circumnarial basin, both frontals should have reached a similar height and anterodorsal projection, with minor differences due to the asymmetric profile of the facial region. In *Pebanista*, the frontals are more enlarged than the condition observed in other platanistoids, due to the great dorsal development of the supraorbital crests. The frontal is exposed lateral to the maxillae in dorsal view, displaying a transversely robust profile. In the circumnarial basin, the frontal greatly elevates over the rest of the facial region, forming the supraorbital crest, which is transversely thinner than in *Zarhachis* and *Pomatodelphis*, although not as thin as in *Platanista*. Furthermore, the dorsomedial region of the crest is excavated by several large vacuities, which may foreshadow the condition of *Platanista*, in which the medial aspect of the crest is totally excavated to house a dorsal expansion of the pterygoid sinus (*70*). In dorsal view, the lateral edge of the orbit roof is not parallel to the anteroposterior axis of the skull as in *Dilophodephis*, but forms an acute angle with the rostrum base, being slightly medially oriented. In other words, the orbits face anterolaterally. Ventrally, only a small portion of the lacrimal can be recognised anteriorly contributing to the preorbital process. The frontal groove is moderately broad and shallow, indicating that optic nerve development was limited as compared to *Zarhachis* or *Pomatodelphis*, thus indicating an intermediate condition between these two genera and the nearly blind *Platanista*. Such condition is also reflected by the proportional reduction in the size of the orbit.

Palatine + pterygoid –The palatine and pterygoid are not easy to distinguish, as the palatal in the holotype specimen is compressed and broken into several small bony fragments, and the palatine-pterygoid suture is fused. In *Pebanista*, the pterygoids have an anterior projection with a round outline. Medially, the pterygoids contact each other but are not fused. Lateral to pterygoid, the palatine is ventrally exposed as a small stripe of bone. Most of the medial part of the palatine has been covered by the pterygoid. As in several platanistoids, the palatine projects dorsolaterally. Both pterygoid sinus fossae are well-developed, displaying an elongated bean-like shape, extending from the level of the antorbital notch to the level of the anterior tip of the squamosal. The hamular process of the pterygoid is mostly missing except for a small area anterior to the choanae. Posteriorly the pterygoid extends towards the pharyngeal and basioccipital crests, contributing to most of their preserved length.

Temporal Region–The skull has undergone a slight to moderate dorsoventral compression during the taphonomic process, being more evident on the right side of the skull, as the temporal crest suffers an abrupt break on its posteriormost portion. Despite this, the overall shape of the temporal fossa has been mostly preserved, presenting an oval outline in lateral view, being transversely broad and much longer anterodorsally than high. The overall extension of the temporal fossa in *Pebanista* is much greater than that of *Platanista* or *Zarhachis*. The fossa projects into the occipital region, displacing the temporal crest to the occipital region, resembling the condition in *Zarhachis*.

Squamosal–Both squamosals are partly preserved, each to a similar extent. Only part of the left zygomatic process is preserved, being much more robust than in *Platanista*, but more slender than in *Zarhachis* or *Pomatodelphis*. The supramastoid crest is only noticeable in dorsal view, near the posterior end of the bone, being broad but not very high. Despite this, the process should have been moderately robust, based on the broken surface of the squamosal. The glenoid fossa is small, with an elliptical outline, and oriented towards the anterolateral portion of the skull.

Occipital Region–*Pebanista* displays an occipital region with a trapezoidal outline delimited by the nuchal crest and the temporal crests. The surface of the occipital shield is mostly perpendicular to the skull main axis, except for its dorsal part, which projects anteriorly. The supraoccipital and the posterior end of the maxilla contribute to the anterodorsally oriented nuchal crest. The foramen magnum and the occipital condyles have been dorsoventrally compressed; despite this, the overall shape of the surrounding bones indicates that the foramen should have had a mostly circular outline. The occipital condyles protrude markedly posteriorly, having a rounded to triangular shape in posterior view.

S3: Description of additional referred specimens

cf. *Pebanista*

Referred specimen– MUSM 3593, an isolated rostral fragment.

