



General palaeontology, systematics and evolution (Vertebrate palaeontology)

A new record of *Notocetus vanbenedeni* (Squalodelphinidae, Odontoceti, Cetacea) from the Early Miocene of Peru



Une nouvelle occurrence de Notocetus vanbenedeni (Squalodelphinidae, Odontoceti, Cetacea) dans le Miocène inférieur du Pérou

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ABSTRACT

An almost complete skull with associated periotics and one cervical vertebra from the Early Miocene strata of the Chilcatay Formation (Pisco Basin, Peru) is described here and referred to *Notocetus vanbenedeni*, a species previously recorded from Argentina, belonging to the extinct odontocete family Squalodelphinidae (Platanistoidea). The fossil was collected in the same locality and approximately the same stratigraphical horizon as *Huavidelphis raimondii*, suggesting the sympatric coexistence of two squalodelphinids during the Early Miocene along the Pacific coast of South America. Considering the new record here described, *N. vanbenedeni* lived both along the Atlantic and Pacific coasts of South America, two marine areas in wide contact during the Late Oligocene and Early Miocene. Despite the relative commonness of squalodelphinids in the Chilcatay Fm., the worldwide record of this family remains globally rather scarce and significant specimens were only found in Italy, France, along the East Coast of USA, Argentina, Peru, and possibly New Zealand.

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RÉSUMÉ

Provenant de couches du Miocène inférieur de la formation Chilcatay (bassin Pisco, Pérou), un crâne subcomplet avec les périotiques et une vertèbre cervicale associés est décrit ici et rapporté à *Notocetus vanbenedeni*, une espèce préalablement connue d'Argentine et appartenant à la famille d'odontocètes éteints Squalodelphinidae (Platanistoidea). Le fossile a été collecté dans la même localité et approximativement le même niveau stratigraphique que *Huavidelphis raimondii*, suggérant la coexistence sympatrique de deux squalodelphinidés durant le Miocène inférieur le long de la côte pacifique de l'Amérique du Sud. En

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considérant la nouvelle occurrence décrite ici, *N. vanbenedeni* vivait aussi bien sur la côte atlantique que sur la côte pacifique de l'Amérique du Sud, deux régions marines connectées durant l'Oligocène supérieur et le Miocène inférieur. Malgré le caractère relativement commun des squalodelphinidés dans la formation Chilcatay, le registre mondial de cette famille reste globalement pauvre, et des spécimens significatifs n'ont été découverts qu'en Italie, en France, sur la côte est des États-Unis, en Argentine, au Pérou et, plus hypothétiquement, en Nouvelle-Zélande.

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1. Introduction

Investigations carried out during the last years in the Pisco Basin (Peru) led to the discovery of numerous well-preserved fossil marine vertebrate skeletons from the Middle Miocene–Pliocene Pisco Formation and from the latest Oligocene–Early Miocene Chilcatay Formation. These fossils are prevalently concentrated in some relatively restricted areas of the Pisco-Ica desert, south of the city of Ica (Fig. 1). The most significant new localities of the Pisco Formation are those of Cerro Colorado, where the giant raptorial sperm whale *Livyatan melvillei* (Lambert et al., 2010) and the long-snouted beaked whale *Messapicetus gregarius* Bianucci et al., 2010 were found, and of Cerro los Que-sos, where we collected the holotype of the beaked whale *Nazzacetus urbinai* Lambert et al., 2009. In Ullujaya and Zamaca, outcrops of the Chilcatay Formation revealed an unexpectedly high concentration of fossils of marine vertebrates (cetaceans, fishes, and sea turtles). Fossil whales are particularly abundant and well-preserved. Surprisingly, the remains belonging to the rare Miocene odontocete family Squalodelphinidae are some of the most common, including the recently described small species *Huaridelphis raimondii* Lambert et al., 2014. Squalodelphinids are Miocene dolphins characterized by a moderately elongated and tapered rostrum, single-rooted posterior teeth retaining ornamentation, and marked skull asymmetry. Our recent phylogenetic analysis (Lambert et al., 2014) confirmed that squalodelphinids belong to the superfamily Platanistoidea (sensu de Muizon, 1987), a large clade of odontocetes whose only surviving species is the Ganges and Indus river dolphin *Platanista gangetica* (see, Bianucci et al., 2013). The aim of this contribution is to describe a squalodelphinid specimen from Chilcatay Formation referred here to *Notocetus vanbenedeni* Moreno, 1892, a species previously recorded from the Late Oligocene–Early Miocene of Argentina (de Muizon, 1987; Lydekker, 1893; Moreno, 1892), and thereby to extend our knowledge on the distribution of squalodelphinids.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MGP, Museo di Geologia e Paleontologia, Padova, Italy; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNUP, Museo di Storia Naturale, Università di Pisa; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; RMNH,

Naturalis, Leiden, The Netherlands; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

1.2. List of specimens directly examined for comparison

H. raimondii MUSM 1396, 1403, 599; *Medocinia tetragorhina* (MNHN cast of holotype); *N. vanbenedeni* MLP 5-5; *Platanista gangetica* IRSNB 1507; MNHN A7943; MSNUP M272; RMNH 31169, USNM 172409, 23456, Pomatodelphininae USNM 206006; Pomatodelphininae cf. *Zarhachis* USNM 214759; *Pomatodelphis bobengi* USNM 299695; *Pomatodelphis* sp. USNM 187414; Squalodelphinidae USNM 21039, 475596; Squalodelphinidae aff. *H. raimondii* MUSM 603; *Squalodelphis fabianii* MGP 26134, 26141, 26378; *Zarhinocetus errabundus* cast USNM; *Zarhachis flagellator* USNM 10911, 10485.

