

EURHINODELPHINIDS FROM THE EARLY MIOCENE OF PERU: FIRST UNAMBIGUOUS RECORDS OF THESE HYPER-LONGIROSTRINE DOLPHINS OUTSIDE THE NORTH ATLANTIC REALM

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Abstract. Among the many hyper-longirostrine dolphins (Odontoceti) from the Miocene, members of the family Eurhinodelphinidae bear two highly distinctive cranial features: a long and edentulous premaxillary portion of the rostrum and a mandible that is significantly shorter than the rostrum. Until now, unambiguously attributed members of this clade were only recorded from early to middle Miocene deposits of the North Atlantic realm (east coast U.S.A., North Sea Basin, and Mediterranean). In this work we describe and compare two partial skulls of longirostrine dolphins from late early Miocene (Burdigalian, 19.25-18 Ma) marine deposits of the Chilcatay Formation, in the East Pisco Basin (southern coast of Peru), preserving rostral and mandibular material, as well as ear bones. Based on these specimens we report diagnostic remains attributable to this family for the first time for the whole Southern Hemisphere and the whole Pacific Ocean. This major expansion of eurhinodelphinids' palaeogeographic distribution contrasts with their proposed shallow-water, coastal environments; it suggests a new dispersal route for members of the family across the Central American Seaway; and it further highlights the similarities between the odontocete faunas of the southeastern Pacific and North Atlantic realm during the Miocene. Better-preserved eurhinodelphinid specimens from the odontocete-rich Chilcatay Formation will allow for a more detailed comparison with North Atlantic members of the family.

INTRODUCTION

Eurhinodelphinidae are a moderately diversified family of hyper-longirostrine dolphins (sensu McCurry & Pyenson 2019) characterized by the unique combination of an elongated, edentulous premaxillary part of the rostrum with mandibles

that are significantly shorter than the rostrum (Abel 1901; Kellogg 1925). Never observed in any other cetacean group, the resulting extreme 'overbite' has been variously interpreted as a probing tool to detect prey in soft sediment of the seafloor or as a contacting or stunning device used higher in the water column, as in istiophorid and xiphiid billfish (Myrick 1979; Lambert 2005a; McCurry & Pyenson 2019). Together with their long snout, the long and relatively flexible neck of eurhinodelphinids

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(as seen for example in *Mycteriaceetus* and *Xiphiacetus*, see Pilleri 1985; Lambert 2005a) suggests that these small to medium-size odontocetes were slow swimmers, possibly living in shallow-water coastal environments (Lambert 2005a; Marx et al. 2016), a hypothesis that should be further tested with stable isotope analyses (see preliminary work by Barrick et al. 1992).

Although fossil odontocete remains from various regions of the world, including Patagonia, Peru, Caucasus, and South Australia, and from deposits dated from the late Oligocene to the late Miocene have been tentatively attributed to the family Eurhinodelphinidae (in some cases named Rhabdosteidae; Lydekker 1893; Cabrera 1926; Mchedlidze 1976; Fordyce 1983; Pilleri 1989), their state of preservation does not allow for the unambiguous recognition of the two apomorphic features listed above (Lambert 2005a; Marx et al. 2016; Supplementary Table 1). Therefore, based on specimens either at least showing one of these two synapomorphies or robustly assigned to species or genera known from better-preserved specimens in other localities, the fossil record of the family is for now restricted to the genera *Eurhinodelphis*, *Mycteriaceetus*, *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis*, from the western North Atlantic, North Sea, and Mediterranean (together grouped here in the North Atlantic realm), in deposits ranging from the early to middle (and possibly up to early late) Miocene (Abel 1901, 1902; Kellogg 1925; Pilleri 1985; Muizon 1988a; Bianucci et al. 1994; Bianucci & Landini 2002; Lambert 2005a,b; Whitmore & Kaltenbach 2008; Marx et al. 2016).

Recently, lower Miocene (Burdigalian) deposits of the Chilcatay Formation, in the East Pisco Basin (southern coast of Peru), yielded a rich odontocete assemblage, including an heterodont longirostrine odontocete (*Inticetus vertizi*), two phaseteroids, several platanistoids (a platanistid, four squalodelphinids, and two other platanistoids), a longirostrine homodont dolphin (*Chilcacetus cavarhinus*), and a kentriodontid (Lambert et al. 2015, 2018, 2020; Bianucci et al. 2018a,b, 2020; Di Celma et al. 2018, 2019). Early field observations lead us to suggest in a previous work (Lambert et al. 2014) that a eurhinodelphinid closely related to *Ziphiodelphis* was present in the Chilcatay Formation. However, a detailed study of collected material lead to the referral of this material to *Chilcacetus*, in another clade of longirostrine odontocetes (Lambert et al. 2015; Bia-

nucci et al. 2018). In the present work we describe and compare two new skulls of longirostrine homodont odontocetes from the Chilcatay Formation in the fossil-rich locality of Zamaca, revealing the presence of eurhinodelphinids in the southeastern Pacific during the early Miocene.

MATERIAL AND METHODS

Institutional abbreviations. **CMM**, Calvert Marine Museum, Solomons, U.S.A.; **IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, U.S.A.; **MGP**, Museo di Geologia e Paleontologia, Padova, Italy; **MLP**, Museo de La Plata, La Plata, Argentina; **MUSM**, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **OU**, University of Otago, Dunedin, New Zealand; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

Anatomical terminology. The terminology for skull anatomical features follows Mead & Fordyce (2009), except where explicitly stated.

SYSTEMATIC PALAEOLOGY

CETACEA Brisson, 1762

Pelagiceti Uhen, 2008

Neoceti Fordyce & Muizon, 2001

Odontoceti Flower, 1867

Eurhinodelphinidae Abel, 1901

Eurhinodelphinidae indet.

Figs. 1-5

Referred specimens: MUSM 632, a fragmentary skull including large portions of the rostrum, part of the bony nares region, part of the basicranium (mainly the basisphenoid, basioccipital, right exoccipital, and right squamosal), and a large part of the mandibles, together with a rib fragment; MUSM 3944, a partial cranium including the proximal portion of the rostrum, part of the facial region, and most of the basicranium, including the two in situ periotics and the two detached tympanic bullae.

Localities: Both specimens were discovered in the odontocete-rich locality of Zamaca (see Lambert et al. 2018, 2020; Di Celma et al. 2019; Bianucci et al. 2020), East Pisco Basin. The exact locality of MUSM 632 is unknown, whereas the geographic

coordinates of MUSM 3944 are the following: S 14°37'34.95" - W 75°38'24.35". MUSM 3944 was reported in the Zamaca fossil map of Di Celma et al. (2019) with the field number ZM 25, and tentatively referred there to "Eurhinodelphinidae indet."

Horizon: Both specimens were collected in the Chilcatay Formation, which is widely exposed in the locality of Zamaca. The precise stratigraphical level of MUSM 632 is unknown, whereas MUSM 3944 was collected at 32.4 m above the contact with the underlying Otuma Formation, in the allomember *Ct1a*, together with other odontocete (*Odontoceti* indet.) and marine turtle (*Testudines* indet.) remains, as well as shark teeth (Di Celma et al. 2019). The allomember *Ct1a* also yielded a rich odontocete fauna including kentriodontids, physeteroids, and squalodelphinids (Di Celma et al. 2019; Bianucci et al. 2020; Lambert et al. 2020). In Zamaca and the nearby Ullujaya locality the cetacean-bearing layers of this formation have been dated through biostratigraphy, ⁴⁰Ar/³⁹Ar and ⁸⁷Sr/⁸⁶Sr radiometric analyses from a 19.25-18.02 Ma interval (Burdigalian, late early Miocene; Di Celma et al. 2018, 2019; Bosio et al. 2020a,b).

