

HUARIDELPHIS RAIMONDII, A NEW EARLY MIOCENE SQUALODELPHINIDAE (CETACEA, ODONTOCETI) FROM THE CHILCATAY FORMATION, PERU

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ABSTRACT—The fossil record of odontocetes (toothed cetaceans) is relatively scarce during the Oligocene and early Miocene compared with later in the Miocene and Pliocene; most of the odontocete families from these epochs are known by a limited number of species and specimens. Among those, Squalodelphinidae is a family of small- to medium-sized platanistoids with single-rooted teeth, which until now has included only four genera based on diagnostic material, from the early Miocene of Europe, Argentina, and North America. Recent field work in the Pisco-Ica desert, southern coast of Peru, has resulted in the discovery of several marine vertebrate-rich localities in various levels of the late Oligocene–early Miocene Chilcatay Formation. Based on three specimens from Ullujaya and Zamaca, including two well-preserved skulls with periotics, we describe a new squalodelphinid genus and species, *Huaridelphis raimondii*. This new species increases the early Miocene diversity of the family and is also its smallest known member. It further differs from other squalodelphinids by its thin antorbital process of the frontal, abruptly tapering rostrum, and higher tooth count. A more fragmentary skull, from Zamaca, is referred to Squalodelphinidae aff. *H. raimondii*. This skull provides information on the morphology of the tympanic, malleus, and incus, currently unknown in *H. raimondii*. Focusing on platanistoids with single-rooted teeth, our phylogenetic analysis suggests that Squalodelphinidae are monophyletic and confirms the sister-group relationship between the latter and Platanistidae. The relationships within Squalodelphinidae are not fully resolved, but *H. raimondii* might be one of the earliest diverging taxa.

INTRODUCTION

This paper represents the first of a series of contributions on the fossil odontocetes discovered by us during the last few years in the upper Oligocene–lower Miocene Chilcatay Formation (Pisco-Ica Basin, Peru; DeVries, 1998, 2001) (Fig. 1). Preliminary observations, both in the field and on the collected material under preparation, indicate a high diversity documented by well-preserved fossils. Some levels of the Chilcatay Formation display an exceptional wealth of fossil marine vertebrates, similar to that in the overlying younger Pisco Formation (e.g., Muizon, 1984, 1988a, 1993; Lambert et al., 2008a, 2009, 2013; Bianucci et al., 2010; Lambert et al., 2010a, 2010b; Lambert and Muizon, 2013). The time interval covered by the Chilcatay Formation spans an important phase of the odontocete radiation, with the appearance of several major extinct and extant clades, but this phase is poorly documented in the fossil record (Fordyce and Muizon, 2001; Uhen and Pyenson, 2007; Uhen, 2008). Consequently, the description of this new material could clarify some crucial aspects of odontocete evolutionary history. In this paper, we describe a new genus and species of Squalodelphinidae, based on well-preserved specimens (including two almost complete skulls) from the early Miocene levels of the Chilcatay Formation outcropping in the new localities of Ullujaya and Zamaca.

Squalodelphinidae are an extinct Miocene family of marine odontocetes characterized by a moderately elongated and tapered rostrum, posterior cheek teeth being single-rooted but retaining accessory denticles, and marked skull asymmetry. Based on some peculiar features, mostly of the ear bones and scapula, squalodelphinids are considered closely related to the family Platanistidae, inside the superfamily Platanistoidea sensu Muizon, 1987, although the relationships among the squalodelphinids and between the squalodelphinids and the other platanistoids are still debated (see below for discussion; Muizon, 1987; Fordyce, 1994; Barnes, 2006; Barnes and Reynolds, 2009; Geisler et al., 2011, 2012). In any case, the closest extant relative of the squalodelphinids is the south Asian river dolphin *Platanista gangetica*, representing the only surviving platanistoid (Bianucci et al., 2013). The fossil record of squalodelphinids is rather limited. Besides a skull associated with a mandible and other more fragmentary specimens referred to the type genus and species *Squalodelphis fabianii* Dal Piaz, 1917 (early Miocene, northern Italy) (Dal Piaz, 1917; Pilleri, 1985), the most significant fossils assigned to this family are (1) three specimens from the early Miocene of southern Argentina referred to *Notocetus vanbenedeni* Moreno, 1892: one skull with mandibles, another skull with a tympanic bulla, mandibles, and a few postcranial bones, and fragments of skull with ear bones, teeth, scapula, and a few other postcranial elements (Moreno, 1892; True, 1910; Muizon, 1987); and (2) one fragmentary skull referred to *Medocinia tetragorhina* Delfortrie, 1875, from the early Miocene of southern France (Muizon, 1988b). More fragmentary remains referred in the past to this family and other significant specimens tentatively assigned to this family are discussed in detail below.

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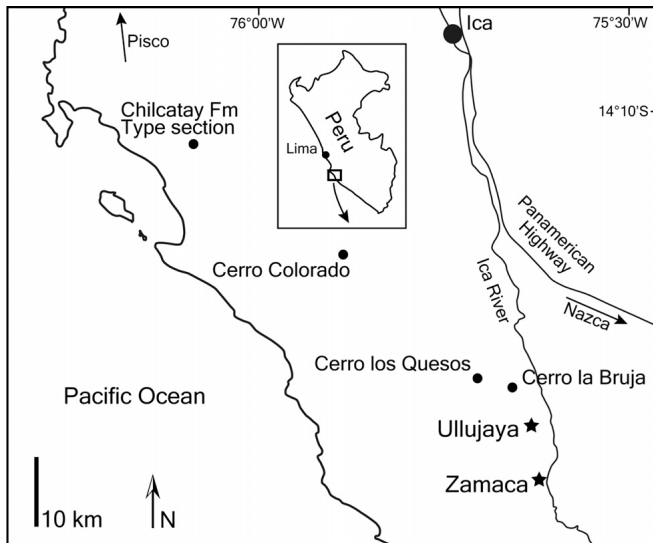


FIGURE 1. Map of the Pisco-Ica desert, southern coast of Peru, showing the two localities of the Chilcatay Formation where squalodelphinids, including *Huaridelphis raimondii*, n. gen. et sp., were found: Ullujaya and Zamaca. Marine vertebrate-rich localities of the Mio-Pliocene Pisco Formation are also indicated: Cerro Colorado, Cerro los Quesos, and Cerro la Bruja.

Besides the *N. vanbenedeni* specimens from Argentina, to our knowledge the only other South American fossil odontocete remains tentatively referred to squalodelphinids are a scapula (Sánchez-Villagra et al., 2001) and poorly diagnostic skulls fragments, with a few vertebrae and ribs (Cozzuol and Aguilera, 2008) from the early Miocene of Venezuela. Hence, the new squalodelphinid from Peru reported here represents an important addition to our knowledge of this extinct family. The cladistic analysis investigating the phylogenetic affinities of this new genus and species gives us the opportunity to propose a new phylogeny for the squalodelphinids and related platanistoids with single-rooted teeth.

MATERIALS

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; BDNLTM, Bunde Doberg und Tabak Museum, Bünde, Germany; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MGP, Museo di Geologia e Paleontologia, Padua, Italy; MNHL, Muséum d'Histoire naturelle de Lyon, Lyon, France; MNHN, Muséum national d'Histoire naturelle, Paris, France; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; MLP, Museo de La Plata, La Plata, Argentina; RMNH, Naturalis, Leiden, The Netherlands; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Anatomical Measurement Abbreviations—BZW, Bizygomatic width of skull; CBL, condylobasal length of skull.

Anatomical Terminology—We mostly follow Muizon (1987), Fordyce (1994), and Mead and Fordyce (2009) for the terminology of skull elements and Rommel (1990) for vertebrae.

List of Specimens Directly Examined for This Work—*Albertocetus meffordorum* USNM 525001; *Eosqualodon lange-wieschei* BDNLTM 326; *Eurhinodelphis cocheteuxi* IRSNB M.294, 295, 296, 297, 299, 1856, 1857; *E. longirostris* IRSNB M.342, 1858; *Huaridelphis raimondii*, n. gen. et sp., MUSM 1396,

1403, 599; *Medocinia tetragorhina* (cast MNHN); *Notocetus vanbenedeni* MLP 5-5; *Phocageneus venustus* USNM 21039; *Platanista gangetica* IRSNB 1507; MNHN A7943; RMNH 31169, USNM 172409, 23456, Pomatodelphininae USNM 206006; Pomatodelphininae cf. *Zarhachis* USNM 214759; *Pomatodelphis bobengi* USNM 299695; *Pomatodelphis* sp. USNM 187414; *Prosqualodon australis* MLP 5-8; *Prosqualodon davidis* (cast USNM 467596); *Simocetus rayi* USNM 256517; Squalodelphinidae USNM 475596; Squalodelphinidae aff. *Huaridelphis raimondii* MUSM 603; *Squalodelphis fabianii* MGP 26134, 26141, 26378; *Squalodon bariensis* MGP 26081, MNHL Dr15; *Squalodon bellunensis* MGP 17715, 26091, 26131, 26322; *Squalodon calvertensis* USNM 10484, 328343; *Squalodon whitmorei* USNM 183023; *Waipatia maerewhenua* cast USNM; *Xiphiacetus bossi* IRSNB M.367, USNM 8842, 10464, 10711, 10714, 16581; *X. cristatus* IRSNB M.361, 1893, 1894, 1895, 1896, USNM 13436, 21303, 21360, 21363; *Zarhinocetus errabundus* cast USNM; *Zarhachis flagellator* USNM 10911, 10485; *Ziphiodelphis abeli* MGP 26187; *Z. sigmoideus* MGP 26395; *Zygorhiza kochii* USNM 4679, 11962.

SYSTEMATIC PALEONTOLOGY

Order CETACEA Brisson, 1762

Suborder ODONTOCETI Flower, 1867

Superfamily PLATANISTOIDEA Gray, 1863

Remarks on the Definition of the Platanistoidea— Since the proposal of Muizon (1987) to include the families Platanistidae, Squalodelphinidae, and Squalodontidae in the superfamily Platanistoidea, the content of the latter has been controversial. In a subsequent work, based respectively on the morphology of the scapula (loss of coracoid process and acromion on the anterior edge of the bone) and the morphology of the periotic, Muizon (1991) included *Prosqualodon* and *Dalpiazina* in Platanistoidea. *Waipatia*, for which no scapula is known, entered the superfamily in the first software-assisted phylogenetic analysis of fossil and extant odontocetes (Fordyce, 1994). With a larger morphological matrix, Geisler and Sanders (2003) excluded *Notocetus*, *Prosqualodon*, and *Squalodon* from the superfamily, and included other river dolphin lineages (iniids, lipotids, and pontoporiids) as well as *Eurhinodelphis*. It should be noted that the diagnostic platanistoid characters of the scapula have not yet been observed in any member of a river dolphin lineage or in a eurhinodelphinid (Muizon, 1991, 1994; pers. observ.). In two steps, Barnes (2006) and Barnes and Reynolds (2009) placed the allodelphinids *Allodelphis* and *Zarhinocetus* in a superfamily incorporating Platanistidae, Squalodelphinidae, Squalodontidae, and Waipatiidae. Recently, with a supermatrix containing both molecular and morphological data, Geisler et al. (2011) did not find support for a monophyletic superfamily Platanistoidea. The definition of Platanistoidea and the relationships between included families are beyond the scope of this work; they will be investigated in detail in a future study. For that reason, we choose to provisionally maintain in the superfamily the less debated families, namely, Allodelphinidae, Platanistidae, and Squalodelphinidae, with a question mark for Squalodontidae and Waipatiidae. And because our group of interest is squalodelphinids, we will mostly comment on presumed members of the superfamily having lost double-rooted teeth.

Among platanistoids, platanistids, squalodelphinids, and at least some allodelphinids (*Zarhinocetus*) share a cranium distinctly shorter than wide, with a ratio between cranium length (longitudinal, from occipital condyles to level of antorbital notches) and postorbital width <0.90. These taxa also share deep fossa in orbit roof (possibly present in *Zarhinocetus*, unknown in *Allodelphis*), which seemingly connects the pterygoid sinus fossa to a crest on the supraorbital process of platanistids; elevated antorbital region, distinctly higher than the dorsal margin of

rostrum base in lateral view (obscured in *Zarhinocetus* by the thick lateral margin of the rostrum at the antorbital notch; unknown in *Allodelphis*); vertex distinctly shifted to the left compared with the longitudinal midline of the skull (present in *Zarhinocetus*; difficult to detect in *Allodelphis*); and loss of double-rooted posterior teeth (present in *Zarhinocetus*; unknown in *Allodelphis*).

Furthermore, platanistids and squalodelphinids share marked asymmetry of premaxillae on the rostrum, at some distance anterior to premaxillary foramina, with the right premaxilla narrower than the left in dorsal view (the opposite occurs in some squalodontids, e.g., *Squalodon bariensis* and *S. bellunensis*); posterior infraorbital foramen(in) along the vertex more medial than the lateral-most margin of the premaxilla in the cranium; thick zygomatic process of the squamosal, with the ratio between maximum distance from the anteroventral margin of the zygomatic process to the posterodorsal margin, in lateral view, and vertical distance from the lower margin of the occipital condyles to the cranial vertex greater than 0.38; development of an articular rim on the lateral surface of the periotic (hook-like in platanistids); and elongated anterior spine on the tympanic bulla, which is associated with a marked anterolateral convexity. Finally, most platanistids and squalodelphinids share a deep longitudinal groove on the posterior apex of the premaxilla (possibly homologous to the premaxillary cleft in *Waipatia*).

