

MIDDLE EOCENE STRATIGRAPHY AND MARINE MAMMALS (MAMMALIA: CETACEA AND SIRENIA) OF THE SULAIMAN RANGE, PAKISTAN

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ABSTRACT

Field work in the Sulaiman Range of southwestern Punjab has yielded four middle Eocene vertebrate faunas with marine mammals, principally archaeocete Cetacea. These are intermediate in age and bridge the temporal and morphological gap between two continental early Eocene faunas with amphibious archaeocetes in Kohat and northern Punjab (Pakistan), and later marine middle Eocene faunas with aquatic archaeocetes and sirenians in Kutch (India) and in Mokattam and Fayum (Egypt). The six Pakistan faunas are correlated to the geological time scale using global sea-level sequence stratigraphy, with planktonic foraminiferal and nannoplankton control (magnetization is weak where this has been sampled, with the present-day field predominating and little or no remanent Eocene primary magnetization). The two oldest faunas come from Kohat and northern Punjab: 1) the *Pakicetus* fluvial fauna comes from the lower Kuldana Formation, which is latest Ypresian in age (about 49.0 to 49.5 million years before present on the Haq et al. time scale); and 2) the *Ambulocetus* transitional-marine fauna comes from the upper Kuldana Formation, which is earliest Lutetian in age (about 49.0 to 48.0 Ma). Four succeeding faunas come from the Sulaiman Range: 3) the

Habib Rahi Formation deep-shelf marine fauna comes from platy limestones and is early Lutetian in age (about 48.0 to 46.5 Ma); 4) the lower Domanda Formation *Rodhocetus-Takracetus* middle-shelf marine fauna comes from green clays and limestones and is early middle Lutetian in age (about 46.5 to 46.0 Ma); 5) the middle Domanda Formation *Gaviacetus-Remingtonocetus-Dalanistes* shallow-shelf marine fauna comes from brown clays and is middle Lutetian in age (about 46.0 to 45.5 Ma); and 6) the middle Drazinda Formation *Babiacetus-Protosiren* middle-shelf marine fauna comes from green clays and is late middle Lutetian in age (about 43.5 Ma). The Drazinda Formation fauna is evidently younger than the long-known Egyptian *Protocetus-Protosiren* fauna of Gebel Mokattam (ca. 45.0 Ma), and the Indian *Indocetus-Remingtonocetus* fauna from Kutch probably lies in the interval spanned by these two (ca. 45.0 to 43.5 Ma). The six Pakistan faunas document successive stages of cetacean evolution through six million years of early and middle Eocene time in eastern Tethys that involved changes first in the dentition for feeding on fish, then in the basicranium and dentaries for hearing in water, and finally in the pelvic girdle and hind limbs for efficient tail-powered swimming.

INTRODUCTION

The first mammalian remains from Eocene strata of the Sulaiman Range of Pakistan were reported by Pilgrim (1940). Pilgrim described three specimens. The first was a maxilla that he identified as anthracotheroid, and the other two were a partial maxilla lacking teeth and a “bear-like” partial right pelvic bone or innominate, both identified as mesonychid creodont. These came from “blue-grey

shales weathering olive-green of the lower Khirthar” at Safed Toba, three to five miles south of Toba Kund, south of Kaha Nala (Fig. 1). This “lower Khirthar” is the “lower Chocolate Clays” of Eames (1952a, 1952b), or, in modern terminology, the Domanda Formation of Hemphill and Kidwai (1973) and Shah (1977, 1991). In Pilgrim’s time, the Khirthar stage of Indo-Pakistan was known to

