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A Miocene relative of the Ganges River dolphin (Odontoceti, Platanistidae) from the Amazonian Basin

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SHORT COMMUNICATION

A MIOCENE RELATIVE OF THE GANGES RIVER DOLPHIN (ODONTOCETI, PLATANISTIDAE) FROM THE AMAZONIAN BASIN

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INTRODUCTION

Today, only three odontocete (toothed whales) genera are restricted to freshwater habitats: the Amazon River dolphin (*Inia geoffrensis*), the possibly extinct Yangtze River dolphin (*Lipotes vexillifer*) (Turvey et al., 2007), and the Ganges and Indus river dolphins (*Platanista gangetica*). Even if their phylogenetic relationships are still debated, *Inia*, *Lipotes*, and *Platanista* are now recognized as belonging to different families (Iniidae, Lipotidae, and Platanistidae, respectively) on the basis of morphological and molecular characters (Muizon, 1988; Cassens et al., 2000; Hamilton et al., 2001; Nikaido et al., 2001; McGowen et al., 2009; Geisler et al., 2011, 2012). Considering their geographic distribution and the discovery of some fossil relatives in marine deposits, for example, the iniid *Meherrinia*, the lipotid *Parapontoporia*, and the platanistids *Prepomatodelphis*, *Pomatodelphis*, and *Zarachis*, the current habitat of freshwater dolphins must be explained by independent episodes of colonization of freshwater environments (Cassens et al., 2000; Geisler et al., 2011, 2012). Several fragmentary fossil specimens, isolated teeth or jaw fragments, have been tentatively attributed in the past to unknown species that are thought to be closely related to extant river dolphin genera (e.g., Zhou et al., 1984; review in Muizon, 1988), but until now there were no diagnostic fossil remains that could provide clues about the early steps of these colonization episodes.

More specifically, the fossil record of Platanistinae, the subfamily including the extant *Platanista*, is scarce, with only one tentative record from early Miocene, coastal deposits of Oregon, north Pacific. This specimen consists of an isolated mandibular symphyseal region that is transversely compressed (Barnes, 2006). Even if we consider this attribution as valid, a long ghost lineage characterizes most of the history of the Platanistinae, the latter having diverged from the extinct subfamily Pomatodelphininae since at least the latest early Miocene (Barnes, 2002, 2006).

We present here a new fossil platanistine specimen: a periotic from the middle Miocene of Peruvian Amazonia. This highly diagnostic ear bone partly fills the ghost lineage mentioned above and provides insights on the shifts to freshwater environments by various odontocete clades, a phenomenon probably underestimated due to the lack of fossils from the freshwater sedimentary record, and probably not just limited to extant clades of freshwater odontocetes (Fordyce, 1983).

Institutional Abbreviations—MSNTUP, Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, Italy; MUSM,

Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru.

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
PLATANISTOIDEA Gray, 1863
PLATANISTIDAE Gray, 1846
PLATANISTINAE Gray, 1846
Gen. et sp. indet.
(Fig. 2A–G)

Referred Specimen—Isolated left periotic MUSM 1611.

Locality and Age—Bone bed DTC-32, Mapuya River, north-western flank of Fitzcarrald Arch, Peruvian Amazonia (Fig. 1). 'Fitzcarrald Local Fauna,' late middle Miocene (Laventan South American Land Mammal Age), ~13.2–12.5 Ma, based on mammal assemblage and paleomagnetism (Salas-Gismondi et al., 2006; Antoine et al., 2007; Goillot et al., 2011).

Description—This well-preserved left periotic only lacks the anterior tip of the anterior process and the posteroventral portion of the posterior process. A thin concretionary layer remains in the notch between the pars cochlearis and the anterior process. The total length, as preserved, is 38 mm; the length of the preserved part of the anterior process is 16.6 mm; the length of the pars cochlearis from its anterior margin to the anteromedial margin of the fenestra rotunda is 16.7 mm. After inferring the sizes of missing parts, this periotic was originally slightly larger than those of *Platanista* (see Fig. 2H–K; total length of the periotic ranging from 33.4 to 42.3 mm in *Platanista*, with a mean length of 37.6 mm, based on seven specimens measured by Kasuya, 1973).