Family SQUALODELPHINIDAE Dal Piaz, 1917

Emended Diagnosis—Squalodelphinidae differ from Allodelphinidae and Platanistidae except *Platanista* by having a proportionally shorter rostrum (rostrum length/condylobasal length <0.70); Allodelphinidae and Platanistidae by lacking a deep lateral groove on the rostrum and a deeper, 'V'-shaped, left antorbital notch, related to anteriorly pointed antorbital process (right notch usually shallower). Squalodelphinidae differ from Platanistidae by having an antorbital-supraorbital region lacking a distinct crest; a square-shaped pars cochlearis; a large, dorsally facing, aperture for the cochlear aqueduct of the periotic; median furrow of the tympanic affecting the whole length of bone, including the anterior spine (except in Squalodelphinidae aff. *Huaridelphis raimondii* MUSM 603); apical extension of the manubrium of the malleus (except in Squalodelphinidae aff. *Huaridelphis raimondii* MUSM 603); retention of ornamentation on posterior teeth; and strong development of the dorsal transverse process of the atlas and extreme reduction of its ventral process.

Remarks on Previous Attributions to Squalodelphinidae—The holotype of the only species of the squalodelphinid genus *Phocageneus*, *P. venustus*, is an isolated single-rooted tooth from Virginia (Leidy, 1869). Later, a partial skeleton from the Calvert Formation, Maryland, USNM 21039, including a part of the mandible, the ear bones, teeth, vertebrae, and ribs, was referred to the species, based on the similar tooth morphology (Kellogg, 1957). In addition, a fragmentary skull from the Miocene of the Lee Creek Mine, USNM 475596, with associated tooth and fragment of periotic was tentatively attributed to the genus *Phocageneus* together with other more fragmentary specimens, including five isolated periotics (Whitmore and Kaltenbach, 2008). The ear bones of USNM 21039 and the skull of USNM 475596 clearly bear resemblances with other squalodelphinid taxa, and we agree with their family attribution. Even if the correlation with the holotype of *P. venustus* is only based on the poorly diagnostic tooth morphology, the specimen USNM 21039 was long considered as belonging to the species, being more often used in comparisons and discussions than the holotype, especially for the ear bones. Therefore, we follow a conservative approach, considering the attribution of the specimen USNM 21039 to the species *P. venustus* as valid. The other specimen, USNM 475596, will be

mentioned below as squalodelphinid USNM 475596, pending a detailed review of its relationships with other squalodelphinids and/or the discovery of more complete specimens. It should be noted that among squalodelphinids, USNM 475596 was only compared with *Notocetus* and *Squalodelphis*, not with *Medocinia* (Whitmore and Kaltenbach, 2008). The latter shares some interesting similarities with the Maryland skull: the frontal much anteroventrally projected on the antorbital process, with a consequently limited overlap of the frontal by the maxilla in this area; and the general outline of the swollen zygomatic process of the squamosal.

The holotype of '*Prosqualodon*' *marplei*, an incomplete skull from the early Miocene of New Zealand with associated ear bones, teeth, parts of the mandible, vertebrae, ribs, one scapula, and one ulna (Dickson, 1964), was later referred to the genus *Notocetus*, based on the morphology of the vertex, the nuchal crest, the supraoccipital, the atlas, and the periotic (Fordyce, 1994). Very schematically illustrated in both papers, the skull displays some differences with *Notocetus vanbenedeni*. The posterior apex of the premaxilla is wider in '*P.*' *marplei*; the medial sutures on the vertex are not shifted to the left side; the frontal is considerably thinner in the proportionally longer and lower orbital region; and the zygomatic process of the squamosal is much less dorsoventrally thickened, with a more distinctly concave anteroventral margin. In addition, the ventral transverse process of the atlas of '*P.*' *marplei* is more developed than in *Notocetus vanbenedeni* AMNH 9485. The cervical vertebra figured by Dickson (1964:fig. 8) shares similarities with the sixth cervical of the *Phocageneus venustus* USNM 21039 (True, 1910: pl. 7, fig. 1), but with a larger transverse foramen. The scapula, bearing platanistoid characters, does not display major differences with the scapula of AMNH 29060, referred to *Notocetus vanbenedeni* by Muizon (1987:fig. 13c). The periotic (Fordyce, 1994: fig. 10) displays similarities with squalodelphinids. Most of the differences at the level of the skull can also be applied to other squalodelphinids. Pending direct observation of the specimen or the publication of more detailed illustrations of the skull, we question its attribution to the genus *Notocetus*.

HUARIDELPHIS RAIMONDII, n. gen. et sp.

(Figs. 3–6)

Holotype—MUSM 1396, well-preserved skull with the ventral-most portion of the basicranium worn along an horizontal plane (basioccipital crests, ventral part of exoccipitals, and postglenoid processes of squamosals missing), with associated fragmented right periotic.

Type Locality—Ullujaya (Figs. 1, 2), Pisco-Ica Basin, 58 km SSE from Ica, 1.5 km N from Cerro Las Tres Piramides (see Alván De la Cruz, 2008:fig. 1). Approximate geographic coordinates: S14°34'30"–W75°38'40".

Type Horizon—Chilcatay Formation, latest Oligocene to early Miocene (Dunbar et al., 1990; DeVries, 1998, 2001). A section has been published at Cerro Buque, 1.65 km NWW to the type locality (Alván De la Cruz, 2008); based on sedimentology and shark teeth (presence of *Isurus desori* and *Carcharocles chubutensis*, absence of *Carcharocles megalodon*), the beds of the Chilcatay Formation in this section were dated to early Miocene. In the type locality and approximately in the same horizon of the holotype, we found a rich vertebrate fossil assemblage represented by other odontocetes (e.g., possible eurhinodelphinid cf. *Ziphiodelphis*, kentriodontids, stem physeteroid), a mysticete, marine turtles, sharks, and teleostean fishes (Fig. 2).

Trophic relationships between odontocetes and sharks are documented; in addition to the close association of odontocete bones and shark teeth, bite marks are observed in two ribs of MUSM 1403, a specimen referred to *Huaridelphis raimondii*.

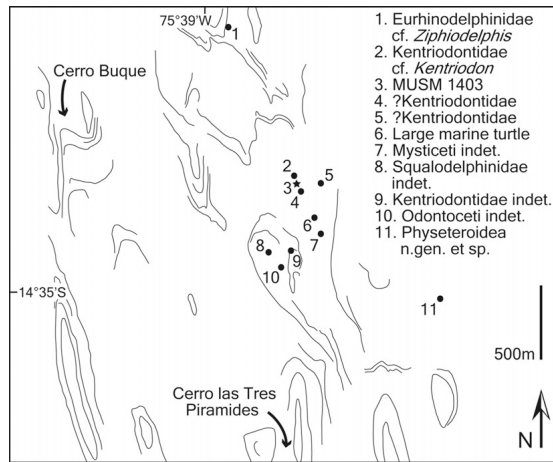


FIGURE 2. Map of the Chilcatay Formation locality Ullujaya, where the holotype of *Huaridelphis raimondii*, n. gen. et sp., was found together with other cetacean remains, marine turtles, and fishes. Cerro Buque, from where a section of the Chilcatay Formation was published (Alvan De la Cruz, 2008), is a short distance northwest to Ullujaya. Curved lines represent limits of more consolidated beds visible from aerial views.

Etymology—From ‘Huari,’ ancient culture of the south-central Andes and coastal area of Peru (500–1000 AD), and from ‘delphis,’ the Latin word for dolphin. Gender masculine. The species name honors Antonio Raimondi (1826–1890), an Italian scientist who first documented fossil whales from Peru (Bianucci, 2010).

Diagnosis—*Huaridelphis raimondii* differs from all the other squalodelphinids in smaller size (as seen in BZW and CBL); thin antorbital process of the frontal, barely thicker than the antorbital process of the maxilla in lateral view. It further differs from *Notocetus* and *Squalodelphis* in more abrupt anterior tapering of rostrum in dorsal view (see quantification below); higher tooth count, more than 28 teeth per row; short and less robust postorbital process of frontal; anteroventral slope of flat dorsal surface of vertex; dorsoventral compression of periotic at level of pars cochlearis and superior process, producing a flat dorsal surface; and posterior process of periotic more ventrally bent, with posterodorsal margin forming a right angle with dorsal surface of body of bone. It further differs from *Medocinia* and *Squalodelphis* in dorsal opening of mesorostral groove narrower than premaxilla in rostrum base; and wider dorsal exposure of maxilla at rostrum base (premaxilla nearly reaches lateral margin of rostrum in *Medocinia* and *Squalodelphis*).

Referred Specimens—MUSM 1403, well-preserved skull with the ventral portion of the basicranium worn along a sub-horizontal plane (right squamosal, occipital condyles, basioccipital, basisphenoid, and paroccipital processes of the exoccipitals missing), with associated anterior symphyseal portion of mandible and posterior part of left dentary, partly preserved vertebrae including a fragment of atlas, axis, four additional cervicals, and four to five partly preserved thoracics, one nearly complete rib, and several smaller rib fragments. Found in the type locality Ullujaya. Accurate geographic coordinates: S14°34′36″–W75°38′39″. MUSM 599, fragmentary skull including the rostrum base, part of the vertex, the supraoccipital shield, the occipital condyles, the squamosals, the basioccipital, and the left periotic, and one caudal vertebra. Found in the locality of Zamaca, Pisco-Ica Basin, along the Ica River, 8 km SSE from the type locality Ullujaya.

DESCRIPTION AND COMPARISON

Skull

The skull of *Huaridelphis raimondii* is small (Table 1); CBL is 494 mm in the holotype, with BZW of 207 mm. This is smaller than in all other known squalodelphinids (holotype of *Notocetus vanbenedeni* MLP 5-8: CBL = 582 mm, BZW = ca. 235; *N. vanbenedeni* AMNH 9485: CBL = 634, BZW = ca. 254 mm; holotype of *Squalodelphis fabianii*: CBL = 640 mm, BZW = 263 mm; the skull of the holotype of *Medocinia tetragorhina* is too fragmentary for providing estimates of these measurements, but other skull measurements, for example, the width at rostrum base, are greater than in *Huaridelphis raimondii*). The rostrum is moderately elongated, constituting 67% of CBL in the holotype, a value in the range (63–70%) of *Notocetus* and *Squalodelphis*. The rostrum is considerably longer in all the known fossil platanistids (e.g., 84% in *Zarhachis flagellator*; Kellogg, 1924) and allodelphinids. The rostrum is only slightly dorsoventrally flattened, contra pomatodelphinines, in which the rostrum is much wider than high, and in platanistines, in which the rostrum is higher than wide (Barnes, 2002, 2006). The anterior two-thirds of the rostrum are slender, with a more abrupt tapering in the proximal third of the rostrum than in *Notocetus* and *Squalodelphis* (Figs. 3–5); in other words, the anterior part of the rostrum is proportionally narrower in *Huaridelphis raimondii* compared with the wide rostrum base.

The cranium is proportionally short, with a ratio between length of the cranium (taken from the level of the antorbital notches to the occipital condyles) and BZW of 79.2% in the holotype. The cranium is roughly as long as wide in *Squalodon* and *Waipatia*, whereas the proportions of the cranium are closer to *Huaridelphis* in other squalodelphinids, allodelphinids, platanistids, and *Prosqualodon*.

The antorbital notches are deep and ‘V’-shaped. They are distinctly asymmetrical: the right antorbital notch is located more posteriorly than the left, and the lateral and medial borders of the right antorbital notch form a more open angle (60° in the holotype and 68° in MUSM 1403) than the equivalent angle on the left side (50° in the holotype and 55° in MUSM 1403). The ratio between right and left angles is around 1.2. A similar morphology and asymmetry of the antorbital notches is observed in *Notocetus* and *Squalodelphis*, although in both *Notocetus* and *Squalodelphis* the antorbital notches are wider and the ratio between the right and left angles is greater in *Notocetus* (ca. 1.7) and slightly smaller in *Squalodelphis* (ca. 1.1). Only the left deep and ‘V’-shaped antorbital notch is known in *Medocinia*. The asymmetry of the antorbital notches observed in *Huaridelphis*, *Notocetus*, and *Squalodelphis* is likely related to the asymmetry of the maxillary crests and antorbital processes: the left antorbital process is more elevated dorsally and longer anteriorly than the right process. A similar asymmetry is recorded in the frontal/maxillary crests of fossil platanistids, with the left crest more developed than the right in *Pomatodelphis* (e.g., USNM 187414) and *Zarhachis* (e.g., USNM 10911), whereas a higher right maxillary crest is at least occasionally observed in the strongly modified *Platanista* (e.g., IRSNB 1507, MNHN A7943). Asymmetry is also observed in the premaxillary sac fossae, the vertex, and surrounding bones laterally shifted on the right side (see below). All these elements of asymmetry are also observed in *Notocetus*, *Squalodelphis*, and platanistids. The temporal fossa of *Huaridelphis* has a shape and extent roughly similar to other squalodelphinids, anteriorly shorter and lower than in *Squalodon* and *Waipatia*.