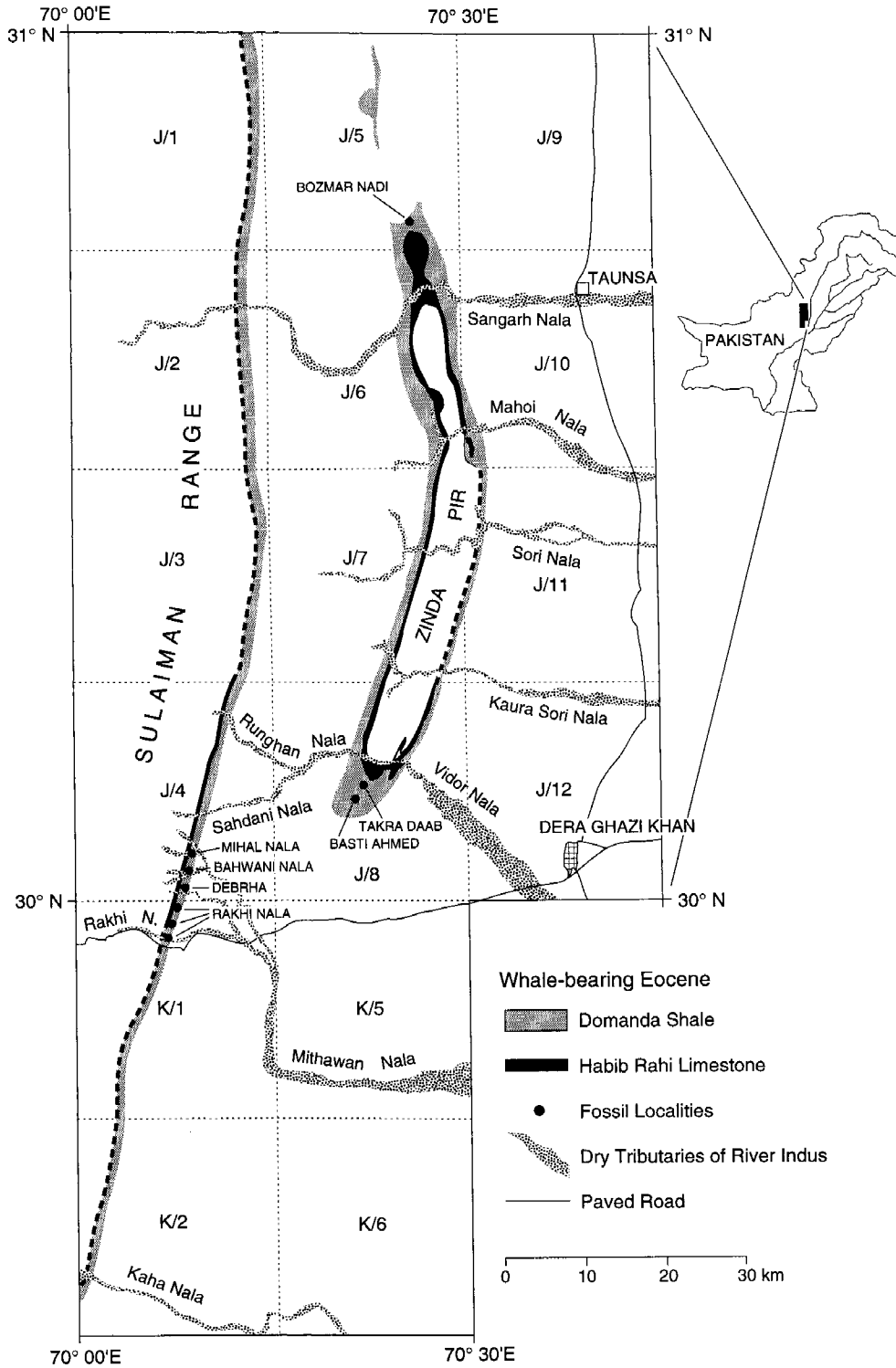


Fig. 1.—Map of Sulaiman Range and Zinda Pir anticlinorium located on the west side of the Indus River in the southwest corner of Punjab, central Pakistan (inset). Northern fossil-bearing localities of Bozmar Nadi and Satta with specimens described by Gingerich et al. (1993, 1994, 1995b) are shown in relation to southern fossil-bearing localities of Takra Daab, Basti Ahmed, Debrha, Bahwani Nala, and Rakhi Nala with specimens described by Gingerich et al. (1993, 1995a). Stratigraphic sections shown in Figure 3 were measured on the north and south sides of the Rakhi Nala stream bed (southernmost Rakhi Nala locality shown here) and in nearby tributaries of Barghan Nala, the next drainage north of Rakhi Nala stream bed (middle Rakhi Nala locality shown here). Lithologies and thicknesses of middle Eocene formations studied here are very uniform over the entire map area, and the sections in Figure 3 are generally representative of sections studied throughout the field area.

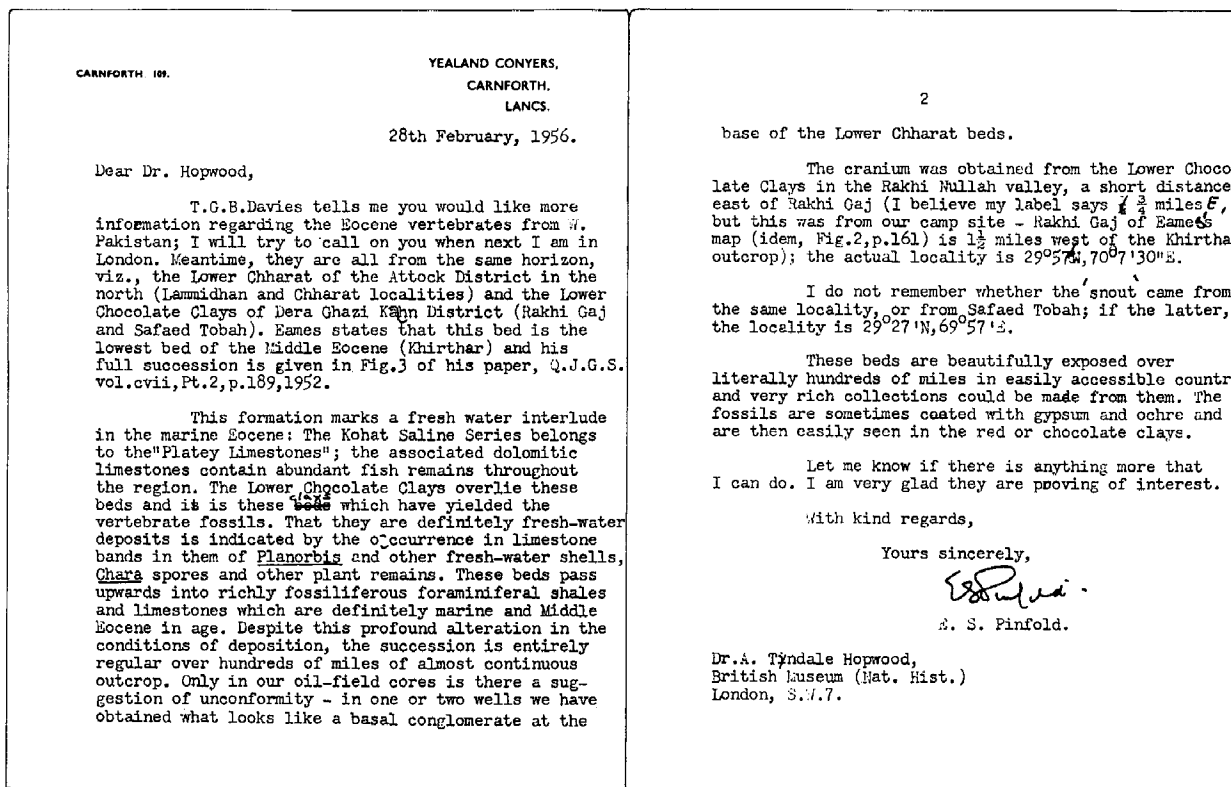


Fig. 2.—Letter from E. S. Pinfold to A. Tyndale Hopwood, dated February 28, 1956, describing the promise of Eocene fossil vertebrate localities in the Domanda Formation or "Lower Chocolate Clays" of the Sulaiman Range of Pakistan. The cranium mentioned by Pinfold is M50719 in the Natural History Museum, London, United Kingdom, which is a partial cranium of *Dalanistes ahmedi* from the north side of Rakhi Nala east of Rakhi Gaj (locality shown in Figure 5). Safaed Tobah, south of Kaha Nala on the map in Figure 1, is the source of the "mesonychid" maxilla described by Pilgrim (1940).

be an eastern-Tethys equivalent of the Lutetian stage of Europe, and the lower Khirthar was (and is) understood to be early middle Eocene in age.

