

# First record of the family Protocetidae in the Lutetian of Senegal (West Africa)

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**Abstract:** The earliest cetaceans are found in the early Eocene of Indo-Pakistan. By the late middle to late Eocene, the group colonized most oceans of the planet. This late Eocene worldwide distribution clearly indicates that their dispersal took place during the middle Eocene (Lutetian). We report here the first discovery of a protocetid fossil from middle Eocene deposits of Senegal (West Africa). The Lutetian cetacean specimen from Senegal is a partial left innominate. Its overall form and proportions, particularly the well-formed lunate surface with a deep and narrow acetabular notch, and the complete absence of pachyostosis and osteosclerosis, mark it as a probable middle Eocene protocetid cetacean. Its size corresponds to the newly described *Togocetus traversei* from the Lutetian deposits of Togo. However, no innominate is known for the Togolese protocetid, which precludes any direct comparison between the two West African sites. The Senegalese innominate documents a new early occurrence of this marine group in West Africa and supports an early dispersal of these aquatic mammals by the middle Eocene.

**Keywords:** innominate, Lutetian, Protocetid, Senegal

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## INTRODUCTION

Africa seems to have played a pivotal role in the evolution of early marine mammals, but the sub-Saharan Paleogene fossil record is very poor and relatively little paleontological work has been carried out in sub-Saharan Africa (Domning *et al.*, 2010; Gingerich, 2010). The great potential to discover early cetaceans and associated fauna in Senegal was demonstrated over half a century ago. In 1966, Elouard reported the discovery of a partial skeleton of an archaeocete from Lutetian deposits in a water well at Tiavandou located 8 km south of Kaolack (west-central Senegal; Fig. 1 and Elouard, 1966).

Fifteen meters deep inside the well, the well-diggers of Tiavandou were surprised to find bones of a gigantic beast in limestone deposits, namely some ten vertebrae and a few teeth. Shocked by this discovery, they finally decided to carefully bury the bones in the vicinity of the well. As chance would have it, one vertebra did not take part to the funeral and was given to the village chief and came to a school teacher in Kaolack, L. Costes, who brought it to Dakar. The members of Laboratory of Geology of the University of Dakar then decided to organize a proper excavation inside the abandoned well.

The excavation led to discovery of numerous vertebrae (18), some fragments of ribs, but no limb or piece of skull except for some teeth enclosed in an altered bone. Elouard (1966) attributed these remains to the genus *Zeuglodon*, an archeocete of 8 to 10 metres long. Gingerich (2010) recently gave a younger estimation (from Bartonian to Priabonian) for the age of these remains based on the recognition of basilosaurid features on the teeth. Frustratingly, the “bête de Tiavandou” (i.e. beast of Tiavandou), which was the only Senegalese specimen of fossil

