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MAKARACETUS BIDENS, A NEW PROTOCETID ARCHAEOCETE (MAMMALIA, CETACEA) FROM THE EARLY MIDDLE EOCENE OF BALOCHISTAN (PAKISTAN)

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PHILP D. GINGERICH[1], IYAD S. ZALMOUT[1],
MUNIR UL-HAQ[2], AND M. AKRAM BHATTI[2]

Abstract — *Makaracetus bidens* is a new genus and species of late Lutetian (early middle Eocene) archaeocete collected from the Kunvit area near Rakhni, in eastern Balochistan Province, Pakistan. *M. bidens* was found in upper Domanda Formation strata deposited in a coastal marine setting of the eastern Tethys Sea. The new cetacean is represented by a partial skull with associated postcranial elements. The cranium of *Makaracetus* is distinctive in having a relatively short rostrum that is bilaterally compressed and slightly down-turned distally, with two incisors rather than three in each premaxilla. The anterior rostrum is T-shaped in cross-section, with paired narial grooves on the dorsal surface, and deep fossae for attachment of hypertrophied facial muscles on the left and right lateral surfaces. *Makaracetus* apparently had a short, muscular proboscis, possibly for specialized feeding on mollusks or other benthic fauna. The centrum of the preserved cervical vertebra is normally proportioned for a protocetid archaeocete, and the first two sacral vertebrae are fused like those of other protocetids. The conformation of the anterior rostrum in *Makaracetus* is so distinctive that it is placed in its own subfamily Makaracetinae (new), distinct from both Protocetinae and from Georgiacetinae (new).

INTRODUCTION

Archaeoceti are primitive Cetacea, intermediate between earlier land-mammal ancestors outside the order and the later living suborders Mysticeti and Odontoceti. Geologically, archaeocetes range in age from the late early Eocene (*Himalayacetus*; Bajpai and Gingerich, 1998) through the late Eocene (*Saghacetus*; Gingerich, 1992) and possibly Oligocene (Fordyce, 2004). Archaeocetes are generally classified in five families: Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae (including Dorudontinae). The first of these to be broadly distributed geographically was Protocetidae (Fig. 1), represented by some 15 named genera and 16 named species (Table 1). The high proportion of monospecific genera named to date probably

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[1] Department of Geological Sciences and Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

[2] Geological Survey of Pakistan, Sariab Road, Quetta, Balochistan, Pakistan

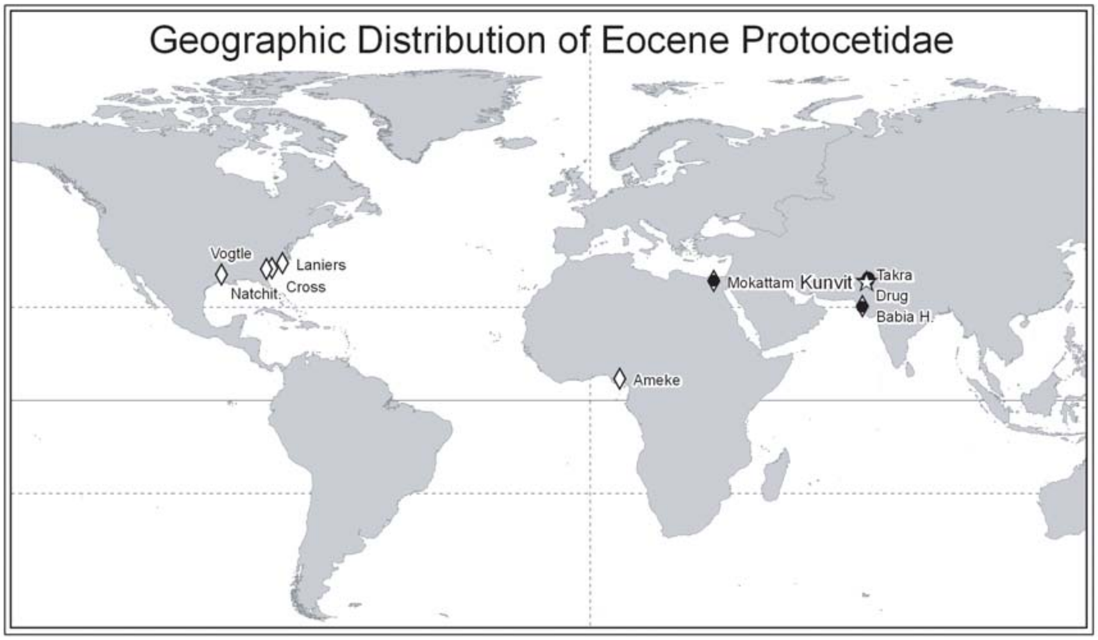

FIG. 1 — Geographic distribution of Eocene Protocetidae plotted on a map showing the present-day distribution of continents. Note that Lutetian or early middle Eocene protocetids including most Protocetinae (solid circles) and Makaracetinae (open star) are concentrated in the Middle East and in Indo-Pakistan, where they are found in deposits of what was then the eastern Tethys Sea. Bartonian protocetids including most Georgiacetinae (open diamonds) are more broadly distributed from Indo-Pakistan in the east to West Africa and eastern North America in the west. Data plotted here are listed in Table 1.

reflects their broad distribution, and also suggests that protocetid diversity is still poorly sampled. When Kellogg (1936) reviewed Archaeoceti he knew only *Protocetus*, *Eocetus*, and *Pappocetus*. Twelve of the 15 protocetid genera were named since 1975, and ten were named since 1990 when the Protocetidae of Pakistan were targeted for intensive study. Much is known and much remains to be learned about protocetids and other primitive archaeocetes.