Pilgrim (1940) also described land mammals from what is now the Kuldana Formation at Lammidhan in the Kala Chitta Range of northern Punjab. Broader exploration of the Kuldana Formation in the Kala Chitta Range was organized by Dehm and Oettingen-Spielberg (1958), who added two named "mesonychids," *Gandakasia potens* and *Ichthyolestes pinfoldi*, to the Kuldana Eocene fauna. In 1972, one of us (P.D.G.) visited Kuldana localities in the Kala Chitta Range and examined Kuldana and other Pakistan specimens at the British Museum (Natural History) in London. Accompanying specimens in a drawer in the British Museum was a letter from the geologist E. S. Pinfold to A. Tyndall Hopwood. The letter (reproduced in Fig. 2) mentions Lammidhan and Chharat in northern Punjab and Rakhi Gaj and Safaed Tobah (or Toba) in the Sulaiman Range, and, citing Eames, implies that the lower Chocolate Clays are "definitely fresh-water,"

and states that these are "beautifully exposed over literally hundreds of miles in easily accessible country" where "very rich collections could be made."

The Lammidhan and Chharat localities were examined in more detail in 1975, when discovery of a "*Gandakasia*" tooth led to the suggestion that this "mesonychid" might be an archaeocete (Gingerich, 1977). At this time a team from Howard University (S. T. Hussain), Utrecht (H. de Bruijn), and the Milwaukee Public Museum (R. M. West) began to prospect the Kala Chitta Eocene intensively (Hussain et al., 1978; West, 1980), and a cooperative Geological Survey of Pakistan—University of Michigan (GSP—UM) research project was organized by P. D. Gingerich and D. E. Russell of the Muséum National d'Histoire Naturelle (Paris) to follow up on Pinfold's letter with exploration of the lower Chocolate Clays and other formations in other parts of Pakistan having the potential to yield land mammals.

In the field in 1977 it quickly became clear, contrary to the implication of Pinfold's letter, that the

lower Chocolate Clays (now Domanda Formation) are predominantly or entirely marine, having been deposited in the Tethys Sea on the passively-subsiding northwestern margin of Eocene Indo-Pakistan before uplift of the Himalayas. Fragmentary cranial and postcranial remains of archaeocete cetaceans were found in 1977, and Pilgrim's edentulous "mesonychid" maxilla from Safed Tobah was reinterpreted as representing, possibly, an archaeocete rather than a land mammal (Gingerich et al., 1979). Several massive sacra and innominates with large acetabula found in 1977 were facetiously dubbed "walking whales" in the field, but such whales were then unknown and the specimens were consequently considered more likely to represent moeritheriid or other amphibious land mammals carried into the sea (as Sahni and Mishra, 1975, had interpreted a sacrum from Kutch). Subsequent study has shown that all of these are archaeocetes, as are Pilgrim's Safed Tobah innominate and "anthracotheroid" maxilla and Sahni and Mishra's sacrum. Although disappointing for land mammals, the Eocene of Pakistan showed promise for investigating the early evolution of whales.

Interest in archaeocetes was rekindled by three developments in the 1960s and 1970s. First, Van Valen (1966, 1968) combined the results of comparative immunological study of myoglobins showing Cetacea to be the sister group of Artiodactyla (Boyden and Gemeroy, 1950) with his own understanding of early Cenozoic condylarthran mammals and proposed that Mesonychidae (or later, Mesonychia) are the group from which cetaceans evolved. Second, an important new archaeocete fauna was found and described from the marine middle Eocene of Kutch in India by Tandon (1971, 1976), Sahni and Mishra (1972, 1975), Satsangi and Mukhopadhyay (1975), Trivedy and Satsangi (1984), and Kumar and Sahni (1986). Finally, the cranium of a new and very primitive archaeocete, *Pakicetus inachus*, was found in fluvial deposits now known to be early Eocene in age at Chorlakkhi in Kohat District in the North-West Frontier Province of Pakistan (Gingerich and Russell, 1981; Gingerich et al., 1983). All of these discoveries served to focus attention on the early-to-middle Eocene as the time of origin, and eastern Tethys as the place of diversification, of the earliest Cetacea.

In 1981 a GSP-UM team including Neil Wells, Hassan Shaheed, David Bardack, and William Ryan returned to the Sulaiman Range to look for archaeocetes and other marine vertebrates. There, in addition to a substantial fauna of fishes, they found:

1) the skull included in *Indocetus* by Gingerich et al. (1993; now identified as *Rodhocetus*), 2) well-preserved dentaries described and named *Rodhocetus* by Gingerich et al. (1994), and 3) a partial skull of *Remingtonocetus* cf. *R. harudiensis* described by Gingerich et al. (1995a; identifications and re-identifications are explained in this paper). These specimens all came from the Domanda Formation. In addition, the GSP-UM team found a partially articulated skull and skeleton of a new archaeocete in the underlying Habib Rahi Formation (Gingerich, 1991), which Rahman and Dunkle (1966) had reported as yielding well-preserved marine fishes. Localities are described in Wells (1984) and in Gingerich et al. (1993, 1995a; see Fig. 1 here). The 1981 expedition proved that well-preserved archaeocetes can be found in the Domanda and other Eocene formations of the Sulaiman Range.

Further expeditions were organized in 1992 and 1994 to follow up on the 1977 and 1981 discoveries. Field work in 1992 was concentrated at the northern plunge of the Zinda Pir anticlinorium, particularly in the Domanda Formation of Bozmar Nadi (Fig. 1), and in the Drazinda Formation near Satta (north of Sangarh Nala, north of an area prospected by West et al., 1991; see also Case and West, 1991, and Nolf, 1991). Field work in 1994 was concentrated at the southern plunge of the Zinda Pir anticlinorium, particularly in the Domanda Formation of Takra Daab (Fig. 1). The 1994 field work yielded some ten cetacean skulls or partial skulls, including several with good associated postcranial remains. These show, when studied together with the Pilgrim-Pinfold specimens and our 1977, 1981, and 1992 collections, that there is considerable morphological and taxonomic diversity in early middle Eocene archaeocetes—much greater diversity than is known in late middle and late Eocene archaeocetes found in Egyptian Tethys or elsewhere. Diversity and its temporal succession are important for understanding the early evolution of whales. Six successive archaeocete faunas are now known from Pakistan, substantially improving our understanding of the timing and adaptive diversification of earliest Cetacea.

This paper combines results of Gingerich et al. (1995a, 1995b), with those of Sahni and Mishra (1975), Gingerich et al. (1983, 1993, 1994), Thewissen (1993), and Thewissen et al. (1994), using a stratigraphic framework to investigate the evolutionary chronology of cetacean evolution in eastern Tethys. Possible cetaceans from the early-to-middle

Eocene of Kashmir (Gingerich and Russell, 1994) are not considered here because of ambiguities concerning their age and identification.