The anterior process is strongly bent anteromedially, and it is separated by a deep notch from the pars cochlearis; the angle between the anterior process and the pars cochlearis in ventral view is 18 degrees. We assume that the missing anterior tip of the anterior process corresponds to a separate ossicle, as observed in several specimens of *Platanista* (see Fig. 2H; Kasuya, 1973:pl. 9; Kellogg, 1924:pl. 7). The anterior bullar facet is transversely concave but shallow. A prominent parabullary ridge is developed lateral to the rectilinear lateral crest of the bullar facet. The lateral tuberosity is long and pointed in ventral view, although this is not apparent because it is merged with the parabullary ridge. Anteromedial to the anterior bullar facet, the anterior process bears a small dome made of more spongy bone. No accessory ossicle is preserved, further emphasizing the transverse constriction at the base of the anterior process. The malleolar fossa is wide and

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FIGURE 1. Map of the Amazonian Basin (A) and northwestern flank of Fitzcarrald Arch (Peru) (B) showing the late middle Miocene locality DTC 32 (star) where the platanistine periotic MUSM 1611 was discovered. (Color figure available online.)

moderately deep, whereas the fossa incudis is not present. The fenestra ovalis is posterior to the level of the small ventral opening for the facial canal. The preserved dorsal and posterodorsal parts of the posterior process suggest that the posterodorsal margin of the latter structure turned abruptly ventrally. The articular process (sensu Muizon, 1987) is only partly preserved as a thin oblique lamina on the lateral surface of the bone, just posterior to the epitympanic hiatus.

The outline of the proportionally high pars cochlearis is more rounded than square-shaped in dorsal and ventral views. The fenestra rotunda is large, roughly circular, opens posteromedially into a short and wide sulcus. The lateral margin of the fenestra rotunda is an elevated and acute crest (caudal tympanic process sensu Mead and Fordyce, 2009) that separates this foramen from the wide and deep stapedial muscle fossa. Identified from computed tomographic (CT) scan images (Fig. 2G), the aperture of the cochlear duct is posterior to the internal auditory meatus (IAM); it is tiny, with a maximum diameter of 1 mm. The margin of the IAM has a sharp crest, and the IAM displays an oval outline, not pointed anterolaterally. In the IAM, the dorsal opening for the facial canal is lateral to the spiral cribriform tract and sep-

arated from it by a very low transverse crest. The aperture of the vestibular duct is much larger than the aperture of the cochlear duct and not anteroposteriorly compressed.

Comparisons—The general shape of the periotic, a cranial element highly diagnostic in odontocetes, is similar to platanistids and squalodelphinids, two platanistoid families considered to be sister groups by several authors (e.g., Muizon, 1987; Fordyce, 1994; Barnes, 2006). This similarity is supported by the presence of an articular process (see Muizon, 1987), even if only partly preserved, that is more distinct than the simple prominence seen, for example, in some eurhinodelphinids and squalodontids. Compared with squalodelphinids, MUSM 1611 exhibits a pars cochlearis less distinctly square-shaped and lacks a large aperture with sharp rim of the cochlear aqueduct (Muizon, 1987). Among platanistids, MUSM 1611 differs from the pomatodelphinines *Pomatodelphis* and *Zarhachis* in having an anterior process not dorsoventrally thickened and an anteromedial corner of the pars cochlearis more angled. Instead, MUSM 1611 shares three to four synapomorphies with *Platanista* (Fig. 3):

- 1—Anterior process strongly anteromedially bent. This derived character is only observed in *Platanista*, in which the parabullary ridge is similarly prominent. Outside of Platanistoidea, a rather similar condition is observed in the pygmy sperm whale *Kogia* (Kasuya, 1973) and related fossil kogiids (e.g., Luo and Marsh, 1996). However, in kogiids, the curved anterior process is associated to an enlarged, often fused, accessory ossicle.
- 2—Tiny aperture of the cochlear aqueduct. This aperture is always larger in pomatodelphinines and squalodelphinids (see Kellogg, 1924; Muizon, 1987). The latter, as described above, have a large thin-edged aperture (Muizon, 1987). The aperture is similarly reduced in some delphinoids (for examples, see Kasuya, 1973).
- 3—IAM oval, with the dorsal opening for the facial canal lateral to the spiral cribriform tract. In platanistoids other than *Platanista* and in many other odontocetes (e.g., *Squalodon*, *Waipatia*; see Fordyce, 1994; Luo and Eastman, 1995), the IAM is pointed anterolaterally, with the opening for the facial canal anterior to the level of the tract.
- 4—Separate ossicle at the apex of the anterior process. Only observed in *Platanista*, this character might constitute another synapomorphy of MUSM 1611 + *Platanista*. We note that this interpretation is somewhat speculative considering that only one specimen of the Amazonian platanistine is known and available for study.