Locality, Age and Horizon– This specimen was donated by Juan Pablo de Molina in 2018, and was recovered from the Fitzcarrald Arch, an area in South Central Peru where the middle Miocene Ipururo Fm. crops out. Despite not having a well-defined locality, the sediments attached to the rostral fragment indicate that it corresponds to the fluvial or tidal deposits in this area. Previous work in the area indicates that the Fitzcarrald Arch was a highly diverse region during the middle Miocene, as a wide array of taxa including, but not restricted to, crocodilians, cingulates, folivores, astrapotheres, notoungulates, litopterns, rodents, odontocetes and a possible marsupial have been reported so far(*57*, *71*).

Description– The rostral fragment is rather robust and reaches a maximum length of 13.5 cm and a maximum width of 8.8 cm, including the premaxillae, maxillae, and vomer. In dorsal view, the maxilla is restricted to a narrow strip lateral to its respective premaxilla. Medially the suture between both premaxillae is somewhat noticeable, being slightly deviated to the left side. The premaxilla-maxilla suture is located within a narrow, moderately shallow recess, like the condition observed in the holotype skull of *Pebanista*. The lateral walls of the rostrum are parallel, except for a minor distortion resulting from to the taphonomic process. Ventrally, both maxillae preserve four well-developed dental alveoli on each side, with the broken teeth preserved in situ within these alveoli. The posteriormost right alveolus reaches an anterodorsal length of 2.9 cm and a transverse width of 1.9 cm. Only two greatly enlarged teeth are preserved on the left maxilla. The largest one reaches a 2.4 cm exposure of the crown and displays several longitudinal ornamentations on the crown. The tooth resembles that of *Platanista*, but proportionally much larger in this fossil. Medially, the vomer is exposed as a narrow strip between both maxillae.

Platanistidae indet.

Referred specimen– MUSM 4759, isolated tympanic.

Locality, Age and Horizon– The isolated tympanic was found in coquina layers of the lower Pebas Fm. (Early to Middle Miocene) along the Napo River.

Description– The isolated tympanic reaches a maximum length of 5.9 cm, being anteroposterioly longer than wide, and resembles in general shape that of other platanistoids such as *Platanista, Pomatodelphis* or *Notocetus* (*40*, *44*). In MUSM 4759 the anterior spine is long, but its overall extension cannot be assessed, as the distal tip is missing. Only the base of the anterodorsal crest is preserved, as the tympanic plate has only been partly preserved. The involucrum is well-developed, being rather robust due to the pachyosteosclerotic growth of the bone. The outer lip exhibits a minor extension anteriorly, similar to the condition observed in *Zarhachis* or *Platanista*. The preserved portion of the outer lip displays a moderately inflated outline, interrupted by the thin and shallow lateral furrow. Posteriorly, the outer posterior prominence has a moderately triangular profile in ventral view, contrasting with the inner posterior prominence, which displays a much rounder profile. The interprominential notch is wide and moderately shallow, along with the median furrow which extends across most of the ventral surface of the tympanic.

Fig. S1. Geographical context. Map indicating the locality where the holotype specimen of *Pebanista yacuruna* gen. et sp. nov., MUSM 4017, was found (A) and photos from the collection of the specimen (B, C) along the banks of the Napo River.

