New Middle Eocene Whales from the Pisco Basin of Peru

NEW MIDDLE EOCENE WHALES FROM THE PISCO BASIN OF PERU

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ABSTRACT—Three new specimens of middle Eocene cetaceans are reported from the Pisco Basin of southern Peru. All three specimens originate from the Paracas Formation and their minimum age is constrained to about 37 Ma using $^{40}Ar/^{39}Ar$ dating of ash collected ~100 m up section from the source localities. Two new genera of archaeocete cetaceans are described along with additional material of another distinctive protocetid, which is not named pending the discovery of more complete material. Phylogenetic analysis resolves the two new genera within Basilosauridae, while the unnamed protocetid is closely related to *Eocetus*. The discovery of crownward protocetids in South America demonstrates that early cetaceans may have dispersed into both hemispheres prior to evolving a fully aquatic lifestyle. Geochronologic constraints on the age of new Peruvian archaeocetes establish them as the oldest whales from South America and among the oldest known from the Southern Hemisphere, which highlights the need for better sampling of marginal marine rocks from this part of the world.

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 Pelagiceti [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 Pelagiceti) 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 collections, Lima, Peru; NCMS, North Carolina Museum of Natural Science, Raleigh, N.C., U.S.A.; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

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
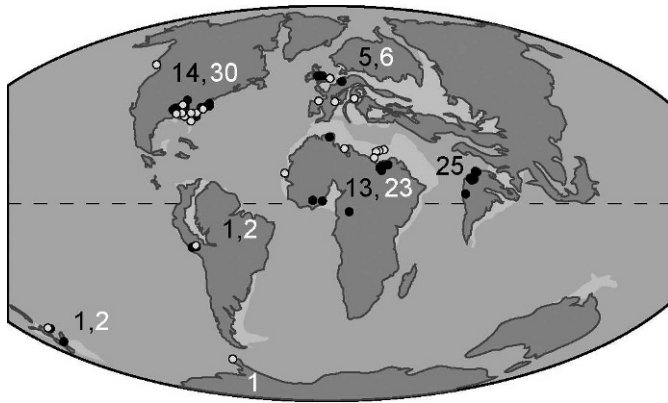
FIGURE 1—Middle and late Eocene fossil cetacean localities of the world. Eocene fossil cetacean collections on a paleogeographic reconstruction, with middle Eocene localities in black circles and late Eocene in white circles (number of collections indicated for each continental region in corresponding black and white text). Numbers of collections are based on data in the Paleobiology Database (<http://pbdb.org>). Map is redrawn from Mollewide projection of Eocene (<http://jan.ucc.nau.edu/~rcb7/50moll.jpg>), with permission from R. Blakey. The paleoequator is denoted by dashed line.

Vertebrados, Museo de Historia Natural de San Marcos collections, 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 dolotimized 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,
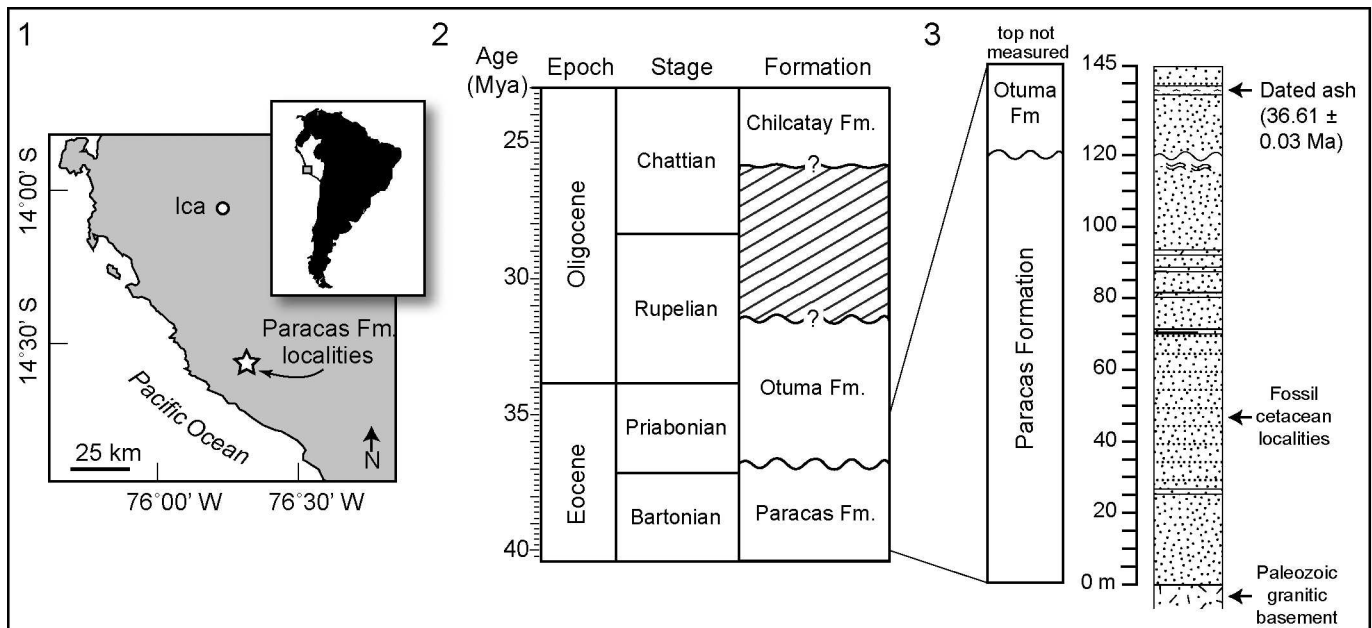
FIGURE 2—Geochronology and stratigraphy of the Pisco Basin, in southern Peru. *1*, area of field localities in Pisco Basin, denoted by a star; inset, map of South America, highlighting Peru (in white) and Ica region (in gray); *2*, general stratigraphy, according to (Dávila, 1993; DeVries, 1998; DeVries et al., 2006); *3*, measured section of the Paracas and Otuma Formations, indicating the provenance of new fossil cetaceans and geochronology constraints from ash beds in the Otuma Formation.