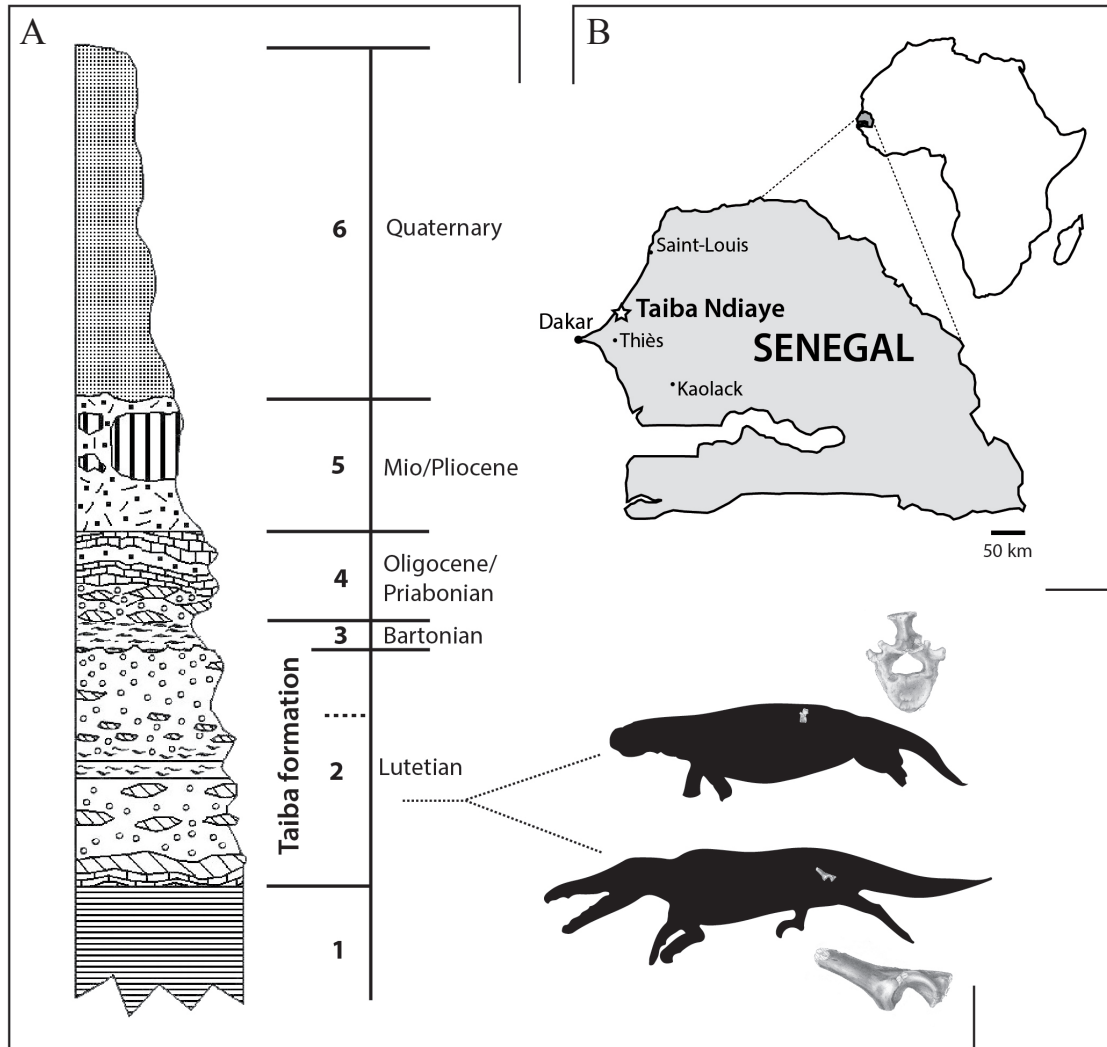
cetacean found to date, seems to have been lost (pers. comm., Institut Fondamental d’Afrique Noire, IFAN).

Recent discovery of a Lutetian stem sirenian (Hautier *et al.*, 2012) in the phosphate quarry of Taïba Ndiaye has demonstrated the great potential for new discoveries in the Senegalese phosphate series, especially of early marine mammals. In 1979, one of us (PMH) was in charge of undertaking the geological survey in the area of Taïba Ndiaye when he discovered a partial innominate in the now abandoned quarry of Ndomor Diop. This discovery occurred at the end of the exploitation period of this part of the quarry, the ore layer becoming thinner and grading laterally into limestone and marl. The partial innominate was found in these latter deposits. We present here the description of this bone, which represents the westernmost African remains of a protocetid.

*Institutional abbreviation:* SN, University of Dakar, Dakar, Senegal.

## GEOLOGICAL OVERVIEW

The phosphate quarry of Taïba Ndiaye is located north of the plateau of Thiès (Western Senegal - Fig. 1B). Previous studies already described precisely the stratigraphical context of the quarries of Taïba Ndiaye and Lam-Lam (Tessier, 1952; Chino, 1963; Castelain, 1965; Marie, 1965; Monciardini, 1966; Brancart & Flicoteaux, 1971; Flicoteaux, 1975, 1982; Tessier *et al.*, 1976; Ducasse *et al.*, 1978; Samb, 2008). In the new stratigraphical nomenclature of the Senegalese sedimentary basin, Roger *et al.* (2009) distinguished two formations, the lower of



**Figure 1.** Stratigraphic position (A) and geographic position (B) of the quarry of Taïba Ndiaye that yielded the fossil of cetacean described in this study. Original arts by Laurence Meslin, © Laurence Meslin - CNRS.

which is the Formation of Lam-Lam and the upper the Taïba Formation (Fig. 1A). The Lam-Lam Formation is composed predominantly of marl and limestones from the lower Lutetian (Fig. 1A, 1) whereas the Taïba Formation mainly consists of phosphate deposits.