Premaxilla—At the dorsoventrally flattened apex of the rostrum, the premaxilla bears the three anterior-most dental alveoli, as seen on the right side of MUSM 1403. The dorsal surface of each premaxilla at the anterior apex is excavated by a narrow

TABLE 1. Measurements (in mm) on the skulls of *Huaridelphis raimondii*, n. gen. et sp., compared with two skulls of *Notocetus vanbenedeni* (measurements partly taken from True, 1910).

Dimension	<i>Huaridelphis raimondii</i> , n. gen. et sp.			<i>Notocetus vanbenedeni</i>	
	Holotype, MUSM 1396	MUSM1403	MUSM 599	Holotype MLP 5-5	AMNH 9485
Measurements of True (1910)					
Condylobasal length	494	+486	—	582	634
Rostrum length	330	317	—	368	433
Maximum width between temporal crests	128	e109	117	140	142
Distance between upper margin of foramen magnum and nuchal crest	69	—	—	91	97
Height of foramen magnum	31	—	29	33	40
Width of foramen magnum	35	—	31	33	40
Height of occipital condyle	37	—	38	47	46
Length of temporal fossa	81	e63	—	102	115
Height of temporal fossa	59	58	—	71	74
Minimum width between temporal crests	109	e90	e102	135	128
Width between orbit centers	173	165	—	230	252
Anterior width of nasals	28	26	e32	46	48
Width at rostrum base	92	90	—	114	142
Width of premaxillae at rostrum base	55	54	e56	—	89
Maximum distance between premaxillae anterior to bony nares	9	7	—	e22	28
Width of maxillae at mid-length of rostrum	30	28	—	44	52
Width of premaxillae at mid-length of rostrum	16	14	—	28	30
Length of posterior alveolus	4.5	5.0	5.6	—	9
Width of posterior alveolus	3.7	e5.0	4.7	—	6.5
Length of alveolus at mid-length of rostrum	5.0	4.1	—	7	9.5
Width of alveolus at mid-length of rostrum	4.5	4.1	—	5.5	8
Length of anterior alveolus	—	5.5	—	11	11.5
Width of anterior alveolus	—	4.2	—	6	9
Length of tooth row	275	268	—	315	363
Additional measurements					
Number of teeth per upper tooth row	+28/28	29/29–30	—	22–23	21–22
Height of rostrum at mid-length	24	24.5	—	—	—
Cranium length from antorbital notches to occipital condyle	177	+148	—	—	—
Postorbital width of skull	183	173	—	—	—
Bizygomatic width of skull	207	e200	—	—	—
Maximum width of premaxillae on cranium	73	79	—	—	—
Width of right premaxillary sac fossa	27	28	—	—	—
Width of left premaxillary sac fossa	28	27	—	—	—
Width of bony nares	33	31	e34	—	—
Maximum length of nasal	15	15	—	—	—
Length of medial suture between nasals	10	15	—	—	—
Minimum distance between maxillae across vertex	40	39	44	—	—
Length of medial suture between frontals on vertex	19	19	—	—	—
Orbit length	55	52	58	—	—
Squamosal length from ventral tip of postglenoid process to anterior tip of zygomatic process	—	—	88	—	—
Width of occipital condyles	78	—	74	—	—

+, incomplete; —, missing data; e, estimate.

sulcus a few centimeters long exiting forward from a small foramen. The two premaxillae are dorsally joined above the mesorostral groove for about half the length of the rostrum, whereas the groove is open until the apex in *Notocetus* (see Moreno, 1892; True, 1910); the medial opening of the groove is distinctly narrower than in *Medocinia* and *Squalodelphis*, and the widening towards the bony nares is progressive, with a 'V'-shaped anterior limit of the nares. At 100–110 mm anterior to the antorbital notch, the right premaxilla is slightly narrower than the left, a condition also observed, but more pronounced, in pomatodelphinines and *Platanista* (see Kellogg, 1924, 1957, 1959; Lambert, 2006; Lee et al., 2012; pers. observ.). In parallel to the posterior widening of the rostrum, the premaxillae widen towards the proximal part of the rostrum, with a convex lateral margin, as in *Medocinia*, *Notocetus*, and even more pronounced in

Squalodelphis. A roughly similar widening is possibly present in some specimens of *Pomatodelphis*, but not in *Platanista*, *Prepomatodelphis*, and *Zarhachis*. In this area the right premaxilla is distinctly wider than the left in both the holotype and MUSM 1403. As in other squalodelphinids, allodelphinids, and pomatodelphinines, each premaxilla displays a marked medial slope at this level, making a depressed area between the antorbital notches, which resembles the prenarial basin of several extinct and extant ziphiids (Lambert, 2005a). A similar medial depression is also present, but less marked, in *Squalodon* and *Eosqualodon*. Each premaxilla is pierced by a single premaxillary foramen. The transverse line through right and left foramina is anterior to the level of the antorbital notches. The ratio between the longitudinal distance from the level of the premaxillary foramina to the level of the right antorbital notch and the width

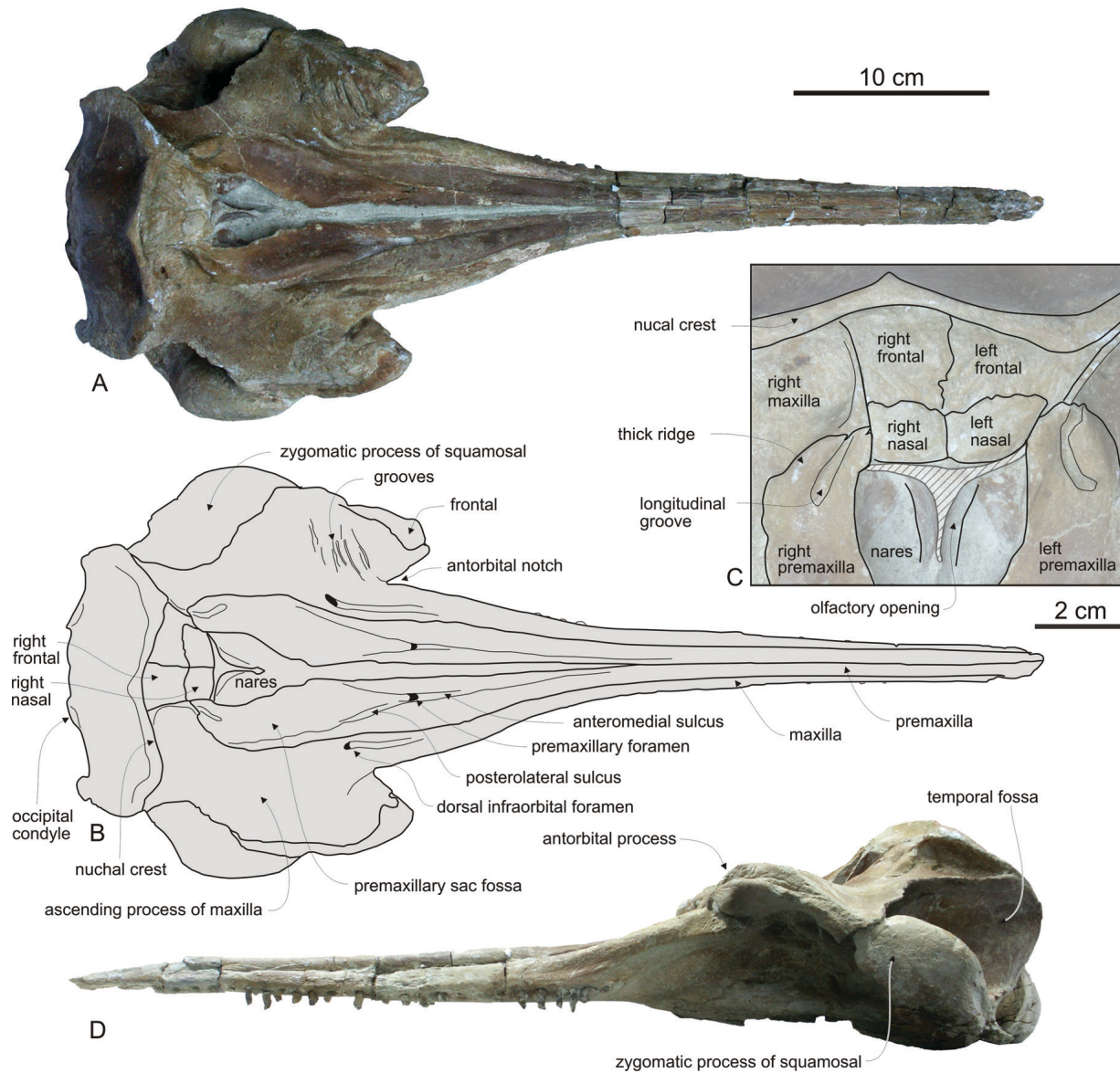


FIGURE 3. *Huaridelphis raimondii*, n. gen. et sp., MUSM 1396 (holotype), skull in dorsal (A, B, C; detail of the vertex) and left lateral (D) views. Diagonal solid lines indicate major breaks. Scale bar for A, B, D equals 10 cm. Scale bar for C equals 2 cm.

of the rostrum base varies between 0.10 and 0.20, close to the condition in *Notocetus* (ratio between 0.20 and 0.27), whereas the premaxillary foramina are more anterior in *Squalodelphis* (ratio ca. 0.40). The anteromedial sulcus is long, discernible for more than 100 mm anterior to the foramen. Among squalodelphinids, a similarly long sulcus is also observed in *Notocetus*. The posteromedial sulcus nearly reaches the anterior limit of the bony nares and the posterolateral sulcus ends at about mid-length of the bony nares. The premaxillary sac fossa is roughly flat, with a medial slope. An angle of the medial margin of the premaxillae marks the anterior limit of the bony nares; this angle is more pronounced than in *Squalodon* or *Waipatia*. The ascending process of the premaxilla narrows abruptly and ends as a pointed apex on the right side, before the level of the nasal-frontal suture. On the left side the premaxilla is slightly longer and its wider apex contacts the frontal. In the pomatodelphinines *Pomatodelphis*, *Prepomatodelphis*, and *Zarhachis* and in *Allodelphis*, this posterior part of the premaxilla is more expanded,

whereas it is narrower in *Platanista*. It should be noted that this part of the premaxilla is also wide in some other archaic odontocetes, such as *Albertocetus* and *Xenorophus* (see Uhen, 2008). The posterior apices of both premaxillae bear a deep longitudinal groove laterally margined by a thick ridge in the premaxilla. A similar combination of a groove and a thickened lateral margin is observed in *Notocetus*, *Prepomatodelphis* (commented in Barnes, 2006, char. 41, therein), *Zarhachis* (see Kellogg, 1926), and possibly *Squalodelphis* and the poorly preserved *Medocinia*. This groove may be homologous to the premaxillary cleft described in *Waipatia* (Fordyce, 1994), as well as to the elongated and shallow depression in the posterior part of the premaxilla of the highly modified *Platanista*.