1998). 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 at >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 CO_2 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 1.003955 ± 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 ^{40}K 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 ($^{40}Ar*/^{39}Ar_K$) 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 $^{40}Ar/^{39}Ar$ 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 $^{40}Ar/^{39}Ar$ dates that have not yet been recalibrated.

PHYLOGENETIC ANALYSIS

The phylogenetic positions of the fossils described herein were determined by a stratocladistic analysis (Fisher, 1994) that was performed in two stages. In the first stage of the analysis, a conventional cladistic analysis was conducted using PAUP (Swofford, 2002) on the morphological data. This analysis consisted of one million replicates in a heuristic search of 20 ingroup taxa and 2 outgroup taxa (*Sus* Linnaeus, 1758 and *Hippopotamus* Linnaeus, 1758) that were scored for 109 morphological characters (after Geisler et al., 2005). The matrix of Geisler et al. (2005) was selected because its taxonomic scope focused specifically on archaeocetes, rather than the relationship of archaeocetes to crown Cetacea, and because it includes many of the characters from previous phylogenetic analyses along with many additional new characters; see Geisler et al. (2005) for character descriptions and descriptions of the character states. The matrix consists of a mixture of binary and multi-state characters, some of which were ordered following Geisler et al. (2005); two additional unordered morphological characters were added, and they are described in Supplemental Tables 2 and 3 (online archives). In addition, the recently described *Maiacetus* was also added as a new taxon to the matrix. Character codings for the new Peruvian taxa and *Maiacetus* Gingerich et al. 2009 are listed in Supplemental Table 4 (online archives). In the second stage of the analysis, a stratigraphic character was added to the analysis and overall most parsimonious trees were explored in MacClade (Maddison and Maddison, 2000). The stratigraphic character state codings are listed in Supplemental Table 3 (online archive). A comprehensive stratocladistic analysis could not be performed because of the size and complexity of the data matrix. Thus, additional equally parsimonious trees or more parsimonious trees may exist.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
ARTIODACTYLA Owen, 1848
WHIPPOMORPHA WADDELL et al. 1999
(=CETANCODONTA ARNASON et al. 2000)

The name Whippomorpha was coined by Waddell et al. (1999) for the clade including Hippopotamidae + Cetacea. The existence of this clade has been supported by many more recent phylogenetic studies (e.g., Geisler and Theodor, 2009; Geisler and Uhen, 2003; Geisler and Uhen, 2005; Spaulding et al., 2009). Arnason et al. (2000) proposed replacing Whippomorpha with the name Cetancodonta for the same clade, a change that was not followed by some (e.g., Geisler and Uhen, 2005), followed by others, (e.g., Agnarsson and May-Collado, 2008) and explicitly supported by Spaulding et al. (2009). Despite the fact that the International Code of Zoological Nomenclature does not include rules for taxa above the family level, we choose to follow the Principle of Priority outlined in Article 23 of the code to preserve stability in the names of higher taxa, despite the linguistic objections to the name Whippomorpha outlined by Arnason et al. (2000) and Spaulding et al. (2009). Also see Asher and Helgen (2010).

CETACEA Brisson, 1762
Family PROTOCETIDAE Stromer, 1908
PROTOCETIDAE new genus and new species
Figures 3, 4