Institutional acronyms used in text are: CGM, Cairo Geological Museum, Cairo, Egypt; GSI, Geological Survey of India, Calcutta, India; GSP-UM, Geological Survey of Pakistan—University of Michigan collection, Islamabad, Pakistan; H-GSP, How-

ard University—Geological Survey of Pakistan collection, Islamabad, Pakistan; LUVP, Lucknow University vertebrate paleontology collection, Lucknow, India; NHML, Natural History Museum, London, United Kingdom; VPL/K, Kumar collection, Vertebrate Paleontology Laboratory, Panjab University, Chandigarh, India; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

EOCENE STRATIGRAPHY

Archaeocetes are known from three principal areas in Pakistan: the Kala Chitta Range in northern Punjab, the Kohat District in the North-West Frontier Province, and the Sulaiman Range in western Punjab. Extensive study of the micropaleontological stratigraphy and sea-level stratigraphy from various parts of the western Indo-Pakistan subcontinent has provided a means to correlate the archaeocete-bearing deposits from all three areas to the geological time scale.

KALA CHITTA RANGE AND KOHAT DISTRICT

The geology of Eocene deposits in the Kala Chitta Range of northern Punjab, whence Pilgrim (1940) and Dehm and Oettingen-Spielberg (1958) described Eocene land mammals, was studied by Cotter (1933). These Eocene deposits extend north and east into Hazara (Latif, 1970), and westward across the Indus River into Kohat District in North-West Frontier Province (Eames, 1952*a*, 1952*b*; Meissner et al., 1975). The principal land-mammal-bearing unit is the lower Kuldana Formation (or Mami Khel Formation), which is red mudstone with thin beds of calcarenite representing reworked soil nodules (Wells, 1983, 1984). These calcarenites sometimes preserve reasonably complete skulls (e.g., the holotype of *Pakicetus inachus*) and even skeletons of mammals (e.g., the *Diacodexis pakistanensis* skeletons described by Thewissen et al., 1983), and the entire vertebrate fauna is continental with no marine taxa (Pilgrim, 1940; Dehm and Oettingen-Spielberg, 1958; Buffetaut, 1978; Hussain et al., 1978; Russell and Gingerich, 1980, 1981, 1987; West, 1980; de Bruijn et al., 1982; Hartenberger, 1982; Gingerich et al., 1983; Thewissen et al., 1983, 1987; de Broin, 1987; Gayet, 1987; Rage, 1987; Roe, 1991), except, possibly, archaeocetes like *Ichthyolestes* and *Pakicetus*. Lower Kuldana red beds are interpreted as clastic low-stand wedge deposits that grade laterally and offshore into Bahadur Khel salt and Jatta gypsum in Kohat District, which are

equivalent to Baska gypsum farther south along strike in the Sulaiman Range.

The upper Kuldana Formation is a thin unit of green shales with oyster beds and other indications of shallow marine deposition (Wells, 1984). Mammals are rare elements of the fauna, and these generally represent more amphibious groups like anthracobunids (Wells and Gingerich, 1983) and *Ambulocetus* (Thewissen et al., 1994). The upper Kuldana shales are overlain by nummulite-rich marine Kohat Limestone, which has not yet been found to yield mammalian fossils. The Kohat Limestone was probably deposited during the TA3.2 sea-level highstand, correlative with Habib Rahi deposition in the Sulaiman Range farther to the south (see below).

SULAIMAN RANGE

In 1994 we spent ten days in the Sulaiman Range studying the classic Eocene stratigraphic section exposed in Rakhi Nala near Rakhi Gaj police post. Five formations were examined: 1) the 122 m-thick Baska Shale, "shales with alabaster," or Baska Formation, consisting of interbedded green shales and thin limestones with 10 m of bedded to massive gypsum near the top (Fig. 3, 4); 2) the 43 m-thick Habib Rahi Formation or "platy limestone" consisting of platy limestone and marl alternating with green shale, with limestones 10 cm thick at the base of the formation thinning and becoming more distantly spaced upward in the section (Fig. 3, 5); 3) the 303 m-thick Domanda Formation or "lower chocolate clays" consisting of green clay shale (sometimes fissile paper shales) at the base, brown clay shales in the middle, and brown shales with a lignite near the top (Fig. 3, 5); 4) the 12 m-thick Pir Koh Limestone or "white marl band" (Fig. 3, 6, 7); and 5) the 331 m-thick Drazinda Formation or "upper chocolate clays" consisting of green clay shales with some *Discocyclus*-rich limestones in the lower part and brown to red shales in the upper part (Fig. 6). The upper contact of the Drazinda For-