Maxilla—In dorsal view, the maxilla is narrower than the premaxilla for the whole posterior third of the rostrum. Nevertheless, it is proportionally wider than in *Medocinia*, *Notocetus*, and *Squalodelphis*. Differing from platanistids and allodelphinids (as well as some other long-snouted odontocetes such as

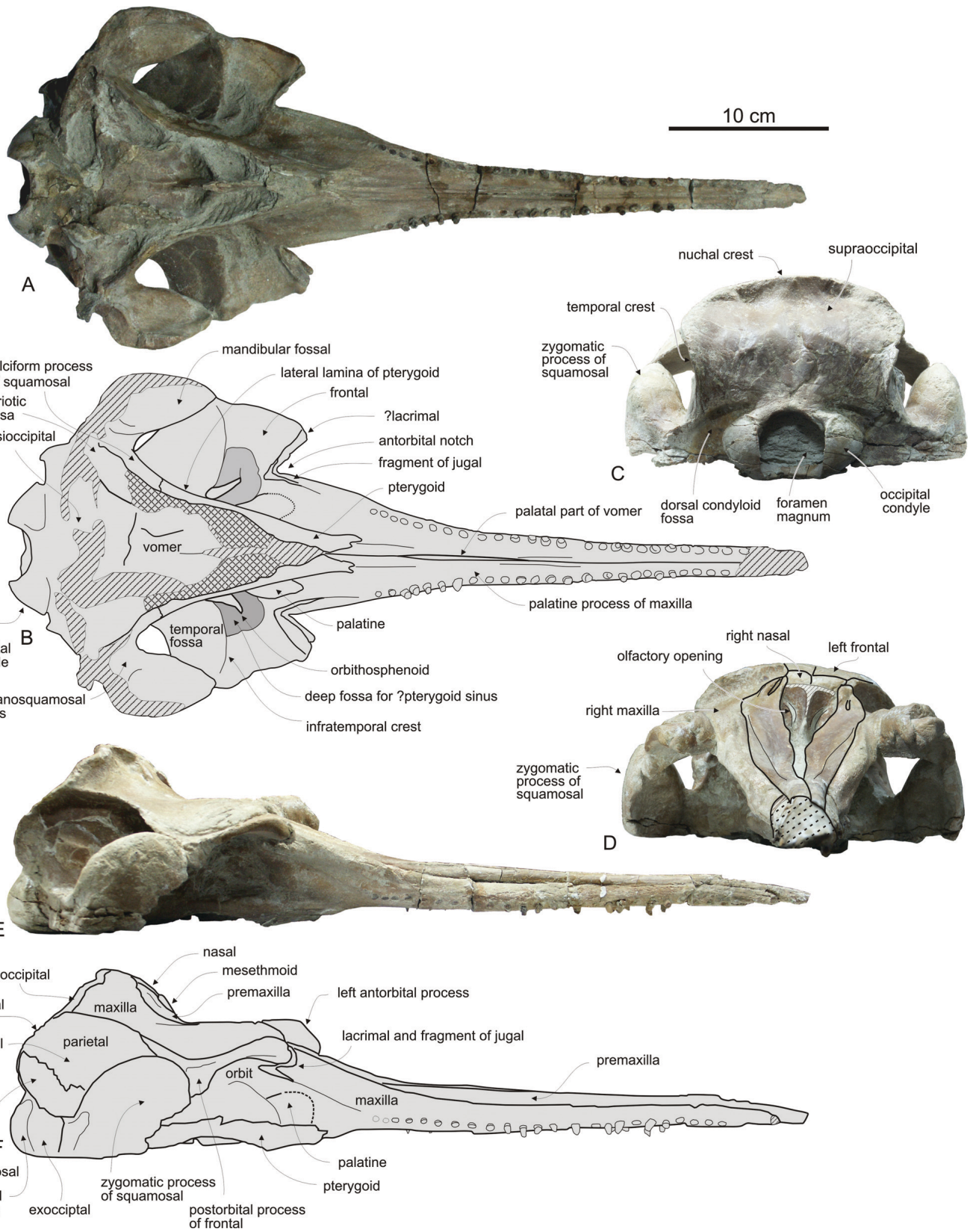


FIGURE 4. *Huaridelphis raimondii*, n. gen. et sp., MUSM 1396 (holotype), skull in ventral (A, B), posterior (C), anterior (D), and right lateral (E, F) views. Diagonal solid lines indicate major breaks.

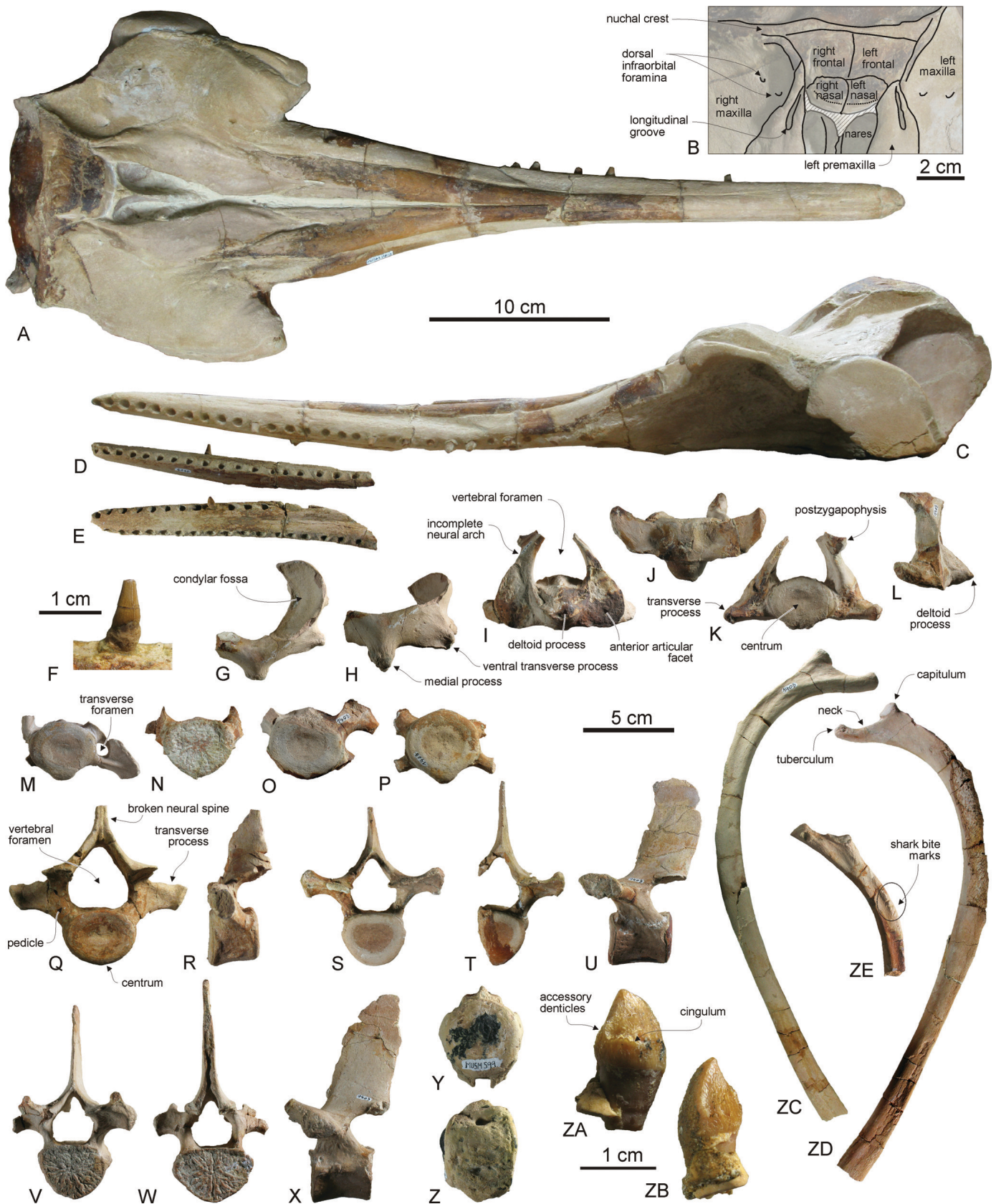


FIGURE 5. *Huaridelphis raimondii*, n. gen. et sp., MUSM 1403, skull in dorsal (A, B; detail of the vertex) and left lateral (C) views; symphyseal portion of mandible in left lateral (D) and dorsal (E) views; mandibular tooth in lateral view (F); incomplete atlas in anterior (G) and ventral (H) views; axis in anterior (I), ventral (J), posterior (K), and right lateral (L) views; four cervical vertebrae in anterior views (M–P); four thoracic vertebrae in posterior (Q, W), anterior (S, T, V), and right lateral (R, U, X) views; almost complete right rib in anterior (ZC) and posterior (ZD) views; proximal fragment of left rib in anterior view (ZE). *Huaridelphis raimondii* n. gen. et sp., MUSM 599, caudal vertebra in anterior (Y) and left lateral (Z) views; posterior tooth in lateral (ZA) and lingual (ZB) views. Diagonal solid lines indicate major breaks. Scale bars for F, ZA, and ZB equal 1 cm. Scale bars for G–Z and ZC–ZE equals 5 cm. Scale bars for A, C, D, and E equals 10 cm.

eurhinodelphinids and eoplatanistids), the lateral maxilla-premaxilla suture on the rostrum is not located in a deep lateral groove. The lateral margin of the rostrum at its base is thick and it increases steeply towards the antorbital notch, as seen in lateral view. This margin is moderately convex in dorsal view, similar to *Notocetus* and *Squalodelphis*. The posterior wall of the deep and 'V'-shaped antorbital notch (see below for a comment on the asymmetry of the notches) is made of the maxilla dorsally and the jugal ventrally. In platanistids, the notch is shallower, less clearly individualized, and often obscured by the maxillary/frontal crest. Just posteromedial to the antorbital notch, each maxilla is pierced by one or two small dorsal infraorbital foramina, followed anteriorly by a sulcus towards the antorbital notch. The antorbital region is elevated compared with the rostrum base, as in other squalodelphinids and platanistids, but more than in *Allodelphis*, *Squalodon*, and *Waipatia*. This thickening does not correspond to an individualized crest, differing from the high crest made of the maxilla and/or frontal in platanistids, even if a slight ridge marks the dorsolateral margin of each maxilla above the orbit, likely corresponding to the outer limit of a facial muscle. A series of deep oblique grooves marks the dorsal surface of the left antorbital process of the holotype (Fig. 3A). First thought to have been produced by a predator or scavenger, similar grooves were observed on the left process of USNM 526604, an undescribed platanistoid from the Calvert Formation, and might correspond to a genuine anatomical feature. The thin posterolateral part of the supraorbital process, roughly complete on the right side of MUSM 1403 (Fig. 5A), narrows posteriorly, leaving uncovered the posterior part of the temporal fossa. Linked to the conspicuous lateral shift of the vertex to the left side, the posterior part of the right maxilla is wider and less pointed backwards than on the left side, a feature also observed in *Notocetus* and *Squalodelphis*. One or two posterior dorsal infraorbital foramina are located at a short distance lateral to the posterior tip of the premaxilla, along the vertex (Fig. 5B). As in *Notocetus* and the platanistids, these foramina are more medial than the lateral-most margin of the premaxilla; this is not the case in *Allodelphis*, *Squalodon*, and *Zarhinocetus*. Due to the even wider premaxilla in this area, the posterior dorsal infraorbital foramen is just posterior to the maxilla-premaxilla suture in the platanistids *Platanista*, *Pomatodelphis*, *Prepomatodelphis*, and *Zarhachis*.

Including the three anterior alveoli that pierce the premaxilla, 28 and 29–30 alveoli for single-rooted teeth were counted on each upper tooth row for the holotype and MUSM 1403, respectively. This tooth count is higher than in *Notocetus* (22–23; Moreno, 1892; True, 1910) and *Squalodelphis* (15), but much smaller than in pomatodelphinines. The alveoli are small, with a diameter ranging from 3.7 mm for the smallest posterior alveoli to 5.5 mm for the largest anterior alveoli. This is smaller than in *Notocetus* and *Squalodelphis*. The spacing of the alveoli is wider posteriorly (6–7 mm), decreasing irregularly in more anterior alveoli (3–6 mm).

Mesethmoid—On the posterior wall of each bony naris, the mesethmoid is pierced by an elongated crescent-like fenestra starting at the dorsolateral corner of the wall, directed ventromedially then ventrolaterally (Fig. 4D). Such a pair of openings is commonly observed in platanistoids, for example, *Notocetus*, *Pomatodelphis*, *Squalodon*, and *Zarhachis* (see Kellogg, 1926; Dickson, 1964; Hoch, 2000), in *Waipatia* (Fordyce, 1994), and in one eurhinodelphinid, together with a possible ethmoturbinal (*Schizodelphis morckhoviensis* IRSNB M.343; Lambert, 2004). Hoch (2000) proposed an olfactory interpretation for this pair of cavities, which probably represent reduced olfactory openings. No olfactory fontanelles have been observed in any extant adult odontocete, including *Platanista*, and the reduction and subsequent loss of the olfactory system is thought to have occurred in parallel in different odontocete lineages (Geisler and Sanders, 2003; McGowen et al., 2008; Godfrey et al., 2013). The dorsal

margin of the mesethmoid roughly reaches the level of the antero-dorsal margin of the nasal.

Nasal—Each small nasal is shorter and narrower than the corresponding frontal on the moderately elevated vertex (more elevated than in *Allodelphis* and *Squalodon*). The right nasal is longitudinally shorter and transversely narrower than the left (Figs. 3C, 5B). The nasal-frontal suture is somewhat irregular, but with a general transverse direction, as in *Pomatodelphis* or *Waipatia*. In *Notocetus*, the suture is more anteromedially pointed, whereas it is posteromedially pointed in *Medocinia* (region not clear in *Squalodelphis*). The nasals are lower than the frontals; together, their flat dorsal surfaces form an anteroventrally inclined plane (slope best seen in lateral view), as in *Pomatodelphis* and the highly modified *Platanista*. In contrast, in *Notocetus*, the vertex is roughly horizontal; it seems to slope posterovertrally in *Squalodelphis*; and it is more dorsally convex in *Zarhachis*. As a whole, the vertex is shorter than in *Allodelphis*, *Squalodon*, and *Waipatia*, as in other squalodelphinids and platanistids.

Frontal—Because the vertex is strongly shifted to the left side, the suture between frontals is far left from the midline of the skull. In relation with this shift, the left frontal exhibits a longitudinally shorter and transversely wider exposure at the vertex than the right frontal, partly due to the anterior projection of the lateral portion of the nuchal crest. The vertex is similarly shifted to the left in at least *Platanista*, *Pomatodelphis*, *Notocetus*, and *Squalodelphis*; this feature is less pronounced in *Squalodon*, *Waipatia*, and *Zarhachis*. Nevertheless, the shorter and wider exposure of the left frontal at the vertex is only similarly observed in *Notocetus* and *Squalodelphis*.