Here we describe the cranium and associated postcranial elements of a new protocetid discovered in 2004 near Kunvit in the western Sulaiman Range of Balochistan. This specimen is important in representing a new and hitherto unknown feeding adaptation in archaeocetes involving, evidently, development of a short proboscis and hypertrophy of the facial muscles. It shows that there is greater morphological disparity in Protocetidae than hitherto appreciated, and leads us to propose a new three-part classification of the family.

ABBREVIATIONS

ChM — Charleston Museum, Charleston, South Carolina (USA)
GSI — Geological Survey of India, Calcutta (India)
GSM — Georgia Southern Museum, Statesboro, Georgia (USA)
GSP-UM — Geological Survey of Pakistan-University of Michigan, Islamabad (Pakistan)
LUVP — Lucknow University Vertebrate Paleontology (India)

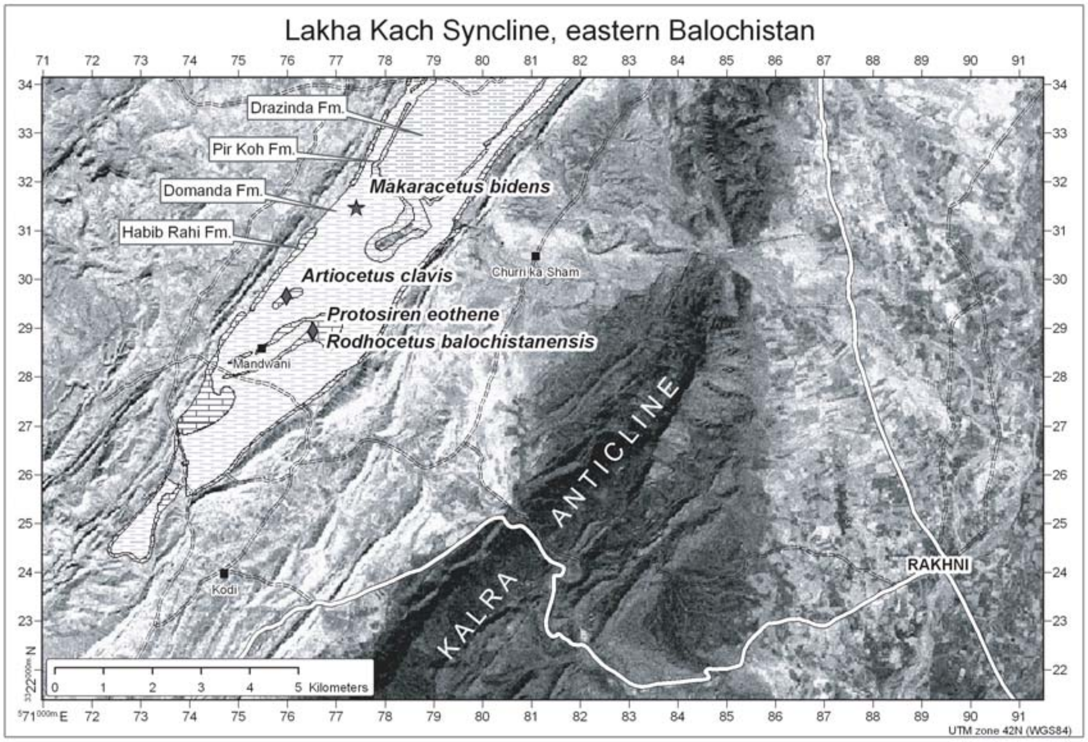

FIG. 2 — Map of the Kunvit area in the southern part of the Lakha Kach syncline, northwest of the town of Rakhni in eastern Balochistan (Pakistan). Star represents the type locality of *Makaracetus bidens* described here. Diamonds are type localities of *Artiocetus clavis* and *Rodhocetus balochistanensis* described by Gingerich et al. (2001), and *Protosiren eothene* described by Zalmout et al. (2003). All are in the Habib Rahi and Domanda formations of early through late Lutetian age (early middle Eocene). Kalra anticline has Paleocene Rakhi Gaj Formation exposed in its core. White lines are metaled roads. Geology is from Haq and Malkani (1999).

NHML — Natural History Museum, London (UK)
SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
UM — Museum of Paleontology, University of Michigan, Ann Arbor, Michigan (USA)
USNM — U. S. National Museum, Smithsonian Institution, Washington, D.C. (USA)

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CETACEA Brisson, 1762
Suborder ARCHAEOCETI Flower, 1883
Family PROTOCETIDAE Stromer, 1908
Subfamily **MAKARACETINAE**, new

Type genus.— *Makaracetus*, new genus.
Diagnosis.— As for the genus. *Makaracetus* is the only genus of the subfamily known to date.

TABLE 1 — Summary classification of Eocene archaeocetes of the family Protocetidae.