Three units are represented in the Taïba Formation, which varies in thickness from 5 to 12 m (Fig. 1A). The basal heterogeneous ore, bearing the specimen described here, consists of a fine brownish phosphate bearing sandstone with flints, rarely interbedded with brown clays (Fig. 1A, 2). It is overlain by homogeneous ore, which consists of pinkish phosphate of lime constituted by phosphatic grains in a phosphatic and/or clay matrix with rare flints (Fig. 1A, 2). A thin layer of variegated clay overlies the homogeneous ore (Fig. 1A, 3). The whole formation is dated from the late Lutetian to the Bartonian based on planktonic foraminifera (Marie, 1965; Flicoteaux, 1975, 1982; Brancart, 1977; Ducasse *et al.*, 1978; Samb, 2008) and sharks (Hautier *et al.*, 2012).

A superficial covering, dominated by quaternary sand dunes of 20 to 40 m high (Fig. 1A, 6), covers the phosphate Taïba Formation. These dunes are part of a system called the “Red Dunes of Ogolian” that cover most of the northern part of the Senegalese coast.

**SYSTEMATIC PALAEONTOLOGY**

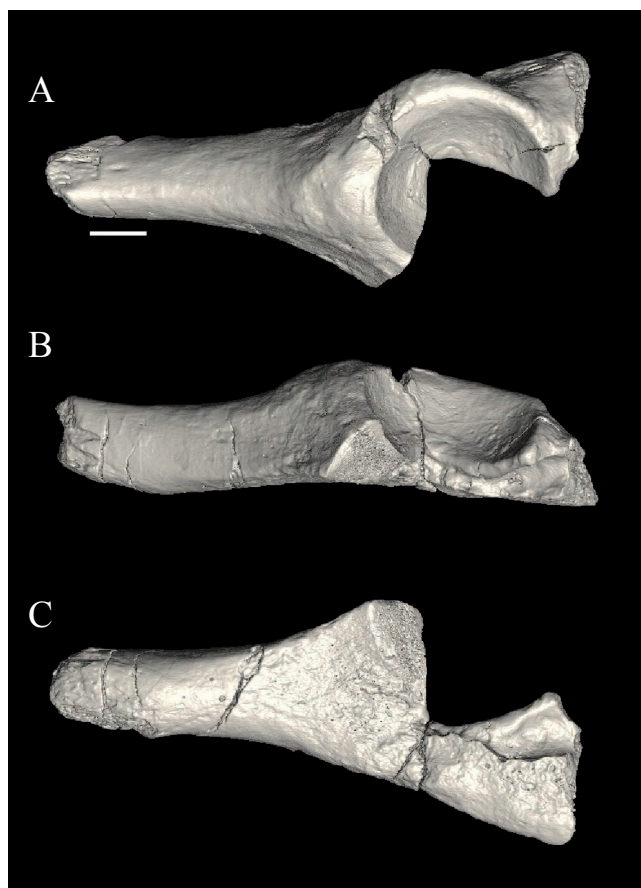
Class MAMMALIA Linnaeus, 1758  
 Order CETACEA Brisson, 1762  
 Suborder ARCHAEOCETI Flower, 1883  
 Family PROTOCETIDAE Stomer, 1908  
 gen. and sp. indet.

**Referred material.** SN103, a partial left innominate. A 3D reconstruction of SN103 was deposited in MorphoMuseum (<http://www.morphomuseum.com/>; M3#5\_SN103).

**Age and occurrence.** Taïba Formation, Lutetian of the near Taïba Ndiaye, quarry of the Industries Chimiques du Sénégal (ICS) (Figs 2, 3, and 4). The innominate, like the prorastomid vertebra (SN102; Hautier *et al.*, 2012), was collected in the area of Ndomor Diop, which was previously exploited but is now completely abandoned.

**Description** (Figs 2 and 3)

Partial left innominate mostly consisting of the ilium. The ilium



**Figure 2.** CT scan of the Senegalese innominate SN103 in lateral (A), ventral (B), and medial (C) views. Scale bar = 1 cm.

is gracile and characterized by the retention of a well-formed acetabulum with a circular lunate surface. Suture lines have been obliterated, so individual bones of the innominate may have fused but the ischium and pubis are largely missing. The rounded acetabulum is 31.5 mm in diameter (measured around the margin of the lunate surface) and 16 mm deep (measured to the deepest part of the lunate surface). It opens caudalventrally (the ventral part is largely broken). A sharp ridge in the lower third of the socket suggests the presence of a deep, well-marked acetabular notch (Figs 2 and 3).

