New Middle Eocene Whales from the Pisco Basin of Peru

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NEW MIDDLE EOCENE WHALES FROM THE PISCO BASIN OF PERU

MARK D. UHEN, NICHOLAS D. PYENSON, THOMAS J. DEVRIES, MARIO URBINA, AND PAUL R. RENNE

INTRODUCTION

The transition from semi- to fully aquatic cetaceans occurred during the Eocene (55–34 Ma). Fossils documenting this transition represent a range of early whales (archaeocetes), including both semi-aquatic and fully aquatic forms that have to date, been found almost entirely in the Northern Hemisphere (Gingerich et al., 2001; Thewissen et al., 2001; Uhen, 2004; Uhen and Gingerich, 2001; but for examples of southern hemisphere archaeocetes see Köhler & Fordyce, 1997; de Muizon, 2009). Protocetids are the most crownward group of semi-aquatic archaeocetes. Recent discoveries from Indo-Pakistan confirm that protocetids locomoted both on land and in the water (Gingerich et al., 2001) but retained the ancestral ability to give birth on land (Gingerich et al., 2009). Also, protocetid material from the southeastern United States shows that the most crownward protocetids lacked tail flukes and thus did not swim like later diverging, fully aquatic cetaceans such as the Basilosauridae and modern whales (which, together, form the clade Pelagigeti [Uhen, 2008b]).

The most crownward clade of archaeocetes, Basilosauridae, has been reported on all continents (Uhen and Pyenson, 2007 and references therein; see Relative Age below). In contrast, protocetids and other more basal archaeocetes have only been found in Indo-Pakistan (e.g., Bajpai and Thewissen, 1998; Gingerich et al., 2005), northern and western Africa (e.g., Andrews, 1920; Bianucci et al., 2003; Gingerich, 1992; Gingerich, 2010), the southeastern United States (e.g., Geisler et al., 2005; Hulbert et al., 1998; McLeod and Barnes, 2008; Uhen, 1999; Uhen, 2008b), and recently Europe (e.g., Uhen and Berndt, 2008) (Fig. 1). The dispersal of protocetids to North America from the Old World previously indicated that semi-aquatic archaeocetes (those basal to Pelagigeti) were swimmers capable of crossing ocean basins either by following the coastlines or by direct dispersal across the open ocean (Uhen, 1999); but to date, none have been described from the Southern Hemisphere.

Three new specimens of middle Eocene cetaceans from the Paracas Formation, Pisco Basin of Peru are described here and confirm the presence of protocetids and early basilosaurids in the Southern Hemisphere. The Pisco Basin, and in particular the Miocene-Pliocene Pisco Formation, has produced a wealth of fossil marine vertebrates including penguins (e.g., Göhlich, 2007), pinnipeds (e.g., de Muizon, 1981), marine sloths (e.g., de Muizon and McDonald, 1995), and cetaceans (e.g., de Muizon, 1984). The Cenozoic marine deposits in the Pisco Basin extend down from the Pisco Formation and include the Chilcatay Formation (late Oligocene!early Miocene! [DeVries, 2007]), the Otuma Formation (late Eocene, discussed herein), and the Paracas Formation (middle Eocene, discussed herein).

Some of these new specimens display a mosaic of characters previously found only in protocetids, or only in basilosaurids, a finding that highlights the increasing need to revise the systematics of these early cetacean groups. Also, the antiquity of these specimens (constrained to the middle Eocene) has implications for resolving the geographic pattern of early cetacean evolution. Lastly, the discovery of protocetids in South America demonstrates that early cetaceans dispersed not only across the Atlantic but also dispersed into both hemispheres prior to the evolution of a fully aquatic lifestyle.

INSTITUTIONAL ABBREVIATIONS—MUSM, Departamento de Paleontología de Vertebrados, Museo de Historia Natural de San Marcos, Lima, Peru; BMNH, Department of Earth and Planetary Science, University of California, Berkeley, Berkeley, CA 94720-4767, USA; and Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, CA 94709, USA.

STRATIGRAPHY

A stratigraphic section was measured from the top of the Paleozoic basement rock through the base of the Otuma Formation, which included a series of ash beds. Using a Jacob’s staff and a Brunton compass as a clinometer, a total of 145 m of section was measured, beginning at the contact of the Paracas Formation with the Paleozoic granitic basement along the exposures located to the west of Rio Ica, approximately 50 km south of Ica, Peru. Bed thicknesses were measured and lithostratigraphic observations were recorded along with paleontological observations moving up section in a northerly direction. The collection locations of all vertebrate specimens collected were marked with GPS coordinates and the specimens were deposited in the Departamento de Paleontología de...
Vertebrados, Museo de Historia Natural de San Marcos, where they are currently housed.

Geologic setting.—The Pisco Basin is a forearc basin on the west coast of South America, extending along the southwestern coast of Peru and into the northern part of Chile (Fig. 2). During the Cenozoic, widespread block faulting in this region resulted in the preservation of broad expanses of both Paleogene and Neogene sedimentary rocks in the basin (DeVries, 1998). Vegetation cover in this arid basin is restricted almost exclusively to river drainages, which improves visibility of exposed rock outcrop on the ground and from satellite imagery.