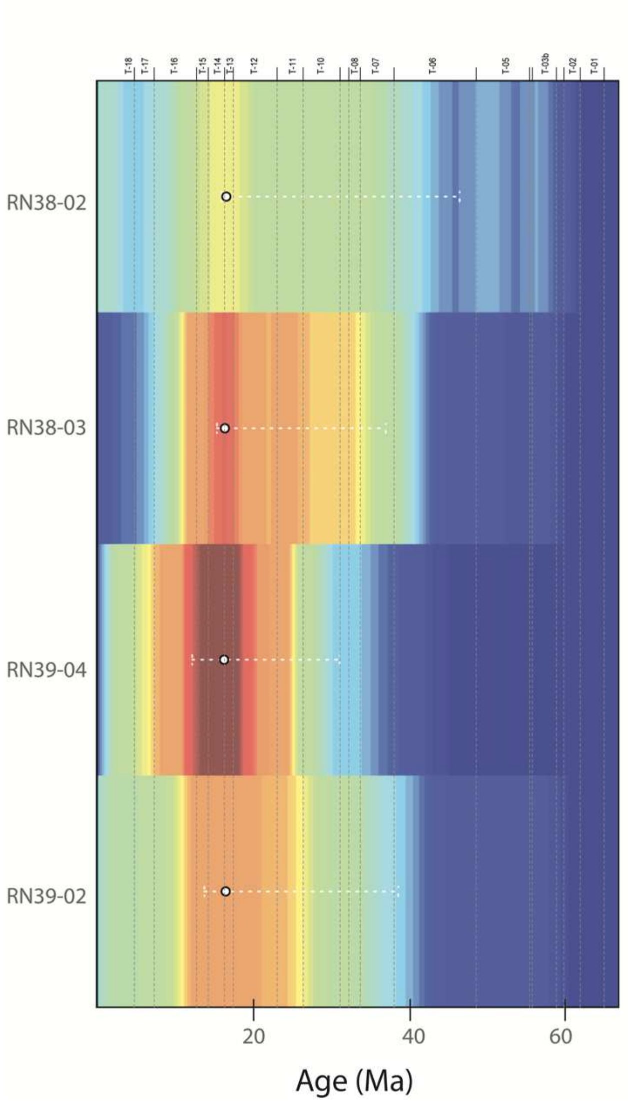

Fig. S2. Stratigraphic ML age estimates for the MUSM 4017-bearing section, calculated using a probabilistic approach based on the taxa abundances. Normalized likelihood values are represented by color, with higher and lower likelihood values symbolized by warmer and colder colors, respectively. The lower horizontal axis shows geologic time (Ma), and vertical axis represents stratigraphic position of specific samples and the upper horizontal axis marks the palynological zones proposed by Jaramillo et al.(*19*).