Specimen.—MUSM 1443, a partial skull and skeleton including the posterior portion of the skull and partial vertebral column and ribs, including vertebrae C1, C4?, C7,
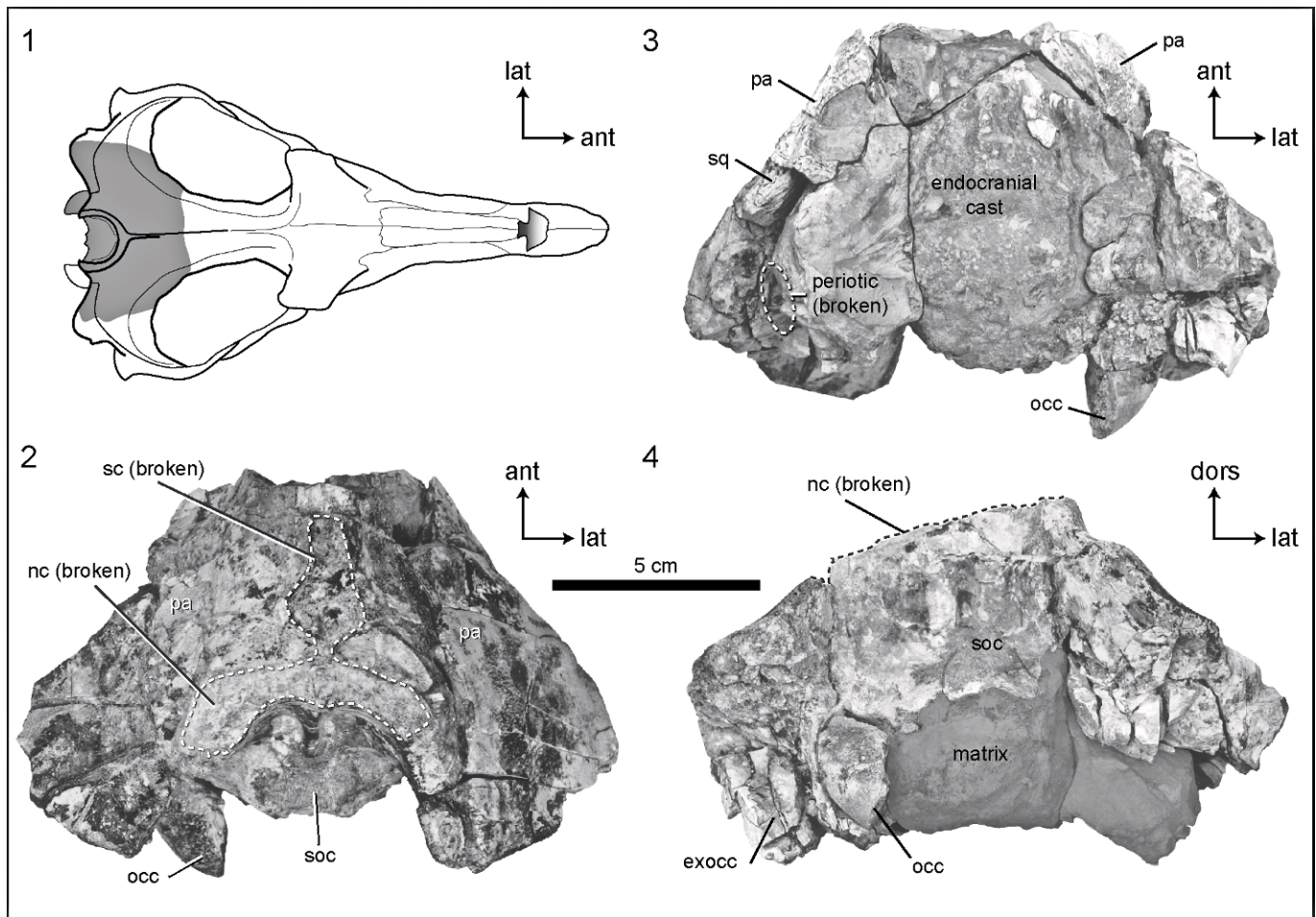
FIGURE 3—MUSM 1443, incomplete cranium. *1*, outline of the preserved cranium, in gray, compared to the complete skull of *Maiacetus*, after Gingerich et al. (2009); cranium views: *2*, dorsal; *3*, ventral; *4*, posterior. Abbreviations: ant=anterior; dors=dorsal; exocc=exoccipital; lat=lateral; nc=nuchal crest; occ=occipital condyle; pa=parietal; sc=sagittal crest; soc=supraoccipital; sq=squamosal.

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
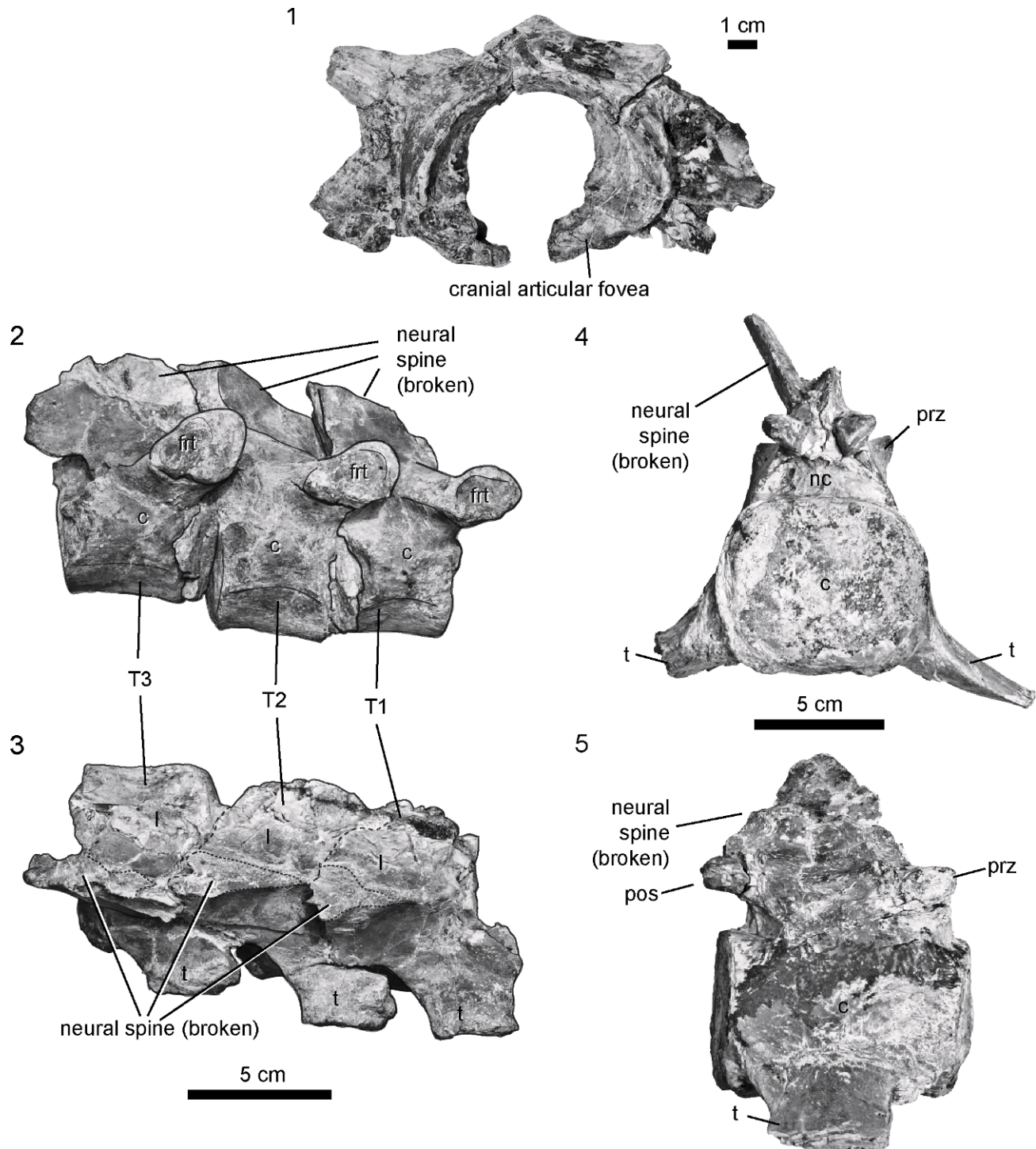
FIGURE *4*—MUSM 1443, associated vertebrae. *1*, atlas vertebra (C1) in anterior view; *2*, vertebrae (T1–T3) in right lateral view and; *3*, dorsal view of the vertebrae; both *2* and *3* include line art superimposed to emphasize osteology; *4*, lumbar vertebrae anterior view; *5*, lumbar vertebrae right lateral view. Abbreviations: c=vertebral centrum; frt=fovea for rib capitulum; l=vertebral lamina; nc=neural canal; pos=postzygapophysis; prz=prezygapophysis; t=transverse process of vertebra.