2. Systematic palaeontology

Order CETACEA Brisson, 1762

Suborder ODONTOCETI Flower, 1867

Superfamily PLATANISTOIDEA Gray, 1863

Family SQUALODELPHINIDAE Dal Piaz, 1917

Type genus: *Squalodelphis* Dal Piaz, 1917

Other genera included: *Huaridelphis*, *Medocinia*, *Notocetus*, *Phocageneus*.

Genus *Notocetus* Moreno, 1892

Type and only included species: *N. vanbenedeni* Moreno, 1892.

Emended diagnosis: Same as for only included species, *N. vanbenedeni*.

Remark: A specimen presumably from the Earliest Miocene of New Zealand was tentatively referred to the genus *Notocetus* (Fordyce, 1994), but a redescription and a more detailed comparison with other known squalodelphinids are needed.

Notocetus vanbenedeni Moreno, 1892

Emended diagnosis: *N. vanbenedeni* differs from *Huaridelphis*, *Phocageneus*, and *Squalodelphis* in the retention of accessory denticles in the distal keels of the posterior teeth (teeth unknown in *Medocinia*). It further differs from *Huaridelphis* in: its larger size; the less abrupt anterior tapering of the rostrum in dorsal view; the lower tooth count (21–24 teeth per row contra 28–30 in *Huaridelphis*); the thicker

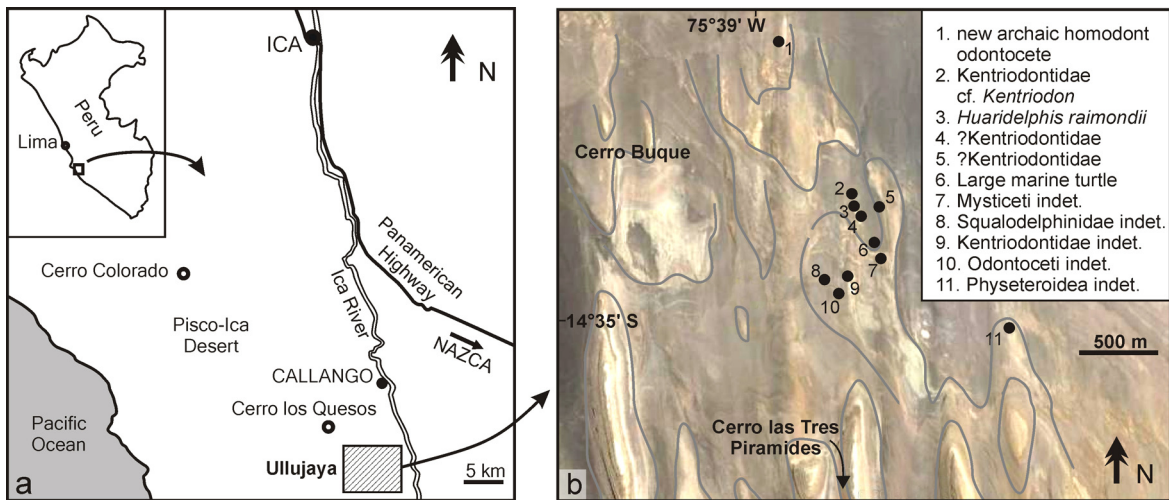


Fig. 1. (Color online.) a: maps of the Pisco-Ica desert indicating some investigated areas, including Ullujaya where *Notocetus vanbenedeni* Museo de Historia Natural 1395 was discovered; b: detail of the Ullujaya locality showing the position of other vertebrate remains. Note that Cerro Buque, from where a section of the Chilcatay Formation was published (Alvan De la Cruz, 2008), is a short distance northwest to Ullujaya.

Fig. 1. (Couleur en ligne.) a : cartes du desert Pisco-Ica localisant plusieurs zones etudiees, incluant Ullujaya, ou *Notocetus vanbenedeni* Museo de Historia Natural 1395 a ete decouvert ; b : detail du site de Ullujaya montrant la position des restes d'autres vertebres. Le site de Cerro Buque, d'ou une coupe de la formation Chilcatay a ete publiee (Alvan De la Cruz, 2008), se situe a une courte distance au nord-ouest de Ullujaya.

antorbital process of the frontal, distinctly thicker than the antorbital process of the maxilla in lateral view; the more elongated and robust postorbital process of the frontal; the flat dorsal surface of the vertex parallel to the horizontal plane, not anteroventrally sloping; the absence of a dorsoventral compression of the periotic at the level of the pars cochlearis and superior process (sensu Kasuya, 1973); and the less ventrally bent posterior process of the periotic. It further differs from *Medocinia* and *Squalodelphis* in: the dorsal opening of the mesorostral groove being narrower than the premaxilla in the base of the rostrum; and the wider dorsal exposure of the maxilla in the base of the rostrum (the premaxilla nearly reaches the lateral margin of the rostrum in *Medocinia* and *Squalodelphis*). It further differs from *Phocageneus* and *Squalodelphis* in the shorter anterior spine of the tympanic bulla. It further differs from *Squalodelphis* in: the higher tooth count (15 per row in *Squalodelphis*); the transversally wider nuchal crest (approximately as wide as the greatest width of the premaxillae in *Squalodelphis* and considerably wider than the greatest width of the premaxillae in *Notocetus*); and the stronger manubrium of the malleus with a rounded rather than pointed apex.

Holotype: MLP 5-5, skull, lacking the ear bones, and associated mandible (Lydekker, 1893; Moreno, 1892), Chubut province, Argentina.