Marine vertebrates from the Paleogene sequences of the Pisco Basin are poorly known, although these sequences contain sediments from depositional environments that are good candidates for preserving cetaceans and other marine vertebrates. The Paleogene units of the Pisco Basin are, from oldest to youngest, the Paracas Formation, the Otuma Formation, and the Chilcatay Formation (DeVries et al., 2006; Fig. 2). Some previous interpretations of the deposits stratigraphically below the Chilcatay Formation have included from three (Dunbar et al., 1990) to four formations (DeVries, 2007), from oldest to youngest: Caballas, Los Choros, Yumaque, and Otuma, Formations. Dunbar et al. (1990) includes what DeVries (2007) identifies as the Otuma Formation within his Yumaque Formation, and the Los Choros and Yumaque Formations in the Paracas Group.

The base of the Paleogene deposits near the protocetid localities overlies lower Paleozoic granitic and granodioritic basement (Montoya et al., 1994). We follow DeVries et al. (2006) and identify a separate Otuma Formation. We also attribute all sediments between the basement and the Otuma Formation as the Paracas Formation based on their original description as a single formation and the similarity in lithology throughout this portion of the measured section. The Paracas Formation is composed of ~120 m of coarse sandstones and siltstones (Dunbar et al., 1990; NDP personal observation), interbedded with dolomitized siltstones that are interspersed in section. All of the new Peruvian archaeocetes described herein originate from localities (AV-15, AV-17, AV-19) that are situated between 45–50 m in the section above the basement (Fig. 2).

In the region with the archaeocetes localities, the Otuma Formation directly overlies the Paracas Formation and the contact between the Paracas and Otuma formations is marked by a regionally extensive angular unconformity, which can be identified by a thin lag of iron-manganese nodules and numerous boulders of granite. This unconformity is burrowed and marked by an accumulation of shark teeth and sea urchin spines. The base of the Otuma Formation consists of yellow-orange, coarse sandstone containing mollusk fossils (DeVries,
The remainder of the formation consists of tuffaceous, fine sandstone with siliceous and calcareous microfossils, thin-shelled pectinid bivalves, fish scales, and vertebrate remains (DeVries et al., 2006), including cetaceans, penguins (Clarke et al., 2007), and sea turtles.

Radioisotopic dating.—At locality AV-18, an ash sample was collected at the base of the Otuma Formation, just above the contact between the Otuma Formation and the top of the Paracas Formation. The ash sample (AV18-NDP), a vitric-crystal rhyolite tuff, was disaggregated and sieved into size fractions. Sanidine was concentrated from the 180–250 micron fraction using standard techniques employing Na-polytungstate heavy liquids and a Frantz Isodynamic separator. The concentrate was viewed under clove oil (refractive index 1.535) to verify purity, which was estimated as >99%. The sample was irradiated for 10.0 hrs (BGC irradiation #354PR) in the cadmium-lined CLICIT facility of the Oregon State University TRIGA reactor, along with the Fish Canyon sanidine (FCs) standard in an adjacent well of an Al disc similar to those used by Renne et al. (1998). Individual analyses of 10 single grains of FCs yielded a J value of 0.0026277 ± 0.000015 (1 standard error of the mean) based on the age of 28.02 Ma for FCs (Renne et al., 1998).

Approximately 20 mg of AV18-NDP sanidine was analyzed by incremental heating in 29 steps with a CO2 laser beam, broadened with an integrator lens. Heating was achieved by maintaining constant laser power for 60 s per step. The resulting gas was purified by 180 s of gettering time for each step. Relative abundances of Ar isotopes from each heating step were determined by peak-hopping (10 cycles of magnetic field switching) with an MAP 215-50 sector mass spectrometry using a Balzers electron multiplier detector in analog mode. Relative abundances were obtained by regression of peak-height versus time data to an initial equilibration time using linear or parabolic fits chosen to minimize residuals. Mass discrimination was monitored by 35 air pipettes bracketing the sample and standards, yielding a mean value of 1.03955 ± 0.00149 per atomic mass unit based on a power law correction. Backgrounds were measured between every three heating steps or fusions (standards), yielding values comparable to those reported by Renne et al. (1998). Average values and their standard deviations were used to make the background corrections.

Isotope data (Supplemental Table 1, online archive available at www.journalofpaleontology.org) corrected for backgrounds, mass discrimination and radioactive decay were also corrected for interfering reactions on K and Ca (Renne et al., 2005) and Cl (Renne et al., 2008). Ages in Supplemental Table 1 are calculated relative to the 40K decay constants (Steiger and Jäger, 1977) and the standard calibration of Renne et al. (1998). The plateau age of 36.61 ± 0.03 Ma (1 σ uncertainty) was determined by computing the inverse variance weighted mean of (39Ar/40Ar) for all plateau steps (in this case, all steps), and applying the age equation (and error propagation) to the resulting value (Supplemental Fig. 1, online archive). The plateau age uncertainty as stated above does not include contributions from decay constants or the age of the standard. A more recent calibration of the 40Ar/39Ar system (Renne et al., 2010) yields an age of 36.98 ± 0.04 Ma that includes systematic errors associated with the decay constants and age of the standard. This latter age is thought to represent the most accurate estimate for the age of the dated ash, but for comparison with existing time scales the value of 36.61 Ma is probably more relevant as existing Cenozoic time scales are dominated by 40Ar/39Ar dates that have not yet been recalibrated.
T1 to T11 and L1 to L11 are partially preserved in the specimen. Epiphyseal fusion state indicates that the specimen was fully mature.