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
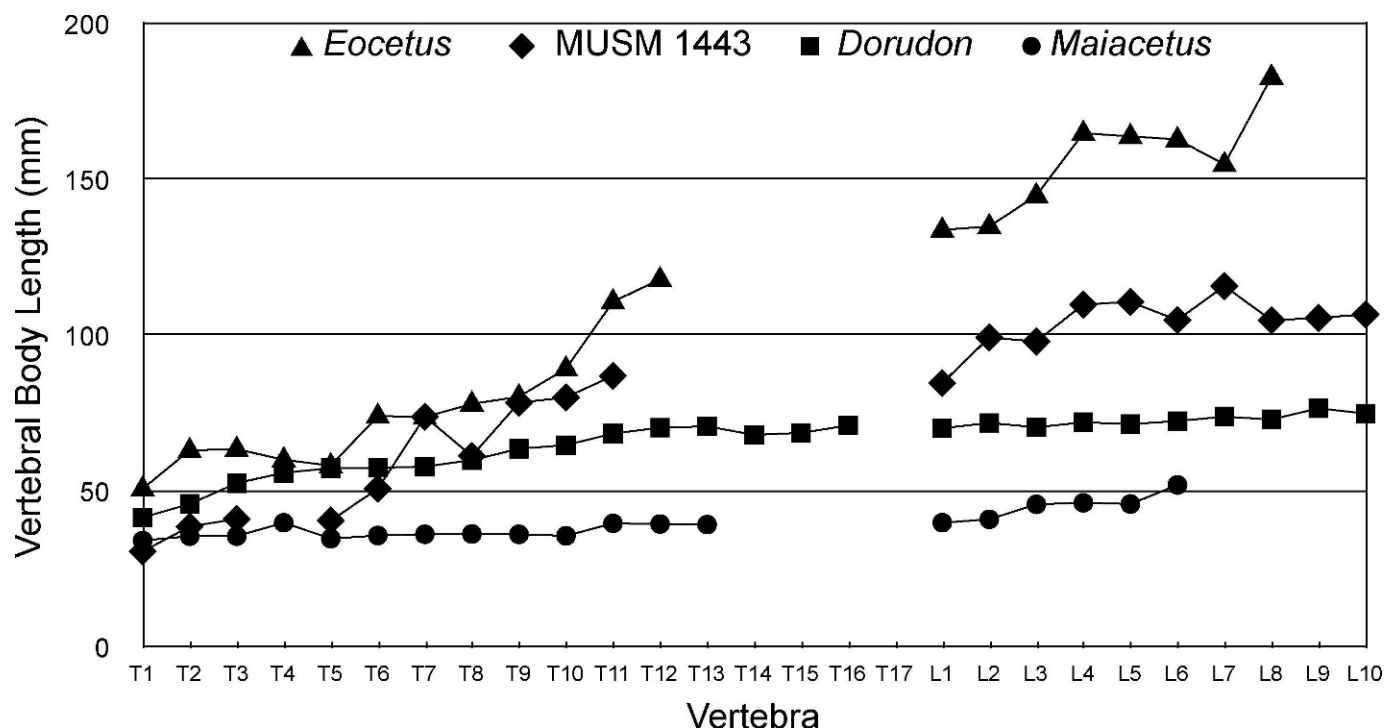
FIGURE 5—Comparison of the sizes of *Eocetus*, *Maiacetus*, *Dorudon* and MUSM 1443 vertebrae. *Eocetus wardii* is a composite of USNM 310633 and NCMS 11284 (Uhen, 1999; Uhen, 2001). *Dorudon* is a composite of UM 101215 and UM 101222 (Uhen, 2004). *Maiacetus* is from specimen GSP-UM 3551 (Gingerich et al., 2009).

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.