MUSM 1611 differs from *Platanista* in having (1) a larger, more circular aperture for the vestibular duct; (2) a less dorsoventrally flattened area lateral to the IAM; (3) a thicker pars cochlearis in medial view; and (4) a dorsoventrally thinner anterior process.

Based on the series of shared apomorphies, MUSM 1611 is considered to represent the sister group of *Platanista* and is therefore placed with the latter in the subfamily Platanistinae (Fig. 3). The only other fossil specimen tentatively identified as a platanistine is a fragment of the symphyseal part of a mandible from the early Miocene of Oregon (Barnes, 2006), which cannot be compared with MUSM 1611.

DISCUSSION

This periotic is the first record of a fossil platanistine based on a diagnostic cranial element. This attribution leads to the recognition of a series of apomorphies for the subfamily, which was previously diagnosed by a transversely flattened mandible, some plesiomorphic characters, and a few specialized characters only observed in *Platanista*, such as the reduction of the eye and the development of the maxillary crests (Barnes, 2006). Our new specimen is from the late middle Miocene (~13 Ma), younger

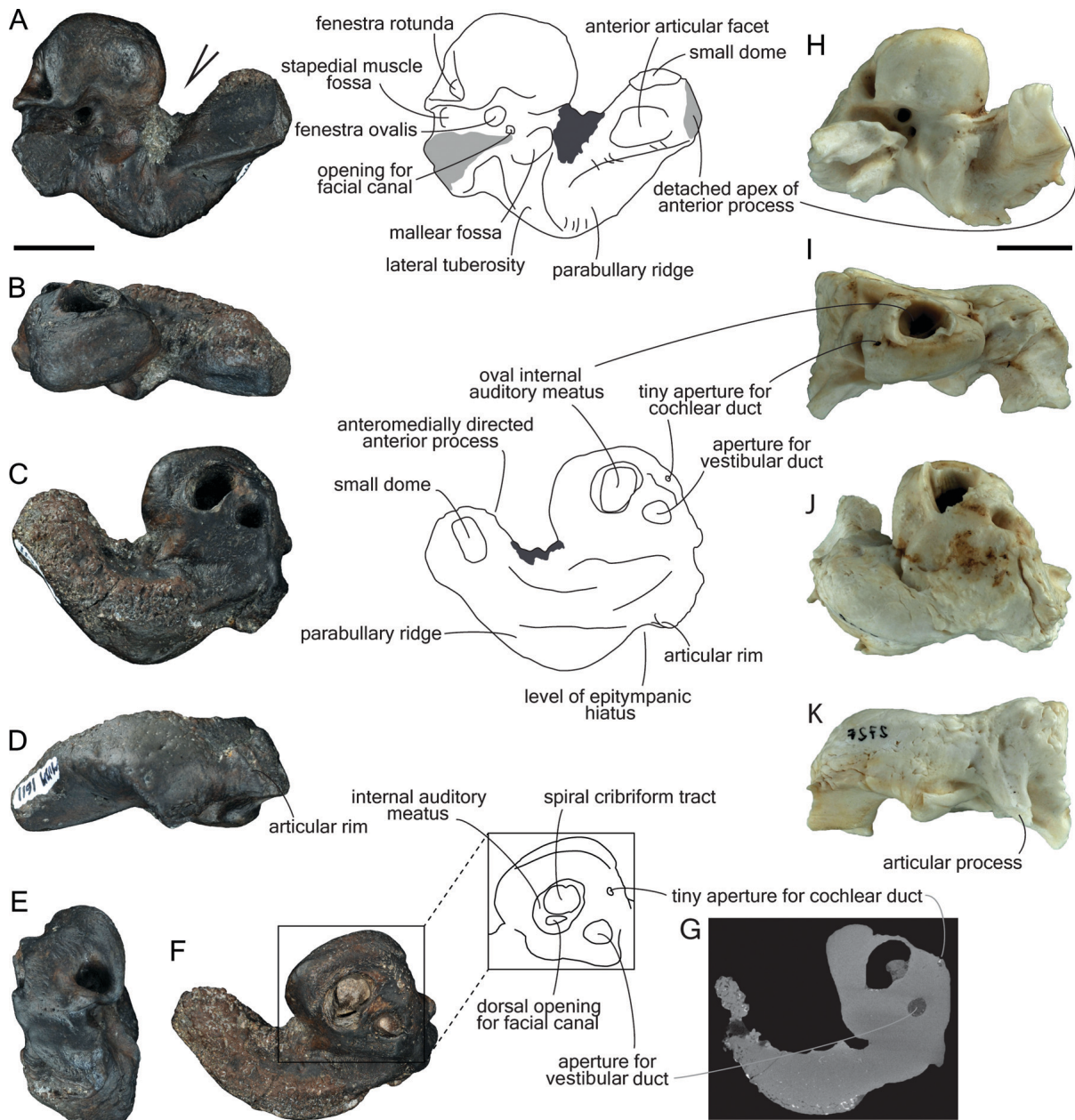


FIGURE 2. Comparison of platanistine periotics. **A–F**, left periotic of *Platanistinae*, gen. et sp. indet., MUSM 1611, late middle Miocene of Peruvian Amazonia, in ventral view with corresponding explanatory drawing (**A**), in medial view (**B**), in dorsal view with corresponding explanatory drawing (**C**), in lateral view (**D**), in posterior view (**E**), and in anterodorsomedial view with corresponding explanatory drawing of the openings in the pars cochlearis (**F**); **G**, CT scan section of MUSM 1611 with an orientation roughly similar to **F**, passing through the tiny opening of the cochlear duct. **H–K**, right periotic (reversed) of *Platanista gangetica* MSNTUP M272, the extant Ganges River dolphin, in ventral (**H**), medial (**I**), dorsal (**J**), and lateral (**K**) views. Light gray, break surfaces; dark gray, concretion. Arrow in **A** indicates the angle between anterior process and pars cochlearis. Scale bars equal 10 mm. (Color figure available online.)

than the fragmentary mandible from Oregon, and thus partly fills the temporal gap between the Oregon specimen and the extant *Platanista*.