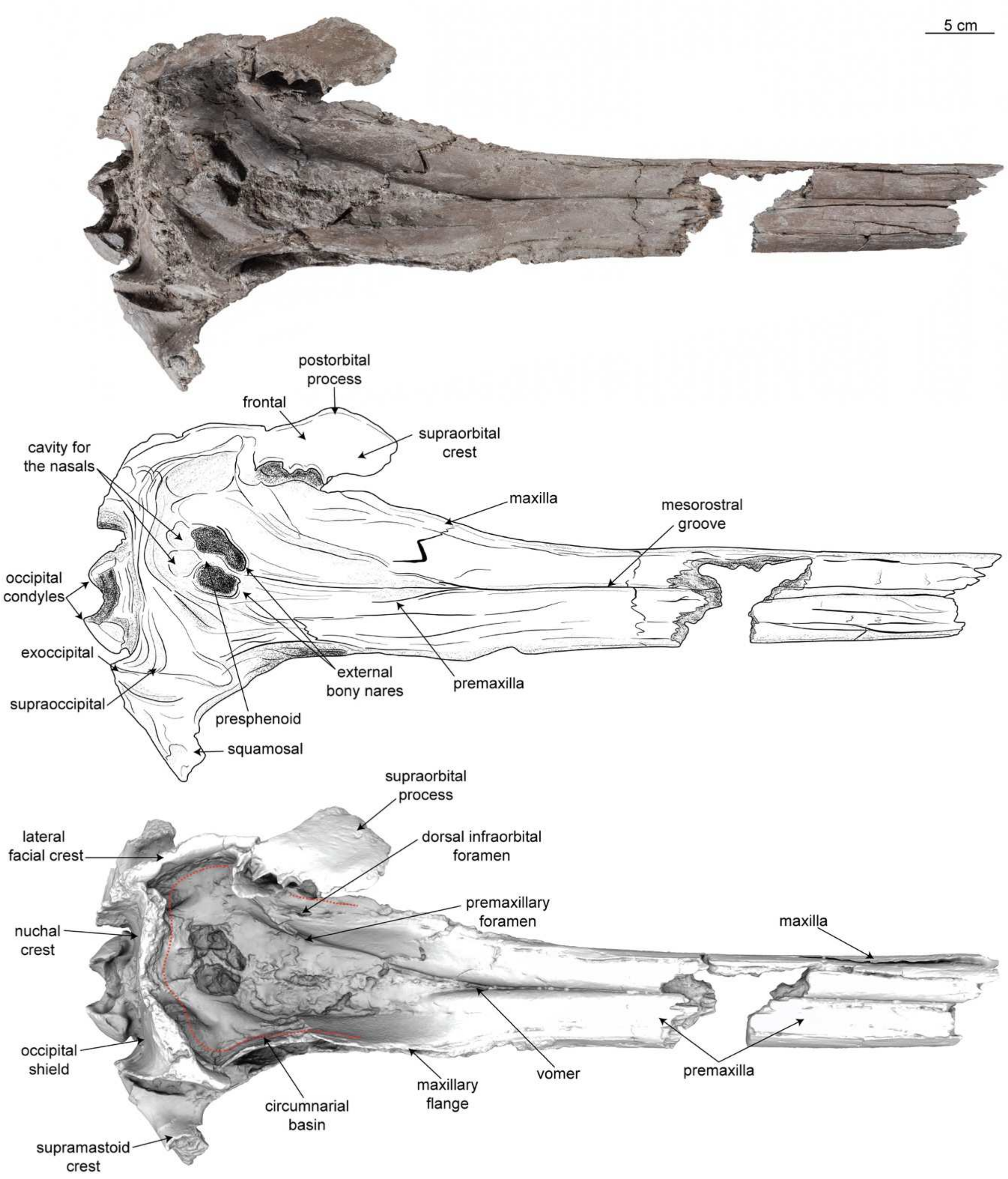

Fig. S3. Holotype skull of *Pebanista yacuruna* gen. et sp. nov. (MUSM 4017). Photograph (top), drawing (middle), and surface (bottom) 3D model in dorsal view.