Remarks: In addition to the large amount of similarities with known eurhinodelphinids (see below), both specimens described here are referred to the family Eurhinodelphinidae based on two synapomorphies: the presence of an extensive premaxillary portion of the rostrum and, for MUSM 632, the mandibles being significantly shorter than the rostrum (see details below). None of these characters is observed in any other odontocete clade. Similarities in cranial dimensions and morphology indicate that the two specimens could belong to the same species; however, the lack of a well-preserved facial region in both specimens and the absence of ear bones in MUSM 632 refrain us from providing a definitive conclusion on that matter. More complete specimens will also be needed for a more detailed comparison with eurhinodelphinid species from the North Atlantic realm.

Description

MUSM 632: The fragmentarily preserved cranium of MUSM 632 has a minimum rostrum length of 540 mm (apex of the premaxillae is missing for an unknown length, see below) and a width of the rostrum at its base estimated at 106 mm; the bizygomatic width is estimated at 218 mm (see Table

1 for additional measurements), in the range of *Xiphiacetus cristatus*, for instance (Lambert 2005a).

The lateral suture between the maxilla and the premaxilla on the rostrum is visible on both sides in lateral view; from a level about 255 mm anterior to the antorbital notch, it starts descending anteroventrally from the lateral groove with a steep slope, reaching the ventral margin of the rostrum 490 mm anterior to the antorbital notch (tip of the maxilla) (Fig. 1B-C). The ratio between length of the maxilla on the rostrum and bizygomatic width is thus estimated at 2.25 in MUSM 632; this is significantly greater than in the type specimens of *Eurhinodelphis cocheteuxi* and *E. longirostris* (1.88 and 1.86, respectively; Lambert 2004, 2005b). Seventy millimeters anterior to the anterior tip of the maxilla, the dorsoventral height of the preserved section of left premaxilla is 16 mm, indicating that the premaxilla was originally considerably anteriorly longer than the maxilla, a diagnostic feature for Eurhinodelphinidae. In dorsal view the premaxillae are narrow for most of the rostrum length, with a convex transverse section, and they contact each other dorso-medially. They more significantly widen from a level 145 mm anterior to the antorbital notch and diverge posterolaterally from a level 120 mm anterior to the notch, gradually opening the mesorostral groove dorsally. At the level of the antorbital notch the dorsal surface of the premaxilla is flattened. At this level the premaxilla is proportionally much wider (compared to the maxilla) in *Mycteriacetus* and *Ziphiodelphis*. Only part of the right anteromedial sulcus is preserved; the premaxillary foramen was posterior to the level of the antorbital notch.

In dorsal view the maxilla is exposed lateral to the premaxilla for its whole length on the rostrum, with an exposure gradually increasing posteriorly (Fig. 1A). The surface of the lateral groove is damaged in many parts of the rostrum; nevertheless, this groove most likely occupied most of the rostrum length, as indicated by a finely preserved region dorsal and anterodorsal to the anterior tip of the maxilla. Level with the antorbital notch the dorsal width of the maxilla is slightly narrower than the width of the premaxilla. Several medium to small-size dorsal infraorbital foramina (at least two on the right side) are present along the maxilla-premaxilla suture anterior to the antorbital notch. The largest posterior foramen marks the start of the lateral groove.

In ventral view, the alveolar groove ends posteriorly 45 mm anterior to the antorbital notch (Fig. 1E-F). Small, closely spaced, circular maxillary alveoli are observed, with diameters ranging between 5.0 and 5.5 mm and interalveolar septa ranging between 2.5 and 4.0 mm. The walls of the alveolar groove are too damaged or not preserved in the anterior part of the maxilla to allow for the identification of individual alveoli. Similarly, the preserved portion of the premaxillary part of the rostrum does not allow for a detailed description of the alveolar groove; no clue for premaxillary alveoli could be found. On the palate, each maxilla is marked by a series of long, anteriorly, anteromedially, and anterolaterally directed sulci, starting in the area of the major palatine foramen. A similar condition is observed in multiple specimens of *Schizodelphis* and *Xiphiacetus* from the USNM collection. A broad ventral exposure of the vomer is observed between the maxillae from a level a few centimeters anterior to the start of the alveolar grooves and for a length of 105 mm.

Together, the palatine-maxilla sutures draw a U shape, reaching a level 26 mm anterior to the antorbital notch, with no significant wedge of the maxillae between the palatines (Fig. 1F). The anterior limit of the transversely broad pterygoid sinus fossa is posterior (20-25 mm) to the level of the antorbital notch. Part of the lacrimojugal complex is preserved along the floor of the right antorbital notch, including the base of the styliform process of the jugal.

Due to the loss of the vertex and occipital shield, the ventral surface of the brain cavity is exposed, revealing small dorsal carotid foramina in the basisphenoid, the jugular foramina and the medial edge of the posterior lacerate foramina in the basioccipital, just posterior to the tentorium (Fig. 1A). Right and left basioccipital crests diverge moderately posterolaterally, drawing an angle of about 45°. Each crest thickens significantly transversely for its last posterior centimeters, whereas its ventral edge remains thin along its whole length (Fig. 1E-F). The distance between the lateralmost margins of the basioccipital crests is 88 mm.

In lateral view the moderately long zygomatic process of the squamosal is robust (maximum height = 32 mm), with a convex, transversely thick dorsal margin, a rounded anterior end, and a rectilinear to slightly concave, transversely thinner

ventral edge (Fig. 1B). Two deep sternocephalic fossae are present; the largest, dorsal fossa extends farther anteriorly, partly excavating the lateral surface of the zygomatic process. The postglenoid process is lost. In dorsal view the long axis of the zygomatic process is oblique, directed anterolaterally. In ventral view the mandibular fossa is vast (transverse width = 32 mm) and anteroposteriorly concave. The tympanosquamosal recess is deep and anteriorly long, reaching the apex of the zygomatic process medial to a prominent tubercle for the short articulation surface of the styliform process of the jugal.