**Description.**—The badly weathered neurocranium of MUSM 1443 demonstrates that it had nuchal and sagittal crests, but the distal margins of these crests are not preserved (Fig. 3). The left occipital condyle is preserved, but the right one is missing. Ventrally, a portion of the right periotic is preserved, but it is badly eroded and fragmented, which prevents detailed description. Virtually all of the basicranial features are missing. The skull is missing anterior to the anterior termination of the sagittal crest.

Much of the first cervical vertebra (C1, atlas) is preserved, however, the dorsal arch of the vertebra and much of the transverse processes are missing. Thus, the vertebrarterial canals are not preserved in C1. Many of the additional intermediate cervical vertebrae (C3, C4, or C5) are also preserved, along with an incomplete vertebral body of a fragmentary posterior cervical vertebra (C7?). The intermediate cervical vertebrae (e.g., C4) present strong hemal processes on the ventral margin. Vertebrarterial canals perforate the flat transverse processes on these vertebrae.

The thoracic and lumbar vertebrae of MUSM 1443 were found in articulation, although they were offset by minor faulting (Fig. 4). The neural spines and transverse processes of the trunk vertebrae in the holotype are anteroposteriorly elongate. The trunk vertebrae increase in size from anterior to posterior, but the posterior lumbar vertebrae are similar in size to one another. Eleven of the trunk vertebrae have been identified as thoracic and another eleven have been identified as lumbar, although this lumbar count is almost certainly incomplete, and the identity of the anteriormost lumbar is questionable (i.e., it may represent a 12th thoracic vertebra) because the transverse processes are incomplete. These thoracic and lumbar (trunk) vertebrae are very similar to those of *Eocetus* in shape and bone texture, but those of MUSM 1443 are considerably smaller in size (Fig. 5). The trunk vertebrae are also somewhat elongate, like those of *Eocetus* (Uhen, 2001) and exhibit anteroposteriorly long neural spines and transverse processes, unlike those of *Basilosaurus*. No skeletal material posterior to the lumbar vertebrae is known for this specimen.

**Occurrence.**—MUSM 1443 was collected from field locality number AV 15, Ica Department, Peru (14.668050°S, 75.35483°W), PaleoDB collection 73780. Paracas Formation, middle Eocene, Bartonian. For details of stratigraphic occurrence, see geochronologic constraints and geologic age below.

**Discussion.**—MUSM 1443 shares a low number of thoracic vertebrae with other contemporaneous protocetids (11 or 12 in MUSM 1443, 12 in *Eocetus* Fraas 1904 [Uhen, 2001], 13 in *Maiacetus* [Gingerich et al., 2009], 13 in *Georgiacetus* Hulbert...
et al. 1998 [Hulbert, 1998], 13 in Rodhocetus Gingerich et al. 2001 [Gingerich et al., 2001]) compared to a much higher number in basilosaurids (17 in Dorudon Gibbes 1845 [Uhen, 2004], at least 15 in Zygorhiza True 1908 [Kellogg, 1936], 17 in Basilosaurus Harlan 1834 [Gingerich et al., 1990]). The trunk vertebrae of MUSM 1443 are moderately elongate, and have a pock-marked texture like that in Eocetus (Uhen, 1999; Uhen, 2001); no protocetids other than Eocetus exhibit this suite of vertebral conditions (Fig. 4). MUSM 1443 and Eocetus share anteroposteriorly elongate neural arches, spines and transverse processes as well as moderately elongate lumbar vertebral bodies. In contrast, Basilosaurus has greatly elongated vertebral bodies lacking anteroposteriorly elongate neural arches, spines and transverse processes. These character states suggest
that MUSM 1443 and Eocetus are closely related but MUSM 1443 differs from Eocetus spp. in possessing trunk vertebrae that are about 35% smaller in linear dimensions (Fig. 5, see also Table 1).

Table 1—Ventral lengths of the vertebrae of MUSM 1443 with measurements in centimeters (cm). Other measurements were difficult or impossible to take because the vertebrae are mostly still articulated. Thoracic vertebrae are listed in order, but there may be some missing from the series.

<table>
<thead>
<tr>
<th>Vertebra</th>
<th>Ventral length</th>
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<tbody>
<tr>
<td>C1</td>
<td>29.5</td>
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<tr>
<td>C2</td>
<td>—</td>
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<tr>
<td>C3</td>
<td>—</td>
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<tr>
<td>C4</td>
<td>23.8</td>
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<tr>
<td>C5</td>
<td>—</td>
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<tr>
<td>C6</td>
<td>—</td>
</tr>
<tr>
<td>C7</td>
<td>34.0</td>
</tr>
<tr>
<td>T1</td>
<td>30.9</td>
</tr>
<tr>
<td>T2</td>
<td>38.9</td>
</tr>
<tr>
<td>T3</td>
<td>41.3</td>
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<tr>
<td>T4</td>
<td>—</td>
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<tr>
<td>T5</td>
<td>40.8</td>
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<tr>
<td>T6</td>
<td>51</td>
</tr>
<tr>
<td>T7</td>
<td>74.1</td>
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<tr>
<td>T8</td>
<td>61.5</td>
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<tr>
<td>T9</td>
<td>78.6</td>
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<tr>
<td>T10</td>
<td>80.3</td>
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<td>T11</td>
<td>87.2</td>
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<tr>
<td>L1</td>
<td>84.9</td>
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<tr>
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<td>99.5</td>
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<tr>
<td>L10</td>
<td>106.9</td>
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<tr>
<td>L11</td>
<td>—</td>
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</tbody>
</table>

Family BASIOSAURIDAE Cope, 1868
Subfamily DORUDONTINAE Miller, 1923
SUPAYACETUS new genus

Type species.—Supayacetus muizoni n. sp.
Diagnosis.—As for the species.
Etymology.—After Supay, the Incan god of death and lord of the underworld and ketos, Greek for whale.