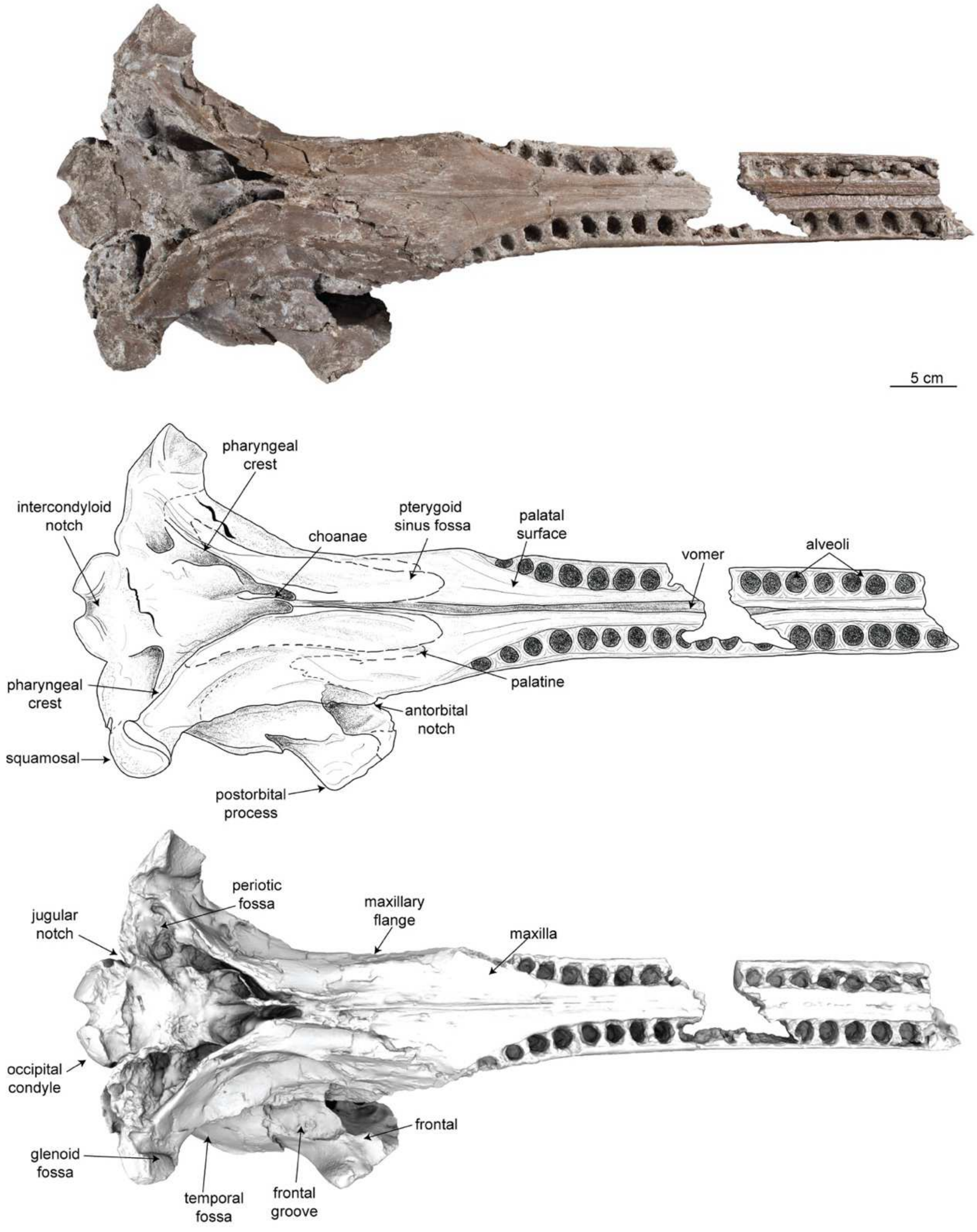

Fig. S4. Holotype skull of *Pebanista yacuruna* gen. et sp. nov. (MUSM 4017). Photograph (top), drawing (middle), and surface (bottom) 3D model in ventral view.