Rakhi Nala Stratigraphic Sections

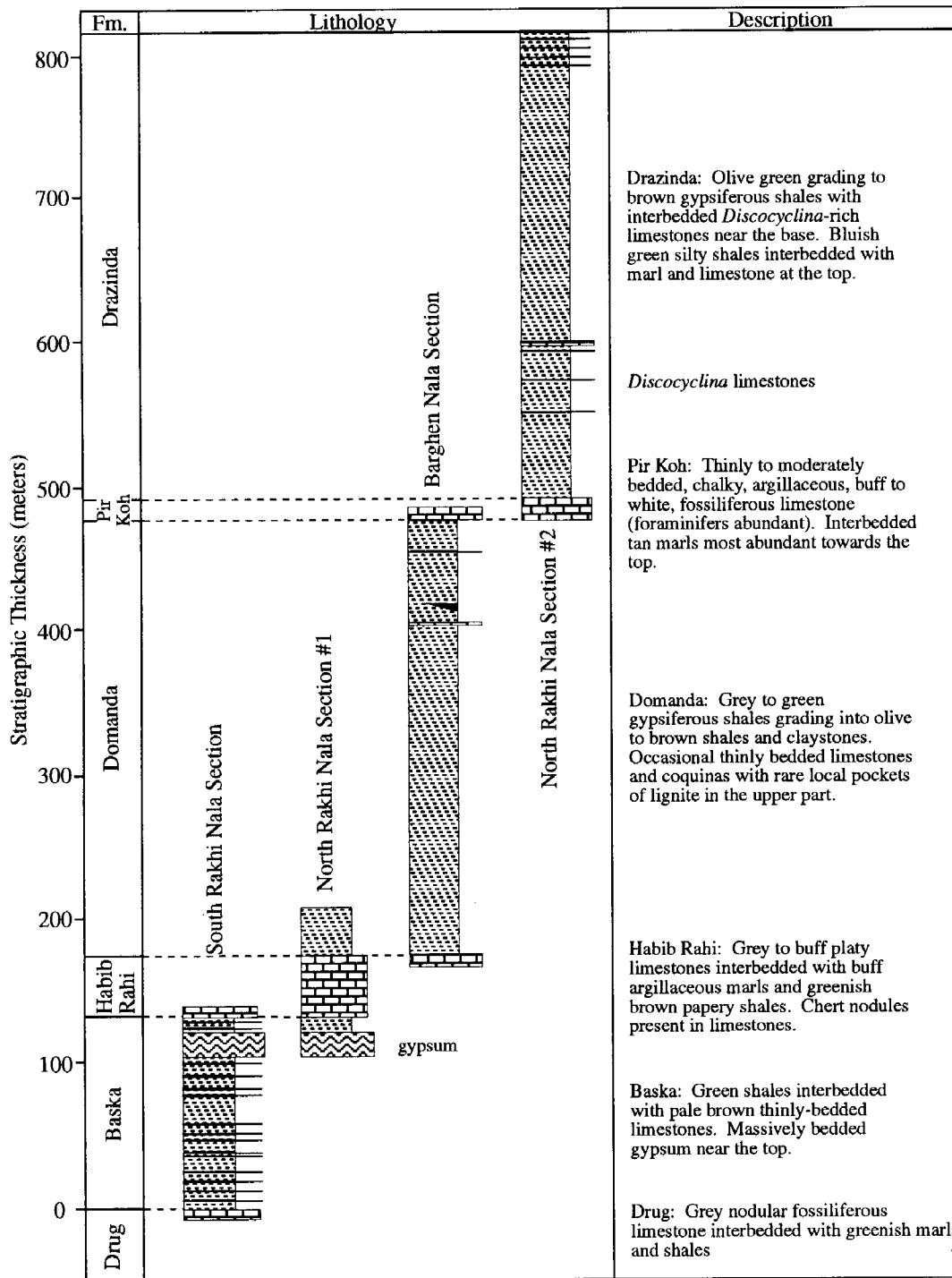


Fig. 3.—Diagrammatic summary of stratigraphic sections of lower and middle Eocene formations measured by the authors in and just north of Rakhi Nala in November 1994. Formational thicknesses are listed Table 1. Baska Formation is best exposed on the south side of Rakhi Nala (Fig. 4). Habib Rahi Formation is best exposed on the north side of Rakhi Nala (Fig. 5). Domanda Formation is best exposed in Barghen Nala just north of Rakhi Nala proper (Fig. 6). Pir Koh Formation (Fig. 7) and Drazinda Formation are best exposed on the north side of Rakhi Nala, where they are overlain disconformably by the continental Miocene Chitarwata Formation.

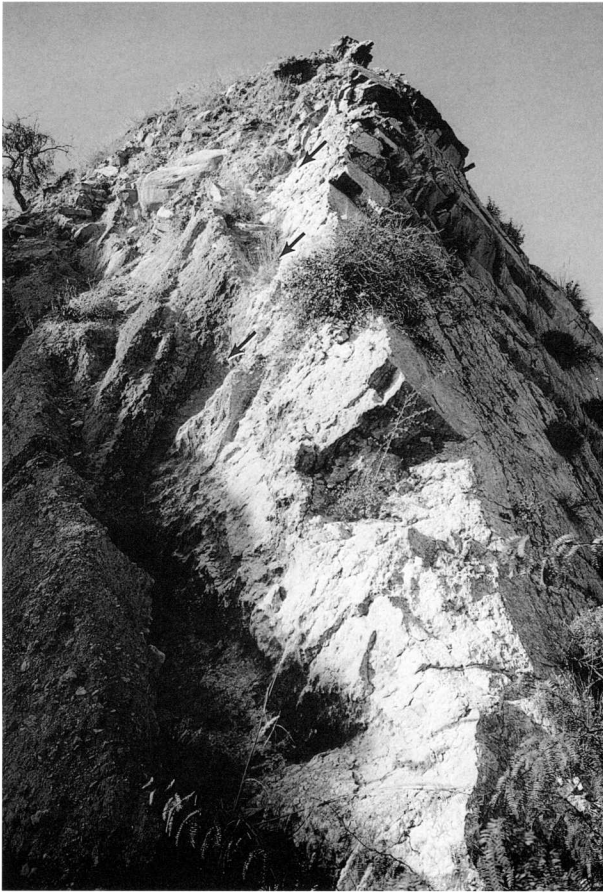


Fig. 4.—Photograph of about 5 m-thick, massive, fine-grained Baska gypsum in the Baska Formation (or Baska Member of the Ghazij Formation), as exposed on the south side of Rakhi Nala (29°56'58"N latitude, 70°6'56"E longitude). View is to the south. Note that the top of the Baska gypsum (white slope dipping toward camera) has an undulating surface (arrows), suggesting subaerial exposure and weathering before deposition of overlying green shale passage beds. This gypsum, like Bahadur Khel salt and Jatta gypsum in North-West Frontier Province, and Kuldana or Mami Khel red beds in North-West Frontier Province and northern Punjab (Meissner et al., 1975), is thought to have been deposited during the latest Ypresian low-sea stand of Haq et al. (1987; see Fig. 8 here).

mation with the overlying lower Miocene Chitarwata Formation (Hemphill and Kidwai, 1973; Downing et al., 1993) is a disconformity and much or all of late Eocene and Oligocene time is lost in this hiatus. Stratigraphic names used here are those of Hemphill and Kidwai (1973) and Shah (1977, 1991).

The Rakhi Nala section is well studied because of its accessibility. The early-to-middle Eocene part of this section of interest here has been studied by Eames and Nagappa (in Eames 1951, 1952a, 1952b, 1952c), who studied the mollusks; by Rieb and

Bayliss in 1956–1957, who concentrated on collecting microfossils (section itself and ostracods published by Siddiqui, 1971; planktonic foraminifera published by Latif, 1961, and Samanta, 1972, 1973); by Rose, Hassan, and Hartenberger (in Gingerich et al., 1979) as part of a project prospecting for fossil vertebrates; and by Bhatti et al. (1988) while mapping the Choti Bala geological quadrangle. Discrepancies in published thicknesses of the formations are all small (Table 1), due to differences in beds chosen as boundaries between formations, differences in precise location where sections were measured, and differences in methods of measurement. These studies and others (Haq, 1967, 1972a, 1972b; Köthe et al., 1988) provide the basic biostratigraphic framework used to correlate the Rakhi Nala section to the geological time scale.