Previously referred specimens from Argentina: AMNH 9485, skull, including the right tympanic bulla, mandible and some vertebrae and ribs, Santa Cruz province (True, 1910); AMNH 29026, fragment of skull, right periotic, tympanic bulla and malleus, several teeth, scapula and fragments of vertebrae and ribs, Chubut province (de Muizon, 1987).

Referred specimen: MUSM 1395, skull lacking the left squamosal and the teeth, with associated periotics (the left one in situ) and one cervical vertebra.

Locality: Ullujaya, the type locality of *H. raimondii*. Pisco Basin, 58 km SSE of Ica, 1.5 km north from Cerro Las Tres Piramides (see Alvan De la Cruz, 2008, fig. 1). Approximate geographic coordinates: S14°34'30"-W75°38'40" (Fig. 1).

Horizon: Chilcatay Formation, latest Oligocene to Early Miocene (DeVries, 1998, 2001; Dunbar et al., 1990). A section of the Chilcatay Formation at Cerro Buque, 1.65 km NWW to the Ullujaya locality has been published (Alvan De la Cruz, 2008). Based on the analysis of the stratigraphical sequence and shark teeth (presence of *Isurus desori* and *Carcharocles chubutensis*, absence of *C. megalodon*), the beds of the Chilcatay Formation in this section were dated to the Early Miocene (Alvan De la Cruz, 2008). In the same locality and approximately in the same stratigraphical horizon of MUSM 1395, we found a rich fossil vertebrate assemblage represented by other odontocetes (e.g., *H. raimondii*, kentriodontids, a stem physteroid and a new archaic homodont odontocete), a mysticete, sea turtles, sharks, and teleostean fishes (Fig. 1b).

Description and comparison: skull (Fig. 2). For most of the skull measurements available (see True, 1910), MUSM 1395 falls in the size interval between the holotype (MLP 5-5) of *N. vanbenedeni* and the somewhat larger referred specimen AMNH 9485 (Table 1). No major morphometric differences are noted, and all the minor dissimilarities can be explained with intraspecific variation and/or slight post-mortem deformation of the specimens. The condylobasal length (CBL) of MUSM 1395 is 600 mm, close to MLP 5-5 (CBL = 582 mm), feebly smaller than AMNH 9485 (CBL = 634) and the holotype of *Squalodelphis fabianii* (CBL = 640), but distinctly larger than the holotype of *H. raimondii* (CBL = 494 mm).

As in other specimens of *N. vanbenedeni* the rostrum of MUSM 1395 is more robust and, in dorsal view, less abruptly tapering in its proximal third than in *Huaridelphis*. In lateral view, the rostrum displays an apex distinctly

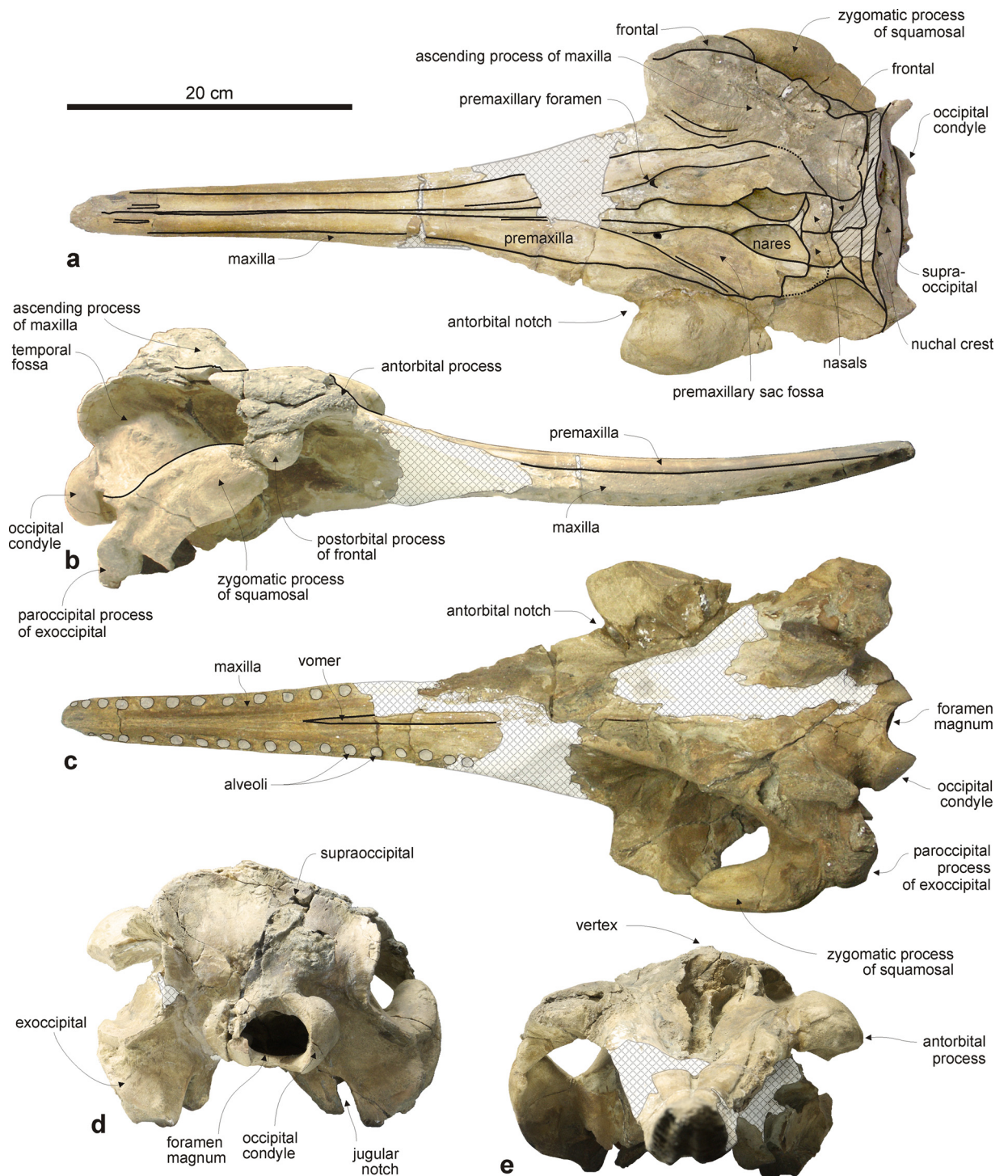


Fig. 2. (Color online.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395: skull in dorsal (a), right lateral (b), ventral (c), posterior (d), and anterior (e) views. Linear hatching indicates major breaks, crosshatching indicates reconstructed missing parts.