Vertebra	Ventral length
C1	29.5
C2	—
C3	—
C4	23.8
C5	—
C6	—
C7	34.0
T1	30.9
T2	38.9
T3	41.3
T4	—
T5	40.8
T6	~51
T7	74.1
T8	61.5
T9	78.6
T10	80.3
T11	87.2
L1	84.9
L2	99.5
L3	98.2
L4	110.1
L5	110.9
L6	105.1
L7	~116
L8	~105
L9	~105.8
L10	~106.9
L11	—

Family BASILOSAURIDAE 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 *Carolinacetus* 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
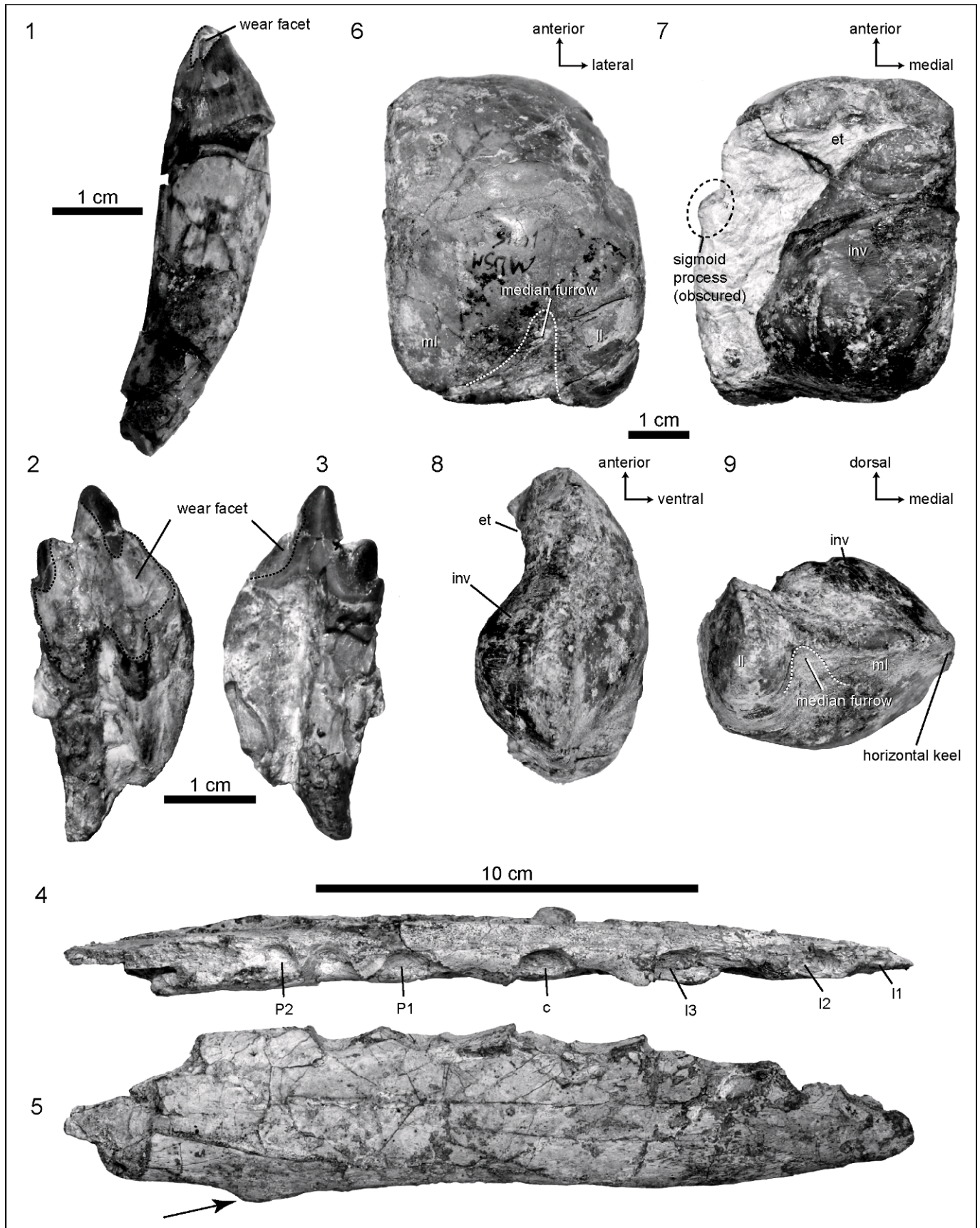
FIGURE 6—MUSM 1465, material belonging to *Supayacetus muizoni*, n. gen. n. sp. (holotype). *1*, isolated incisor tooth; isolated cheek tooth in: *2*, medial; *3*, lateral views; right dentary in: *4*, dorsal (arrow denotes the posterior extent of the mandibular symphysis); *5*, right lateral views; 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.
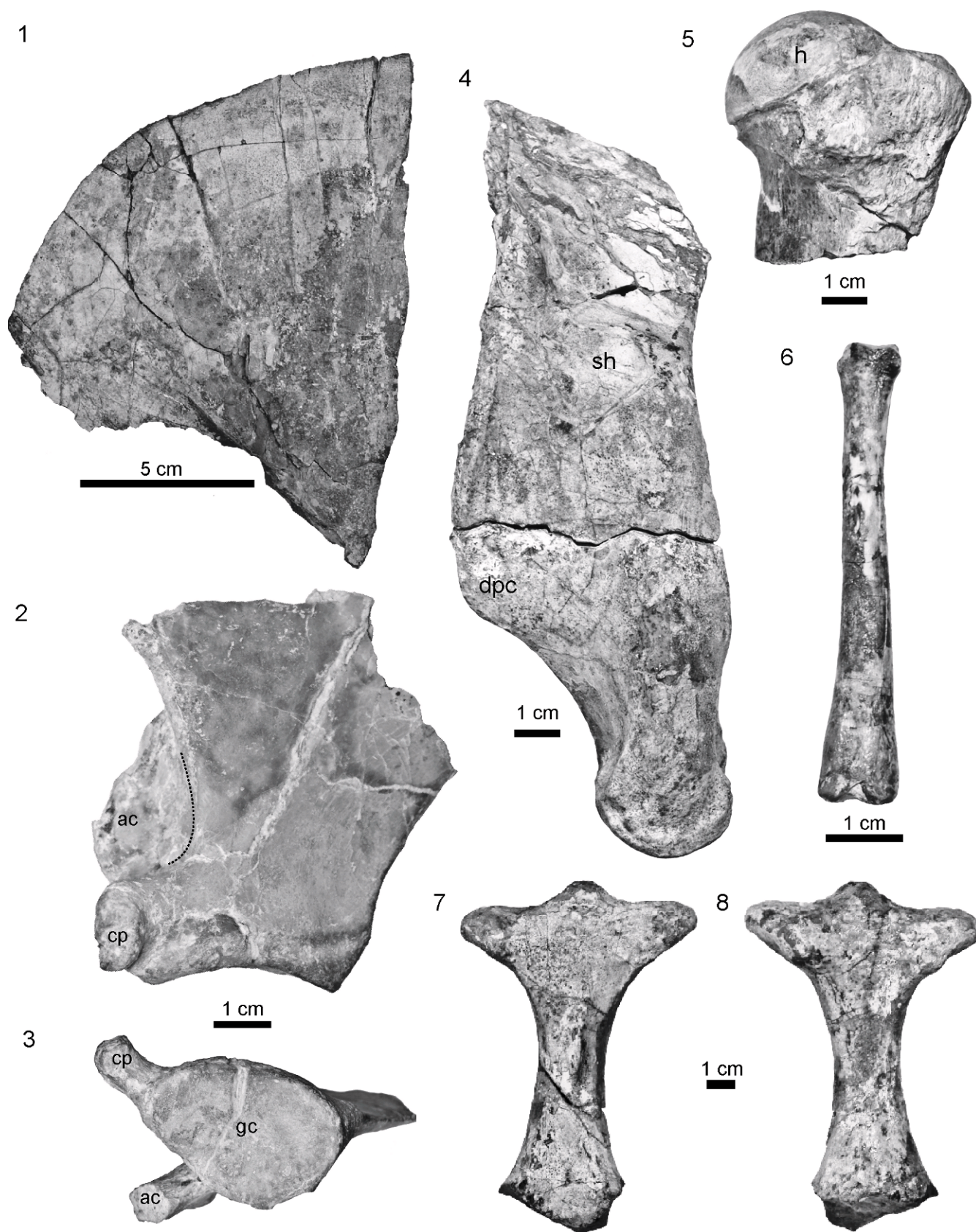
FIGURE *7*—MUSM 1465, postcranial material belonging to *Supayacetus muizoni*, n. gen. n. sp. (holotype). *1*, left scapular blade in lateral view; *2*, glenoid process of scapula in lateral view; *3*, glenoid process of scapula in distal view; *4*, incomplete left distal humerus in lateral view; *5*, 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 I_1 to P_2 (Fig. 6), while the left dentary is preserved from I_3 to P_1. The medial surface of both dentaries shows that the mandibular symphysis was unfused and