Genus and species	Reference	Holotype	Age	Type locality	Geodetic coordinates N latitude	Geodetic coordinates E longitude
Protocetinae						
Protocetus atavus	Fraas, 1904: 201	SMNS 11084-7	M. Lutetian	Gebel Mokattam (Egypt)	30.035278	31.272222
Indocetus ramani	Sahni & Mishra, 1975: 18	LUVP 11034	E. Bartonian	Harudi (India)	23.505500	68.687500
Rodhocetus kasranii	Gingerich et al., 1994: 844	GSP-UM 3012	E. Lutetian	Bozmar Nadi (Pakistan)	30.773333	70.446111
Takracetus simus	Gingerich et al., 1995: 300	GSP-UM 3041	E. Lutetian	Takra (Pakistan)	30.143920	70.363880
Gaviacetus razai	Gingerich et al., 1995: 305	GSP-UM 3095	M. Lutetian	Basti Ahmed (Pakistan)	30.125812	70.365258
Artiocetus clavis	Gingerich et al., 2001a: 2242	GSP-UM 3458	E. Lutetian	Kunvit (Pakistan)	30.095650	69.788583
R. balochistanensis	Gingerich et al., 2001a: 2242	GSP-UM 3485	E. Lutetian	Kunvit (Pakistan)	30.089017	69.794033
Qaisracetus arifi	Gingerich et al., 2001b: 295	GSP-UM 3410	L. Lutetian	Ander Dabh Shumali (Pak.)	30.909833	70.229500
Makaracetinae						
Makaracetus bidens	Gingerich et al., 2005: 201	GSP-UM 3570	Late Lutetian	Kunvit (Pakistan)	30.112030	69.803560
Georgiacetinae						
Eocetus schweinfurthi	Fraas, 1904: 217	SMNS 10986	Bartonian	Gebel Mokattam (Egypt)	30.029444	31.270833
Pappocetus lugardi	Andrews, 1920:309	NHML-M 11414	Bartonian	Ameke (Nigeria)	5.555400	7.515200
Babiacetus indicus	Trivedy & Satsangi, 1984: 322	GSI 19647	E. Bartonian	Babia Hill (India)	23.700000	68.775000
Georgiacetus vogtlensis	Hulbert et al., 1998: 912	GSM 350	E Bartonian	Plant Vogtle (U.S.A.)	33.148610	-81.755800
Natchitochia jonesi	Uhen, 1998: 664	USNM 16805	E. Bartonian	Natchitoches (U.S.A.)	31.692900	-93.080000
Eocetus wardii	Uhen, 1999: 514	USNM 310633	Lut.-Bart.	Laniers Pit (U.S.A.)	34.625000	-77.675000
Carolinacetus gingerichi	Geisler et al., 2005: 6	ChM-PV 5401	M. Bartonian	Cross Quarry (U.S.A.)	33.350000	-80.332222

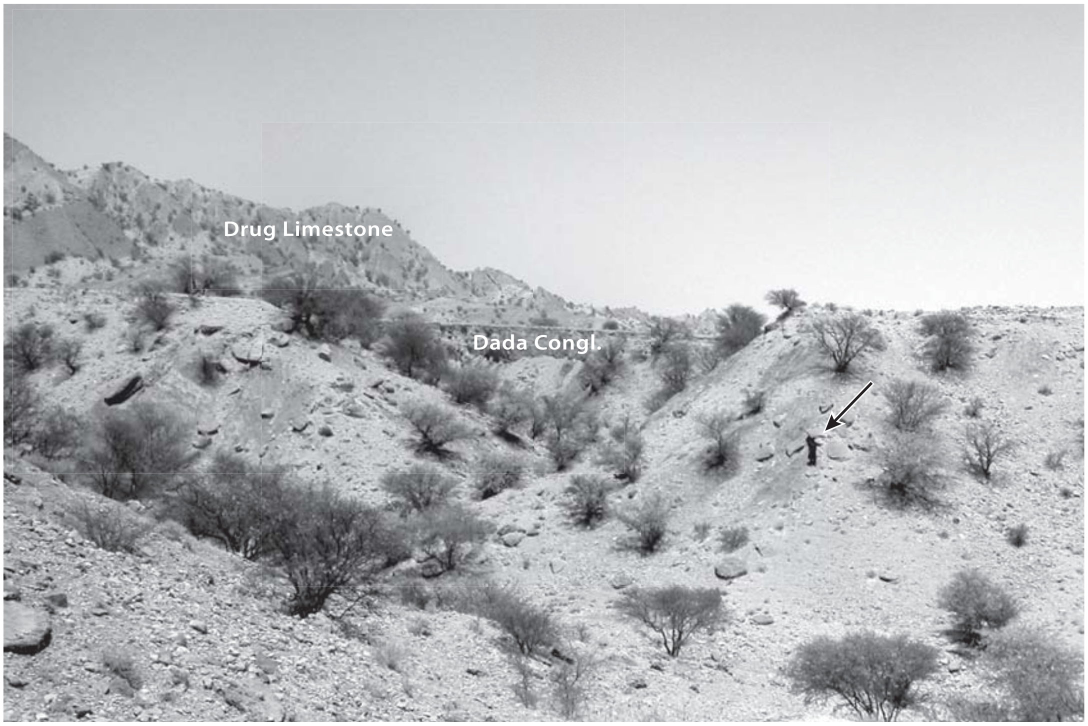

FIG. 3 — Field photograph of the type locality of *Makaracetus bidens* in the Kunvit area on the west flank of the Lakha Kach syncline, northwest of Rakhni, in eastern Balochistan (Pakistan). GSP-UM 3570 was found in the lower part of the upper Domanda Formation where the man is standing (arrow). View is to northwest. Eocene strata in foreground are dipping at approximately 45° to east (right side of photograph). Locality is approximately 150 m above the top of the Habib Rahi Formation, and a few meters below a 2-3 m massive gypsum bed present in the upper Domanda Formation in this area. Steeply dipping formation in the background is the Drug Limestone of Ypresian early Eocene age. Flat-lying unit in the center of the photograph is Dada Conglomerate of Pleistocene age.