Fig. 2. (Couleur en ligne.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395 : crâne en vues dorsale (a), latérale droite (b), ventrale (c), postérieure (d) et antérieure (e). Les lignes diagonales pleines indiquent les surfaces de cassure principales, les hachures entrecroisées indiquent les parties reconstruites.

curved upward, a feature seemingly absent in the holotype and AMNH 9485. A similar variation is observed in *H. raimondii*, with an apex of the rostrum horizontal in the holotype and curved upward in MUSM 1403.

We observed a wide intraspecific variation of this character in the extant delphinids, particularly in some species with a proportionally elongated and thin rostrum (e.g., *Steno bredanensis*). Contrary to platanistids, the lateral

Table 1

Cranial measurements (in mm) for three specimens of *Notocetus vanbenedeni* from the Late Oligocene–Early Miocene of Argentina (AMNH 9485 and holotype MLP 5-5) and Peru (MUSM 1395). Measurements of the Argentinean specimens are taken from True (1910) and slightly reformulated.

Tableau 1

Mesures crânielles (en mm) pour trois spécimens de *Notocetus vanbenedeni* de l'Oligocène supérieur–Miocène inférieur d'Argentine (AMNH 9485 et holotype MLP 5-5) et du Pérou (MUSM 1395). Les mesures des spécimens argentins sont légèrement reformulées à partir de True (1910).

	MUSM 1395	MLP 5-5 (holotype)	AMNH 9485
Measurements from True (1910)			
Condylobasal length	600	+582	634
Rostrum length	403	368	433
Width across occipital shield	145	140	142
Height between upper margin of foramen magnum and nuchal crest	93	91	97
Height of foramen magnum	e29	33	40
Width of foramen magnum	e39	33	40
Height of occipital condyle	48	47	46
Length of temporal fossa	108	e102	115
Height of temporal fossa	66	e71	74
Minimum posterior distance between temporal fossae	134	e135	128
Width between orbit centers	227	230	e252
Anterior width of nasals	43	e46	e48
Width of rostrum at base	136	e114	142
Width of premaxillae at antorbital notches	78	–	89
Maximum distance between premaxillae anterior to bony nares	e15	e22	28
Width of maxillae at midlength of rostrum	49	e44	52
Width of premaxillae at midlength of rostrum	28	e28	30
Length of alveoli at midlength of rostrum	9.0	e7.0	9.5
Transverse width of alveoli at midlength of rostrum	9.0	–	8
Length of anteriormost alveoli	11.0	11.0	11.5
Transverse width of anteriormost alveoli	7.0	6.0	9.0
Length of upper tooth row	+302	e315	363
Number of teeth in upper tooth row	+18	22–23	21–22
Additional measurements for MUSM 1395			
Maximum width across premaxillae on cranium	e105		
Width of bony nares	45		
Distance between maxillae across the vertex	40		
Maximum length of nasal	24		
Length of median suture between nasals	14		
Length of median suture between frontals	28		
Orbit length	55		
Squamosal length from anterior tip of zygomatic process to ventral tip of postglenoid process	91		
Width of occipital condyles	88		
Width of right premaxillary sac fossa	40		
Width of left premaxillary sac fossa	41		

AMNH: American Museum of Natural History; MLP: Museo de La Plata; MUSM: Museo de Historia Natural; e: estimate; +: nearly complete; –: data unavailable.

maxilla-premaxilla suture is not located in a deep groove along the rostrum. The mesorostral canal is dorsally closed by the joined premaxillae along the distal third of the rostrum, whereas a narrow gap is observed in the holotype and AMNH 9485. Toward the base of the rostrum, the dorsal opening of the mesorostral canal feebly and progressively broadens. A similar condition is observed in AMNH 9485, whereas in the holotype a narrow separation between the premaxillae is observed along the whole length of the rostrum. The maxillary alveoli are larger than in *Huaridelphis*, and the original upper tooth count was likely close to the count in the holotype of *N. vanbenedeni* and AMNH 9485 (21–23), lower than in *Huaridelphis* (28–30), but higher than in *Squalodelphis* (15).