On the mandibles, the anterior tip of each dentary is missing, as well as the coronoid processes, the condyles, and part of the angular processes (Fig. 2). Based on the gradual anterior narrowing and lowering of the slender anterior part of the mandibles we estimate that no more than 20-30 mm are missing anteriorly. Taking account of the missing mandibular condyles, the slope of the anterior part of the coronoid process, and the corresponding slope of the ventrolateral margin of the rostrum, we could position the mandibles in an approximately anatomically correct position along the anteroposterior axis of the rostrum (Fig. 1B). In such a position, the dorsoventral height of the preserved anterior section of the mandible is markedly lower than the corresponding section on the rostrum. Furthermore, the reconstructed tip of the mandible reaches an anterior level where the rostrum is still dorsoventrally high. Together, these features suggest that the mandible was originally significantly shorter than the rostrum in MUSM 632, a derived character similarly observed or deduced from preserved sections of the rostrum and mandible in the genera *Mycteriaetus*, *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis* (Kellogg 1925; Myrick 1979; Pilleri 1985; Lambert 2005a). The tooth-bearing part of the mandible is slender (dorsoventrally low), with a slightly anterodorsally recurved outline (Fig. 2A). Posterior to the alveolar groove the dorsal edge of the ramus becomes concave in lateral view, raising abruptly towards the coronoid process and possibly indicating the presence of a precoronoid crest (sensu Fordyce et al. 2002), whereas in the same region the ventral margin is slightly convex and directed posteroventrally. The resulting abrupt increase of the height of the ramus posterior to the alveolar groove is similarly observed in *Mycteriaetus*,

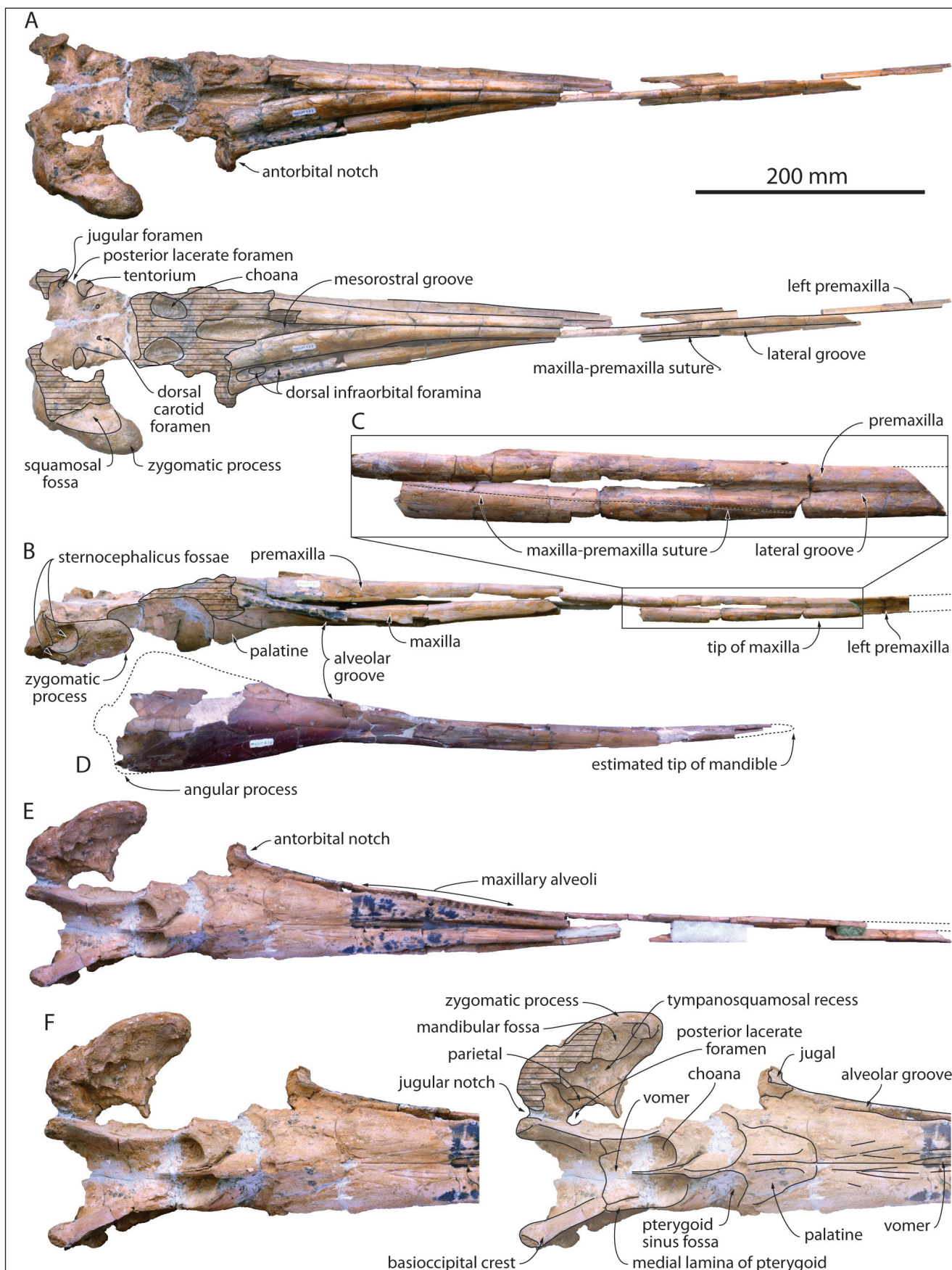


Fig. 1 - Skull of MUSM 632, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. A) cranium in dorsal view (photo and interpretive drawing); B) cranium in right lateral view; C) detail of the anterior part of the rostrum in right lateral view, showing the descent of the maxilla-premaxilla suture; D) mandibles in right lateral view; E) cranium in ventral view; F) neurocranium and rostrum base in ventral view (photo and interpretive drawing).

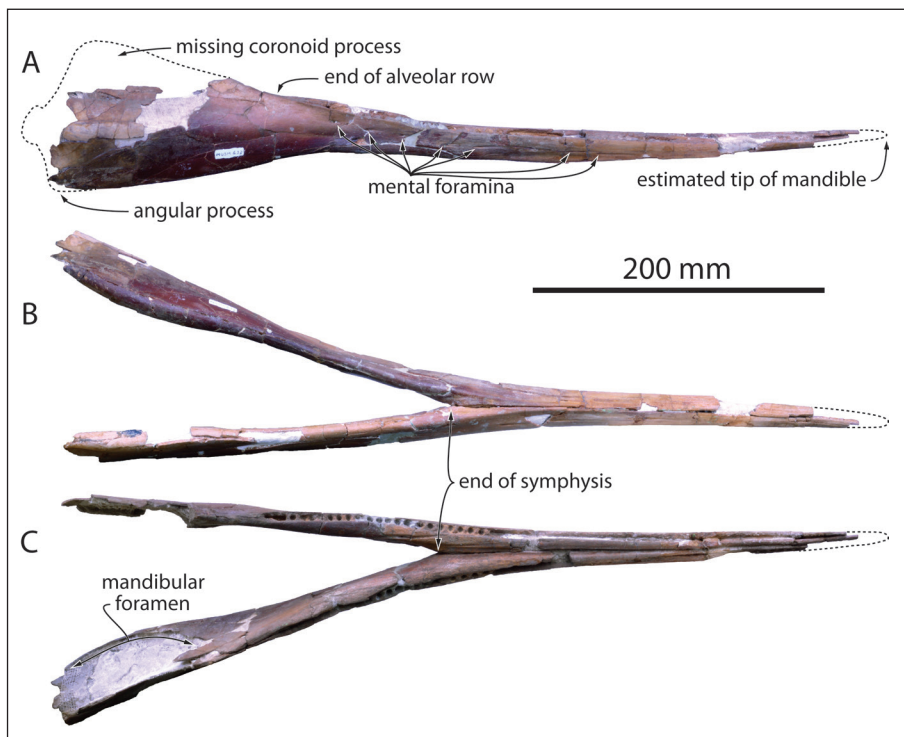


Fig. 2 - Mandibles of MUSM 632, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. A) right lateral view; B) ventral view; C) dorsal view.