Makaracetus bidens, new genus and species
Fig. 4

Holotype.— GSP-UM 3570, cranium, cervical and thoracic vertebrae, and partial sacrum. All were found as parts of one associated skeleton.

Type locality.— Kunvit area, Lakha Kach syncline, northwest of the town of Rakhni in eastern Balochistan Province, central Pakistan (Fig. 2; coordinates of the type locality are given in Table 1). The type specimen of *Makaracetus bidens* was found weathering from a unit of green and brown clay shale interbedded with thin limestones several meters below the massive gypsum bed in the lower part of the upper Domanda Formation at this locality (Fig. 3).

Diagnosis.— *Makaracetus* is distinctive among archaeocetes in having a relatively short, bilaterally compressed, down-turned rostrum, with two rather than three teeth in each premaxilla. The anterior rostrum is T-shaped in cross-section, with paired narial grooves on the dorsal surface, and deep lateral fossae in the posterior premaxillae and anterior maxillae. *M. bidens* is the only species of the genus known to date.

Age and distribution.— GSP-UM 3570 was found in the lower part of the upper Domanda Formation. This part of the section is late Lutetian in age, but is not precisely calibrated chronologically. *Makaracetus bidens* is known only from the type locality on the east side of the Sulaiman Range, Balochistan Province, in central Pakistan. This was in the eastern Tethys Sea (Neotethys) paleogeographically.

Etymology.— *Makara*, mythological animal in South Asia that is half-mammal, half-fish, sometimes described as having the head of an elephant and the body of a fish, generally large and ocean-dwelling; and *cetus*, L., whale. Species name *bidens*, L., two-teeth; refers to the apparent retention of only two incisors in each premaxilla.

DESCRIPTION

Cranium in general.— The cranium of *Makaracetus*, GSP-UM 3570, was found in four pieces: (1) anterior rostrum; (2) middle rostrum; (3) middle cranium section with the frontal shield and temporal constriction; and (4) posterior cranium section with the braincase and occiput. The contact between the two rostral pieces is well preserved and these pieces fit together unambiguously. It does not appear that there is very much bone missing between the middle rostrum and middle cranium pieces, nor between the middle and posterior cranium pieces, but these do not fit together well and the contacts had to be rebuilt.

Many cranial bones have their surfaces well preserved, with sutures visible between adjacent bones, but other surfaces have been damaged by erosion. This damage is particularly serious on the ventral surface of the cranium, both on the posterior part of the palate where none of the alveoli for molar teeth can be identified, and on the basicranium where none of the sinuses, foramina, or other landmarks can be identified.

The reconstructed cranium of *Makaracetus* is illustrated in Figure 4. For scale, the total condylobasal length of the cranium, from the tip of the rostrum to the posterior surface of the better-preserved occipital condyle is 53 cm. Cranial measurements are listed in Table 2.

Dentition.— Many upper teeth in the premaxillae and maxillae are represented by alveoli or tooth roots, but none has a crown preserved. The left and right premaxillae each preserve a root or alveolus for two upper incisor teeth, which are interpreted as I^1 and I^2. The incisors are well spaced, and there is no trace of the normal third incisor. The canine is single-rooted, and relatively long anteroposteriorly compared to other anterior teeth. It is clear from the alveolus that C^1 had an unusually bluntly tapering root. The alveolus and part of a root show that P^1 was small. Alveoli and roots show that P^2 was larger and double-rooted. P^3 was larger still and similarly double-rooted, with a more broadly expanded posterior root. Nothing can be determined with certainty about the remaining cheek teeth because the tooth-bearing portions of the left and right maxillae are heavily damaged. Dental measurements, where these can be estimated reliably, are listed in Table 3.

Cranial rostrum.— The anterior rostrum is the most distinctive part of the skull of *Makaracetus*. It is literally T-shaped in cross-section, and the palatal or ventral part of the rostrum, the base of the T, is very narrow. The premaxillae together measure 29.6 mm at their narrowest, palatally, behind I^2 (with each being 14.8 mm wide when measured from the midline of the skull). The maxillae together measure 26.8 mm at their narrowest, palatally, behind P^1(with each being 13.4 mm wide when measured from the midline). In contrast, the dorsal part or crown of the rostral T is very broad. The premaxillae together at their broadest were approximately 70 mm wide, dorsally, above the canines (with each being approximately 35 mm wide when measured from the midline).