The widening of the premaxilla towards the base of the rostrum is more developed on the right side, as in the holotype and AMNH 9485. The ratio between the width of the rostrum and the transverse width of the premaxillae at the level of the antorbital notches is 0.61, a value

intermediate between AMNH 9485 (0.56) and the holotype (0.68). A similar widening of the premaxillae is observed in *Huaridelphis* (ratio 0.60–0.61), whereas in *Medocinia* and *Squalodelphis* the premaxilla nearly reaches the lateral margin of the rostrum (ratio 0.82). As in all squalodelphinids, allodelphinids, and pomatodelphinines the dorsal surface of the premaxillae at the base of the rostrum shows a deep medial depression. Both premaxillary foramina are slightly posterior to the level of the antorbital notches, whereas they are anterior, with longer premaxillary sac fossae, in the holotype and AMNH 9485. The left and right premaxillary sac fossae are distinctly separated medially, leaving the mesethmoid uncovered. The latter is ossified on a short length anterior to the bony nares. A similar condition is observed in AMNH 9485, whereas in the holotype the premaxillae are almost in contact medially. The right antorbital notch is shallower than the left; the anterior margin of the right antorbital process is roughly rectilinear and transversely directed, a condition differing from the narrower

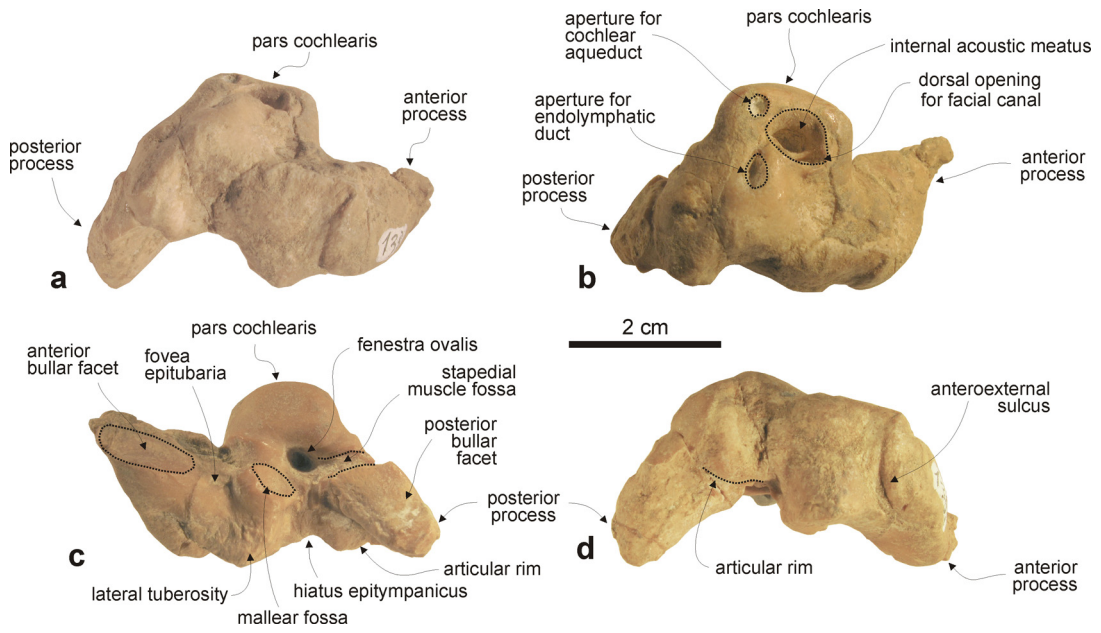


Fig. 3. (Color online.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395: right periotic in dorsal (a), dorsomedial (b), ventral (c) and lateral (d) views.
Fig. 3. (Couleur en ligne.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395 : périotique droit en vues dorsale (a), dorsomédiale (b), ventrale (c) et latéral (d).

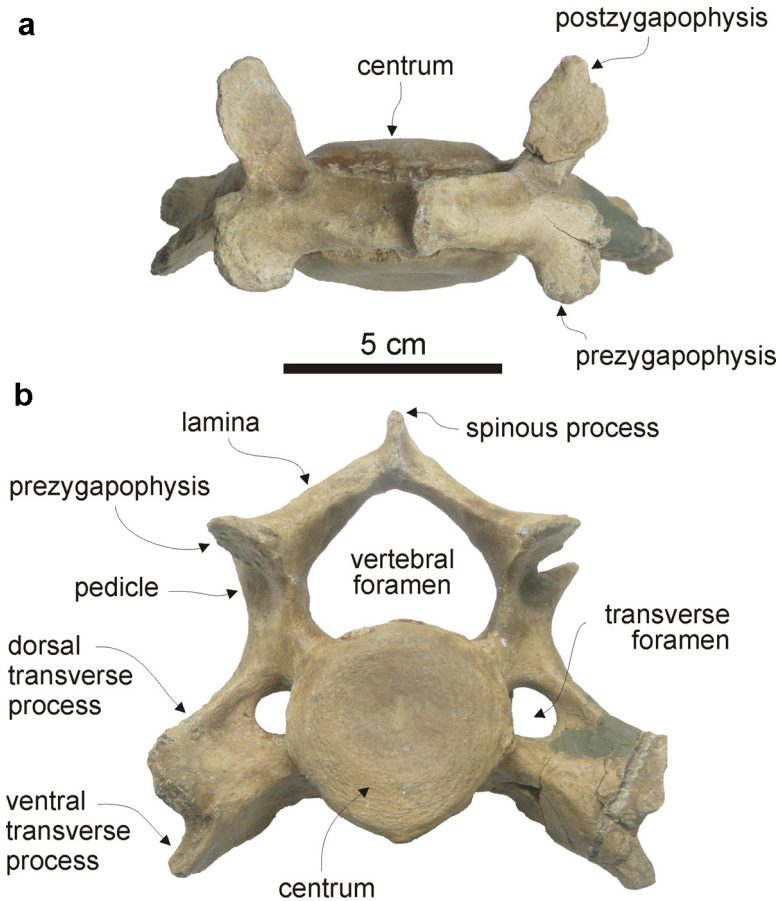


Fig. 4. (Color online.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395: cervical vertebra in dorsal (a) and anterior (b) views.
Fig. 4. (Couleur en ligne.) *Notocetus vanbenedeni*, Museo de Historia Natural 1395 : vertèbre cervicale en vues dorsale (a) et antérieure (b).