The depositional environment of the western Amazonian Neogene layers has long been debated; Miocene deposits have been interpreted as continental, fluvio-lacustrine, or marine in origin, or combinations thereof (Wesselingh et al., 2002; for review, Hoorn et al., 2010a). Middle Miocene deposits in the Fitzcarrald area have been proposed to correspond to a freshwater, tidally

influenced megalake with occasional marine incursions (Espurt et al., 2007, 2010; Hoorn et al., 2010b; Roddaz et al., 2010). In addition to numerous terrestrial and semiaquatic mammals, the Fitzcarrald vertebrate fauna includes fish taxa (mostly characiforms and siluriforms) and two turtles (*Chelus* sp. and *Podocnemis* sp.), the extant relatives of which live in freshwater environments. Other fish taxa from the fauna have extant relatives that live in marine to freshwater (*Carcharhinus* sp., *Pristis* sp., or Sciaenidae indet.), and marine to estuarine (*Rhinoptera* sp.)

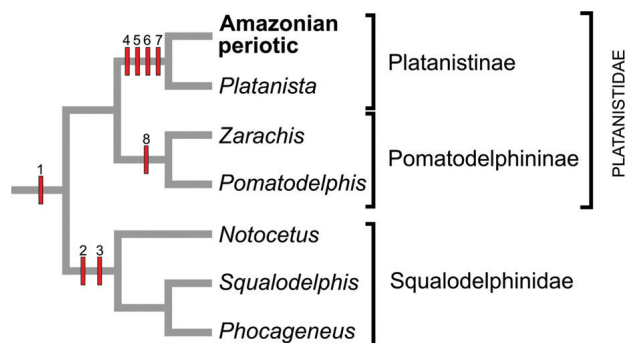


FIGURE 3. Cladogram, modified from Muizon (1987), showing the relationships of the late middle Miocene Amazonian platanistine (MUSM 1611) to other platanistids and squalodelphinids based on the main characters of the periotic discussed in the text. (1) development of an articular process sensu Muizon, 1987, on the lateral surface of the anterior process of the periotic; (2) square-shaped pars cochlearis; (3) large, thin-edged dorsal opening of the cochlear aqueduct, which faces dorsally; (4) anterior process strongly anteromedially bent; (5) tiny aperture of the cochlear aqueduct; (6) internal auditory meatus oval, with the dorsal opening for the facial canal lateral to the spiral cribriform tract; (7) separate ossicle at the apex of the anterior process; (8) transverse thickening of the anterior process. Characters from other parts of the skeleton are discussed in other works (Muizon, 1987; Fordyce, 1994; Barnes, 2006; Geisler et al., 2011). (Color figure available online.)

environments (e.g., Lundberg et al., 2010), in good agreement with the proposed marine influences for these deposits. A few other fragmentary cetacean remains have been collected from the same deposits (IN-008 locality; Goillot et al., 2011); only one tympanic bulla could be referred to an indeterminate delphinidan.