The slightly anteroventrally projected antorbital process of the frontal is only moderately dorsoventrally thickened, less than in *Notocetus* and *Squalodelphis*; it is less anteroventrally developed than in *Medocinia* and the possibly related USNM 475596. The postorbital process is also less robust, corresponding to a proportionally larger orbit than in other squalodelphinids. The ventral surface of the orbit roof is hollowed by a large fossa, with an abrupt lateral border at about 20–25 mm from the lateral margin of the frontal, and occupying the whole length from the lacrimal to the postorbital crest (Fig. 4A, B). Also present in *Notocetus*, and possibly in *Zarhinocetus*, this deep fossa is interpreted as the support for an extension of the pterygoid sinus in the orbit region. In *Squalodelphis* and *Medocinia*, this part of the skull is covered with sediment; therefore, this character cannot be assessed. A similar fossa, likely homologous, is even deeper in *Pomatodelphis* (e.g., *P. bobengi* USNM 299695) and *Zarhachis* (e.g., *Z. flagellator* USNM 10911), seemingly connecting the ventral surface of the orbit roof with the crest in the antorbital-supraorbital region. This interpretation is supported by the morphology of the pterygoid sinus in the extant *Platanista*. Indeed, in the latter, Fraser and Purves (1960) propose a continuum between the pterygoid sinus cavity and the sinus in the maxillary crest, with bony channels connecting the two regions. The condition in squalodelphinids, with a moderately elevated antorbital region and a fossa in the orbit roof, might be considered as an intermediate grade towards the development of a large maxillary and/or frontal crest connected to a deeper sinus fossa in the orbit roof of platanistids. No such fossa has been detected in *Squalodon*, *Waipatia*, or other archaic odontocetes. The condition observed in squalodelphinids and platanistids, a single fossa in the frontal groove, is interpreted as not homologous to the fossae for the pre- and/or postorbital lobes of the pterygoid sinus on anterior and posterior flanks of the frontal groove of many delphinidans and some other odontocete taxa (e.g., several eurhinodelphinids; Lambert, 2005b), even if phocoenids display a somewhat similar extension of the preorbital lobe of the sinus into a space between maxilla and frontal (Fraser and Purves, 1960).

Supraoccipital—The anterodorsal margin of the supraoccipital is slightly posteriorly convex, with a short medial posterior projection. A similar projection is present in adult specimens of several extant delphinid species (external occipital crest sensu Fordyce and Mead, 2009). Just below the prominent nuchal crest, the supraoccipital shield is concave on a short height, before the two convex surfaces corresponding to the cerebral hemispheres. In dorsal view, the temporal crest is only posteriorly projected on a short distance, somewhat less than in *Pomatodelphis* and *Zarhachis*, and much less than in *Platanista*, the latter displaying a much narrower supraoccipital shield than other platanistoids.

Palatine—The extent of the palatine in the palate is interpreted as similar to what is observed in pomatodelphinines: limited exposure lateral to the lateral lamina of the pterygoid (see Muizon, 1987, for *Pomatodelphis*), with an anterior apex slightly anterior to the antorbital notch in the holotype of *Huaridelphis raimondii* (Fig. 4A, B). Previously thought to represent a synapomorphy of the platanistids (Muizon, 1987), the lateral exposure of the palatine seems to be a feature also present in *Medocinia* and *Notocetus* (Muizon, 1988b; pers. observ.; character not assessable in *Squalodelphis*). In *Platanista*, the palatine is completely covered by the pterygoid. The lateral lamina of the palatine borders the infraorbital foramen medially and reaches posteriorly to a level beyond two-thirds of orbit length, ventrally overhanging the deep fossa for the pterygoid sinus in the frontal groove.

Pterygoid—The pterygoid is long and narrow on the palate, with an apex 60 mm anterior to the antorbital notch; right and left apices are separated by a wedge of maxillae. As mentioned above, the pterygoid directly contacts the maxilla for most of its rostral portion. The pterygoid sinus fossa is similarly elongated, until a level more than 35 mm anterior to the antorbital notch. The fossa is also long in other squalodelphinids and platanistids; it is not anterior to the level of the antorbital notch in *Squalodon*, and it is even shorter in *Waipatia*. The lateral lamina is a continuous high plate posteriorly contacting the falciform process of the squamosal, as in all the other platanistoids, including *Notocetus* and *Squalodelphis*.

Jugal-Lacrimal—Only a thin and long oblique element along the anteromedial margin of the antorbital process is detected in the holotype, bearing a thin crest (Fig. 4A, B). It corresponds either to the jugal alone, or to jugal + lacrimal. The second interpretation would match the condition reported in *Waipatia* (see Fordyce, 1994:fig. 7). The jugal sends a narrow anteromedial projection along the medial wall of the antorbital notch.

Squamosal—In lateral view, the zygomatic process of the squamosal is strongly swollen. Its dorsal and posterior margins are highly convex, as in *Medocinia* and *Pomatodelphis*, but more so than in *Notocetus*. Compared with *Huaridelphis*, the subhorizontal part of the dorsal margin of the zygomatic process is considerably longer and the dorsal margin is dorsoventrally lower in *Platanista*, *Squalodon*, and *Waipatia*, whereas a more distinct posterodorsal angulation is present in *Prepomatodelphis* and *Zarhachis*. As in other squalodelphinids, platanistids, and some specimens of *Squalodon*, the anteroventral margin of the process is rectilinear to slightly convex (not taking account of the postglenoid process), due to a ventral bulge of the lateral surface, whereas it is clearly concave in *Allodelphis* and *Waipatia*. To quantify the robustness of the zygomatic process, we calculated a ratio between the maximum distance from the anteroventral margin of the zygomatic process to the posterodorsal margin, in lateral view, and the vertical distance from the lower margin of the occipital condyles to the vertex of the skull. This ratio is higher than 0.38 in all the measured squalodelphinids (including *Huaridelphis*) and platanistids (*Platanista*, *Pomatodelphis*, and *Zarhachis*), whereas it is lower or equal to 0.38 in other presumed platanistoids (*Allodelphis*, *Squalodon*, and *Waipatia*),

with the exception of *Zarhinocetus errabundus*. As in other squalodelphinids, platanistids, and *Squalodon*, the postglenoid process, only preserved in MUSM 599, is an anteroposteriorly flattened and short plate, anteroventrally pointed, and more slender in lateral view than in *Allodelphis*, eurhinodelphinids, *Simocetus*, and *Waipatia*. The mandibular fossa is vast, laterally closed by the ventrally bulging thin lateral wall of the zygomatic process. The tympanosquamosal recess is a shallow and narrow depression, short anteriorly along the falciform process and extending on the medial wall of the postglenoid process. The falciform process is a dorsoventrally high plate, widely contacting the lateral lamina of the pterygoid sinus.

Exoccipital—The occipital condyles are large and salient, with an individualized neck and a deep dorsal condyloid fossa. The ventral-most parts of the exoccipitals, including the paroccipital processes, are not preserved in any of the three known specimens of *Huaridelphis*.

Basioccipital—The ventral margins of the basioccipital crests, preserved in MUSM 599, are thick and moderately divergent posteriorly, with an angle between the crests of about 65 degrees.

Alisphenoid—The foramen ovale is widely separated by a bony bridge from the reduced posterior lacerate foramen, but the identity of the constituting bones cannot be established with certainty. On the ventral surface of the alisphenoid, the pterygoid sinus fossa is a slightly concave area anteromedial to the foramen ovale.

Periotic—The two known periotics (MUSM 1396: incomplete right periotic, total length as preserved = 33.7 mm; MUSM 599: nearly complete left periotic, total length as preserved = 35.4 mm) are similar in shape (Fig. 6). As for the skull, these periotics are smaller than in other squalodelphinids.

The periotic of *Huaridelphis* is similar to *Notocetus* and *Squalodelphis* in several characters: (1) anterior process elongated, not transversely thickened, moderately dorsally inflated, and only slightly bent anteromedially (less than in platanistids); (2) posterior process ventrally bent, bearing a narrow and smooth posterior bullar facet (incomplete in both periotics but probably originally elongated as in the other squalodelphinids) and a distinct articular rim; (3) pars cochlearis square-shaped in dorsal and ventral views; and (4) large, thin-edged dorsal opening of the cochlear aqueduct, which faces dorsally. A distinctive feature of the periotic of *Huaridelphis*, compared with *Notocetus* and *Squalodelphis*, is the dorsoventral compression of the pars cochlearis and of the body of the periotic; the compression of the latter is evidenced by a wide, flat dorsal surface lateral to the pars cochlearis (superior process sensu Kasuya, 1973). Moreover, the posterior process is more ventrally bent than in *Notocetus* and *Squalodelphis*, with its posterodorsal surface forming a straight angle with the dorsal surface of the body of the periotic. Among the other platanistoids, a similar right angle is observed in *Phocageneus*, *Platanista*, and *Zarhachis*.

As in the other squalodelphinids, the anterior bullar facet covers most of the length of the anterior process; it is transversely deeply concave, limited by prominent medial and lateral margins. Lateral to the anterior bullar facet, a well-developed anteroexternal sulcus is visible. On the medial surface of the anterior process is an irregular protuberance, possibly a small piece of bone fused to the periotic. A similar structure of unknown origin is observed in *Xenorophus* and in a squalodontid-like periotic by Luo and Marsh (1996:fig. 3E, F, tuberosity of anterior process), as well as in the other squalodelphinids, the squalodontids, and some eurhinodelphinids. The ventral margin of this protuberance is marked by a narrow groove, specially visible in MUSM 1396, likely corresponding to one of the 'anterointernal sulci' noted in *Waipatia* by Fordyce (1994). The fovea epitubaria is a longitudinally concave depression between the anterior bullar facet and the malleolar fossa. The latter is wide, circular, distinctly concave, anteromedially oriented, and bounded laterally by a

prominent lateral tuberosity, followed posteriorly by a deep hiatus epitympanicus. On the lateral margin of the posterior process is a prominent articular rim more developed than in *Notocetus*, less pointed than in *Squalodelphis*, and probably more reduced than the easily broken prominent hook-like articular process of platanistids (see Muizon, 1987).

As in *Notocetus* and *Squalodelphis*, the internal acoustic meatus is almost circular, deep, and tubular. An anterolateral notch in the outline of the meatus delimits the dorsal opening of the facial canal, which is located slightly anterolateral to the spiral cribriform tract. A similar location of the dorsal opening of the facial canal is observed in *Phocageneus* and *Squalodelphis*, whereas in *Notocetus* this foramen is less anterolaterally shifted and the internal acoustic meatus does not display a distinct notch. A narrower and longer notch is seen in *Squalodon* and *Waipatia*, both having a dorsal opening of the facial canal clearly more anteriorly located, whereas in *Platanista* and a Miocene platanistine from the Amazonian Basin (Bianucci et al., 2013) the dorsal opening of the facial canal is lateral to the spiral cribriform tract, with an oval internal acoustic meatus lacking an anterior notch. The foramen singulare is close to the opening of the facial canal, and both are separated from the spiral cribriform tract by a distinct transverse crest. As in the other squalodelphinids, the aperture for the cochlear aqueduct is wide and circular and it opens on the dorsal surface of the pars cochlearis, whereas the aperture for the endolymphatic duct is a small fissure. The fenestra rotunda is large and semicircular. The stapedial muscle fossa is deep, and its posterior opening is transversely wider than high.

Mandible

The symphyseal portion of the mandible is more than 168 mm long in MUSM 1403 (Fig. 3D, E), with the two dentaries nearly completely fused. The symphysis is similarly ankylosed in *Notocetus*, *Phocageneus*, and *Squalodelphis*. As for the rostrum, this part is dorsoventrally flattened, with a section wider than high for the whole preserved anterior 80 mm. Eighteen circular alveoli are counted on 161 mm of the right alveolar groove; their diameter ranges from 4 to 5 mm, with an irregular spacing (3–7 mm). The first right and left alveoli are anterolaterally directed and separated by 4 mm. Several mental foramina are present on each side, within a very shallow lateral groove.

Teeth

As in other squalodelphinids, allodelphinids, and platanistids, the teeth are conical and single-rooted, whereas the posterior teeth of *Squalodon*, *Waipatia*, and other archaic odontocetes remain double-rooted.