What makes the anterior rostrum T-shaped is the presence of paired left and right fossae that are extraordinarily deep between the roots of successive incisors, canines, and premolars. Midline bone separating these fossae is literally paper-thin in the deepest fossae in both the premaxillae and the anterior maxillae. There is a shallow depression in the lateral surface of the anterior premaxilla between the roots of I^1 and I^2, and there is a deep lateral fossa of the posterior premaxilla between the roots of I^2 and the premaxillary-maxillary suture. This suture is well marked on

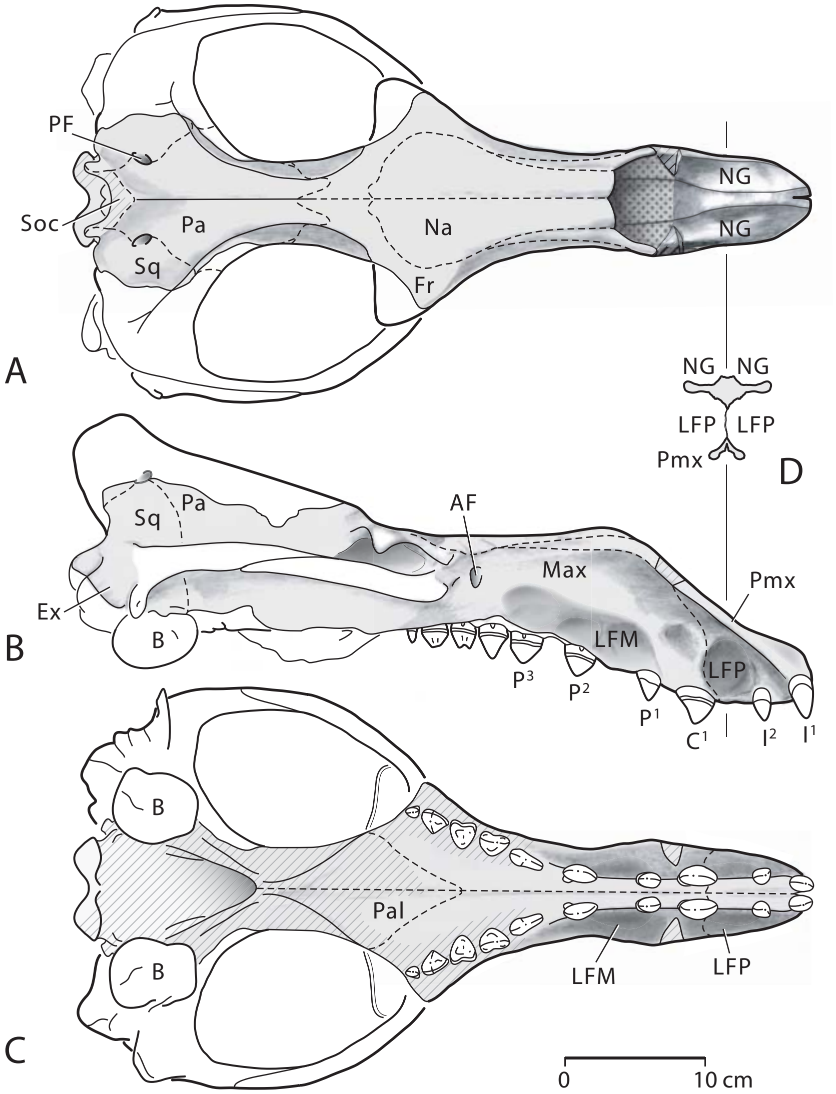

FIG. 4 — Cranium of holotype of *Makaracetus bidens*, GSP-UM 3570. Specimen is shown in dorsal (A), right lateral (B), and palatal view (C). Skull is 53 cm in condylobasal length. Note relatively short, bilaterally compressed, and down-turned rostrum with two rather than three incisors in each premaxilla. The anterior rostrum is T-shaped in cross-section (inset D), with paired narial grooves (*NG*) on the dorsal surface, and deep fossae (*LFP*, *LFM*) for origination of hypertrophied facial muscles on left and right lateral surfaces. *Makaracetus* apparently had a short, muscular proboscis for specialized feeding, possibly on mollusks or other shallow benthic organisms. Roots or alveoli representing $I^{1\text{-}2}$, C^1, and $P^{1\text{-}3}$ are present in the specimen, but none of the teeth has crowns preserved. Gray core of the skull is present in the holotype, while white portions are reconstructed. Hatching covers bone surfaces damaged by weathering. Abbreviations: ***AF***, antorbital foramen; ***B***, auditory bulla; ***Ex***, exoccipital; ***Fr***, frontal; ***LFM***, lateral fossa of the anterior maxilla; ***LFP***, lateral fossa of the posterior premaxilla; ***Max***, maxilla; ***Na***, nasal; ***NG***, narial groove; ***Pa***, parietal; ***Pal***, palatine; ***PF***, parietal foramen; ***Pmx***, premaxilla; ***Soc***, supraoccipital; ***Sq***, squamosal.

TABLE 2 — Measurements of the cranium of the holotype of *Makaracetus bidens*, GSP-UM 3570. All measurements are in cm. A.-p. position is place where a transverse breadth intersects the midline, measured from the tip of the rostrum. Asterisks denote estimates.