Schizodelphis, and *Xiphiacetus* (Kellogg 1925; Myrick 1979; Pilleri 1985). The partly ankylosed mandibular symphysis (Fig. 2B-C) is long (more than 292 mm) with a triangular cross section, as seen in *Mycteriacetus*, *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis*. Transverse width of the joined mandibles and dorsoventral height at the posterior end of the symphysis are 44 and 25 mm, respectively. In the anterior part of the mandibles, the alveolar groove bears small circular alveoli with a diameter of 4.5 mm and interalveolar septa of about 2 mm (Fig. 2C). At the posterior end of the symphysis alveoli retain a diameter of about 4.6 mm and septa ranging from 3.0 to 3.5 mm. 18 post-symphyseal alveoli are counted on a length of 120 mm on the left side. The lateral surface of the mandible is pierced by a series of obliquely organized mental foramina (at least seven on the right side), extended anteriorly by long sulci. No conspicuous lateral groove is observed on the mandibles. Deep longitudinal sulci mark the dorso-medial surface of each dentary in the region of the end of the symphysis. The large mandibular foramen has a rounded anterior margin located 175 mm posterior to the symphysis.

MUSM 3944: Though missing a longer anterior part of the rostrum, including the premaxillary portion, this cranium is better preserved than MUSM 632 for the proximal part of the rostrum,

the right side of the facial region, and most of the basicranium, including the two in situ periotics (Figs. 3-4). The dorsal surface of the neurocranium is unfortunately heavily abraded, especially on the left side of the facial region, the vertex, and most of the occipital shield (Fig. 3A).

The bizygomatic width is estimated at 224 mm, only slightly greater than in MUSM 632, whereas the width of the rostrum at its base is estimated at 117 mm, also slightly greater than in the latter. In general, dimensions do not differ significantly from MUSM 632 (Table 1).

At the preserved anterior end of the rostrum, 385 mm anterior to its base, as in MUSM 632 the premaxillae are narrow in dorsal view and contact each other. Their medial margins similarly diverge posterolaterally, but the maximum dorsal opening of the mesorostral groove is somewhat more anterior than in MUSM 632, 20 mm anterior to the level of the antorbital notch. Better preserved in that region, MUSM 632 displays an abrupt narrowing of the opening of the mesorostral groove towards the bony nares, in a way reminiscent of squaloziphiids (Muizon 1991; Lambert et al. 2019). The dorsal opening of the mesorostral groove is much more reduced in *Mycteriacetus* and *Ziphiodelphis*. The anterior outline of the bony nares is V-shaped. Preserved on both sides the premaxillary foramen is posterior to the level of the antorbital notch (more so than in

Tab. 1 - Measurements (in mm) on the skulls MUSM 632 and MUSM 3944, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. +, incomplete; e, estimate; -, missing data.

	MUSM 632	MUSM 3944
Cranium		
Condylobasal length (as preserved)	+ 720	+ 600
Length of rostrum (as preserved)	+ 540	+385
Width of rostrum at its base	e106	117
Width of premaxillae at level of antorbital notches	-	71
Maximum transverse width of right premaxilla	-	42
Length of medial palatal exposure of vomer	105	120
Distance between posterior end of medial palatal exposure of vomer and rostrum base	85	100
Distance between posterior end of right maxillary alveolar groove and rostrum base	45	50
Longitudinal distance between anterior end of palatine and rostrum base	26	20
Distance from paroccipital process to antorbital notch	185	188
Bizygomatic width	e218	e224
Transverse width at lateral margins of exoccipitals	e168	188
Maximum width between the basioccipital crests	88	95
Width of occipital condyles	-	76
Height of left occipital condyle	-	39
Width of left occipital condyle	-	32
Width of foramen magnum	-	32
Height of foramen magnum	-	24
Mandibles		
Length of mandible parallel to longitudinal axis of the skull (as preserved)	-	+ 570
Length of mandibular symphysis (as preserved)	-	+ 292
Width of joined mandibles at posterior end of symphysis	-	44
Height of joined mandibles at posterior end of symphysis	-	25
Distance between posterior end of symphysis and posteriormost mandibular alveolus	-	130
Number of alveoli in the postsymphyseal portion	-	18
Left periotic		
Maximum length	-	+38
Right tympanic bulla		
Maximum length (without posterior process)	-	43.9
Maximum width	-	26.5
Left tympanic bulla		
Maximum length (without posterior process)	-	44.8
Maximum width	-	27.7

Eurhinodelphis cocheteuxi and *Mycteriaetus*), followed anteriorly by a medium-length anteromedial sulcus and posteriorly by a well-defined posterolateral sulcus, reaching at least the level of bony nares' mid-length. The right premaxillary sac fossa is moderately transversely concave.

In lateral view, the lateral groove becomes conspicuous about 200 mm anterior to the level of the antorbital notch (Fig. 3D); although this region is not as well preserved in MUSM 632, the lateral groove may have started more posteriorly in the latter. The maxilla-premaxilla suture leaves the ventral floor of the lateral groove about 250 mm anterior to the antorbital notch, displaying an anteroventral slope similar to MUSM 632. The anterior tip of the

maxilla being lost, there is no direct evidence for the presence of an extended premaxillary portion of the rostrum. However, the strong similarities with MUSM 632 for the shape of the premaxillae on the rostrum and the slope of the suture, as well as the height of the maxilla at its preserved anterior section (ratio between this height and the total height of the rostrum at that level equals 0.4 in MUSM 3944) strongly suggest that the premaxillae were similarly significantly longer than the maxillae on the rostrum in MUSM 3944.

Related to the proportionally broader rostrum base compared to MUSM 632, the dorsal exposure of the maxilla at this level is wider than in the latter. Three dorsal infraorbital foramina are vis-