One detached tooth of MUSM 599 (Fig. 5ZA, ZB), presumably a right upper posterior, has a low crown (crown height 6.4 mm) roughly equal to its maximum mesiodistal diameter (6.35 mm). Its transverse section is buccolingually flattened with sharp mesial and distal keels. Both keels are slightly crenulated. The apex of the crown is pointed. An 'S'-shaped cingulum on the lingual side bears several accessory denticles. Additional denticles are observed above the line of the cingulum on the lingual surface. The surface of the enamel is rough, with an ornamentation made of partly anastomosed grooves. This crown is similar to crowns of posterior teeth of *Phocageneus venustus* USNM 21039 (Kellogg, 1957:pl. 3, figs. 5, 6, fourth and sixth lower teeth counting forward), an isolated tooth of aff. *P. venustus* (Whitmore and Kaltenbach, 2008:fig. 8), and posterior teeth of *Squalodelphis fabianii* (Dal Piaz, 1917:pl. 5, figs. 3–6). The cingulum is more developed than in the holotype of *P. venustus* (Kellogg, 1957:pl. 3, figs. 1–3). The crown is slightly lower than in one posterior tooth of *Notocetus vanbenedeni* (Muizon, 1987:fig. 1b, c). In *Notocetus*, one to three accessory denticles are observed on

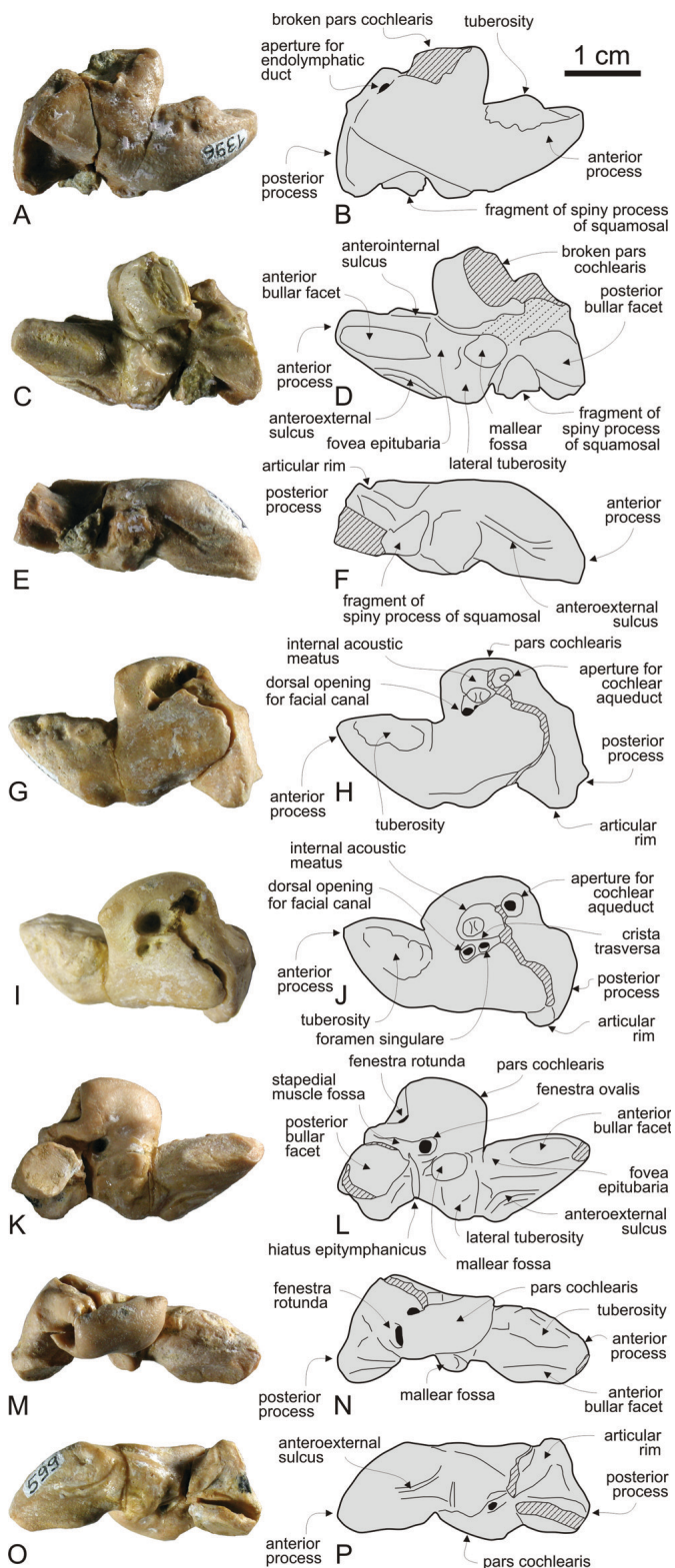


FIGURE 6. *Huaridelphis raimondii*, n. gen. et sp., MUSM 1396 (holotype), incomplete right periotic in dorsal (A, B), ventral (C, D), and lateral (E, F) views. *Huaridelphis raimondii*, n. gen. et sp., MUSM 599, left periotic in dorsal (G, H), dorsolateral (I, J), ventral (K, L), medial (M, N), and lateral (O, P) views. Diagonal solid lines indicate major breaks.

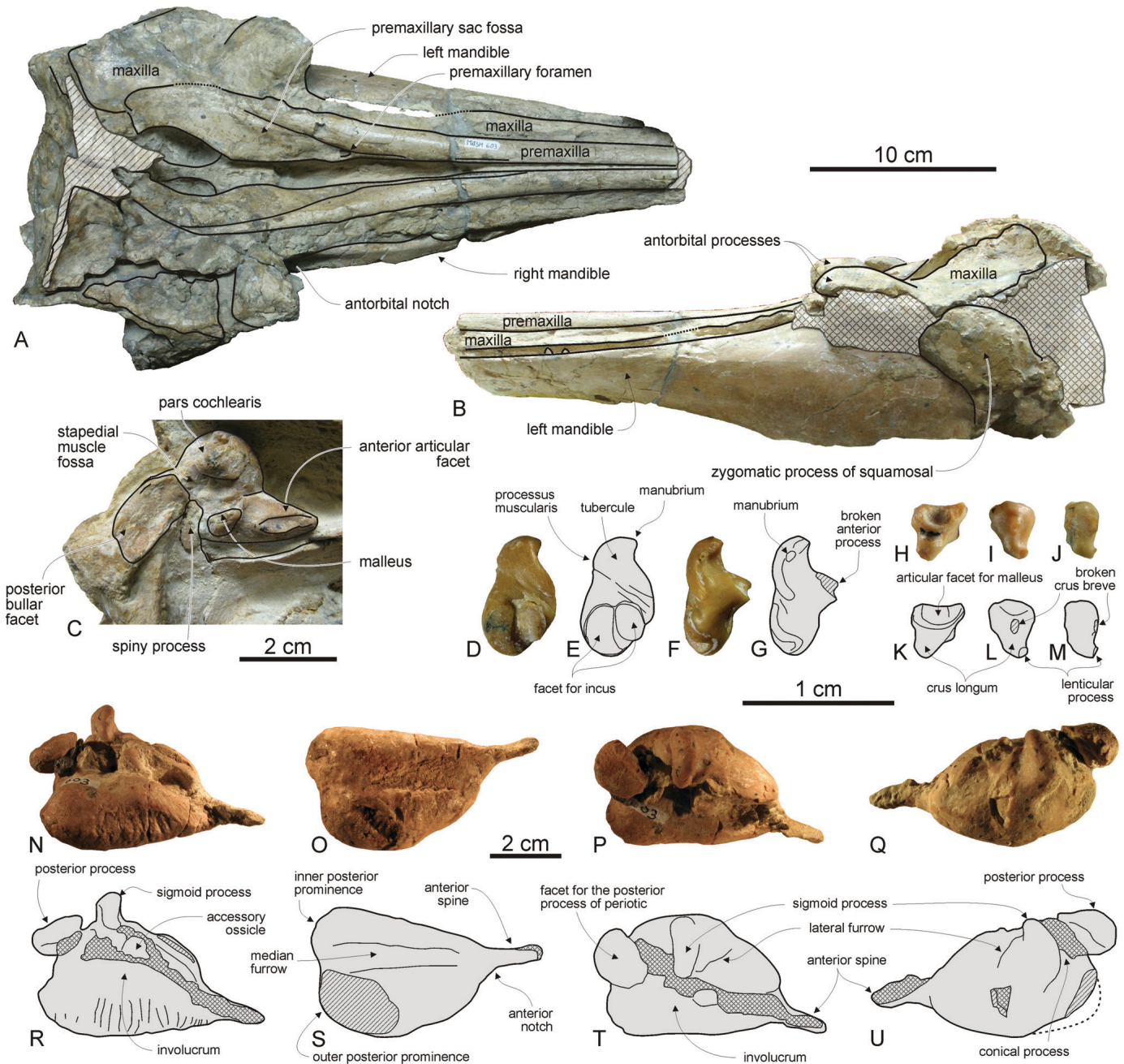


FIGURE 7. *Squalodelphinidae* aff. *Huaridelphis raimondii*, MUSM 603, incomplete skull in dorsal (A) and left lateral (B) views; left periotic articulated to the skull in ventral view (C); left malleus in posterior (D, E), and medial (F, G) views; left incus in medial (H, K), lateral (I, L), and dorsal (J, M) views; left tympanic bulla in medial (N, R), ventral (O, S), dorsal (P, T), and lateral (Q, U) views. Diagonal solid lines indicate major breaks. Scale bar for A and B equals 10 cm. Scale bars for C and N–U equal 2 cm. Scale bar for D–M equals 1 cm.

the distal keel, whereas these denticles seem to be lost in *Phocaenus*, *Squalodelphis* (Muizon, 1987), and *Huaridelphis*. Posterior teeth of platanistids, including *Platanista*, also have a low crown (Lambert et al., 2008b; pers. observ.), but the teeth are simpler and lack cingula, accessory denticles, and papillae.

A more anterior lower tooth of MUSM 1403 (Fig. 3F), the right ninth counting backward, displays a simple, elongated, moderately posteromedially curved, and conical crown with a less marked ornamentation made of more regular thin and low longitudinal grooves. The mesiodistal and buccolingual diameters of the crown base are respectively 3.7 and 3.35 mm. The

morphology of this tooth is also similar to more anterior teeth of *N. vanbenedeni* and *Squalodelphis fabianii* (Dal Piaz, 1917:pl. 5, figs. 8–11; Muizon, 1987:fig. 1a; pers. observ.), corroborating the retention of some degree of heterodonty, both in terms of proportions and development of ornamentation (grooves, accessory denticles, cingulum), in squalodelphinids.

Vertebrae

As in other platanistoids, atlas and axis are not fused and both are anteroposteriorly long (medial length of the ventral surface

of the atlas and axis respectively 31 and 37 mm). The degree of preservation of the ventral and dorsal transverse processes of the partly preserved atlas (Fig. 5G, H) does not allow an estimation of their length, even if the ventral process was probably shorter than in *Zarhachis*, possibly more similar to *Notocetus* (see True, 1910). The dorsal transverse process is thicker dorsoventrally than in *Zarhachis*, and dorsal and ventral processes are less divergent than in *Zarhachis*, closer to *Phocageneus*. The medial process projecting posteriorly from the posteroventral margin of the atlas is broad, as in *Notocetus*, *Phocageneus*, and *Zarhachis*.

In addition to the measurements presented in Table 2, the distance between the lateral margins of the anterior articular facets of the axis is 69.5 mm. The shape of the axis of MUSM 1403 (Fig. 5I–L) generally matches the axis of USNM 206006, an undescribed platanistid from the Calvert Formation showing affinities with *Zarhachis*. The transverse process is distinctly less ventrally projected in MUSM 1403, more similar, even if shorter, to the possible platanistid *Araodelphis* (see Kellogg, 1957) and *Platanista*. The centrum is less ventromedially pointed, more regularly oval in posterior view than in the platanistid USNM 206006. The neural spine is missing.

One of the other preserved cervicals (C; Fig. 5M) displays similarities with the third cervical of the *P. venustus* USNM 21039 (Kellogg, 1957:pl. 7, fig. 2). In MUSM 1403, with a maximum diameter of 8.5 mm, the transverse foramen for the vertebral canal is located at a lower level relative to the centrum than in *Phocageneus*, with a dorsoventrally thinner parapophysis. In *Platanista*, the transverse foramen is much smaller in the third cervical and laterally open in the next vertebrae. The centrum is more transversely flattened here than in *Phocageneus*. The three other cervicals preserved (D–F; Fig. 5N–P) are too fragmentary to allow a comparison. Only some measurements are provided in Table 2.

A series of four well-preserved thoracic vertebrae (A–D; Fig. 5Q–X) is close to the first thoracics of *P. venustus* USNM 21039. The anterior-most vertebra A (Fig. 5Q–R) is shorter than T1 in *P. venustus*. The centrum becomes more ventrally pointed in anterior/posterior view backwards, more than in T3 or T4 of *P. venustus*. The preserved neural spines of the two last vertebrae C and D (Fig. 5U–X) of this series tend to be slightly tilted posteriorly, more than in T3–T5 of *P. venustus* and closer to the thoracics of *Platanista*. The anterior thoracic vertebrae of *Notocetus* illustrated by True (1910) bear longer transverse processes.

With a centrum slightly higher than wide, the caudal vertebra of MUSM 599 (Fig. 5Y, Z) probably originates from the tail stock, just before the fluke (sensu Buchholtz and Schur, 2004). Pairs of ventral protuberances indicate the articulation of chevron bones.

More complete vertebral columns, both for *Huaridelphis* and other squalodelphinids, are needed for a detailed comparison.

Ribs

The preserved ribs are less transversely flattened than in *Platanista*. One nearly complete, double-headed, right rib (Fig. 5ZC, ZD), with a preserved maximum length of 260 mm, has a prominent tuberculum and a long neck; it does not differ significantly from two ribs of *Notocetus* (True, 1910:pl. 4, figs. 2, 4), also close, even if more slender, to the fourth to seventh ribs of *Zarhachis* (Kellogg, 1924:pl. 15, 16). Another proximal rib fragment (Fig. 5ZE), more robust with a nearly square section of the body, probably occupied a more posterior position in the rib cage.