The lithological pattern that stands out in all descriptions of the Rakhi Nala early-to-middle Eocene section is the following: 1) Baska Formation massive fine-grained gypsum or alabaster evaporite deposits, indicating major regression (and possibly some subaerial exposure). This is overlain by 2) Habib Rahi Formation alternating platy limestones with brown and black chert interbedded with green clay shales, indicating relatively deep-water deposition with clastic input (clay) possibly controlled by Milankovich cycles of continental weathering. The spacing of Habib Rahi Formation platy limestones increases up-section and limestone thicknesses decrease up-section until the Habib Rahi Formation has graded insensibly into overlying Domanda Formation clay shales. These 3) Domanda Formation clay shales are rich in fuller's earth and predominantly green at the base of the formation and brown to reddish brown and more silty higher up, indicating a single prolonged regression from early Habib Rahi deposition through all of Domanda deposition. The lithological transition from Domanda clay shales to 4) Pir Koh deeper-water limestone deposition is sharp, indicating a rapid return to deep-water deposition. The Pir Koh Formation gives way to 5) green and then brown and reddish-brown clay shales of the Drazinda Formation, indicating a second single, prolonged regression from early Pir Koh deposition through all or most of the Drazinda Formation. There are *Discocyclina*-filled foraminiferal limestones in the middle part of the Drazinda Formation that suggest the presence of foraminiferal shoals in relatively shallow water. The upper part of the Drazinda Formation (Eames' "Tapti beds") may indicate a brief interval of de-

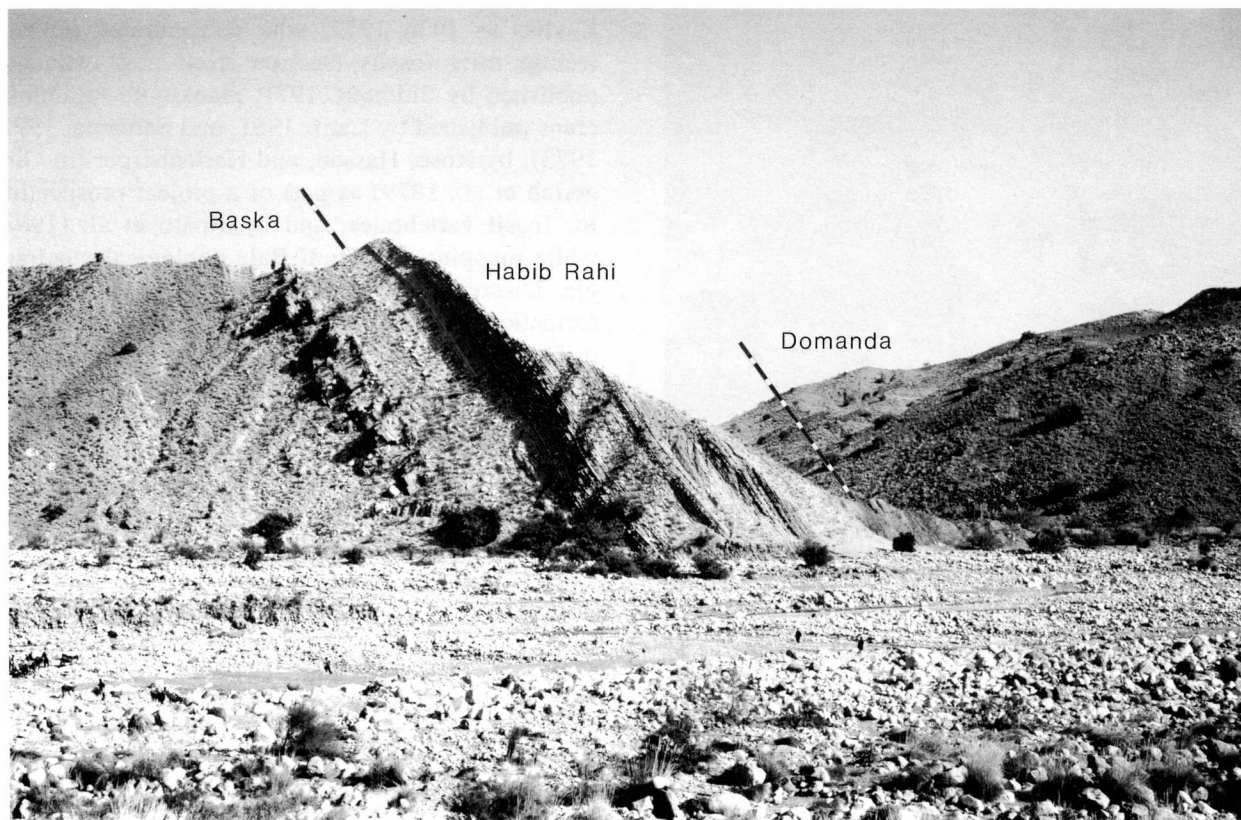


Fig. 5.—Photograph of north side of Rakhi Nala showing North Rakhi Nala section #1 of Figure 3. View is to the north. Section shows ridge-forming gypsum and softer overlying passage beds at the top of the Baska Formation, Habib Rahi Formation platy limestones, and interbedded green shales at the base of the Domanda Formation (right middle of photograph, near stream bed). The British Museum specimen of *Dalanistes ahmedi* (NHML M50719) collected by Pinfold evidently came from the low spit of green shales at the edge of Rakhi Nala ($29^{\circ}57'3''N$ latitude, $70^{\circ}7'3''E$ longitude; Pinfold's coordinates given in his letter reprinted as Figure 2 must be erroneous because they would place the locality in Miocene Vihova Formation much farther to the east). Search for additional parts of the specimen was unsuccessful, possibly because the original site has been eroded by flood waters. Beds here strike $N20^{\circ}E$ and dip $70^{\circ}SE$.

position in deeper water at the very top of the formation.