terminates posteriorly just anterior to P_2. The mandibles are also very thin and gracile, broadening dorsally around the alveoli for the teeth. The alveoli demonstrate that I_1–P_1 were single rooted, while P_2 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 basilosaurids 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 manual phalanges 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, 75.635150°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 basilosaurids 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 nares 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 *Artiocetus* (Gingerich et al., 2001). The orbit is large and round in lateral view and is proportionally similar in size to those of other basilosaurids. 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 M_1–M_3 are preserved, as well as portions of upper right M^1–M^2. The roots of the left upper P^3–M^2 are also preserved (Fig. 8). Of the two roots on P^4, the posterior root is lingually expanded. The presence or absence of M^3 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.
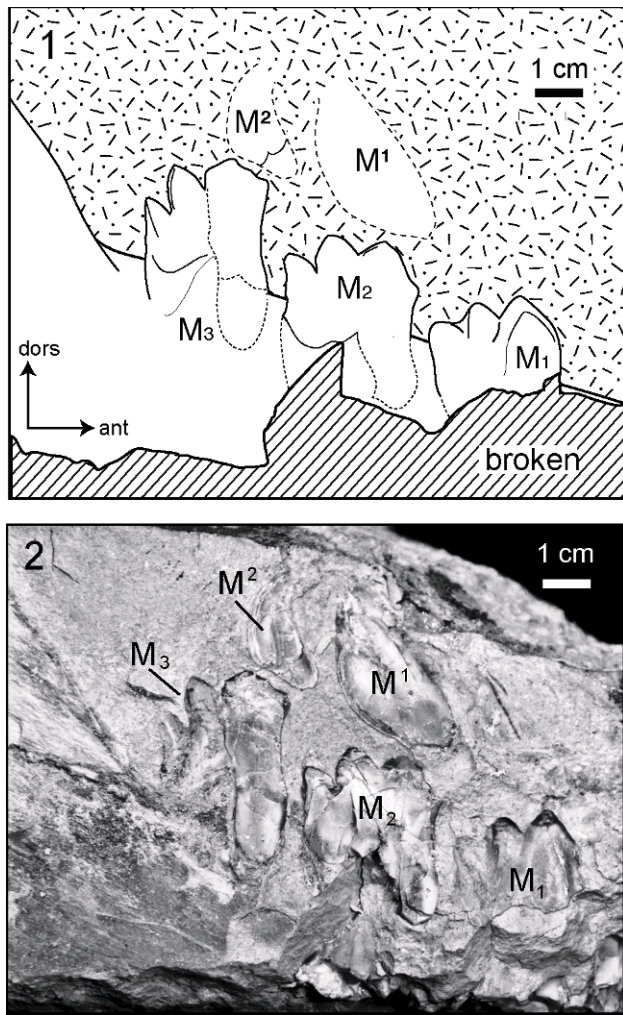
FIGURE 8—Fragmentary molar dentition of *Ocucajea picklingi* (MUSM 1442) n. gen. n. sp. *1*, interpretive illustration; *2*, image of right upper cheek tooth roots, P⁴–M², left lower molars M¹–M³ and left upper molars, M¹–M².