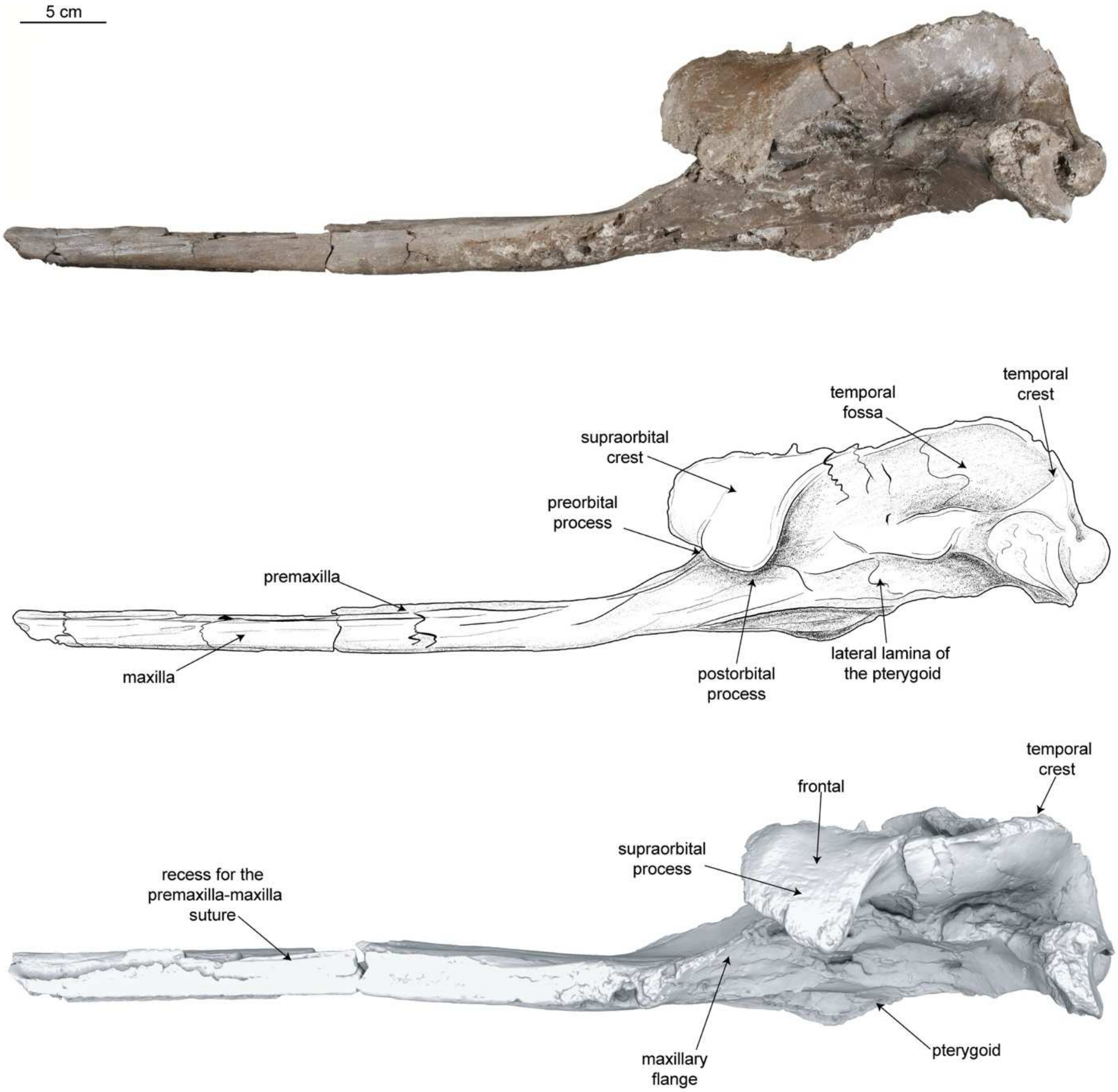

Fig. S5. Holotype skull of *Pebanista yacuruna* gen. et sp. nov. (MUSM 4017). Photograph (top), drawing (middle), and surface (bottom) 3D model in left lateral view.