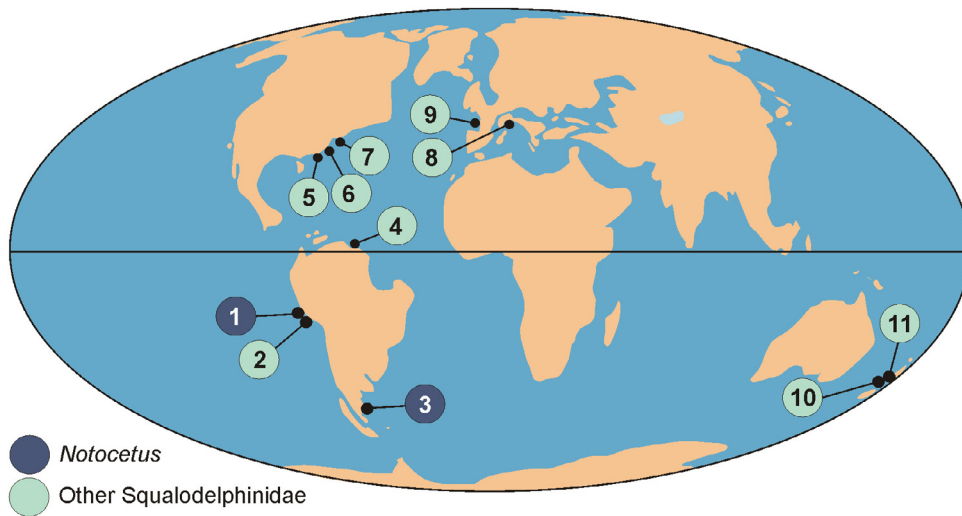


Fig. 5. (Color online.) Worldwide Late Oligocene–Early Miocene distribution of Squalodelphinidae. **1**, *Notocetus vanbenedeni*, Peru; **2**, *Huaridelphis raimondii*, Peru; **3**, *N. vanbenedeni*, Argentina; **4**, ?Squalodelphinidae indet., Venezuela; **5**, Squalodelphinidae indet., North Carolina; **6**, *Phocageneus venustus*, Virginia; **7**, *Phocageneus venustus*, Maryland; **8**, *Squalodelphis fabianii*, Italy; **9**, *Medocinia tetragorhina*, France; **10**, '*Prosqualodon*' *marplei*, New Zealand; **11**, Squalodelphinidae indet., New Zealand.

Fig. 5. (Couleur en ligne.) Distribution des Squalodelphinidae à travers le monde durant l'Oligocène supérieur–Miocène inférieur. **1**, *Notocetus vanbenedeni*, Pérou; **2**, *Huaridelphis raimondii*, Pérou; **3**, *N. vanbenedeni*, Argentine; **4**, ?Squalodelphinidae indet., Venezuela; **5**, Squalodelphinidae indet., Caroline du Nord; **6**, *Phocageneus venustus*, Virginie; **7**, *Phocageneus venustus*, Maryland; **8**, *Squalodelphis fabianii*, Italie; **9**, *Medocinia tetragorhina*, France; **10**, « *Prosqualodon* » *marplei*, Nouvelle-Zélande; **11**, Squalodelphinidae indet., Nouvelle-Zélande. Carte modifiée d'après Smith et al. (2004).

Map modified after Smith et al. (2004).

V-shaped notch and anteriorly pointed antorbital process on the left side. Asymmetrical antorbital notches are also observed in the holotype, AMNH 9485, and, less accentuated, in *Huaridelphis* and *Squalodelphis*. In lateral view, the antorbital process is robust, with a thick frontal covered by a proportionally thinner sheet of the maxilla, as in AMNH 9485, whereas the limit between maxilla and frontal is more difficult to distinguish in the holotype. Together with the massive postorbital process, this condition leads to a proportionally smaller orbit than in *Huaridelphis*. As in several other squalodelphinids, the left antorbital region is more elevated than the right, a condition best seen in anterior view.

The posterior apex of the premaxilla is pointed and narrower than in pomatodelphinine platanistids. As in many other platanistoids, the mesethmoid of MUSM 1395 is pierced by a pair of crescent-like fenestrae on the posterior wall of the bony nares. Also observed in *Huaridelphis*, these fenestrae much likely represent reduced olfactory openings (Godfrey, 2013; Hoch, 2000; Lambert et al., 2014).

The lateral shift of the vertex on the left side is similar to the other known specimens of *N. vanbenedeni* for which this area is preserved. The nasal-frontal suture is anteromedially pointed, as in AMNH 9485 (obscured in the holotype), and the dorsal surface of the frontals and nasals on the vertex is subhorizontal, a clear difference between *Notocetus* and other squalodelphinids, the latter displaying a marked anterior slope of that surface.

As in the two other known skulls of *Notocetus*, the nuchal crest is transversely wider than in *Squalodelphis*. In the latter, the nuchal crest is approximately as wide as the greatest width of the premaxillae, whereas in *Notocetus* it is considerably wider.

The pterygoid reaches 50–60 mm beyond the level of the antorbital notch. As in other squalodelphinids and pomatodelphinines, the palatine is probably only exposed on the ventral surface of the base of the rostrum, as a thin plate lateral to the pterygoid and slightly anteriorly longer than the antorbital notch. The lateral lamina of the pterygoid forms a continuous plate until its contact with the long and wide falciform process of the squamosal, a feature also seen in AMNH 9485.

On the roof of the orbit, the frontal is excavated by a large fossa anterior to the postorbital ridge, a character also present in the holotype; its presence in other squalodelphinids and pomatodelphinines has been interpreted as the indication of an extension of the pterygoid sinus in the orbit region (Lambert et al., 2014).