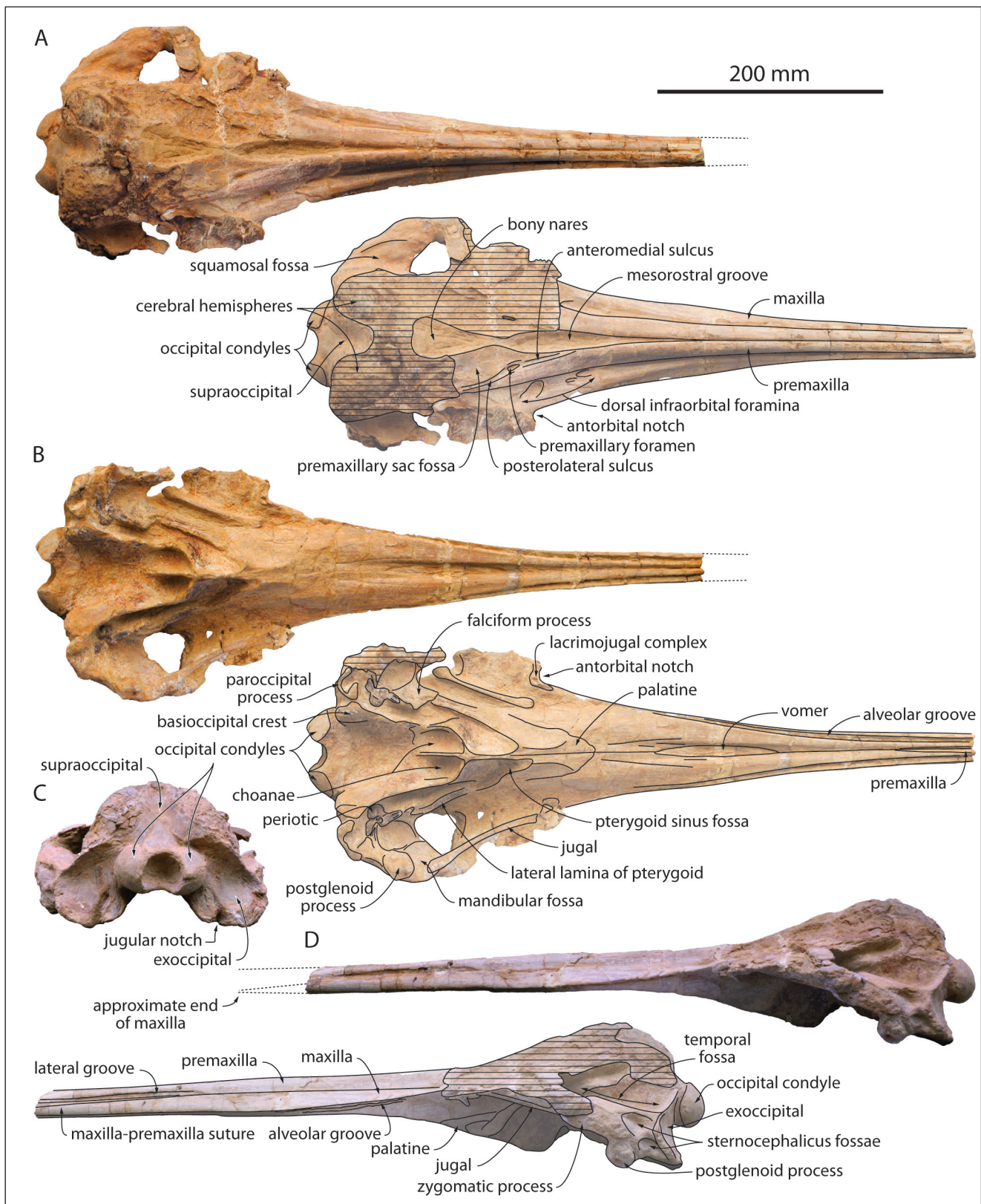


Fig. 3 - Cranium of MUSM 3944, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. A, dorsal view (photo and interpretive drawing); B, ventral view (photo and interpretive drawing); C, posterior view; D, left lateral view (photo and interpretive drawing).

ible in the same region as in MUSM 632, medial and anteromedial to the antorbital notch (Fig. 3A).

The walls of the alveolar groove are too abraded in MUSM 3944 to allow for the measure-

ment of individual alveoli. Nevertheless, the width and orientation of the groove in the maxilla are similar to MUSM 632. Also, the ventral exposure of the vomer between the maxillae occurs in the same region as in the latter (for a slightly greater length of 120 mm) and long sulci are similarly observed in the ventral surface of the maxilla anterior to the palatine (Fig. 3B). The palatine-maxilla suture is also U-shaped and the pterygoid sinus fossa does not reach anteriorly the level of the antorbital notch. Better preserved in that region, MUSM 3944 displays on the lateral side of both pterygoid sinus fossae an elongated plate reaching the falciform process of the squamosal; it is identified here as the lateral lamina of the pterygoid. Such a feature is observed in several eurhinodelphinids (e.g., multiple specimens of *Schizodelphis* and *Xiphiacetus* from the USNM collection; Kellogg 1925; Muizon 1988a; Lambert 2005a), and was proposed to be absent in *Chilcacetus cavirhinus*, the only other non-platanistoid homodont and longirostrine medium-size dolphin recorded from the Chilcatay Formation (Lambert et al. 2015). We cannot exclude the possibility that part of this lateral lamina is made of the palatine, as proposed for *Eurhinodelphis cocheteuxi* (Lambert 2005b); better-preserved specimens would be needed to test this hypothesis. Slightly shifted from its original position (more so on the right side), the styliform process of the jugal is slender and it contacts the ventral side of the zygomatic process of the squamosal at the level of the prominent tubercle described in MUSM 632 (Figs. 3B, 4A). As in the latter, the zygomatic process is transversely broad in dorsal view and directed anterolaterally. As in MUSM 632, two deep sternocephalic fossae are present, with the dorsalmost being anteriorly longer (Fig. 3D). The squamosal fossa is widely open anterolaterally, ventrally limiting an anteroposteriorly long and most likely dorsoventrally low temporal fossa (as suggested by the low position of the anteromedial portion of the fossa's roof; Fig. 3D). Not preserved in MUSM 632, the postglenoid process is anteroposteriorly thick and transversely wide in MUSM 3944 (Figs. 3B, D, 4A), in a way similar to other eurhinodelphinids, *Eoplatanista*, and at least some members of the *Chilcacetus* clade (e.g., *Argyrosetus joaquinensis*) (Kellogg 1932; Pilleri 1985; Lambert et al. 2015), but it is anteroposteriorly thinner and ventrally shorter than in squaloziphiids (Lambert et al. 2019), not reaching farther ventrally than

the paroccipital process of the exoccipital.

The preserved posteromedial part of the occipital shield displays a broad medial groove separating the artificially exposed, posterodorsally inflated cerebral hemispheres (Fig. 3A, C). In ventral view the basioccipital crests are thickened posteriorly, as in MUSM 632. The large occipital condyles are prominent, reaching farther posteriorly than the exoccipitals; they project slightly posteroventrally.

Both periotics of MUSM 3944 display tight contacts with the spiny process and posteromedial edge of the falciform process of the squamosal (Fig. 3B, 4). The left periotic has a complete length of more than 38 mm (anterior tip of anterior process partly hidden by the falciform process). The anterior process is long, making more than 96 per cent of the length of the pars cochlearis (measured until the anteroventral margin of the fenestra rotunda), as in other eurhinodelphinids. Its ventral surface is excavated by a deep and long anterior bullar facet with ventrally high medial and lateral walls (Fig. 4B). No accessory ossicle is preserved in the anteroposteriorly short fovea epitubaria; the accessory ossicle is fused to the anterior process in some eurhinodelphinids (e.g. *Eurhinodelphis cocheteuxi* IRSNB M.1856). The medium-size lateral tuberosity extends anterolaterally, bounding with the lateral edge of the posterior process a deep and broadly open hiatus epitympanicus. The large malleolar fossa faces posteroventrally. A small fossa (submalleolar fossa sensu Tanaka & Fordyce 2017; additional small fossa sensu Lambert 2005b) is wedged between the malleolar fossa and the ventral opening for the facial canal. Such a fossa is observed in many other odontocetes, including eurhinodelphinids, physeteroids, ziphiids, *Inticetus*, *Waipatia*, and several related forms (Muizon 1984; Lambert 2005b; Fordyce 1994; Tanaka & Fordyce 2017; Lambert et al. 2018). The posterior process is longer than the pars cochlearis (more so than in part of the specimens of *Schizodelphis* sp. and *Xiphiacetus cristatus* at the USNM; see Lambert 2005a) and directed posterolaterally. The posterior bullar facet displays a slightly undulating surface along the mediolateral axis. The facial crest is ventromedially prominent; it gives the medial margin of the process a highly convex outline, as in other eurhinodelphinids. The area where the articular rim could have been located is hidden by the spiny process. The pars cochlearis has a rounded outline in ventral view, with the anteromedial region