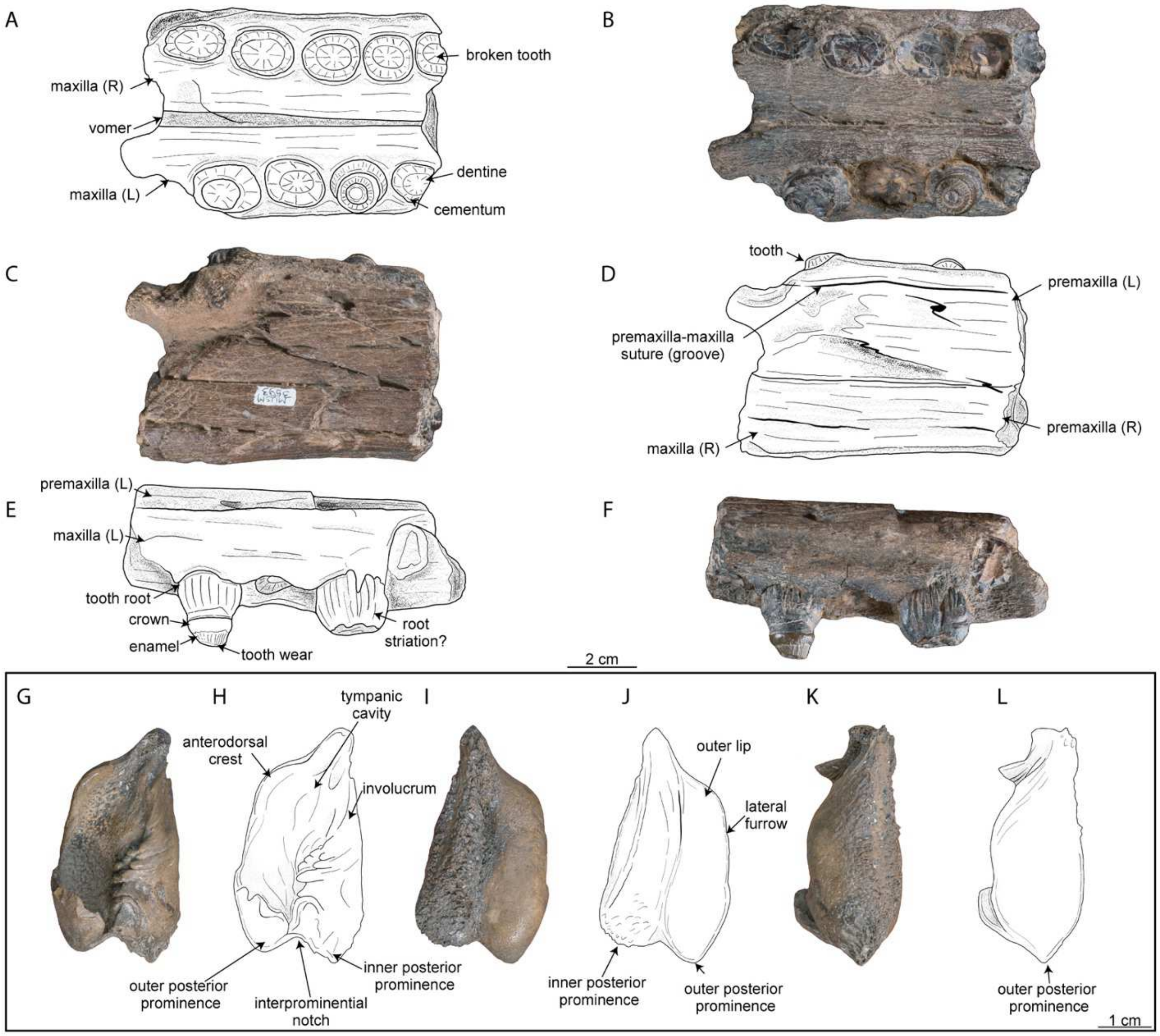

Fig. S6. Additional specimens: cf. *Pebanista* MUSM 3593 rostral fragment in ventral (A,B), dorsal (C,D) and right lateral (E, F) views; Platanistidae indet. MUSM 4017 isolated tympanic in dorsal (G,H), ventral (I, J) and lateral (K, L) views.