Considering the data reported above about the depositional environment and the associated vertebrate assemblage, it is tempting to hypothesize that the Amazonian platanistine lived in a freshwater/oligohaline megalake that experienced only occasional contact with the sea. This hypothesis would be consistent with the scenario of an invasion of a South American freshwater environment by a close relative of *Platanista*. However, a marine origin for the Amazonian platanistine cannot be completely excluded.

Based on our new specimen and considering the large geographical distance between the Amazonian Basin and the Ganges and Indus region, we can infer that in the past the subfamily Platanistinae had a wider geographical distribution and that, at least in a first phase of its evolutionary history, was not restricted to strictly freshwater environments. Moreover, because the fragmentary Oregon specimen is the oldest, even if tentative, record of the subfamily (early Miocene; Barnes, 2006), we propose the following sequence of events: (1) a marine origin for platanistines, possibly in the North Pacific Ocean, before or during the early Miocene; (2) some marine platanistines entered the freshwater Amazonian basin before the end of middle Miocene, probably by the Venezuelan-Colombian corridor (for paleogeographic maps, see Hoorn et al., 2010b); and (3) other marine platanistines reached the Indian Ocean and adapted to the Ganges and Indus rivers, where they survived as the sole representatives of this subfamily. The most parsimonious scenario, from an eco-physiological perspective, would be that the ancestors of both the Amazonian platanistine and *Platanista* already lived in shallow marine and estuarine waters, a scenario supported by the record of members of its sister group Pomatodelphininae from shallow marine to near estuarine (Barnes, 2006) and even freshwater (Hulbert and Whitmore, 2006) Miocene deposits. Additional

support for this hypothesis comes from the following morphological observations: (1) all the extant odontocetes with a narrow and elongated rostrum live in freshwater (*Inia*, *Lipotes*, and *Platanista*) or in coastal and estuarine (*Pontoporia*) environments; (2) the only fossil platanistids for which the rostrum is known have a much elongated snout with a narrow anterior portion; and (3) the fragmentary platanistine mandible fragment from Oregon (Barnes, 2006) most likely corresponds to a long and narrow snout. Therefore, a narrow and elongated rostrum might have been a preadaptation favoring the colonization of freshwater environments, a hypothesis that should be tested in future phylogenetic and morphofunctional analyses. In a recent supermatrix analysis of cetaceans, Geisler et al. (2011) conducted one analysis of their morphology partition by constraining morphology with a molecular scaffold. On this tree, among characters possibly related to the rostrum length, the high number of mandibular teeth was interpreted as plesiomorphic among river dolphin lineages, whereas an elongated mandibular symphysis evolved twice in taxa inferred to inhabit marine environments. This optimization is consistent with our preadaptation hypothesis. The feeding technique, irrespective of the habitat, is in some cases even more strongly correlated to the length of the snout (raptorial versus suction feeding; see Werth, 2006).

It is also interesting to note that the area where the new platanistine was found is occupied today by the iniid *Inia*, the Amazon River dolphin. The evolutionary history of iniids is still poorly understood, but *Ischyrorhynchus*, from several late Miocene South American freshwater deposits, has long been considered as an iniid (Cozzuol, 2010; Negri et al., 2010). Recent phylogenetic results surprisingly proposed *Ischyrorhynchus* as the sister group of *Platanista* (Geisler et al., 2012). Additional work and material are clearly needed, but the remains of *Ischyrorhynchus* and the platanistine periotic described here might prove to belong to a single taxon. Regardless, the Miocene paleogeographic and paleoecological evolution of the Amazon basin (e.g., Hoorn et al., 2010b; Roddaz et al., 2010) might have been conducive for the iterative isolation of several lineages of previously shallow marine or estuarine dolphins, an argument already proposed for different groups of marine-derived fishes from Amazonian rivers (Lovejoy et al., 2006). Only the lineage leading to *Inia geoffrensis* survived, whereas platanistines went extinct everywhere else, except in the distant Ganges and Indus river basins. Such a scenario would corroborate the well-supported hypothesis that repeated freshwater colonization events occurred during the evolutionary history of odontocetes (Cassens et al., 2000; Hamilton et al., 2001; Geisler et al., 2011, 2012).

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