Measurement	A.-p. length or position	Transverse breadth	Height
Skull length (condylobasal skull length: apex–condyles)	53.0		
External narial opening (apex–nares)	13.0		
Posterior extent of nasals (apex–nasal-frontal contact; max. breadth)	29.0	9.0	
Anterior border of orbits (apex–intersection at midline)	27.0	14.5	
Posterior border of frontal shield (apex–intersection at midline)	34.0	15.0*	
Junction of sagittal and nuchal crests (apex–intersection at midline)	50.0		
Posterior margin of nuchal crests (apex–intersection at midline)	52.0	6.0*	
Second incisor (I^2; apex–intersection at midline; max. breadth)	3.0	3.5	
First premolar (P^1; apex–intersection at midline; max. breadth)	11.0	2.5	
Last upper molar (M^3; apex–intersection at midline; max. breadth)	29.0*	12.0*	
Internal nares (choanae; apex–intersection at midline; max. breadth)	41.0*	4.0*	
Maximum width of skull (apex–intersection at midline; max. breadth)	—	—	
Squamosal width of skull (apex–intersection at midline; max. breadth)	—	—	
Exoccipital (apex–intersection at midline; max. breadth)	51.5	13.6	
Tympanic bulla length and width	—	—	—
Orbit diameter		—	
Foramen magnum width and height		3.7	2.4
Occipital condyles		7.7	2.4
Infraorbital canal, width and height		1.5	0.7
Highest point of nuchal crest above base of occipital condyles			—
Highest point of nuchal crest above base of tympanic bulla			—
Dentary maximum length	—		
Mandibular symphysis length (unfused)	—		
Dentary at C_1 width and height		—	—
Dentary height at position of M_3			—
Mandibular foramen width and height		1.25*	3.1*

both sides of the rostrum, where it runs up a pillar of bone defining the posterior margin of the deep posterior lateral premaxillary fossa.

There is a shallow lateral depression in the anterior maxilla between the sutural pillar and the root of C^1, and there is a long deep lateral fossa of the anterior maxilla between the roots of C^1 and P^2. The palate begins to flare laterally at the position of P^2, and left and right P^3 were well separated from each other and from the midline of the skull. A large antorbital foramen opens above P^3 on each side of the skull, and these antorbital foramina help to define the posterior border of the deep anterior lateral fossa of the maxilla on each side. The antorbital foramina are the facial openings of infraorbital canals measuring approximately 15 mm dorsoventrally and 7 mm laterally. We interpret these canals to have been enlarged in *Makaracetus* to supply blood to hypertrophied facial muscles originating from the lateral fossae of the premaxillae and maxillae.

The external nares of the skull of *Makaracetus* open dorsal and a little posterior to P^1. Here the narial opening is wide, measuring about 48 mm from side to side (24 mm on each side of the midline). There is a single narial opening, but the nasal vestibule was undoubtedly divided into left and right chambers by a cartilaginous septum. Anterior to the bony narial opening, the dorsal surface of the rostral T bears broad, shallow grooves indicating that the cartilaginous septum and

TABLE 3 — Measurements of teeth in the holotype of *Makaracetus bidens*, GSP-UM 3570. Measurements in parentheses are based on alveoli. All measurements are in mm.

Tooth position	Crown length	Crown width	Apical height	Trailing diastema
Upper dentition				
I^1	(17.3)	(10.7)	—	21.0
I^2	(13.2)	(10.0)	—	29.0
—	—	—	—	—
C^1	(28.0)	(11.8)	—	12.0
P^1	(14.8)	(8.3)	—	35.8
P^2	(18.0)	(9.0)	—	20.0
P^3	(25.0)	(13.0)	—	—
P^4	—	—	—	—
M^1	—	—	—	—
M^2	—	—	—	—
M^3	—	—	—	—

the left and right vestibular chambers extended forward, in parallel, to the anterior end of the rostrum. We interpret anterior extension of the cartilaginous vestibular chambers and development of extraordinary lateral fossae in the premaxillae and anterior maxillae to indicate the presence of a muscular proboscis of some kind and development of hypertrophied facial musculature, developments otherwise unknown in Archaeoceti or in Cetacea.

Middle cranium.— The middle part of the cranium of *Makaracetus* has the broad frontal shield followed by a narrow temporal constriction typical of Protocetidae. The nasals are broadly expanded on the dorsal surface of the frontal shield. The optic tracts are well marked on both sides of the cranium, but the supraorbital processes of the frontals and the margins of the orbits are broken. Ventrally, a part of the bony palate is preserved on the midline, but tooth bearing parts of the maxillae are missing on both sides. Behind the maxillae, the palatines were removed by erosion, exposing the overlying paired narial canals separated by a narrow vomer. The narial canals are each on the order of 20 mm in diameter. The posterior surface of the middle part of the cranium shows the cross-section of a sediment-filled olfactory peduncle overlying, in turn, sediment-filled left and right optic nerve canals, the presphenoid, and sediment-filled left and right internal nares.

Posterior cranium.— The anterior surface of the posterior part of the cranium shows the same cross-section of a sediment-filled olfactory peduncle and optic nerves seen on the posterior surface of the middle part of the cranium. These overlie the basisphenoid of the basicranium.

The dorsal surface of the posterior cranium preserves a clear suture between parietals and squamosals. The former rise to a sagittal crest (damaged by erosion), and there is a large parietal emissary foramen (measuring about 12 × 4 mm in cross-section) at the apex of the parietal-squamosal suture. The suture between the parietals and supraoccipital is largely woven within the nuchal crest.