The lunate surface overhangs the acetabular notch dorsally. A groove is defined medially behind this ridge. A bulge delineates the lateral edge of the acetabulum, forming a thick ridge. A distinct bulge is visible on the lateral side anterior to the acetabulum for origination of ligaments or muscles (Figs 2 and 3). The foramen obturator and the iliopectineal eminence are not preserved. The body of the ilium is slender and constricted, trihedral in cross-section close to acetabulum and oval more anteriorly.

The ventral border of the iliac neck is relatively flat, whereas the dorsal border is convex; the surface of the innominate dorsal to the acetabulum is rugose. The medial surface is relatively smooth and flat. The rest of the body is missing, especially the auricular surface for articulation of the sacral vertebrae. The ilium shows no sign of pachyostosis and osteosclerosis (Fig. 4), the medullar region is occupied by an open cavity composed by a network of thin trabeculae. The preserved part of the body of the ischium is D-shaped in cross section. A flat lateral surface of the ischium overhangs the acetabulum posteriorly

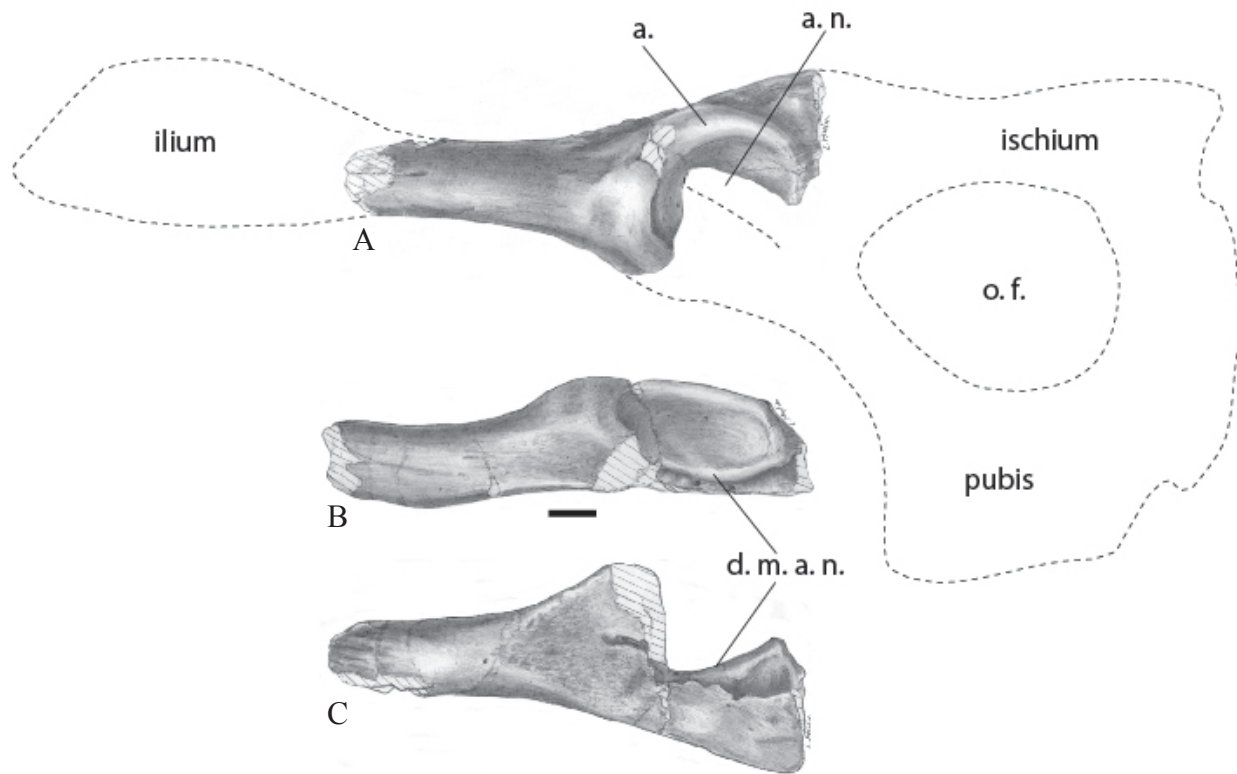
## Comparison

Gingerich *et al.* (1993) and Beatty and Geisler (2010) noticed that the morphology of the pelves of protocetid archaeocetes can be confused with pelves of protosirenids or moeritheriids (Fig. 5). In fact, the present innominate closely resembles the one of Protosirenidae such as *Protosiren fraasi* and *P. sattaensis* characterized by a dorsoventrally slender ilium (Fig. 5A and B; Gingerich *et al.*, 1995a). However, the identity of SN103 as a sirenian can be ruled out because its ilium shows no sign of pachyostosis or osteosclerosis (Fig. 4). The most primitive sirenian, *Pezosiren portelli* has been shown (Domning, 2001; de Buffrénil *et al.*, 2010) to be already pachyosteosclerotic like other sirenians. With the exception of a few posterior ribs, the skeleton of *Protosiren* is known to be pachyosteosclerotic (Beatty and Geisler, 2010; Zalmout, 2008; Zalmout *et al.*, 2003). As a matter of fact, the innominate of *Protosiren* recently recovered from the late Middle Eocene of South Carolina (Beatty and Geisler, 2010) was shown to be clearly osteosclerotic.

Besides this, some other distinct morphological features were observed. The acetabulum of *Protosiren fraasi* is delineated by a sharp edge (Gingerich *et al.*, 1995a) that contrasts with the bulge-like acetabular edge of SN103. The ilium of *Protosiren sattaensis* is characterized by a distinct bulge on the lateral side anterior to the acetabulum. It resembles SN103 in this way, but clearly differs in having a very shallow and wide acetabular notch (Gingerich *et al.*, 1995a).