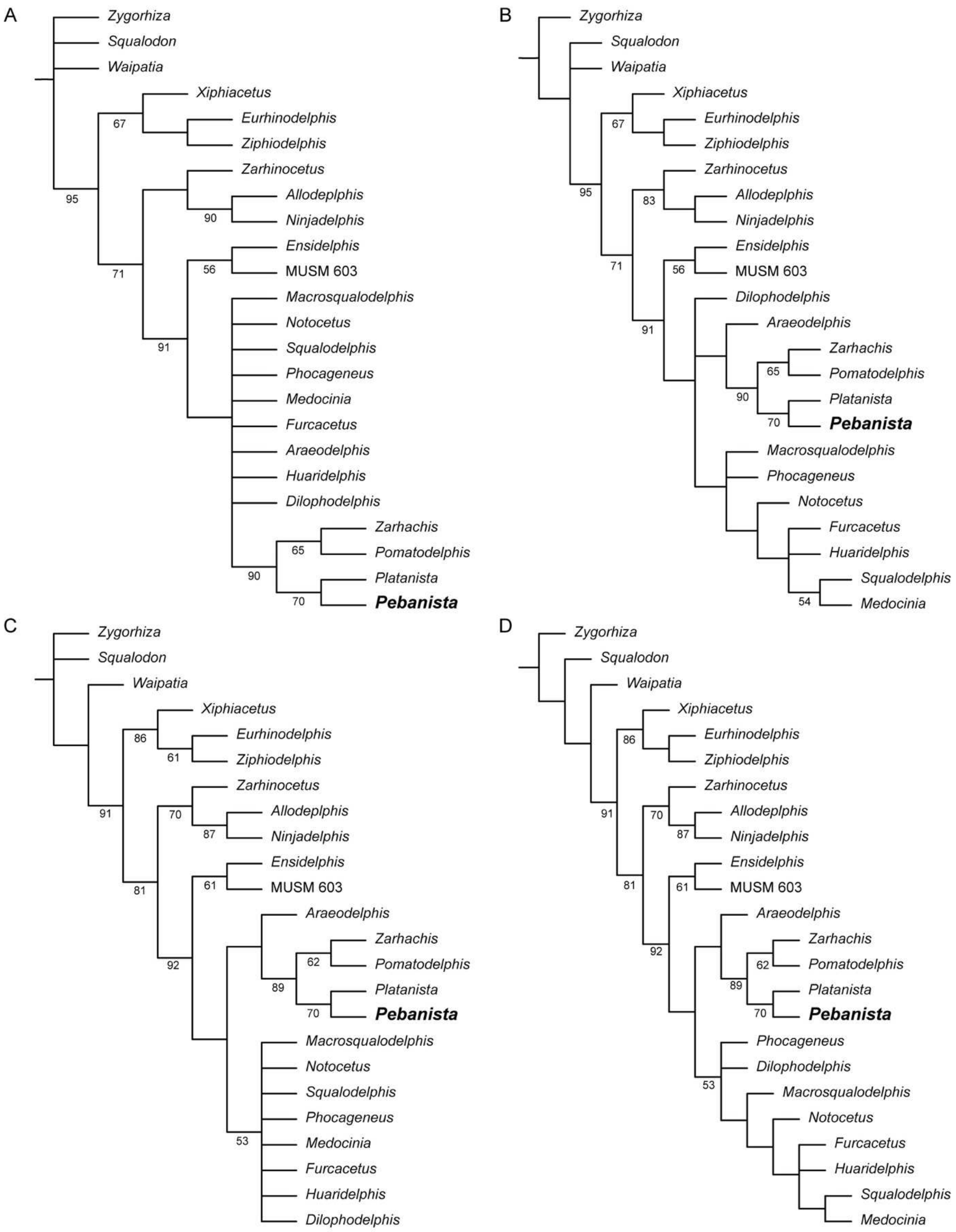

Fig. S7. Phylogenetic relationships of *Pebanista yacuruna* gen. et sp. nov. (MUSM 4017). Related to Figure 2. Strict (a) and Adams (b) consensus trees of the heuristic search without downweighting of characters; and with down-weighting (c,d) homoplastic characters (k=2), indicating the relationships of *Pebanista yacuruna* gen. et sp. nov. (MUSM 4017) to other platanistoids.

Table S1. Cranial measurements (e, estimate; + measurement on incomplete element) of the holotype skull of *Pebanista yacuruna* gen. et sp. nov., MUSM 4017 (in mm)

Dimensions	**MUSM 4017**
Condylobasal length (preserved)	698+
Length of the rostrum (preserved)	489+
Width of rostrum at base	116
Width of the rostrum at 60mm anterior to the line across hindmost limits of antorbital notches	102
Width of rostrum at mid preserved length	66
Width of premaxillae at mid preserved length of the rostrum	71
Width of rostrum at 3⁄4 of the preserved length, measured from posterior end (taken on preserved portion)	74
Height of rostrum at base (including rostral basin)	46
Height of rostrum at base (without rostral basin)	27
Height of rostrum at mid preserved length	21
Maximum width of the external right bony naris	22
Maximum width of the external left bony naris	18
Greatest postorbital width (width across postorbital processes)	261
Minor width within the supraorbital processes	115
Maximum width of external nares	46
Greatest width across zygomatic processes of squamosal	281e
Greatest width of premaxillae	94
Width across both the temporal fossae (minimum)	131
Greatest width between lateral margins of exoccipitals	242e
Dorsoventral length of temporal fossa	94
Anteroposterior width of temporal fossa perpendicular to greatest length (dorsoventral height)	124
Length of left orbit from apex of preorbital process of frontal to apex of postorbital process	54+
Length of antorbital process of left lacrimal taken horizontally	17e
Greatest width of internal nares	23
Greatest length of pterygoid	134
Maximum width across occipital condyles	78
Height of foramen magnum	21e
Width of foramen magnum	35

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