The posterior surface of the cranium is best represented on the right side, where the right occipital condyle and right exoccipital process are well preserved. These are present but not so well preserved on the left side. The foramen magnum is largely filled with matrix, but the basioccipital is missing below the foramen magnum. The jugular foramen or posterior lacerate foramen is preserved on the right side of the basicranium, but virtually all other basicranial morphology has been removed by erosion.

Dentary.— There is a single piece of a left dentary preserved, which appears to be relatively shallow compared to dentaries of other protocetids (the dorsal margin is not intact). This has the root of a tooth and part of an alveolus preserved, presumably for M_3, and it preserves the opening of the mandibular canal. The mandibular canal measures approximately 26 × 12 mm in cross-section.

Cervical vertebrae.— GSP-UM 3570 includes parts of two cervical vertebrae. The first is the right side of the atlas (C1) including much of the right transverse process. This partial atlas includes the ventral part of the cranial surface for articulation with the right occipital condyle, and the entire caudal surface for articulation with C2. The lateral part of the facet for articulation with C2 is circular and about 27 mm in diameter. The foramen for the intervertebral artery is large, measuring about 10.5 mm in diameter where it passes through the transverse process itself. Dorsal to this, the anterior lamina of the transverse process is broken, but much of the foramen passing through it is preserved, measuring again about 10.5 mm in diameter. This intermediate foramen is characteristically present in protocetids but not later basilosaurids.

The second cervical vertebra is a centrum interpreted as that of C5. It is normally proportioned for a protocetid, and is identified as C5 because it lacks the well developed hypapophysis expected for more anterior cervicals.

Vertebral measurements are listed in Table 4.

Thoracic vertebrae.— GSP-UM 3570 includes parts of five thoracic vertebrae. The best preserved is an anterior thoracic interpreted as T2, with a virtually complete centrum and the left half of the neural arch. Typically for anterior thoracics, the centrum is heart-shaped and the neural canal is large and broad. The centrum has anterior and posterior costal foveae. The left prezygapophysis is intact and positioned high on the neural arch at the lateral margin of the lamina. The zygapophyseal surface is flat, and faces dorsally and slightly laterally. The left diapophysis is present but the facet for articulartion with the rib tuberculum is not preserved.

Parts of two additional thoracic centra are tentatively identified as T7 and T11. T7 has both anterior and posterior costal foveae preserved on the right side, and the centrum appears to have been relatively narrow relative to its length or height. T11 has a distinct anterior costal fovea preserved on the right side, and the centrum appears to have been broader relative to its length and height.

The most complete vertebrae of GSP-UM 3570 are two posterior thoracics found together almost in articulation in the same block of matrix. These are identified as T12 and T13, respectively. T12 includes the centrum, neural arch, and neural spine. The centrum is more kidney-shaped than heart-shaped in transverse section, and it has anterior and posterior costal foveae.. T12 has, on one side or the other, concave prezygapophyses facing medially, distinct metapophyses, rudamentary anapophyses, flat to slightly concave tubercular facets, and lacunae for costal ligaments. The neural spine is almost vertical, indicating that T12 is the anticlinal vertebra. The presence of concave prezygapophyses facing medially indicates that T12 is postdiaphragmatic. T13 is not as well preserved, but seems to differ only in having the neural spine slightly anteriorly-inclined.

Sacrum.— The sacrum of *Makaracetus bidens* is distinctive in preserving two vertebrae, S1 and S2, with both centra and zygapophyses solidly fused. Pleurapophyses are not well enough preserved to see if they were fused as well. S1 is relatively complete, but it is missing pleurapophyses, auricular processes, and the neural spine. The prezygapophyses are present but not well preserved. S2 is broken through the middle of the centrum, and posterior and dorsal parts of the vertebra are missing. Nothing is preserved of the sacrum behind S2.

DISCUSSION

The most distinctive characteristics of *Makaracetus* are all related to its unusual mode of feeding. These include: (1) broad, shallow grooves on the dorsal surface of the premaxillae prolonging the narial passages and indicating anterior extension of the nasal vestibule forward to the anterior end of the rostrum; (2) ventral deflection of the anterior rostrum and reduction in the number of

TABLE 4 — Measurements of vertebrae in the holotype of *Makaracetus bidens*, GSP-UM 3570. All measurements are in cm, except neural spine angle (degrees, measured backward from vertical). Asterisks denote estimates. Abbreviations: ant. hgt., anterior height; ant. wid., anterior width; neur. can., neural canal; neur. sp., neural spine; pos. hgt., posterior height; pos. wid., posterior width.

Vertebra	Centrum length	Centrum ant. wid.	Centrum ant. hgt.	Centrum pos. wid.	Centrum pos. hgt	Neur. can. width	Neur. can. height	Neur. sp. height	Neur. sp. angle (°)
Cervicals									
C1	—	—	—	—	—	—	—	—	—
C5	2.15	—	—	3.66	2.75	2.05*	—	—	—
Thoracics									
T2	2.94	4.42	2.94	5.68	2.82	2.42	1.80	—	—
T7?	3.10	—	—	—	—	—	—	—	—
T11?	3.74	—	—	—	—	—	—	—	—
T12	3.40	4.36	—	—	—	2.65	1.60	—	Vert.
T13	—	—	—	—	—	—	—	—	—
Lumbars									
—	—	—	—	—	—	—	—	—	—
Sacrals									
S1	4.72	5.57	3.49	—	—	2.52	1.47	—	—
S2	—	—	—	—	—	—	—	—	—
Caudals									
—	—	—	—	—	—	—	—	—	—

incisor teeth; (3) development of extraordinary lateral fossae in the premaxillae and anterior maxillae; and (4) enlarged antorbital canals augmenting blood supply to the anterior rostrum. This combination of characteristics is not found in any living mammal, but suggests development of a short, muscular proboscis of some kind for specialized feeding.