Some morphological features of SN103 also recall the morphology of the innominate of *Moeritherium* from Egypt (Fig. 5C; Andrews, 1906; Gingerich 1992), an Eocene to Oligocene proboscidean that did not have pachyosteosclerotic bones. However, the specimen can be clearly differentiated from the proboscidean innominates in that *Moeritherium* has a horseshoe-shaped acetabulum flattened dorsoventrally with a prominent rim interrupted posteroventrally by a wide but shallow acetabular notch (Andrews, 1906). Unlike SN103, the surface of the ilium of *Moeritherium* is concave on the lateral side anterior to the acetabulum (Andrews, 1906). The same is true for the innominate of *Numidotherium koholense*, which is bigger than SN103 and characterized by an iliac blade more dorsoventrally flattened, a horseshoe-shaped acetabulum with a widely opened and almost oval acetabular notch (pers. obs.; specimen UOK 215, Université de Montpellier 2). Moreover, even if post-mortem transport cannot be discarded, early proboscideans were likely restricted to a freshwater environment (Clementz and Holroyd, 2007; Liu *et al.*, 2008); such an ecology contrasts with the marine depositional environment previously proposed for the formation of Taïba.

This incomplete but well-preserved innominate shows a suite of morphological features of Cetacea. Eocene cetacean innominates are very rare in the fossil record but partial or subcomplete ones are known from remingtoncetids (Gingerich *et al.*, 1993, 1995b), protocetids (Gingerich *et al.*, 1993, 1994, 2001a, 2009; Hulbert, 1998; Uhen, 2014), and basilosaurids (Kellogg, 1936; Gingerich *et al.*, 1990). The innominate of the remingtoncetid *Dalanistes* (GSP-UM 3106, Gingerich *et al.*, 1995b) can be clearly discriminated from SN103 in displaying a massive ilium with a larger and deeper acetabulum, and a characteristic triangular depression on the lateral surface of the ilium just anterior to the acetabulum (Gingerich *et al.*, 1995b). Basilosaurid innominates clearly differ from SN103 in displaying a rectangular shape with ischial and pubic rami



**Figure 3.** Drawings of the Senegalese innominate SN103 in lateral (A), ventral (B), and medial (C) views. Dashed line represents missing portion of pelvis based on the morphology of the innominate of *Georgiacetus vogtlensi* (Hulbert et al., 1998, holotype GSM 350) Abbreviations: a., acetabulum; a. n., acetabular notch; d. m. a. n., dorsal margin of the acetabular notch; o. f., obturator foramen. Scale bar = 1 cm. Original arts by Laurence Meslin, © Laurence Meslin - CNRS.

directed ventrally, a much shallower acetabulum, and a very short ilium (Fig. 5D; Gingerich et al., 1990).