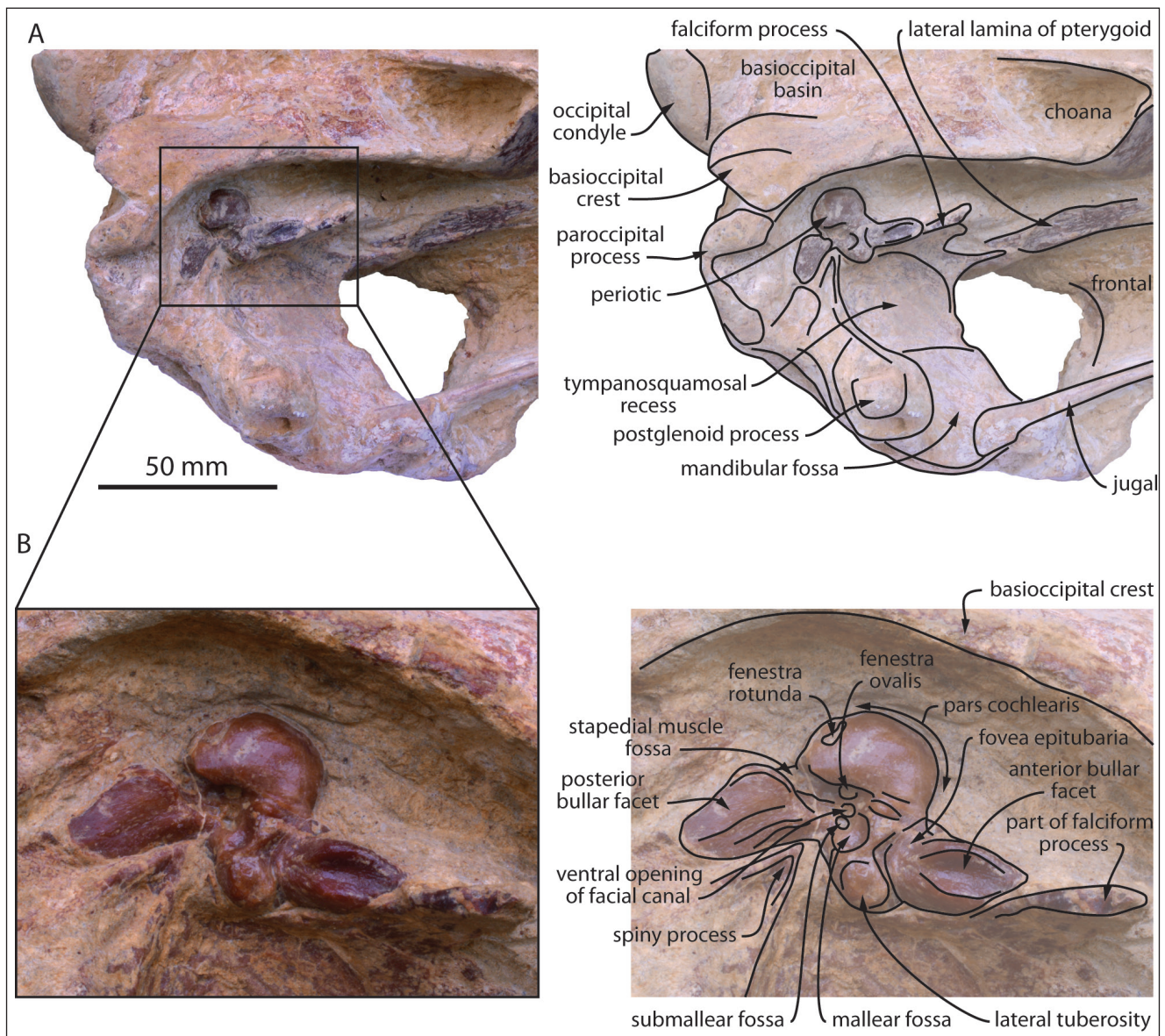


Fig. 4 - Cranium of MUSM 3944, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. A) detail of the left side of the basicranium in ventrolateral view (photo and interpretive drawing); B) left periotic in ventral view (photo and interpretive drawing).

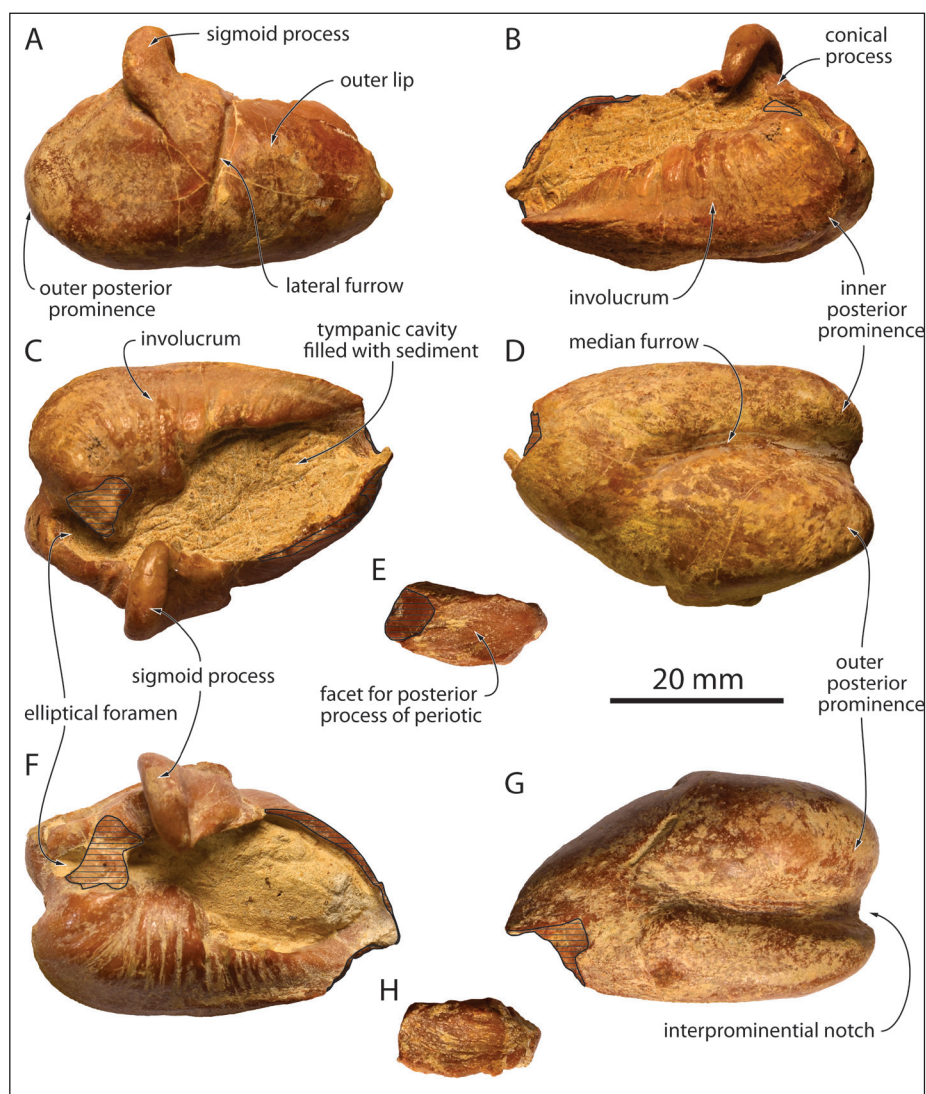
being slightly more angular. The fenestra rotunda is bounded dorsally by a small tuberosity, the latter being medially and laterally defined by a narrow groove leaving from the fenestra. The lateral caudal tympanic process is not prominent.