SUPAYACETUS MUIZONI new species
Figures 5, 6

Diagnosis.—Supayacetus is distinguished from all other fossil cetaceans by the unique combination of the following characters: manubrium of the sternum T-shaped with a rod-shaped mesosternal element; cheek teeth bearing two posterior accessory denticles; scapula broadly fan-shaped with a large infraspinous fossa; humerus has a large, hemispherical head, well-defined greater and lesser tuberosities, a long deltopectoral crest, and an anteroposteriorly broad shaft; larger than Protocetus Fraas 1904, based on the size of the preserved cranium, with a much more square bulla in ventral view; and comparatively small size of its skull and vertebrae, compared with other known basilosaurids (Figs. 6, 7).

Description.—The skull of the type specimen of Supayacetus was mostly destroyed by weathering. The left tympanic bulla is well preserved (Fig. 6), and it is quadrate in outline with a sharp horizontal keel. In ventral view, the median furrow divides the bulla into lateral and medial portions, but only extends about one third the length of the bulla. The eustachian outlet of the bulla is much less prominent than in Carolina cetus Geisler et al. 2005, and the involucrum is more similar in shape to that of Georgiacetus (Hulbert et al., 1998). The horizontal keel of the bulla is visible on the posterior surface of the involucrum, continues along the entire medial side, and around the anterior end of the bulla. The base of a large...
Figure 6—MUSM 1465, material belonging to *Supayacetus muizoni*, n. gen. n. sp. (holotype). 1, isolated incisor tooth; isolated cheek tooth in: 2, medial; 3, lateral views; right dentary in: 4, dorsal (arrow denotes the posterior extent of the mandibular symphysis); 5, right lateral views; left tympanic bulla in tympanic bulla in: 6, ventral; 7, dorsal; 8, medial; 9, posterior views. Abbreviations: et=eustachian outlet; inv=involucrum; ml=medial lobe of tympanic bulla; ll=lateral lobe of tympanic bulla; alveoli are identified by the corresponding tooth that they held.
FIGURE 7—MUSM 1465, postcranial material belonging to *Supayacetus muizoni*, n. gen. n. sp. (holotype). 1, left scapular blade in lateral view; 2, glenoid process of scapula in lateral view; 3, glenoid process of scapula in distal view; 4, incomplete left distal humerus in lateral view; 5, humeral head in lateral view; 6, proximal phalanx in dorsal view; 7, manubrium in ventral view; 8, manubrium in dorsal view. Abbreviations: ac=acromion process; cp=coracoid process; dpc=deltopectoral crest of the humerus; gc=glenoid cavity; h=humeral head; sh=humeral shaft.
sigmoid process is partially preserved on the lateral side of the bulla. The posterior process of the bulla is not preserved.

The stylohyal is slender and arched, with a slight broadening into a shallow cup-shaped articular surface on the proximal end. The distal end of the stylohyal is missing. Portions of the left and right dentaries are also preserved. The right dentary is preserved from I1 to P2 (Fig. 6), while the left dentary is preserved from I1 to P1. The medial surface of both dentaries shows that the mandibular symphysis was unfused and terminates posteriorly just anterior to P2. The mandibles are also very thin and gracile, broadening dorsally around the alveoli for the teeth. The alveoli demonstrate that I1–P1 were single rooted, while P2 was double rooted.

The known dentition for *Supayacetus* is represented by a single incisor and a single cheek tooth (Fig. 6). The preserved incisor bears heavy apical wear, while much of the anteromedial portion of the cheek tooth is worn away, including any anterior cusps (Fig. 6). The identity of the cheek tooth cannot be determined precisely. It may represent a premolar or an upper molar (the latter being more likely), but it is definitely not a lower molar. This tooth bears two roots, and two accessory denticles: the anterior one is much larger, and the posterior much smaller as well as being connected with the cingulum. These denticles are much larger than those seen in either *Georgiacetus* (Hulbert et al., 1998) and much more prominent than those described in remingtonocetids (Thewissen and Bajpai, 2001).

Two cervical vertebral bodies preserved for the holotype of *Supayacetus* most likely represent C6 and C7. Ten additional vertebrae are represented mostly by thoracic vertebral bodies, based on the processes that remain attached to the isolated vertebral bodies. Many fragments of ribs were preserved, along with the manubrium of the sternum and another sternal element.

*Supayacetus* has a T-shaped manubrium of the sternum (Fig. 6) as well as a rod-shaped mesosternal element. The manubrium is similar to those of *Rodhocetus* (personal observation; Gingerich et al., 1994), *Eocetus* (Uhen, 2001) and *Georgiacetus* (personal observation), in contrast to the thick and broad sternal elements of the Basilosauridae (Kellogg, 1936; Uhen, 2004), indicating a retention of this protocetid characteristic. The mesosternal element is more similar to those of *Rodhocetus*, but differs from those of *Eocetus* which are more broad and flat (Uhen, 2001).