Tapirs, sirenians, and walruses provide imperfect models for *Makaracetus*. Maxillary fossae are found in suid artiodactyls, where they provide origination sites for maxillolabialis muscles (Gregory, 1920). Tapirs (*Tapirus*) have an expanded nasal vestibule associated with a trunk-like proboscis (Witmer et al., 1999) but it is not clear how this might be used for aquatic feeding. Sirenians (*Manatus*, *Dugong*) are aquatic and have a down-turned rostrum used for bottom feeding, but they are herbivorous (Domning, 1978, 1981). A better ecological model for *Makaracetus* might be the walrus (*Odobenus*), which has a different rostral morphology but is similarly aquatic and uses specialized buccal and facial musculature to feed on mollusks (Kastelein and Gerrits, 1990; Kastelein et al., 1991; Born et al., 2003). We speculate that *Makaracetus* may have used its specialized rostrum, inferred trunk, and narrow, down-turned rostrum to feed on shallow benthic mollusks, which are abundant in the upper Domanda Formation. Recovery of more complete cranial remains, including, especially, a good dentary, will be required to test and constrain our mollusk-feeding hypothesis. Testing will be complicated too because it is unlikely that direct evidence clarifying the nature of the proboscis will ever be recovered.

We cannot make a precise stratigraphic correlation from the Kunvit type area yielding *Makaracetus*, described here, to the Drug type area yielding *Qaisracetus*, described by Gingerich et al. (2001b), farther northeast in the Sulaiman Range of eastern Balochistan. This is partly because Domanda Formation facies change and partly because the formation as a whole thins on the west side of the Sulaiman Range. However, we are confident that both genera and species are from the lower part of the upper Domanda Formation, and they were thus approximately contemporaeous.

We place *Makaracetus* in its own subfamily of Protocetidae, distinct from typical protocetines and more advanced georgiacetines, to reflect its distinctive adaptations for feeding. Previous attempts at subdivision of Protocetidae include separation of Pakicetinae by Gingerich and Russell

(1990) and separation of Indocetinae by Gingerich et al. (1993). Pakicetinae was subsequently raised to the family level as Pakicetidae (Thewissen et al., 1996). Indocetinae proved to be a misnomer when new collections showed distinctive postcranial remains referred to *Indocetus* to belong to *Remingtonocetus* instead (Gingerich et al., 1995; the systematic position of *Indocetus* within Protocetidae is still ambiguous).

With *Makaracetus* and Makaracetinae removed, remaining Protocetidae fall naturally into two groups based on the degree of their adaptation to water. Protocetinae sensu stricto (Table 1) are generally Lutetian in age. Protocetines have generalized skulls retaining three incisors in the premaxilla and three molars in the maxilla. Most or all retain a primitively land-mammal-like pelvic girdle, with a sacrum consisting of two or more vertebrae fused into a single unit, and substantial transverse or auricular processes on the sacrum that articulate with ilia of the innominates. The sacrum plus the innominates comprise a full pelvis. The hind limbs, where known, are large, and the principal propulsion in water was foot powered (Gingerich, 2003). *Protocetus* itself has been described as having a single-centrum sacrum (Fraas, 1904), but close inspection of the type shows that this is almost certainly an artifact of breakage (Gingerich, in prep.).

A third major subdivision of Protocetidae includes *Georgiacetus* (Hulbert and others, 1998), which is here placed in a new subfamily **Georgiacetinae**. Georgiacetinae (Table 1) are generally Bartonian in age, and are probably transitional to later Basilosauridae. Georgiacetines, like protocetines, have generalized skulls retaining three incisors in the premaxilla and three molars in the maxilla. Most or all have a derived, reduced pelvic girdle, with the sacrum consisting of a single centrum with or without substantial auricular processes that articulated with the ilia of the innominates. Hind limbs are not yet known, but reduction of the sacrum suggests that these were probably reduced as well. *Georgiacetus* itself appears not to have had a distinct sacral vertebra, and the ilium of the preserved innominate shows no evidence of articulation with an auricular process (Hulbert et al., 1998). Locomotion was probably powered more by the tail than the feet.

There are ambiguities in this three-part classification of Protocetidae. For example, the protocetine *Rodhocetus kasranii* of early Lutetian age has a four-centrum sacrum, but none of the centra are fused to each other (Gingerich et al., 1994, 2001b). The protocetine *Gaviacetus razai* of middle Lutetian age has a single-centrum sacrum (Gingerich et al., 1995, 2001b), and it is possible that *Gaviacetus* is really an early Georgiacetine. Nevertheless, a three-part classification of Protocetidae represents the adaptive groups that we know today. Protocetidae includes a diverse set of older and more generalized feeders and swimmers (Protocetinae), a highly specialized feeder *Makaracetus* with primitive postcranial morphology (Makaracetinae), and a diverse set of younger, more aquatic forms (Georgiacetinae). Each subfamily is interesting and important, in its own way, for understanding the early evolution of Cetacea.

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