The importance of this very clear pattern of relative sea-level change is twofold: 1) it shows that a range of depositional environments are represented, suggesting changes in living environments being sampled through time (we return to this below); and 2) it invites interpretation in the context of global sea-level sequence stratigraphy (Haq et al., 1987). This in turn offers much greater chronological precision than might otherwise be possible using biostratigraphy alone. Use of the sequence-stratigraphic record within the biostratigraphic framework from Rakhi Nala allows precise correlations of the Eocene deposits in the Sulaiman Range (and their associated archaeocete faunas) to the geological time scale (Gingerich et al., 1995a, 1995b).

Baska Formation

The Baska Shale has long been considered to be the uppermost member of the Ghazij Formation, but

Shah (1991) recently raised this to formational status. Haq (1967) gave a preliminary report of limited usefulness on calcareous nannoplankton from the Ghazij shales of Zinda Pir, based on a sample collected by Y. Nagappa. Haq's more important work is that of 1972, again on calcareous nannoplankton (Haq, 1972a:7–9; 1972b:139), in which he specified that the Ghazij shale sample came from the *Marthasterites tribrachiatus* zone, nannoplankton zone NP12, of middle Ypresian age. Samanta (1972, 1973) studied planktonic foraminifera from the Rakhi Nala section and concluded that the lower and middle Ghazij Formation belong to Paleogene planktonic foraminiferal zone P8, but samples from the upper Ghazij Formation (now equivalent to the Baska Formation) were characterized by very poor preservation. Haq (1972a, 1972b) and Samanta (1972) agree in placing the lower and middle Ghazij shale in P8 and NP12, which overlap in time and include a sequence of sea-level fluctuations in the

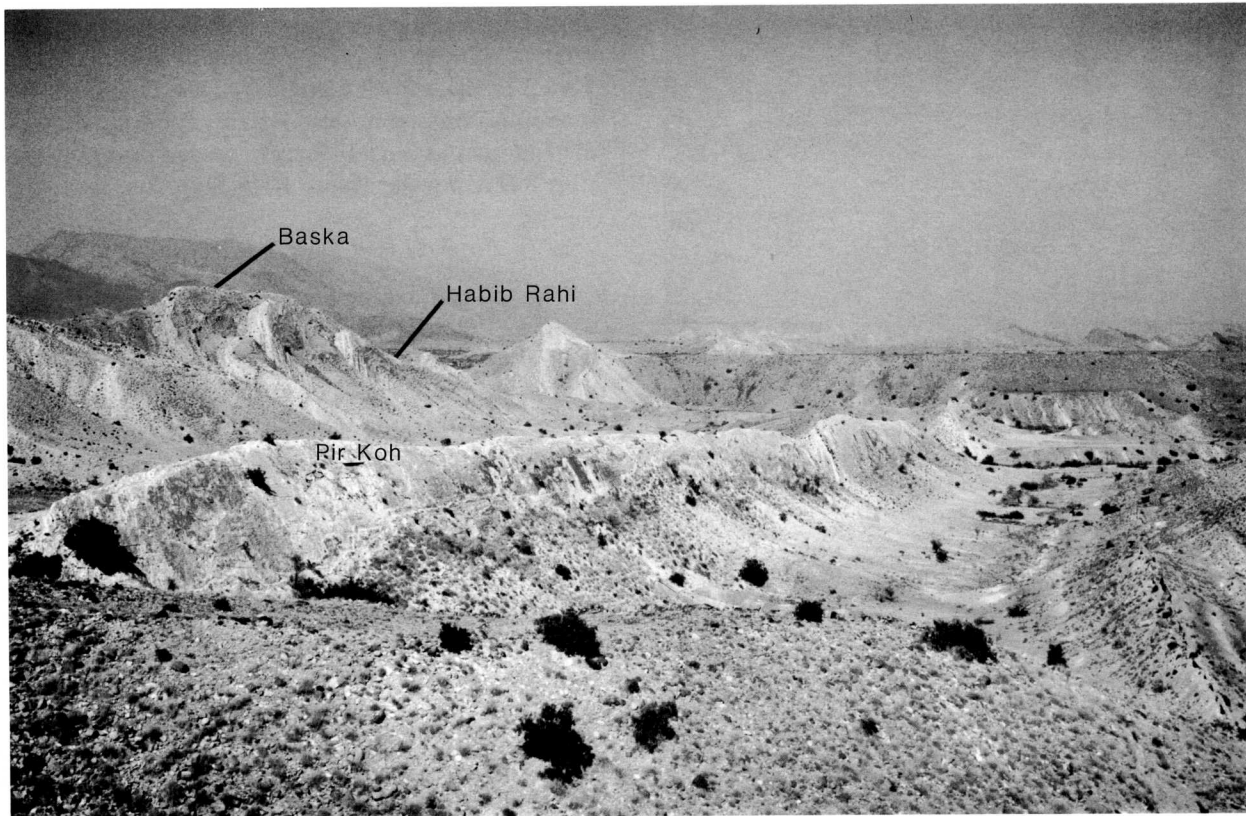


Fig. 6.—Photograph of area north of Rakhi Nala showing general location where Barghen Nala section of Figure 3 was measured. View is to the north, with Sulaiman Range in distance at left. Highest white flatirons at left are ridge-forming Baska gypsum. These are overlain by Habib Rahi platy limestone, which also forms flatiron ridges. Ridge running through center of photograph is Pir Koh limestone. Domanda shales form the valley between Habib Rahi and Pir Koh; these can be seen in cross section in small, sharply eroding nalas (dry stream beds). Shales of lower Drazinda Formation form the valley in the right center of the photograph. Ridges at right margin of photograph are *Discocyclina* limestones. An attempt was made to mine a thin bed of upper Domanda lignite located at 29°57'40"N latitude, 70°7'28"E longitude, which is just to the right of center in this photograph, behind (and stratigraphically below) the ridge of Pir Koh limestone.

middle and late Ypresian (Haq et al., 1987). Köthe et al. (1988) placed the overlying Habib Rahi limestones in late NP14 and early NP15 (see below), which is correlative with the high-sea stand in sea-level cycle TA3.2 in the early Lutetian (Haq et al., 1987). These two ages bracket the massively bedded gypsum in the Baska formation (Fig. 4), which is interpreted to represent the major sea-level fall at the end of the Ypresian. This means that the Baska Formation was deposited during latest Ypresian time.