Although no clear apomorphic feature of the family Eurhinodelphinidae could be found on these bones, the periotics of MUSM 3944 do not display any significant difference with previously figured eurhinodelphinid periotics from the North Atlantic realm (see Muizon 1988a; Bianucci et al. 1994; Lambert 2004, 2005a,b; Benoit et al. 2011). In *Eoplatanista*, the anterior process of the periotic is shorter and more pointed (Muizon 1988a). For

a detailed comparison with platanistoid periotics, the dorsal and lateral surfaces of the bone, which are not available in these in situ periotics, would be needed.

The two tympanic bullae were detached from the basicranium during preparation (Fig. 5); the accessory ossicle is lost on both tympanics; each posterior process is separated from the rest of the bone (Fig. 5E, H); and each tympanic is missing part of its anterior tip. The tympanic is proportionally broad in dorsal/ventral view (Table 1), with a maximum width at about mid-length. The inner posterior prominence is transversely narrower than the outer posterior prominence, but reaches nearly the

Fig. 5 - Tympanic bullae of MUSM 3944, Eurhinodelphinidae indet. from the early Miocene of the Chilcatay Formation, East Pisco Basin, Peru. Right tympanic in lateral (A), medial (B), dorsal (C), and ventral (D) views; E, right posterior process in dorsal view; left tympanic in dorsal (F) and ventral (G) views; H) left posterior process in dorsal view. Hatching highlights main break surfaces.



same posterior level. The interprominential notch is wide and shallow, followed on the ventral surface of the bone by a well-defined median furrow, extending forwards for two thirds of the tympanic's preserved length. Differing from platanistids, squalodelphinids, and the closely related *Ensidelphis*, the median furrow does not reach the tapering anterior part of the bone; on the other hand, *Eoplatanista* lacks any median furrow (Muizon 1988a; Bianucci et al. 2020). Due to the incompleteness of the anterior tip for the two tympanics, the presence and degree of development of an anterior spine cannot be assessed in MUSM 3944. In dorsal view the sigmoid process is slightly oblique, being directed medially and slightly anteriorly. In lateral view the vertical posterior margin of the sigmoid process gradually takes an anteroventral direction, lacking the posterior projection seen in most ziphiids and being ventrally shorter than in the latter (see Lam-

bert et al. 2013). The deep lateral furrow occupies three quarters of the dorsoventral height of the outer lip. As preserved the conical process is low. In dorsal view the dorsal edge of the involucrum is cut at mid-length by a major indentation, more pronounced on the left tympanic; this indentation is less conspicuous in medial view, with the dorsal margin of the involucrum more gradually lowering in an anteroventral direction. Whereas a somewhat similar condition is observed in *Eoplatanista* and ziphiids (e.g. Muizon 1988a; Lambert et al. 2013), there is no marked indentation in several other clades of longirostrine to hyper-longirostrine odontocetes (e.g. Muizon 1987; Fordyce 1994; Tanaka & Fordyce 2014; Kimura & Barnes 2016; Bianucci et al. 2020). The ventral margin of the involucrum is ventrally bulging at two thirds of its length, before raising anterodorsally towards its dorsoventrally thin anterior tip. The whole morphology of the in-

volucrum closely matches the condition observed in several eurhinodelphinids, for example *Eurhinodelphis cocheteuxi* IRSNB M.1856, *Xiphiacetus bossi* USNM 167629, *X. cristatus* IRSNB M.1902, and *Ziphiodelphis abeli* MGP 26194. A moderate size elliptical foramen is visible on both tympanics. The detached posterior process is narrow, and proportionally longer on the right tympanic.

Discussion

Comparison. In addition to general similarities with other eurhinodelphinids as mentioned above, MUSM 632 is attributed to the family Eurhinodelphinidae based on (1) the presence of an extensive premaxillary portion of the rostrum and (2) the mandibles being significantly shorter than the rostrum; these two derived features are absent in other clades of longirostrine to hyper-longirostrine odontocetes (e.g. Kellogg 1924; Muizon 1988a; Fordyce 1994; Kimura & Barnes 2016; Bianucci et al. 2020). Similarities at the level of the rostrum suggest that MUSM 3944 was also characterized by an extensive premaxillary portion of the rostrum. The latter shares multiple characters with other known eurhinodelphinids (at the level of the rostrum, palate, lateral lamina of the pterygoid, postglenoid process of the squamosal, periotic, and tympanic), but each of these features can be individually found to some degree in other odontocete clades and cannot be considered as synapomorphic for Eurhinodelphinidae (see comparison above).

Although displaying a series of minor differences, these two specimens roughly have the same size and share many anatomical similarities (see above). The lack of most of the facial region in both crania and of the periotic in MUSM 632 makes their referral to the same species only tentative. Their fragmentary state of preservation further refrains us either from referring them to a known eurhinodelphinid genus or species from the North Atlantic realm, or from naming any new taxon. Among the available morphological features, these two specimens depart from *Mycteriaetus bellunensis*, *Ziphiodelphis abeli*, and *Z. sigmoideus* in the mesorostral groove being more widely dorsally open and in the premaxillae being significantly narrower at rostrum base. The maxillary portion of the rostrum of MUSM 632 is proportionally longer than in *Eurhinodelphis cocheteuxi* and *E. longirostris*, and the premaxillary foramen is more posteriorly located than in *E.*

cocheteuxi and *M. bellunensis*. More complete crania, including the highly diagnostic vertex, will be needed for a detailed comparison with species of the genera *Schizodelphis* and *Xiphiacetus*, not displaying obvious differences with MUSM 632 and MUSM 3944 at the level of preserved parts (including the periotic and tympanic).

The preservation state of the two specimens does not allow to precisely quantify the portion of the rostrum that was only occupied by the premaxillae and to assess the degree of development of premaxillary alveoli. Nevertheless, their attribution to the family Eurhinodelphinidae suggests that, as in other eurhinodelphinids, premaxillary teeth were either vestigial (not held in distinct alveoli) or completely absent.

The only other longirostrine dolphin from the Miocene of the whole Southern Hemisphere that is known from a reasonable part of the rostrum and mandible and that has been previously referred to the family Eurhinodelphinidae is *Argyrosetus patagonicus*, from the early Miocene of Argentina (Lydekker 1893; Cabrera 1926; Muizon 1988a). The poorly preserved type specimen displays a very long mandible; much longer than reconstructed in MUSM 632, it actually reaches forward much farther than the preserved tip of the rostrum. The anterior part of the mandible being apparently edentulous, Cabrera (1926) suggested that the missing anterior part of the rostrum was also edentulous and would thus correspond to the edentulous premaxillary portion of the rostrum as observed in eurhinodelphinids. If correct, this relatively hypothetical interpretation would mean that the mandibles were not shorter than the rostrum in *A. patagonicus*, a major difference with MUSM 632 (and at least part of the other eurhinodelphinids). In addition, the mandible of *A. patagonicus* bears a distinct lateral groove, a feature absent in MUSM 632, and it displays a lower number of post-symphyseal alveoli. Although the postglenoid process of the squamosal is anteroposteriorly thick in *A. patagonicus*, this character is not exclusively observed in eurhinodelphinids (see above; Muizon 1991; Lambert et al. 2015, 2019), and this process reaches farther ventrally in *A. patagonicus* compared to MUSM 3944. Other parts of the skull are either too poorly preserved in the type of *A. patagonicus* or lost in MUSM 632 and MUSM 3944 (e.g. the nasals, typically projecting anterodorsally in *A. patagonicus*). The observed differences are

nevertheless sufficient to conclude that the Peruvian specimens belong to a different taxon and that more complete specimens would be needed to further test the affinities of *A. patagonicus* with eurhinodelphinids. In a previous phylogenetic analysis, *A. patagonicus* was recovered outside Eurhinodelphinidae, in a clade also including a series of early Miocene, northeastern and southeastern Pacific longirostrine odontocetes (*Chilcacetus* clade; Lambert et al. 2015).