Portions of the forelimb are also preserved in the type specimen of *Supayacetus muizoni* (Fig. 7). The scapula of MUSM 1465 is broad and fan-shaped like basilosaurusids and *Eocetus* with a shallow glenoid cavity that is broadly oval in outline. Not enough of the scapular blade is preserved to determine the relative sizes of the scapular fossae, but the overall shape indicates the presence of a large infraspinous fossa. The glenoid is broadly oval in outline and shallow. The humeral head is hemispherical in shape, like that of *Dorudon, Zygorhiza*, and *Basilosaurus*. The greater tubercle is lower than the head and similar in relative size to that of *Dorudon*. The shaft of the humerus is broad and flattened with a large deltopectoral crest near the distal end, again similar to that of *Dorudon, Zygorhiza*, and *Basilosaurus*. The distal articular surface of the humerus bears a common articular surface for the radius and ulna, with no division into a capitulum and trochlea. Several metacarpals and omniocelal bones are also present.

*Etymology.*—The specific epithet honors Christian de Muizon for his extensive contributions to understanding the fossil marine mammals of Peru.

Type.—MUSM 1465, consisting of a partial skeleton, including teeth, a partial vertebral column, ribs, forelimb elements and the manubrium of the sternum.

*Occurrence.*—The holotype was collected from field locality number AV-17, Ica Department, Peru (14.666783°S, 75.65150°W), PaleoDB collection 90021. Paracas Formation, middle Eocene, Bartonian. For details of stratigraphic occurrence, see geochronologic constraints and geologic age below.

*Discussion.*—*Supayacetus muizoni* is considered a member of the Basilosauridae presence of large accessory denticles on the cheek teeth, a condition found only in basilosaurusids among archaeocetes. *Supayacetus* is further considered to be a member of the Dorudontinae based on its small size and lack of elongation in any of the known vertebral bodies.

**Ocucajea** new genus

*Type species.*—*Ocucajea picklingi* n. sp.

*Diagnosis.*—As for the species.

*Etymology.*—After the town of Ocucaje, in the Department of Ica, Peru, near where the type specimen was found.

**Ocucajea picklingi** new species

Figures 8, 9

*Diagnosis.*—*Ocucajea* can be distinguished from all other dorudontines based on its small size and the configuration of bones at the cranial vertex (Fig. 9). In *Ocucajea*, the nasals and maxillae extend about the same distance posteriorly, whereas in *Saghacetus* and *Dorudon*, the nasals extend farther posteriorly than the maxillae. *Ocucajea* lacks a narial process of the frontal, a feature present in *Saghacetus*.

*Description.*—Much of the dorsal surface of the skull of MUSM 1442 is preserved but the ventral side of the skull is mostly destroyed, including all of the features of the basicranium, and the left occipital condyle (Fig. 9). The rostrum anterior to the external nare is also missing but the nasals are complete. The dorsal surface of the skull shows that *Ocucajea* had relatively long and straight nasals. Because the ventral surface of the rostrum is badly damaged, it is not clear where the anterior nasals terminate relative to the tooth row. The skull lacks a strong projection of the frontal between the posterior ends of the nasals. The nasals do not taper anteriorly. The anterior margins of the nasals form an oblique angle dorsal to the external nares.

The palate is neither particularly broad as in *Takracetus*, nor particularly narrow as in *Gaviacetus* Gingerich et al. 1995. The shape of the rostrum and frontal shield in dorsal view is similar to that of *Dorudon* and *Zygorhiza* but not narrow like *Arcticetus* (Gingerich et al., 2001). The orbit is large and round in lateral view and is proportionally similar in size to those of other basilosaurusids. The premaxilla abuts the nasal and terminates about halfway along the anterioposterior length of the nasal. The maxilla bounds the nasal more posteriorly, reaching the posterior limit of the nasal.

The lower right M1–M3 are preserved, as well as portions of upper right M1–M2. The roots of the left upper P3–M2 are also preserved (Fig. 8). Of the two roots on P4, the posterior root is lingually expanded. The presence or absence of M3 cannot be determined for certain. The lower molars all have two roots, with primary cusps and at least two accessory denticles. They also bear re-entrant grooves on the anterior face of the crowns.

*Etymology.*—Honors José Luis Pickling Zolezzi, naturalist, artist and valued contributor to paleontology in Peru.

*Type.*—MUSM 1442, a partial skull and partial skeleton, including skull, jaws and fragmentary teeth.
Ocucajea picklingi is here interpreted and is shown in an unresolved clade with Eocetus and MUSM 1443, and Uvigerina Bolivina nez-...supplementary material
8
Dorudon Ocucajea Supayacetus
2
is of particular interest with Supayacetus

whether the type specimen lacks an upper third molar. molars are present in the type specimen, but it is not clear
saurid archaeocete based on the presence of well-developed
cheek tooth roots, P1–M3, left lower molars M1–M3 and left upper molars, M1–M2.

Occurrence.—The holotype was collected from field
locality number AV-19, Ica Department, Peru (14.66830°S,
75.63505°W), PaleoDB collection 90022. Paracas
formation, middle Eocene, Bartonian. For details of stratigraphic
occurrence, see geochronologic constraints and geologic age below.

Discussion.—Ocucajea picklingi represents a small basilosaur
archaeocete based on the presence of well-developed
accessory denticles on the distal surface of the lower molars, a
synapomorphy of Basilosauridae (Fig. 8). At least two upper
molars are present in the type specimen, but it is not clear
whether the type specimen lacks an upper third molar. Ocucajea
is placed in the subfamily Dorudontinae because it lacks the vertebral elongation seen in members of the
subfamily Basilosaurinae.