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 basilosaurid 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 (Clupeoidea) 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 Dunbar 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 analysis 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, Remingtonocetidae, 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 *Basilosaurus*, *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
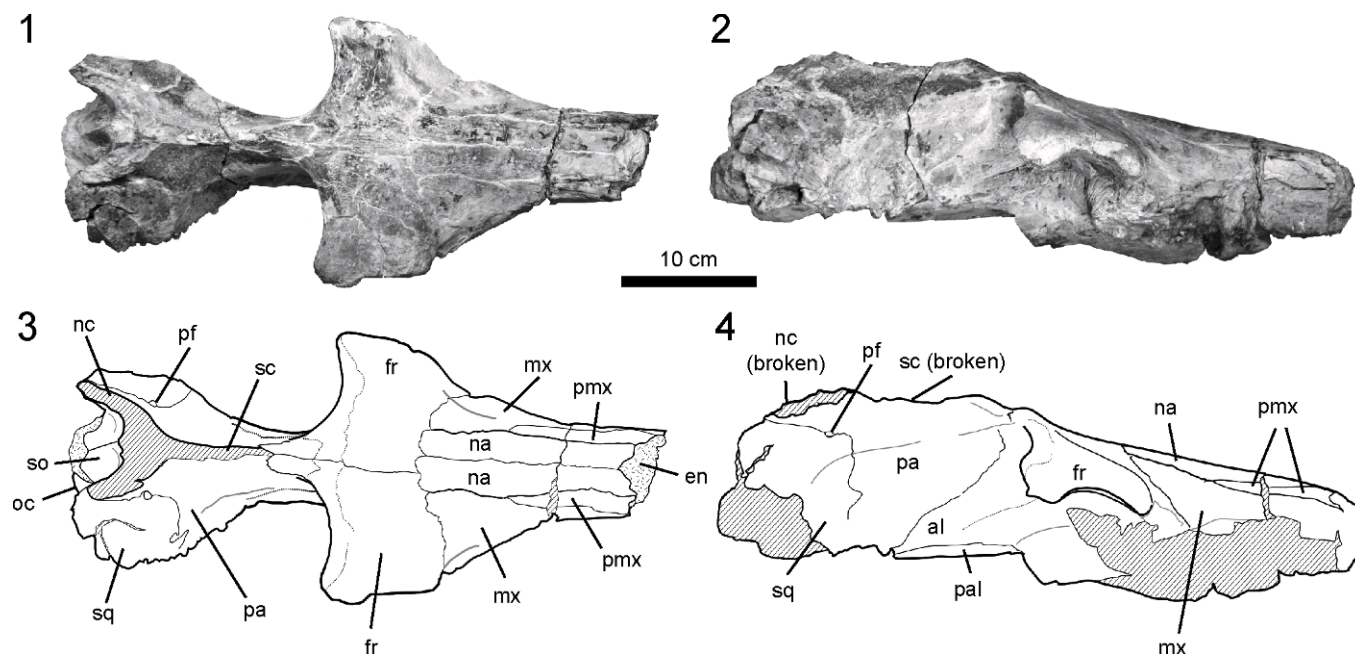
FIGURE 9—Skull of *Ocucajea picklingi* (MUSM 1442) n. gen. n. sp. Incomplete skull in: *1*, dorsal view; *2*, right lateral view; illustration of skull in: *3*, dorsal view; *4*, right lateral view. Abbreviations: al=alisphenoid; en=aperture of external nares; fr=frontal; mx=maxilla; na=nasal; nc=nuchal crest; oc=occipital condyle; pa=parietal; pal=palatine; pf=parietosquamosal foramen; pmx=premaxilla; sc=sagittal crest; sq=squamosal; so=supraoccipital.

Supayacetus will become better resolved when more material of this genus is available for study.