In lateral view, the swollen zygomatic process of the squamosal is similar to that of the holotype and AMNH 9485, with a moderately convex posterodorsal margin and a slightly convex anteroventral margin. As in AMNH 9485, the postglenoid process is slender. Somewhat higher than in the holotype, the temporal fossa has a general outline similar to AMNH 9485 (in the latter, the fossa is likely somewhat dorsoventrally crushed).

In general, the ventral view of the squamosal resembles those of the fragmentary skull AMNH 29026 of *N. vanbenedeni* (de Muizon, 1987). A small but deep fossa dorsal to the spiny process of the squamosal likely corresponds to the subcircular fossa mentioned by de Muizon (1987) in *Notocetus*, *Squalodelphis*, and platanistids, a feature considered as homologous with the anterior part of the periotic fossa by Fordyce (1994). The tympanosquamosal recess is only deep on the medial flank of the postglenoid process. The anterior wall of the paroccipital process of the

exoccipital is excavated by the fossa for the posterior sinus, as in AMNH 29026 (see de Muizon, 1987, fig. 3).

Periotic (Fig. 3). The periotic of *N. vanbenedeni* AMNH 29026 has been described in detail by de Muizon (1987). The periotic of MUSM 1395 is similar to AMNH 29026 in having a square-shaped pars cochlearis in ventral view, an elongated anterior process, an anteroexternal sulcus on the anterior process, an articular rim, a subrectangular posterior bullar facet, and approximately the same size and position for the openings in the pars cochlearis.

Cervical vertebra (Fig. 4). No cervical vertebra other than the atlas has been described for *Notocetus* (True, 1910: pl 5, figs. 1 and 2). The only preserved cervical of MUSM 1395 shares similarities with the third cervical of *Phocageneus* USNM 21039 (Kellogg, 1957). In MUSM 1395, the transverse foramen is more rounded and located lower relative to the centrum than in USNM 21039, being more similar in this regard to a cervical vertebra of *Huaridelphis* (MUSM 1403) that is presumably from a roughly similar position. However, the ventral lamina is more ventrally directed in MUSM 1395 and USNM 21039 than in *Huaridelphis*, and the centrum is more dorsoventrally flattened in the latter. As in USNM 21039, the neural canal is proportionally higher than in *Platanista*.

3. Discussion and conclusion

The new record of *N. vanbenedeni* in the same locality and approximately same horizon of *H. raimondii*, suggests the sympatric coexistence of two squalodelphinids during the Early Miocene along the Pacific coast of South America. This joined record contrasts with the globally scarce record of squalodelphinids (Fig. 5). Indeed, outside of Peru, diagnostic material of squalodelphinids has only been reported from a few Late Oligocene–Early Miocene localities of Argentina, Europe and possibly New Zealand (Cozzuol, 1996; Dal Piaz, 1917; de Muizon, 1988; Fordyce, 1994). The published Argentinean records, from marine beds outcropping in Patagonia, consist of three significant specimens, all referred to *N. vanbenedeni* (de Muizon, 1987; Moreno, 1892; True, 1910). Considering the new record described here, *N. vanbenedeni* lived both along the Atlantic and Pacific coasts of South America. During the Late Oligocene and Early Miocene, contacts between these two distant marine areas were possible through the widely open Panama Seaway and via the southern tip of South America (Smith et al., 2004). Unfortunately, the only other South American records for the family are fragmentary undiagnostic specimens from the Early Miocene of Venezuela (Sánchez-Villagra et al., 2001). More complete specimens from the North of the continent and the Caribbean region will be necessary to better apprehend the South American distribution and migration patterns of *N. vanbenedeni*. To our knowledge, this is the only fossil marine mammal species currently recognized from both South Pacific and South Atlantic.

The European record of squalodelphinids includes the holotype (skull with associated mandible) and referred material of *Squalodelphis fabianii* from the molasses of Belluno (northeastern Italy) and the fragmentary skull referred to *Medocinia tetragorhina* (Delfortrie, 1875) from

the Atlantic coast of southern France (de Muizon, 1988). Squalodelphinids are also reported from the Early Miocene of the East Coast of the USA: an isolated tooth from Virginia described as the holotype of *Phocageneus venustus* Leidy, 1869, a partial skeleton lacking the skull (USNM 21039) from Maryland referred to the same species (Kellogg, 1957), and a damaged skull (USNM 475596) and isolated ear bones and teeth from the Lee Creek Mine, North Carolina (Kellogg, 1957; Whitmore and Kaltenbach, 2008).

The presumable squalodelphinid record of New Zealand includes the holotype of '*Prosqualodon*' *marplei* Dickson, 1964, an incomplete skull with associated ear bones, teeth, parts of the mandible, vertebrae, ribs, one scapula, and one ulna (Fordyce, 1994), and another unnamed *Notocetus*-like specimen (Tanaka and Fordyce, 2012).

In conclusion, based on the new Peruvian specimen referred to *N. vanbenedeni* and other published accounts, Squalodelphinidae represent a poorly diversified Late Oligocene–Early Miocene group of marine platanistoids, with a scarce fossil record but a wide palaeogeographic distribution, including northern and southern Atlantic realms and the southern Pacific.