ENVIRONMENT AND AGE

Depositional environment.—Previous paleontological work
in the Pisco Basin of Peru has mainly focused on Neogene
sediments, with the exception of a recent report on cetaceans
from the Paracas Peninsula (de Muizon, 2009; Martínez-
Cáceres and de Muizon, in press) and Eocene age penguins
(Clarke et al., 2007; Ksepka and Clarke, 2010). Based on
previous studies and our own fieldwork in this area, we
conclude that the Paracas Formation preserves a nearshore
and inner shelf setting (Dunbar et al., 1990) and represents a
cool water depositional environment. The evidence for this
interpretation derives from several lines of evidence. First,
lithostratigraphic observations, such as the lack of cross-
beds and ripple marks, indicate an inner shelf depositional
environment below wave base for the Paracas Formation.
Second, foraminifera (e.g., Bolivina, Uvigerina, and Nonion),
and nannofossils (e.g., Coccolithus pelagicus) (DeVries et al.,
2006; Dunbar et al., 1990) from the Paracas Formation
represent cool water species. Third, beds yielding the fossil
cetaceans reported herein (at localities AV-15, AV-17, and
AV-19) have also produced abundant anchoveta and sardine
(Clupeoides) scales. Because the presence of clupeoid scales
consistently correlates with relatively cool water environments
in the Quaternary record of the Humboldt Current off the
Peruvian coast (DeVries and Pearcy, 1982), their presence in
the Paracas Formation suggests a similar environment in the
Eocene of the same region.

Geochronologic constraints and geologic age.—Previously,
DeVries et al. (2006) reported 40Ar/39Ar dates from three beds
near the base of the Otuma Formation as 37.2, 36.5, and
35.7 Ma, citing L. Snee (personal commun.). These dates are
largely consistent with the age that we obtained, although the
oldest date at 37.2 Ma places it at the Bartonian/Priabonian
boundary according to the Gradstein et al. (2004) geologic
time scale (Luterbacher et al., 2004).

Previously, the range of Turritella lagunillasensis was stated
as middle to late Eocene (DeVries, 2007) but this species is
actually restricted to the Paracas Formation, and it is not
found in the overlying Otuma Formation. In the stratigraphic
nomenclature adopted here, microfossil evidence from Dun-
bar et al. (1990) with new additional microfossil reported by
DeVries et al. (2006) restricts the Paracas Formation to the
middle Eocene, with the hiatus between the deposition of the
top of the Paracas Formation and the deposition of the base of
the overlying Otuma Formation dating to around 37 Ma
(DeVries et al., 2006).

Thus, both the microfossil and radioisotopic age dates
support a middle Eocene (Bartonian) age for the Paracas
Formation, and a late Eocene (Priabonian) age for the Otuma
Formation. These age assignments are consistent with the
presence of more basal protocetids in the middle Eocene
deposits, and the lack of protocetids in the late Eocene
deposits (MDU personal observation), as no protocetids are
known globally later than the middle Eocene (Uhen, 2005a).

Results of phylogenetic analysis.—The initial cladistic anal-
ysis resulted in 90 equally most parsimonious trees of length
342. A strict consensus of those trees (Fig. 10) shows a
relatively resolved tree with four polytomies. Clades that are
clearly represented in the tree include: Cetacea, Remington-
ocetidae, a clade including Eocetus and MUSM 1443, and
Basilosauridae. The addition of the stratigraphic character
offered no additional resolution among the 90 equally most
parsimonious morphological trees. In all results, the family
Protocetidae is paraphyletic.

Supayacetus is shown in an unresolved clade with Basilo-
saurus, Dorudon and Ocucajea. Supayacetus is here interpreted
as a basilosaurid because of the shared presence of large
accessory denticles on the cheek teeth of Supayacetus and
other basilosaurids. Supayacetus is of particular interest with
respect to the derivation of basilosaurids because it retains
some less derived characteristics such as the thin, T-shaped
sternum, which it shares with protocetids such as Rodhocetus,
Eocetus, and Georgiacetus. We posit that the position of
Supayacetus will become better resolved when more material of this genus is available for study.

Ocucajea is classified as a dorudontine basilosaurid based, in part, on the accessory denticles on the molar teeth. The uncertainty in the phylogenetic relationships among the new Peruvian taxa, relative to other archaeocetes, underscores the need for substantial revisions in the taxonomy and systematics of Protocetidae and Basilosauridae. Protocetidae is universally accepted as paraphyletic (Geisler et al., 2005; Spaulding et al., 2009; Uhen, 2008b), giving rise to Basilosauridae, and Basilosauridae is also considered paraphyletic, giving rise to Neoceti (Uhen, 2008c). Future work will hopefully provide a stronger phylogenetic framework that will be necessary for any rigorous tests of morphological and biogeographic patterns in the evolution of early cetaceans.

**DISCUSSION**

*Paleoenvironmental setting.*—Previous interpretations of the archaeocete fossil record indicated that cetaceans originated in Indo-Pakistan, dispersed throughout the western Northern Hemisphere during the middle Eocene, and then later spread globally during the late Eocene (Uhen, 2008b). The range of depositional environments reflected in this record includes relatively warm tropical, subtropical, to temperate waters. New Peruvian fossils of middle Eocene archaeocetes reported here refine these generalizations about the geographic and environmental settings of early cetacean evolution. Based on microfossil evidence, the Paracas Formation was deposited in an area of relatively cool water (DeVries et al., 2006). The known faunal associations in the Paracas Formation support the notion that the nearshore environment represented by the Paracas Formation was a comparatively cold water zone, as it is today along the coast of Peru (DeVries and Pearcy, 1982). A study from New Zealand found sea surface temperatures of 23–25°C and bottom water temperatures of 11–13°C during the middle Eocene, along with no indication of Antarctic ice (Burgess et al., 2008). Also, Tripati and Zachos (2002) calculated sea surface temperatures of 26°C in Panama during the late Eocene. No detailed geochemical analysis has yet been performed on middle or late Eocene sediments from Peru, and thus no precise value for temperature of the water can be determined. Further geochemical study is needed to determine the exact sea surface temperature in this area of Peru during the middle Eocene.