SQUALODELPHINIDAE aff. *HUARIDELPHIS RAIMONDII* (Fig. 7)

Referred Specimen—MUSM 603, skull lacking the anterior portion of the rostrum, associated to a partial mandible. Both

periotics and the right tympanic are still attached to the skull, whereas the left tympanic bulla, malleus, and incus are detached. Found in the locality of Zamaca, Pisco-Ica Basin, along the Ica River, 8 km SSE from Ullujaya. Because a specimen of *Huaridelphis raimondii* (MUSM 599) was also found in this locality, we suspect that the locality of Zamaca corresponds to levels roughly temporally equivalent to the levels of Ullujaya, in the early Miocene of the Chilcatay Formation.

DESCRIPTION AND COMPARISON

With a cranium more heavily damaged than MUSM 1396 and MUSM 1403, this specimen (Fig. 7A, B) shares several similarities with *Huaridelphis raimondii*: the size and proportions of the cranium are roughly similar; the antorbital process is similarly elevated and weakly thickened; and the zygomatic process of the squamosal has the same outline in lateral view. However, the width of the rostrum, as well as the width of the premaxillae on the rostrum, decrease less abruptly anteriorly than in *Huaridelphis raimondii* (see Table 3). Furthermore, the lateral margin of the premaxilla is less distinctly convex in the proximal region of the rostrum, differing from all other squalodelphinids. The antorbital notch is also shallower, more widely open as in *Notocetus*.

The periotics are similar in size and shape to those of *Huaridelphis raimondii* MUSM 1396 and MUSM 1403 (Fig. 7C). The posterior process, complete in both periotics, exhibits a narrow and elongated posterior bullar facet, as in the other squalodelphinids. The left tympanic bulla, malleus, and incus deserve particular attention, because they are unknown in the specimens referred to *Huaridelphis raimondii*.

The tympanic bulla (Fig. 7N–U) is peculiar in its thin and extremely elongated anterior spine, representing 27% of the tympanic length (ca. 20% in *Squalodelphis fabianii* MGP 26134 and in the squalodelphinid USNM 21036; ca. 14% in *Notocetus vanbenedeni* AMNH 29026). Differing from the other squalodelphinids (especially *Phocageneus* and *Squalodelphis*), the median furrow does not extend anteriorly on the anterior spine, and, as in *Notocetus* and unlike *Phocageneus* and *Squalodelphis*, the lateral furrow is not deep. The outer posterior prominence is posteriorly shorter than the inner posterior prominence, whereas the outer and inner posterior prominences have approximately the same posterior extent in *Notocetus*, *Phocageneus*, and *Squalodelphis*. By contrast, in the platanistids *Platanista*, *Pomatodelphis*, and *Zarhachis*, the outer posterior prominence extends farther posteriorly than the inner posterior prominence. The dorsal margin of the involucrum is convex in medial view, but this margin is not as elevated as in *Pomatodelphis*.

The malleus (Fig. 7D–G) does not display the apical extension of the manubrium observed by Muizon (1987) in *Notocetus*, *Phocageneus*, and *Squalodelphis*. On the whole, the tuberculum is not pointed and elevated as in the other squalodelphinids, but hook-shaped as in *Pomatodelphis*, with an outline even more similar to *Squalodon* (see Muizon, 1991:fig. 14).

The incus (Fig. 7H–M) is similar to *Squalodelphis* in having a short and tapered crus longum and a relatively wide articular facet for the malleus. The broken base of the crus breve is located at about half the length of the crus longum. This is probably the plesiomorphic condition among odontocetes, differing from the condition observed, for example, in the physeteroids, with a crus breve located close to the lateral margin of the articular facet for the malleus.

Based on these limited observations, with both similarities and differences with *Huaridelphis raimondii*, and the fragmented state of the specimen, we propose to identify it as *Squalodelphinidae* indet., aff. *Huaridelphis raimondii*, pending the discovery of more complete specimens.

TABLE 2. Measurements (in mm) of vertebrae of *Huaridelphis raimondii*, n. gen. et sp., MUSM 1403 (cervicals and thoracics) and MUSM 599 (caudal).

Element	Centrum length	Maximum centrum height	Width of anterior epiphysis	Width of posterior epiphysis	Width of neural canal	Height of neural canal	Maximum width
MUSM 1403							
Axis	—	29.5	—	39	29	—	87
Cervical C	18	32	—	36.5	—	—	e80
Cervical D	+22.5	33	—	37	—	—	—
Cervical E	+20	+36	—	36	—	—	—
Cervical F	+17	35.5	—	33.5	—	—	—
Thoracic A	27.5	31	34	36	32.5	32.5	98
Thoracic B	+32	30.5	36	—	27	31.5	79
Thoracic C	36	+29	—	—	—	30	—
Thoracic D	+34	30	e36	e44	23.5	27	e69
MUSM 599							
Caudal	36	44	42	36.5	—	—	—

The vertebrae of MUSM 1403 are listed in an anteroposterior sequence reflecting the relative position of each vertebra, but intermediary vertebrae are missing (one cervical and an unknown number of thoracics). +, incomplete; —, missing data; e, estimate.

PHYLOGENY

The aim of the cladistic analysis was to investigate the phylogenetic relationships of *Huaridelphis raimondii*, n. gen., n. sp., and MUSM 603 (a specimen referred here to Squalodelphinidae aff. *Huaridelphis raimondii*) with the other Squalodelphinidae, as well as the relationships of the latter with Allodelphinidae and Platanistidae, the other Platanistoidea (sensu Fordyce, 1994; Muizon, 1987; Barnes, 2006) lacking double-rooted teeth. We think that a much broader taxon sample would be needed to elucidate relationships with other presumable platanistoids retaining double-rooted teeth. The considered Squalodelphinidae are, in addition to *Huaridelphis* and MUSM 603, four genera (*Medocinia*, *Notocetus*, *Phocageneus*, and *Squalodelphis*) and one indeterminate specimen (USNM 475596; see above for the discussion). Allodelphinidae includes *Allodelphis* and *Zarhinocetus*, following Barnes and Reynolds (2009). Platanistidae includes *Platanista*, *Pomatodelphis*, *Zarhachis*, and MUSM 1611 (an isolated periotic from the Amazonian Basin; see Bianucci et al., 2013). The genus *Prepomatodelphis*, also assigned to Platanistidae by Barnes (2002), was not included in the cladistic analysis because of the difficulty to code this more fragmentarily known taxon based on published data alone. Because previous studies proposed relationships between the eurhinodelphinid *Xiphiacetus* and part of the platanistoids (Geisler and Sanders, 2003; Geisler et al., 2011), we include in the analysis the eurhinodelphinids *Eurhinodelphis*, *Xiphiacetus*, and *Ziphiodelphis*.

Presumed platanistoids with double-rooted teeth *Squalodon* and *Waipatia* are also coded, whereas the basilosaurid *Zygorhiza* is used as outgroup. Thirty-seven morphological characters (Appendix 1), partly taken and modified from previous analyses (e.g., Muizon, 1987, 1988b, 1994; Fordyce, 1994; Lambert, 2005c; Bianucci et al., 2013), were coded for the 19 taxa (data matrix in Appendix 2). All characters are binary with the exception of five multistate characters (5, 16, 20, 22, 29). All characters are parsimony-informative in this analysis. The analysis was executed, considering all characters as non-additive (unordered) and unweighted, with the software PAUP (version 4.0b10; Swofford, 2001), using the heuristic search option, optimized by ACCTRAN using the tree bisection and reconnection (TBR) algorithm.

The cladistic analysis produced 60 equally parsimonious trees, with tree length = 55, consistency index (CI) = 0.76, and retention index (RI) = 0.90. The consensus tree, the 50% majority consensus tree, and the bootstrap values are presented in Figure 8 and discussed below.

The cladistic analysis supports the monophyly of the clade formed by Allodelphinidae + Platanistidae + Squalodelphinidae, representing members of the superfamily Platanistoidea without double-rooted teeth. The monophyly of this large clade is supported by a bootstrap value of 75 and by the following 11 synapomorphies: (1) rostral suture between premaxilla and maxilla deeply grooved (char. 3, state 1; reversal to state 0 in the Squalodelphinidae); (2) elevation of antorbital region, distinctly

TABLE 3. Comparison of rostral measurements (width of rostrum and premaxillae at different levels, in mm) in the squalodelphinids *Huaridelphis raimondii*, n. gen. et sp., MUSM 1396 and aff. *Huaridelphis raimondii* MUSM 603.

Dimension	<i>Huaridelphis raimondii</i> MUSM 1396		aff. <i>Huaridelphis raimondii</i> MUSM 603	
	Rostrum	Premaxillae	Rostrum	Premaxillae
Width at antorbital notches	92	55	91	62
Width anterior to notches				
30 mm	78	51	—	50
60 mm	61	38	—	40
90 mm	44	26	65	34
120 mm	33	20	55	28
150 mm	31	16	48	26
180 mm	27	15	41	23
210 mm	23	13	—	—
240 mm	20	13	—	—
270 mm	19	—	—	—
300 mm	19	—	—	—

—, missing data.

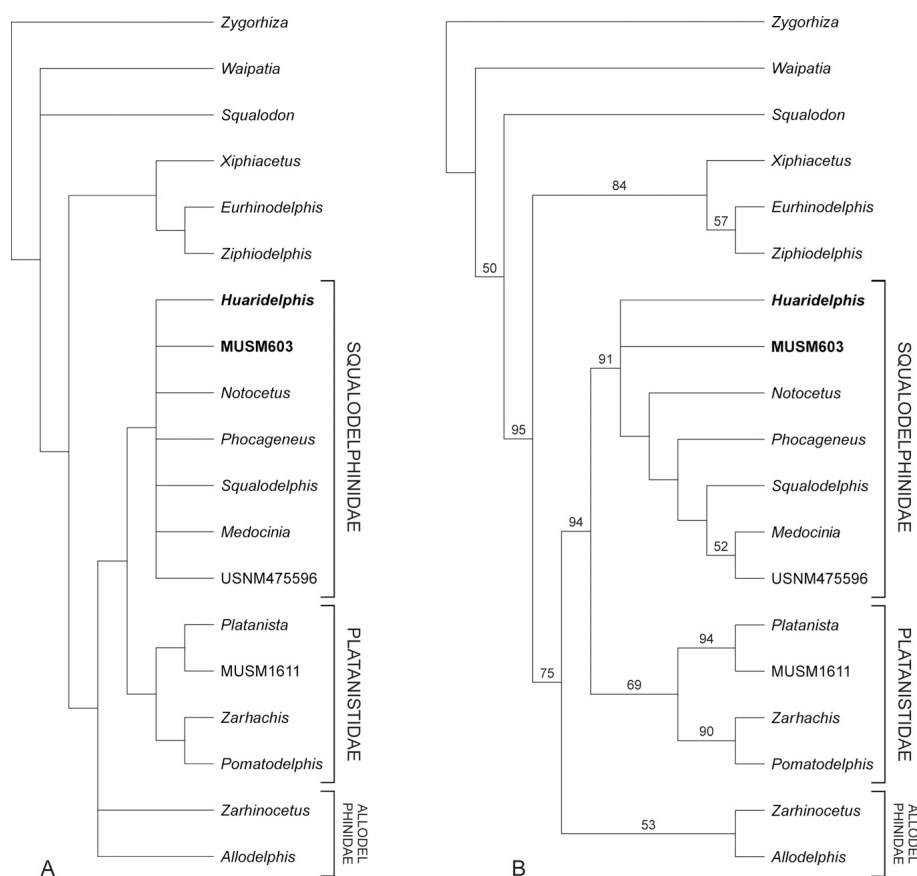


FIGURE 8. Consensus tree (A) and 50% majority consensus tree (B) of 60 equally parsimonious cladograms showing the relationships of *Huaridelphis raimondii*, n. gen. et sp., with the other Platanistoidea having lost double-rooted teeth. Tree length = 55, consistency index = 0.76, and retention index = 0.90. Numbers associated with the nodes in B are bootstrap values. See text for discussion and Appendices 1 and 2 for description of characters and data matrix.

higher than the dorsal margin of the rostrum base in lateral view (char. 8, state 1; absent in *Allodelphis*); (3) widening of the cranium (char. 11, state 1); (4) presence of a deep fossa in the orbit roof (char. 13, state 1); (5) vertex distinctly shifted to the left compared with the sagittal plane of the skull (char. 14, state 1); (6) reduction of the ventral exposure of the palatine (char. 16, states 1 and 2; absent in *Zarhinocetus*); (7) hamular fossa of the pterygoid sinus extended anteriorly on the palatal surface of the rostrum (char. 17, state 1); (8) presence of an articular rim on the lateral surface of the periotic (char. 20, states 1 and 2); (9) elongation of the anterior spine on the tympanic bulla, associated to a marked anterolateral convexity (char. 27, state 1); (10) loss of double-rooted posterior teeth (char. 32, state 1); and (11) tooth count greater than 25 (char. 34, state 1; reversal to state 0 in *Notocetus* and *Squalodelphis*).