It is worth clarifying here another tentative eurhinodelphinid record from South America, as the studied remains originate from Peru. Contradicting an earlier comment on the observed absence of eurhinodelphinids in the Pisco Formation (Muizon 1988b), Pilleri (1989) suggested that two fossils found in layers of this unit in the locality of Aguada de Lomas, Sacaco Basin, could be referred to this family. The first specimen is a highly damaged odontocete neurocranium, only illustrated in dorsal view (Pilleri 1989, pl. 1). The U-shaped anterior margin of the bony nares and the abrupt posterior narrowing of the left premaxilla on the anterolateral corner of the corresponding bony naris are major differences with known eurhinodelphinids. These features are more reminiscent of delphinidans, and among those, more specifically of phocoenids. The latter are especially common in the upper part of the Pisco Formation (see Muizon 1984, 1988b) and this specimen is identified here as Phocoenidae indet. The second specimen figured by Pilleri (1989, pl. 2) is an isolated, highly abraded humerus, whose state of preservation does probably not allow for a more precise attribution than Cetacea indet.

BIOGEOGRAPHY

The two new Peruvian specimens described here constitute the only unambiguous eurhinodelphinid records, based on diagnostic rostral and mandibular material, outside the western coast of the North Atlantic, North Sea, and Mediterranean (= North Atlantic realm), and thus the first clear records for the whole Pacific and the whole Southern Hemisphere (for a revision and comments on more fragmentary remains, see Muizon 1988a; Lambert 2005a, and Marx et al. 2016; Supplementary Table 1). As such, these new specimens from the East Pisco Basin greatly expand the biogeographic distribution of

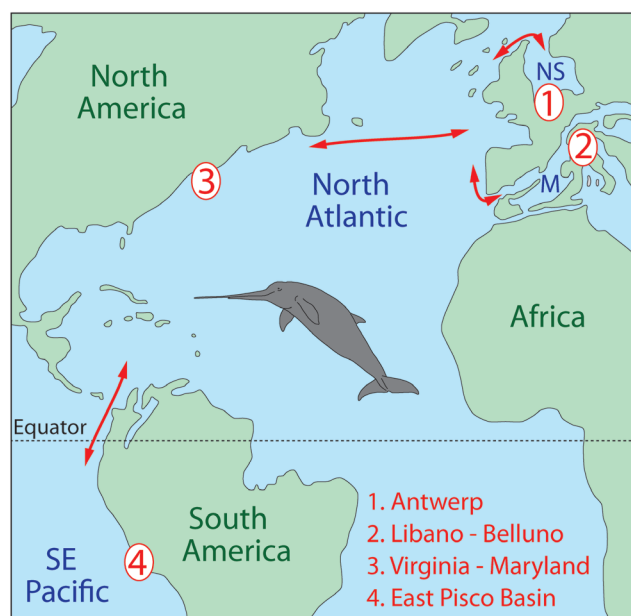


Fig. 6 - Palaeogeographic map of the Atlantic and southeastern Pacific during the early Miocene (ca. 20 Ma) showing the main eurhinodelphinid localities (red numbers) from the North Sea Basin (Berchem Formation, Antwerp, Belgium), Mediterranean (Libano Sandstone, Libano and Belluno, Italy), Atlantic Coastal Plain (Calvert Formation, Virginia and Maryland), and East Pisco Basin (Chilcatay Formation, Peru). M, Mediterranean; NS, North Sea. Red arrows indicate probable dispersal routes of eurhinodelphinids across the Central American Seaway, the North Atlantic, the Mediterranean-Atlantic gateways, and the northern part of the North Sea. Map redrawn from an original map by R.C. Blakey (available at deeptimemaps.com). Reconstruction of the body shape for the eurhinodelphinid *Xiphiacetus bossi* redrawn from original art by T. Scheirer (courtesy of Calvert Marine Museum).

the family. In addition to the crossing of the North Atlantic and of the Mediterranean-Atlantic gateways (see Flecker et al. 2015 and references therein), as well as a dispersal via the northern part of the North Sea (strait of Dover was closed from the late Oligocene to the Tortonian; Van Vliet-Lanoë et al. 2010), a new dispersal route for members of the family can thus be proposed, during the early Miocene or earlier, across the Central American Seaway (Fig. 6); the latter remained fully open at least until the early middle Miocene, before a Pliocene final closure (O'Dea et al. 2016; Jaramillo et al. 2017). Previous reports of marine mammals crossing this seaway during the Miocene (e.g. Bianucci et al. 2010, 2016; Uhen et al. 2010) further support this migration route. These records from the southeastern Pacific also potentially indicate that early Miocene eurhinodelphinids from other Southern Hemisphere or North Pacific localities are still awaiting discovery or proper identification.

The addition of the family Eurhinodelphinidae to the taxonomic list of the Chilcatay Formation further increases the similarities noted between the East Pisco Basin and early to middle Miocene localities of the North Atlantic realm. This early Burdigalian odontocete assemblage now shares five higher rank clades (Eurhinodelphinidae, Kentriodontidae, Physeteroidea, Platanistidae, and Squalodelphinidae) with the Aquitanian to Langhian of the Calvert Formation, Atlantic Coastal Plain (Virginia and Maryland, U.S.A.; Gottfried et al. 1994), three (Eurhinodelphinidae, Physeteroidea, and Squalodelphinidae) with the late Aquitanian to early Burdigalian Libano Sandstone (Libano and Belluno, Italy; Pilleri 1985; Bianucci & Landini 2002), and at least three (Kentriodontidae, Physeteroidea, and Squalodelphinidae, including the species *Notocetus vanbenedeni*, see above for the affinities of *Argyrosetus patagonicus*) with the Aquitanian to early Burdigalian Monte León and Gaiman formations (eastern Patagonia, Argentina; Viglino et al. 2018; Cuitiño et al. 2019; Paolucci et al. 2019). Similarities with early Miocene assemblages from the North Atlantic realm were recently further supported by the tentative report of inticetids in France, North Carolina (U.S.A.), and Italy (Lambert et al. 2018; Boessenecker 2019; Peri et al. 2019). Additional work on the rich cetacean assemblages of the Chilcatay Formation and the lower part of the Pisco Formation will most likely reveal further connections, probably also at lower taxonomic ranks, between the southeastern Pacific and the North Atlantic realm for both the odontocetes and mysticetes, as alluded to in earlier works (Muizon & DeVries 1985; Bianucci et al. 2010, 2019; Marx et al. 2019).

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