The presence of archaeocetes in these deposits also confirms that archaeocetes were fully capable of dealing with the full range of thermal environments in middle Eocene oceans (Marino et al., 2008). Given relatively small brain size of archaeocetes (Marino et al., 2004), our findings also provide further evidence that the evolution of large brains in crown cetaceans was not linked to invasion of cold water habitats (contra Manger, 2006).

*Origin of Pelagoceti.*—Although many Bartonian (middle Eocene) sites have yielded basilosaurids, only two other geologic formations of this age, besides the Paracas Formation, have produced both protocetids and basilosaurids together: the Castle Hayne Formation (North Carolina, U.S.A.) and the Domanda Formation (Pakistan). The Castle Hayne Formation ranges from the middle to late Eocene. No localities within the Castle Hayne Formation have produced both protocetids and basilosaurids from the same stratigraphic level (MDU, personal observation). Thus, the reported Castle Hayne protocetid occurrences (i.e., *Eocetus wardii*) (Beatty and Geisler, 2010; Uhen, 1999; Uhen, 2001) are probably from lower in the formation (Bartonian [Geisler, 2010]) than the stratigraphic occurrence of basilosaurids (Bartonian to Priabonian, [Uhen, 2005b]). Basilosaurids from the Domanda Formation (*Basilosaurus drazindai*, *Basilotherium hussaini*) (Gingerich et al., 1997) are known only from vertebrae (a single and pair of lumbar vertebrae, respectively) and these vertebrae are similar in many respects to those of *Eocetus*, suggesting that they too might represent *Eocetus*-like protocetids rather than basilosaurids (Uhen, 2008a). The association of protocetids and basilosaurids in...
one formation, although unusual in the Eocene record, is not wholly unexpected because it is likely that these two groups shared overlapping marine resources and potentially the same prey items, even if their locomotory modes and feeding strategies differed.

Relative age.—Several Southern Hemisphere fossil localities have previously produced archaeocetes prior to the occurrences reported herein (Table 2), including: the Otuma Formation of Peru (Fordyce and de Muizon, 2001; Marocco and de Muizon, 1988; de Muizon, 2009); the La Meseta Formation of Seymour Island, Antarctica (Fostowicz-Frelik, 2003); the Gambier Limestone of Australia (Fitzgerald, 2004); and several localities in New Zealand (Köhler and Fordyce, 1997).

The Priabonian Otuma Formation of Peru has produced both a large species similar to *Cynthiacetus* from the Northern Hemisphere (de Muizon, 2009; Martínez-Cáceres and de Muizon, in press), as well as a smaller species similar to *Dorudon* or *Zygorhiza* (Uhen et al., 2008). Other additional species of basilosaurids may also be present. Specimens of archaeocetes have been noted from Antarctica by several authors (e.g., Borsuk-Bialynicka, 1988; Fordyce, 1989; Fostowicz-Frelik, 2003; Tambussi et al., 2006; Wiman, 1905), but it is not clear from the published figures and descriptions that these specimens can be differentiated from basal Neoceti, such as the basal mysticete *Llanocetus denticrenatus*. Thus, until these specimens can be confidently assigned to new or currently known species of archaeocetes, or at least confidently assigned to a family of archaeocetes, these Antarctic archaeocetes previously identified as *Zeuglodon* (Wiman, 1905), *Zygorhiza* (Tambussi et al., 2006), and *Dorudontinae* indet. (Borsuk-Bialynicka, 1988) should best be identified as Cetacea indet. The only currently published archaeocete specimen from Australia is “*Squalodon* gambierensis”, from the late Oligocene, which is currently thought to be a late-occurring basilosaurid (Fitzgerald, 2004; Fordyce, 2002).

All of these Southern Hemisphere localities are late Eocene in age or younger (Fordyce and de Muizon, 2001), except Waimate, New Zealand. This locality produced a specimen identified as *Zygorhiza* sp. from the late Bortonian Waihao Greensand of New Zealand (Köhler and Fordyce, 1997) a unit that has been considered middle rather than late Eocene. When the latter specimen was reported, the late Bortonian New Zealand stage was correlated to the early Bartonian of the North Atlantic Ocean (Köhler and Fordyce, 1997), but now the Bortonian New Zealand stage correlates with the late Lutetian (43 Ma) through the Bartonian, with the end of the Bortonian and Bartonian coincident at 37 Ma (Gradstein et al., 2004; Köhler and Fordyce, 1997). Thus, the late Bortonian of New Zealand is now approximately correlated to the international late Bartonian age, which is still considered to be middle Eocene, but is certainly younger than 40 Ma (Morgans et al., 2004). Thus, the Waimate specimen from New Zealand and the Paracas Formation specimens from Peru are approximately the same age, at least as far as the relative ages of the deposits can be resolved.