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References

- Alvan De la Cruz, A., 2008. Geologa de Ocucaje: aportes en la sedimentologa y paleontologa de Lomas de Ullujaya (Ica, Peru). *Rev. Inst. Invest. FIGMMG* 11 (21), 51–59.
- Bianucci, G., Lambert, O., Post, K., 2010. High concentration of long-snouted beaked whales (genus *Messapicetus*) from the Miocene of Peru. *Palaeontology* 53, 1077–1098.
- Bianucci, G., Lambert, O., Salas-Gismondi, R., Tejada, J., Pujos, F., Urbina, M., Antoine, P.-O., 2013. A Miocene relative of the Ganges River dolphin (*Odontoceti*, *Platanistidae*) from the Amazonian Basin. *J. Vert. Paleontol.* 33, 741–745.
- Brisson, M.-J., 1762. *Regnum Animale in classes IX distributum, sine synopsis methodica*. Theodorum Haak, Paris (296 p.).
- Cozzuol, M., 1996. The record of aquatic mammals in southern South America. *Munch. Geowiss., Abhand. A* 30, 321–342.
- Dal Piaz, G., 1917. Gli *Odontoceti* del Miocene Bellunese. Parte terza *Squalodelphis*. *Mem. Ist. Geol. R. Univ. Padova* 5, 1–34.
- Delfortrie, E., 1875. Un dauphin d'espe nouvelle dans les faluns du Sud-Ouest. *Act. Soc. Linn. Bordeaux* 30 (2), 3–7.

- de Muizon, C., 1987. The affinities of *Notocetus vanbenedeni*, an Early Miocene platanistoid (Cetacea Mammalia) from Patagonia, southern Argentina. *Am. Mus. Novit.* 2904, 1–27.
- de Muizon, C., 1988. Le polyphylétisme des Acrodelphidae, odontocètes longirostres du Miocène européen. *Bull. Mus. Nat. Hist. Nat. Paris* 10, 31–88.
- DeVries, T.J., 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). *J. South Am. Earth Sci.* 11, 217–231.
- DeVries, T.J., 2001. Molluscan evidence for an Oligocene-Miocene age of 'Paracas' beds in southern Peru. *Bol. Soc. Geol. Perú* 92, 57–65.
- Dickson, M.R., 1964. The skull and other remains of *Prosqualodon marplesii*, a new species of fossil whale. *New Zeal. J. Geol. Geophys.* 7, 626–635.
- Dunbar, R.B., Marty, R.C., Baker, P.A., 1990. Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 77, 235–261.
- Flower, W.H., 1867. Description of the skeleton of *Inia geoffrensis* and the skull of *Pontoporia blainvillii*, with remarks on the systematic position of these animals in the Order Cetacea. *Trans. Zool. Soc. London* 6, 87–116.
- Fordyce, R.E., 1994. *Waipatia maerewhenua*, new genus and new species (Waipatiidae, new family), an archaic Late Oligocene dolphin from New Zealand. In: Berta, A., Deméré, T.A. (Eds.), Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. *Proc. San Diego Soc. Nat. Hist.*, pp. 147–178.
- Godfrey, S.J., 2013. On the olfactory apparatus in the Miocene odontocete *Squalodon* sp. (Squalodontidae). *C. R. Palevol* 12, 519–530.
- Gray, J.E., 1863. On the arrangement of the cetaceans. *Proc. Zool. Soc. London* 31, 197–202.
- Hoch, E., 2000. Olfaction in whales: evidence from a young odontocete of the Late Oligocene North Sea. *Hist. Biol.* 14 (1–2), 67–89.
- Kasuya, T., 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. *Sci. Rep. Whales Res. Inst.* 25, 1–103.
- Kellogg, R., 1957. Two additional Miocene porpoises from the Calvert Cliffs, Maryland. *Proc. Un. St. Nat. Mus.* 107, 279–337.
- Lambert, O., Bianucci, G., Post, K., 2009. A new beaked whale (Odontoceti, Ziphiidae) from the Middle Miocene of Peru. *J. Vert. Paleontol.* 29, 910–922.
- Lambert, O., Bianucci, G., Post, K., de Muizon, C., Salas-Gismondi, R., Urbina, M., Reumer, J., 2010. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* 466, 105–108.
- Lambert, O., Bianucci, G., Urbina, M., 2014. *Huaridelphis raimondii*, a new Early Miocene Squalodelphinidae (Cetacea, Odontoceti) from the Chilcatay Formation, Peru. *J. Vert. Paleontol.* 34, 987–1004.
- Leidy, J., 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *J. Acad. Nat. Sci. Phila. new series* 7, 1–472.
- Lydekker, R., 1893. Contribution to the knowledge of the fossil vertebrates of Argentina. Part II. Cetacean skulls from Patagonia. *An. Mus. La Plata* 2, 1–15.
- Moreno, F.P., 1892. Noticias sobre algunos cetáceos fósiles y actuales de la República Argentina. *Rev. Mus. La Plata* 3, 383–400.
- Sánchez-Villagra, M.R., Gasparini, Z., Lozán, R., Moody, J.M., Uhen, M.D., 2001. New discoveries of vertebrates from a near-shore marine fauna from the Early Miocene of northwestern Venezuela. *Paläontol. Zeitschrift* 75, 227–232.
- Smith, A.G., Smith, D.G., Funnell, B.M., 2004. Atlas of Mesozoic and Cenozoic coastlines. Cambridge University Press, Cambridge, 99 p.
- Tanaka, Y., Fordyce, R.E., 2012. Another look at the origin of the enigmatic Ganges river dolphin *Platanista*, and the content of the superfamily Platanistoidea (Odontoceti: Cetacea). *J. Vert. Paleontol.* 32 (supp.), 183.
- True, F.W., 1910. Description of a skull and some vertebrae of the fossil cetacean *Diochotichus vanbenedeni* from Santa Cruz, Patagonia. *Bull. Am. Mus. Nat. Hist.* 28, 19–32.
- Whitmore Jr., F.C., Kaltenbach, J.A., 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. *Virginia Mus. Nat. Hist. Sp. Pub.* 14, 181–269.