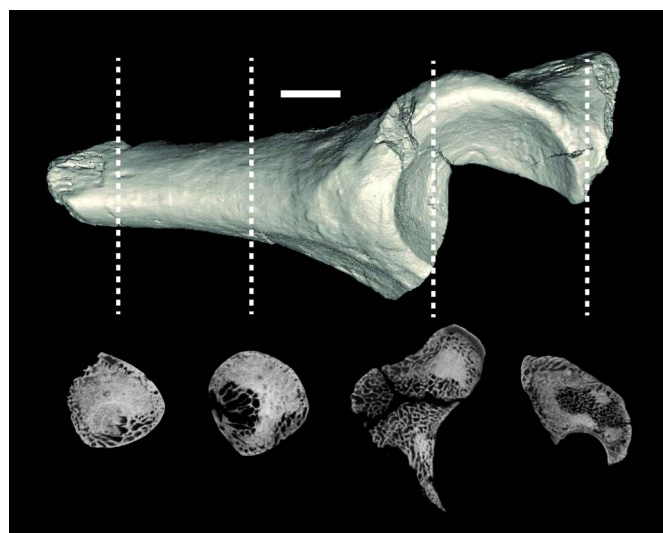
SN103 almost certainly belongs to the family Protocetidae based on its size and morphology. The most complete protocetid innominates are known from *Rodhocetus* (Lutetian, Pakistan; Gingerich et al., 1994, 2001b), *Maiacetus* (Lutetian, Pakistan; Gingerich et al., 2009), *Qaisracetus* (Lutetian, Pakistan; Gingerich et al., 2001a), *Georgiacetus* (Bartonian, Georgia; Hulbert, 1998; Hulbert et al., 1998), *Natchitochia* (Bartonian, Mississippi; Uhen, 2014), and questionably referred to *Indocetus* (Lutetian, India and Pakistan; Gingerich et al., 1993). They all share a suite of morphological features of the ilium: a deep acetabulum with well-formed lunate surface, which overhangs dorsally a deep acetabular notch (Uhen, 2014). All these features are visible on SN103.

The ilia of *Rodhocetus* and *Maiacetus* (Fig. 5F and G) are broader dorsoventrally than SN103. On the contrary, the ilia of *Indocetus*, *Qaisracetus*, *Natchitochia*, and *Georgiacetus* (Fig. 5H, I and J) are much narrower, displaying a deep and narrow acetabular notch and thickened acetabular edges, which closely resemble SN103. Interestingly, SN103 presents a mixture of morphological characters between the lower middle Eocene *Indocetus* and more recent protocetids such as *Qaisracetus*, *Georgiacetus*, and *Natchitochia*. The acetabulum of SN103 is nearly as ventrally positioned as the one of *Indocetus* and is overhung posteriorly by a flat lateral surface of the ischium; however the acetabulum of *Indocetus* is delineated by a sharpened edge and no bulge is visible anterior to it.