**Paleobiogeography.**—The presence of archaeocetes in the middle Eocene of Peru and New Zealand indicates that archaeocetes spread into the Pacific during the middle Eocene. Although hind limb material of the Peruvian protocetids has not yet been recovered, no known protocetids have been
interpreted as fully aquatic, tail-propelled swimmers (Uhen, 2008b). This latter constraint, in conjunction with the austral occurrence of these new fossils, suggests that archaeocetes crossed into the Southern Hemisphere, and perhaps became globally distributed before they evolved their modern mode of locomotion.

Three alternative dispersal routes to South America are possible for Peruvian archaeocetes. First, they could have come from the southeastern United States. During the Eocene, there was open water separating North and South America prior to the emergence of the isthmus of Panama much later in the Neogene (Coates et al., 1992). In the Eocene, there was also a long isthmus extending north from South America, including the Greater Antilles in a landmass known as GAARlandia (Iturralde-Vincent and MacPhee, 1999). This would have provided a nearshore dispersal route from the southeastern United States, across the Gulf of Mexico to northern South America, much of which was covered by a shallow seaway at the time. Second, archaeocetes could have arrived in northern South America directly from North or West Africa after crossing the Atlantic Ocean. A similar dispersal route has been hypothesized to explain the occurrences of archaeocetes in the southeastern United States (Uhen, 1999). Third, archaeocetes could have arrived in Peru from across the Pacific Ocean. This dispersal route would have required crossing of the Indian Ocean to Australia or New Zealand followed by the crossing of the open Pacific Ocean. This final dispersal route seems the most unlikely of the three because of the two long transoceanic crossings that may have been beyond the capabilities of protocetids in the middle Eocene. In addition, no protocetid fossils have yet been found in southern Africa, Southeast Asia, or Oceania.

SUMMARY AND CONCLUSIONS

The discovery of middle Eocene protocetids and basilosaurids in Peru as well as the presence of middle and late Eocene basilosaurids in New Zealand underscore the need for more research on fossil cetaceans from the Southern Hemisphere. The phylogenetic analysis presented here, along with the stratigraphic and geographic occurrence of the most crownward protocetids suggests that the transition from semi-aquatic to fully aquatic cetaceans took place in the Southern Hemisphere. A fuller understanding of this transition and the origin of the Pelagoceti will require more and better fossils from these locales, including additional cranial, axial, and appendicular elements, along with additional exploration in southern and eastern Africa, Southeast Asia, and Oceania.

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Table 2—Southern Hemisphere occurrences of Eocene cetaceans. All fossil cetaceans of Eocene age are listed along with their corresponding ages and geographic locality information. Collection numbers refer to Paleobiology Database (PBDB) collection numbers. Full information on each collection is available at <http://pbdb.org>. Protocetids from equatorial Africa (Togo) (Gingerich et al., 1992) are middle Eocene, but the site was north of the paleoequator during the middle Eocene.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Geographic locality</th>
<th>Formation</th>
<th>Taxa</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>63838</td>
<td>Paracas peninsula, Peru</td>
<td>Otuma</td>
<td><em>Cynthiaecetus peruvianus</em></td>
<td>Priabonian</td>
</tr>
<tr>
<td>73779</td>
<td>AV-10, Archaeocete Valley, Peru</td>
<td>Otuma</td>
<td>Basilsauridae indet.</td>
<td>Priabonian</td>
</tr>
<tr>
<td>73780</td>
<td>AV-15, Archaeocete Valley, Peru</td>
<td>Paracas</td>
<td>MUSM 1443</td>
<td>Bartonian</td>
</tr>
<tr>
<td>90022</td>
<td>AV-19, Archaeocete Valley, Peru</td>
<td>Paracas</td>
<td><em>Ocucajea picklingi</em></td>
<td>Bartonian</td>
</tr>
<tr>
<td>90021</td>
<td>AV-17, Archaeocete Valley, Peru</td>
<td>Paracas</td>
<td><em>Supayacetus muizoni</em></td>
<td>Bartonian</td>
</tr>
<tr>
<td>45723</td>
<td>Seymour Island, Antarctica</td>
<td>La Meseta</td>
<td><em>Llanocetus dentirenuatus</em></td>
<td>Priabonian</td>
</tr>
<tr>
<td>100190</td>
<td>Seymour Island, ZPAL 3, Antarctica</td>
<td>La Meseta</td>
<td>Cetacea indet.</td>
<td>Priabonian</td>
</tr>
<tr>
<td>100290</td>
<td>Seymour Island, DVP 10/84, Antarctica</td>
<td>La Meseta</td>
<td>Cetacea indet.</td>
<td>Priabonian</td>
</tr>
<tr>
<td>32900</td>
<td>Waimate, New Zealand</td>
<td>Waiaho Greensand</td>
<td>'Zygoryza sp.'</td>
<td>Bartonian</td>
</tr>
<tr>
<td>45041</td>
<td>McCulloch's Bridge, New Zealand</td>
<td>Waiaho Greensand</td>
<td>Dorudontinae indet.</td>
<td>Priabonian</td>
</tr>
<tr>
<td>74594</td>
<td>Burnside, New Zealand</td>
<td>Burnside Marl</td>
<td>archaeocete indet.</td>
<td>Priabonian</td>
</tr>
<tr>
<td>79346</td>
<td>Opuha River, New Zealand</td>
<td>?</td>
<td>archaeocete indet.</td>
<td>Priabonian</td>
</tr>
</tbody>
</table>


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