This clade is sister group to the Eurhinodelphinidae, a result that partly confirms several previous analyses (Geisler and Sanders, 2003; Geisler et al., 2011, 2012). However, as mentioned above, a larger sample, including among others *Eoplatanista*, physeteroids, ziphiids, *Prosqualodon*, and other odontocetes with double-rooted teeth, is needed to test this relationship.

The Squalodelphinidae appear to be sister group to the Platanistidae, as suggested in several previous works (e.g., Muizon, 1987; Fordyce, 1994), with Allodelphinidae in a more stemward position. The clade Platanistidae + Squalodelphinidae has a bootstrap value of 94 and is diagnosed by the following three synapomorphies: (1) widening of the premaxillae at the rostrum base (char. 5, states 1 and 2); (2) posterior infraorbital foramen (ina) along the vertex more medial than the lateral-most margin of the premaxilla in the cranium (char. 12, state 1); and (3) thickening of the zygomatic process of the squamosal (char. 18, state 1).

The monophyly of Squalodelphinidae is supported by a bootstrap value of 91 and by the following five synapomorphies: (1) deeper, 'V'-shaped, left antorbital notch, related to an anteriorly pointed antorbital process (char. 7, state 1); (2) circle-shaped dorsal margin of the zygomatic process of the squamosal in lateral view (char. 19, state 1; reversal to state 0 in *Notocetus* and *Squalodelphis*); (3) square-shaped pars cochlearis of the periotic (char. 21, state 1); (4) large, thin-edged dorsal opening of the cochlear aqueduct of the periotic, which faces dorsally (char. 22, state 1); and (5) strong development of the dorsal transverse process of the atlas and extreme reduction of its ventral process (char. 35, state 1). Moreover, squalodelphinids seemingly lost the deep lateral groove along the rostral suture between premaxilla and maxilla (char. 2, state 1), observed in all other platanistoids lacking double-rooted teeth.

Relationships within squalodelphinids are unresolved, as evidenced by the consensus tree of all 60 cladograms (Fig. 8A) and by the bootstrap analysis. Nevertheless, the 50% majority consensus of the 60 trees (Fig. 8B) provides a tentative reconstruction of the relationships within the squalodelphinids, with *Huaridelphis* and MUSM 603 being the first to diverge, followed by *Notocetus* and by the clade formed by *Medocinia*, *Phocageneus*, *Squalodelphis*, and USNM 475596. Although *Huaridelphis* and MUSM 603 are the first diverging squalodelphinids, they are not conclusively sister groups. Consequently, their generic affinities as hypothesized in the systematic section are not strongly supported in the phylogenetic analysis. Analyzing the 60 equally parsimonious trees, the early divergence of *Huaridelphis* and MUSM 603 is supported in 52 trees (87%). Among these 52 trees, 20 (33% of the total) identify MUSM 603 as the earliest diverging taxon, 18 (30%) place *Huaridelphis* as sister group to MUSM 603, and 14 (23%) identify *Huaridelphis* as the earliest diverging taxon. In the remaining eight trees (13%), MUSM 603

is the earliest diverging taxon, with two possibilities for *Huaridelphis*: (1) a polytomy with *Phocageneus* and the clade containing all other squalodelphinids (8%), or (2) an intermediate position between the earlier divergence of *Phocageneus* and the clade containing all other squalodelphinids (5%). These last two topologies contradict the 50% majority consensus of the 60 trees, evidencing that further data (e.g., additional characters from more complete specimens of *Phocageneus*) should be added to improve the resolution of the phylogenetic analysis. A sister-group relationship between *Medocinia* and USNM 475996 is proposed in the 50% majority consensus of the 60 trees, as already suggested in the systematic section. However, it is weakly supported, with a bootstrap value of 52. With a bootstrap value of 94, the close relationships between *Platanista* and MUSM 1611, an isolated periotic from the Miocene of Peruvian Amazonia, confirms the preliminary phylogeny of Bianucci et al. (2013).

CONCLUSIONS

Based on three specimens, including two well-preserved skulls, from early Miocene localities of the Chilcatay Formation (Ullujaya and Zamaca), Pisco-Ica desert, southern coast of Peru, we describe a new genus and species of Squalodelphinidae, *Huaridelphis raimondii*. In addition to periotic characters, *H. raimondii* differs from other known squalodelphinids in, among others, its smaller size, the thin antorbital process of the frontal, the more abrupt tapering of the rostrum, and the higher tooth count. Another fragmentary skull from the Chilcatay Formation in Zamaca is referred to Squalodelphinidae aff. *Huaridelphis raimondii*. It brings additional information on the morphology of the tympanic, malleus, and incus, not yet known in *H. raimondii*. Our phylogenetic analysis of platanistoids with single-rooted teeth suggests that the family Squalodelphinidae is monophyletic; the analysis also confirms the sister-group relationship between the latter and Platanistidae. The relationships within Squalodelphinidae are not fully resolved, but *H. raimondii* might be one of the first diverging taxa of the family.

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APPENDIX 1. List of the characters used in phylogenetic analysis. Characters are polarized with respect to *Zygorhiza* as the outgroup.

- (1) Rostrum elongation (Bianucci et al., 2010, modified): short, ratio between rostrum length and condylobasal length <0.70 (0); elongated, ratio >0.70 (1).
- (2) Apex of the rostrum constituted by the only premaxillae on more than 10% of its total length and lacking alveoli (Lambert, 2005c): absent (0); present (1).
- (3) Lateral rostral suture between premaxilla and maxilla deeply grooved (Fordyce, 1994): no (0); yes (1).

- (4) Marked asymmetry of the premaxillae on the rostrum, at some distance anterior to the premaxillary foramina, with the right premaxilla distinctly narrower than the left in dorsal view: absent (0); present (1).
- (5) Widening of the premaxillae at the rostrum base: narrow premaxillae, ratio between the width of the rostrum and the transverse width of the premaxillae at the antorbital notch <0.60 (0); wide premaxillae, ratio between 0.60 and 0.75 (1); extremely wide premaxillae nearly reaching the lateral margin of the rostrum, ratio >0.75 (2).
- (6) Dorsal opening of the mesorostral groove anterior to the rostrum base (Geisler and Sanders, 2003, modified): narrower than the premaxilla (0); wider than the premaxilla (1).
- (7) Deep, 'V'-shaped, left antorbital notch, related to an anteriorly pointed antorbital process: no (0); yes (1).
- (8) Elevated antorbital region, distinctly higher than the dorsal margin of the rostrum base in lateral view: no (0); yes (1).
- (9) Distinct dorsal crest in the antorbital-supraorbital region: no (0); yes (1).
- (10) Thickening of the antorbital process of the frontal: absent, ratio between the height of the antorbital process of the frontal, measured in lateral view perpendicular to the maxillary-frontal suture above the orbit, and the vertical distance from the lower margin of the occipital condyles to the vertex of the skull <0.25 (0); present, ratio >0.30 (1).
- (11) Widening of the cranium: cranium roughly as long as wide or longer than wide with ratio between cranium length (longitudinal, from occipital condyles to level of antorbital notches) and postorbital width >0.90 (0); cranium distinctly shorter than wide with ratio <0.90 (1).
- (12) Posterior infraorbital foramen(ina) along the vertex more medial than the lateral-most margin of the premaxilla in the cranium: no (0); yes (1).
- (13) Deep fossa in the frontal on orbit roof, at the level of the frontal groove: no (0); yes (1).
- (14) Vertex distinctly shifted to the left compared with the sagittal plane of the skull: no (0); yes (1).
- (15) Transverse premaxillary crest on the vertex (Lambert, 2005c): absent (0); present (1).
- (16) Ventral exposure of the palatine (Muizon, 1987, modified): palatine widely exposed anterior to the pterygoid (0); palatine only exposed laterally to the lateral lamina of the pterygoid (1); palatine completely covered by the pterygoid (2).
- (17) Hamular fossa of the pterygoid sinus (Lambert et al., 2013): small, not reaching anteriorly the level of the antorbital notch (0); wide, extending anteriorly on the palatal surface of the rostrum (1).
- (18) Thickening of the zygomatic process of the squamosal: absent, ratio between the maximum distance from the anteroventral margin of the zygomatic process to the postero-dorsal margin, in lateral view, and the vertical distance from the lower margin of the occipital condyles to the vertex of the skull <0.35 (0); present, ratio >0.35 (1).
- (19) Circle-shaped dorsal outline of the zygomatic process of the squamosal in lateral view: no (0); yes (1).
- (20) Articular rim on the lateral surface of the periotic (Muizon, 1987, modified): absent (0); present (1); present and hook-like (2).
- (21) Pars cochlearis of the periotic square-shaped in ventral view (Muizon, 1987): no (0); yes (1).
- (22) Aperture of the cochlear aqueduct of the periotic (Muizon, 1987, modified; Bianucci et al., 2013): small (0); very small (1); large and thin-edged (2).
- (23) Aperture of the cochlear aqueduct of the periotic (Muizon, 1987, modified): faces mediadorsally (0); faces dorsally (1).
- (24) Transverse thickening of the anterior process of the periotic (Muizon, 1987): no (0); yes (1).
- (25) Internal auditory meatus of the periotic oval, with the dorsal opening for the facial canal lateral to the spiral cribriform tract (Bianucci et al., 2013): no (0); yes (1).
- (26) Separate ossicle at the apex of the anterior process of the periotic (Bianucci et al., 2013): no (0); yes (1).
- (27) Elongated anterior spine on the tympanic bulla, associated to a marked anterolateral convexity (Muizon, 1987): no (0); yes (1).
- (28) Ventral groove of the tympanic affecting the whole length of the bone, including the anterior spine (Muizon, 1987): no (0); yes (1).
- (29) Extent of the inner and outer posterior prominences of the tympanic: both prominences with approximately the same posterior extent (0); outer posterior prominence posteriorly longer than the inner posterior prominence (1); outer posterior prominence posteriorly shorter than the inner posterior prominence (2).
- (30) Dorsal margin of the involucrum of the tympanic cut by a median indentation, in medial view (Lambert, 2005c): absent (0); present (1).
- (31) Apical extension of the manubrium of the malleus (Muizon, 1987): no (0); yes (1).
- (32) Loss of double-rooted posterior teeth: (Muizon, 1987): no (0); yes (1).
- (33) Retention of accessory denticles on posterior teeth (Muizon, 1987, modified): yes (0); no (1).
- (34) Tooth count per upper or lower row: <25 (0); >25 (1).
- (35) Strong development of the dorsal transverse process of the atlas and extreme reduction of its ventral process (Muizon, 1987): no (0); yes (1).
- (36) Great reduction of coracoid process of the scapula (Muizon, 1987, 1991, 1994): no (0); yes (1).
- (37) Great reduction or loss of supraspinatus fossa, with acromion located on anterior edge of scapula (Muizon, 1987, 1991, 1994): no (0); yes (1).

APPENDIX 2. Data matrix of 37 characters for one outgroup (*Zygorhiza*), 13 platanistoids with single-rooted posterior teeth (*Allodelphinidae*, *Platanistidae*, and *Squalodelphinidae*), and other possibly related odontocetes (*Squalodon*, *Waipatia*, and the eurhinodelphinids *Eurhinodelphis*, *Xiphiacetus*, and *Ziphiodelphis*). All characters are treated as unordered; 0, primitive state; 1, 2, derived states; a, variable between 0 and 1; ?, missing character.

	5	10	15	20	25	30	35	37
<i>Huaridelphis</i>	00011	01100	11110	11111	12100	0????	?1011	??
MUSM 603	? ?011	01100	1??10	?1111	1??0?	01020	01???	??
<i>Notocetus</i>	00011	01100	11110	11111	12100	01100	11001	11
<i>Squalodelphis</i>	00012	11100	1?110	?1101	12100	01100	1100?	??
<i>Medocinia</i>	??012	11101	1?110	1110?	?????	?????	?1???	??
USNM 475596	??0??	?1101	11110	?110?	?????	?????	?10??	??
<i>Phocageneus</i>	? ????	?????	?????	?????	12100	01100	110?1	??
<i>Platanista</i>	00111	00110	11110	21102	01001	11010	01110	11
MUSM 1611	?????	?????	?????	?????	01001	1????	?????	??
<i>Zarhinocetus</i>	10111	00111	11110	11102	00010	01010	01110	??
<i>Pomatodelphis</i>	10111	00111	11110	11102	00010	01010	01110	??
<i>Zarhinocetus</i>	10100	10100	10?10	0100?	00000	0????	?1?1?	??
<i>Allodelphis</i>	10100	10000	10?10	1100?	?????	?????	?1?1?	??
<i>Eurhinodelphis</i>	11101	00000	10001	00000	00000	00011	01?10	??
<i>Xiphiacetus</i>	11101	001a0	10000	000a0	00000	00011	?1010	??
<i>Ziphiodelphis</i>	11101	00100	10001	00000	00000	00011	01010	00
<i>Waipatia</i>	00001	00000	00000	00000	00000	00000	00000	??
<i>Squalodon</i>	10000	00000	00000	00000	00000	00000	00000	??
<i>Zygorhiza</i>	00000	00000	00000	00000	00000	00000	00000	00