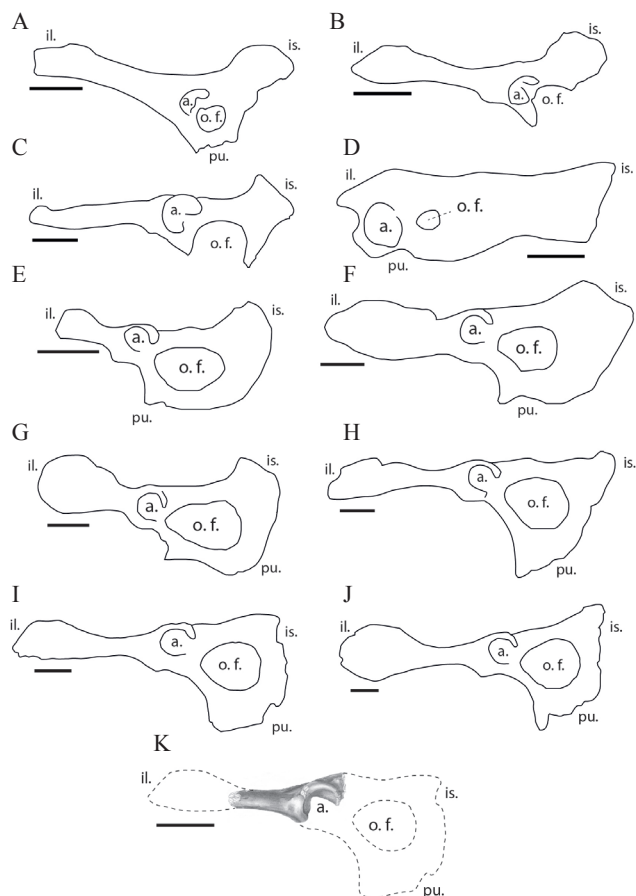
The iliac neck of SN103, like those of *Qaisracetus*, *Georgiacetus*, and *Natchitochia*, is slender and convex anterior to the acetabulum. However, it differs from the latter two in

displaying a more robust iliac neck; the innominates of *Georgiacetus* and *Natchitochia* are also significantly larger, with an acetabulum measuring 49.1 mm and 55.6 mm in height respectively (Uhen, 2014). Moreover, the lunate surface in *Georgiacetus* is more dorsally oriented whereas it is more lateral in SN103, *Qaisracetus*, and *Natchitochia*.

Uhen (2014) noted that the two main differences between *Georgiacetus* and *Natchitochia* reside in the shape of the ventral



**Figure 4.** Bone compactness distribution in cross-sections of the Senegalese innominate SN103. In the cross-sections, gray areas do not represent pachyosteosclerotic bone, but portions of the medullar region filled with sediment. Scale bar = 1cm.



**Figure 5.** Innominate outlines (lateral views) in several mammalian species that were used for comparisons. **A**, *Protosiren smithae* (left, CGM 42292 holotype; Gingerich *et al.*, 1995), **B**, *Protosiren fraasi* (left, SMNS 43976b; Gingerich *et al.*, 1995); **C**, *Moeritherium* (right, reversed; Andrews, 1906); **D**, *Basilosaurus cetoides* (right, reversed; Kellogg, 1936); **E**, *Pakicetus sp.* (left, H-GSP 18507; Uhen, 2014); **F**, *Rodhocetus kasranii* (right, reversed, GSP-UM 3012; Uhen, 2014); **G**, *Maiacetus inuus* (left, and pubis partly reconstructed, GSP-UM 3551; Uhen, 2014); **H**, *Qaisracetus arifi* (right, reversed, GSP-UM 3410; Uhen, 2014); **I**, *Georgiacetus vogtlensis* (left, GSM 350; Hulbert, 1998); **J**, *Natchitochia jonesi* (right, reversed, MMNS 4849; Uhen, 2014); **K**, Senegalese innominate SN103. Abbreviations: a., acetabulum; il., ilium; is., ischium; o. f., obturator foramen; pu., pubis. Scale bar = 5 cm.

margin of the pubis and the presence/absence of clearly defined auricular surface, two features that are missing on SN103. The morphology of SN103 is overall quite similar to the innominate of *Qaisracetus* both in size and morphology. However, the lateroventral margin of the iliac neck of *Qaisracetus* is distinctly characterized by the presence of a sharp ridge whereas this margin is more rounded in SN103. The acetabulum diameter of *Qaisracetus* is 38 mm (Gingerich *et al.*, 2001a), which is larger than the one of SN103 (i.e. 31.5 mm). However, such a difference in size can be attributed to individual variation, especially considering that some protocetids (i.e. *Maiacetus inuus*; Gingerich *et al.*, 2009) have been shown to present sexual dimorphism, with male having a significantly greater body length and distinct pelvic morphology.