Ocucajea is clasified 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 Pelagiceti.—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 [Beatty and Geisler, 2010]) than the stratigraphic occurrence of basilosaurids (Bartonian to Priabonian, [Uhen, 2005b]). Basilosaurids from the Domanda Formation (*Basilosaurus drazindai*, *Basiloterus 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
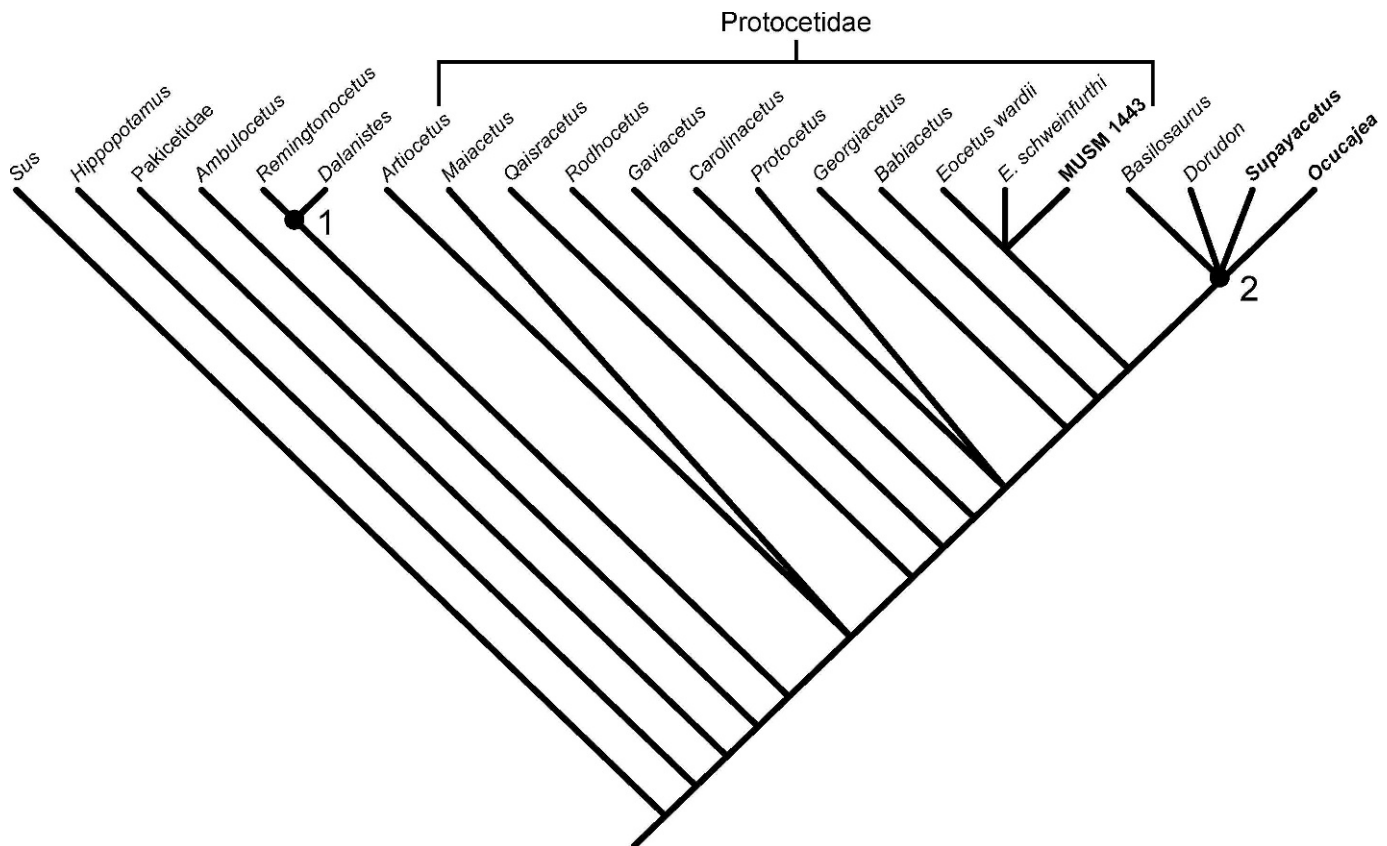
FIGURE *10*—Consensus tree showing the results of the phylogenetic analysis. Clade 1 is the family Remingtonocetidae, while clade 2 is the base of the clade Pelagiceti. Within Pelagiceti, only members of the paraphyletic family Basilosauridae were included in this analysis. The paraphyletic family Protocetidae is shown in a pectinate arrangement between Remingtonocetidae and Pelagiceti. Note that MUSM 1443 groups with members of the genus *Eocetus*, while *Ocucajea* and *Supayacetus* group with basilosaurids despite the retention of a protocetid sternum in *Supayacetus*.

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

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.

Collection	Geographic locality	Formation	Taxa	Age
63838	Paracas peninsula, Peru	Otuma	*Cynthiacetus peruvianus*	Priabonian
73779	AV-10, Archaeocete Valley, Peru	Otuma	Basilosauridae indet.	Priabonian
73780	AV-15, Archaeocete Valley, Peru	Paracas	MUSM 1443	Bartonian
90022	AV-19, Archaeocete Valley, Peru	Paracas	*Ocucajea picklingi*	Bartonian
90021	AV-17, Archaeocete Valley, Peru	Paracas	*Supayacetus muizoni*	Bartonian
45723	Seymour Island, Antarctica	La Meseta	*Llanocetus denticrenatus* Cetacea indet.	Priabonian
100190	Seymour Island, ZPAL 3, Antarctica	La Meseta	Cetacea indet.	Priabonian
100290	Seymour Island, DVP 10/84, Antarctica	La Meseta	Cetacea indet.	Priabonian
32900	Waimate, New Zealand	Waihao Greensand	?*Zygorhiza* sp.	Bartonian
45041	McCulloch's Bridge, New Zealand	Waihao Greensand	Dorudontinae indet.	Priabonian
74594	Burnside, New Zealand	Burnside Marl	archaeocete indet.	Priabonian
79346	Opuha River, New Zealand	?	archaeocete indet.	Priabonian

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-Vinenet 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 crown-

ward 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 Pelagiceti 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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