Several postcranial remains of the protocetid *Pappocetus* have been described from the middle Eocene of Nigeria (Halstead and Middleton, 1974, 1976), but no innominate was reported. Teeth and bone fragments, first identified as *Pap-*

*pocetus*-like, were also reported from the Lutetian deposits of Kpogamé-Hahotoé basin (Cappetta & Traverse, 1988). A recent reconsideration of these specimens (Gingerich *et al.*, 1992; Gingerich and Cappetta, 2014) allowed identifying several Togolese archeocetes, the most common of which is the protocetid *Togocetus traversei*. Unfortunately, only a pubic portion of a left innominate of *T. traversei* is known from Kpogamé; this portion is absent on SN103. For Gingerich and Cappetta (2014), this pubic portion very closely matches the left pubis of *Rodhocetus kasranii* and recalls the right pubis of *Maiacetus inuus*. Despite the absence of a more complete innominate in the Togolese material, it worth mentioning that the spherical femoral head of *T. traversei* measures 28.5 in diameter and so it closely matches the size of the acetabulum of the innominate SN103.

From a paleobiological point of view, the retention of a well-formed lunate surface and acetabular notch in acetabulum suggests a locomotor function for the hind limb (Hulbert *et al.*, 1998). *Rodhocetus*, *Qaisracetus*, *Protocetus*, and *Natchitochia* were probably swimming using simultaneous pelvic paddling (e.g. *Lutra*) due to the presence of a well-developed articulation of the innominate with the sacrum, while *Georgiacetus* was probably using dorsoventral pelvic undulation (e.g. *Enhydra*) because of the lack of such an articulation (Uhen, 2014). The pelvic region likely to show the iliosacral synarthrosis (the auricular surface) is not preserved on the Senegalese innominate, so no interpretation can be made on the locomotor function of the hind limb in terms of terrestrial or marine locomotion.

## DISCUSSION

The earliest cetaceans are found in the early Eocene (Ypresian) of Indo-Pakistan, but by the late middle to late Eocene (Bartonian and Priabonian), the group has colonized most of the oceans of the planet from Egypt (Gingerich, 1992; Gingerich and Uhen, 1996), Europe (e.g. Uhen and Tichy, 2000), North America (e.g. Hulbert *et al.*, 1998; Uhen, 2014), and New Zealand (Köhler and Fordyce, 1997). This late Eocene worldwide distribution clearly indicates that their dispersal took place during the middle Eocene (Lutetian). The new fossils from Senegal and Togo are then of primary importance as they have the potential to considerably improve our knowledge of the African diversification and subsequent global dispersion of these early marine mammals. Startlingly, despite some geological and temporal similarities, the Senegalese and Togolese phosphate basins have yielded somewhat different mammalian fossil remains. Perhaps the most intriguing case is that of the sirenians: while a prorastomid sirenian was described in Senegal (Hautier *et al.*, 2012), this family is absent from the phosphates of Togo where, in contrast, protosirenid and dugongid sirenians have been reported (Gingerich and Cappetta, 2014). The Senegalese innominate may belong to *Togocetus*; however, in order to confirm this, more material will be needed both from Senegalese and Togolese deposits. We show that this innominate is more similar to the one of the Asian *Qaisracetus* than to the one of the North American *Georgiacetus* and *Natchitochia*.

Protocetids were not nearly as sophisticated swimmers as extant cetaceans, probably swimming by undulation of the body and tail (Buchholtz, 1998) or using alternate or simultaneous hind limb paddling (Gingerich, 2003; Uhen, 2014). It is believed that their dispersal occurred from the eastern Tethys of Indo-Pakistan via coastal water circling the Tethys Ocean.

The fact that similar protocetids could be restricted to coastal waters of West Africa, and share morphological features with a Pakistani form, is consistent with this biogeographic scenario. Such a scenario of dispersal via coastal water has also been proposed to explain their dispersal in North America (Geisler *et al.*, 2005), which most likely took place along the continuous, warm-climate North Atlantic shoreline.

However, Gingerich and Cappetta (2014) showed that *Togocetus* was unusual among protocetids in being a more aquatic foot-powered swimmer because it displays heavily muscled shoulder and knee joints, as well as hind limbs that were unable of supporting their own body weight on land. The protocetids that reached the western coasts of Africa might happen to be forerunners in showing more sophisticated swimming abilities. Such protocetids might have also been able to migrate straight across the (then-narrower) Atlantic Ocean with the help of favourable westward paleocurrents and paleowinds from Africa (Bandoni de Oliveira *et al.*, 2009; Uhen, 1999; Hautier *et al.*, 2012). New West African discoveries would undoubtedly provide pivotal data to examine the potential connections in deep time between contemporaneous localities in Africa and Americas.

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