Habib Rahi and Domanda Formations

The rhythmically-bedded Habib Rahi Formation overlies the Baska Formation in Rakhi Nala and contains closely-spaced platy limestones with brown and black cherts, alternating with green shales that thicken upward, making a smooth transition to Domanda shales as the platy limestones

become thinner and finally disappear (Fig. 5). The Domanda Formation, the formation yielding the most archaeocetes to date, was deposited on a passive continental margin on the northwestern flank of the Indo-Pakistan subcontinent before final closure of Tethys and uplift of the Himalayas. Within the Domanda Formation there is a clear transition from green shales to green and brown shales to red-brown shales. Taken together, these lithological changes indicate a shallowing-upward cycle of marine regression from the Habib Rahi Formation through the Domanda Formation.

Köthe et al. (1988) studied calcareous nannoplankton and dinoflagellates from the Rakhi Nala section and analyzed three samples from the Habib Rahi Formation. Their analysis concluded that the Habib Rahi Formation is late nannoplankton zone NP14 to early NP15 (Köthe et al. 1988:25, fig. 17). Haq (1972a, 1972b) studied the nannoplankton



Fig. 7.—Photograph of Pir Koh “white marl” or limestone where this intersects Rakhi Nala at the base of north Rakhi Nala section #2 (29°56′58″N latitude, 70°7′11″E longitude). View is to the north. Beds here strike N17°E and dip 65°SE. Upper right part of photograph is lower and middle Drazinda Formation with ridges of *Discocyclina* limestone.

from two sites in the Domanda Formation and concluded that it was probably from the *Chiphragmalithus quadratus* zone, NP15. Combining the sequence stratigraphic and biostratigraphic informa-

tion suggests that the Habib Rahi Formation is correlative with the high-sea stand in sea-level cycle TA3.2 in the early Lutetian, and the Domanda Formation is consistent with deposition during the middle Lutetian as a shelf-margin wedge during regression following the Habib Rahi high stand.

Pir Koh and Drazinda Formations

The top of the Domanda Formation is marked by a sharp lithological change, and is overlain by a second regressive cycle of deeper-water Pir Koh limestone shallowing upward through green and red-brown Drazinda shales (Fig. 6, 7). Köthe et al. (1988:25, fig. 17) studied two samples from the Pir Koh white marl band for calcareous nannoplankton and dinoflagellates and concluded that it is in nannoplankton zone NP15. This is consistent with deposition during the high-sea stand in sea-level cycle TA3.3 of the middle Lutetian (Haq et al., 1987). Köthe et al. (1988) also analyzed seven samples from the Drazinda Formation and concluded that the “*Discocyclina* marl” overlying the Pir Koh Formation includes NP16 at the base but is mostly NP17 of Bartonian age; and the uppermost part of the Drazinda is in NP18–NP19/20 of Priabonian age. Haq analyzed an assemblage from two sites in the upper Drazinda Formation and concluded that it is probably from the *Discoaster tani nodifer* zone, NP16, of late Lutetian age. Reference to the Rieb and Bayliss section and sample numbers published by Siddiqui (1971), shows that Samanta (1972, 1973) analyzed samples for planktonic foraminifera from the lower Drazinda, “upper” Drazinda with *Discocyclina*, and “*Pellatispira*” or Tapti beds, which he interpreted as belonging to Paleogene zones P12–13, P14, and P15–17, respectively. Studies in India are also relevant for dating the *Discocyclina* interval of the lower and middle Drazinda

Table 1.—Thicknesses of middle Eocene formations in Rakhi Nala as measured by five independent field parties (Eames, 1952a:163; Rieb and Bayliss in Siddiqui, 1971; Rose, Hassan, and Hartenberger in Gingerich et al., 1979:108; and Bhatti et al., 1988:15–18). Note general similarity of formational thicknesses in all studies: discrepancies can be attributed to slight differences in beds chosen as boundaries between formations, differences in precise location where sections were measured, and differences in methods of measurement.

	Thickness (m)				
	Eames and Nagappa 1943	Rieb and Bayliss 1956–1957	Rose et al. 1977	Bhatti et al. 1985–1986	This study 1994
Drazinda (upper chocolate clays)	297	291	—	225	331
Pir Koh (white marl band)	12	9	—	8	12
Domanda (lower chocolate clays)	283	200	297	208	303
Habib Rahi (platy limestones)	21	27	—	21	43
Baska (shales with alabaster)	229	141	—	55	122
Total	842	668	—	517	811

Formation, which was first found in Kutch (Nuttall, 1926a, 1926b).

Discocyclina is found in the Babia Stage of Biswas (1965, 1992), which includes the interval yielding archaeocetes described by Sahni and Mishra (1972, 1975) and Kumar and Sahni (1986). In the principal reference section in the Berwali stream section at Harudi, where the Harudi and Fulra formations of the Babia Stage are reported as being 40 m thick, archaeocetes come from the interval between about 7.5 and 12.5 m within this (Sahni and Mishra, 1975:5). The same section is published at almost the same scale by Mohan and Soodan (1970:39). Comparison of these two sections shows the relevant archaeocete-bearing interval to be at or near the base of the *Globigerinoides kugleri*–*Globigerina frontosa* or *Globorotalia lehrneri* Paleogene planktonic foraminiferal zone (P12). Singh and Singh (1991) studied calcareous nannoplankton in the Rato Nadi stream section at Harudi, where the Harudi and Fulra formations are reported as being about 20 m thick. The lower part of the Harudi Formation did not yield calcareous nannoplankton, but the upper part of the Harudi section, and by inference the entire whale-bearing Harudi–Fulra transgressive phase, is attributed to Paleogene nanofossil zones NP16 and CP14a (Singh and Singh, 1991:30). Haq (1972a, 1972b) placed upper Drazinda shales in NP16, while Köthe et al. (1988) concluded some of the *Discocyclina* limestones at the base of the Drazinda were NP16 but most of the Drazinda was NP17 or even NP18 and NP19/20 (which is also consistent with Samanta's study of the planktonic foraminifera). Köthe et al.'s and Samanta's interpretation would span such major changes in sea level (Haq et al., 1987) that it is difficult to see how these would not be reflected in more obvious ways in the sedimentary record, and study of *Discocyclina*-bearing strata in Kutch indicating that these belong in NP16 (Singh and Singh, 1991) casts further doubt on the records of NP18 and NP19/20 from the Drazinda Formation. Thus, on the basis of both planktonic foraminifera and nannoplankton from correlative strata in Kutch, the age of *Discocyclina*-rich limestones in the Sulaiman Range would appear to be middle to late Lutetian (P11–P12 and NP15–NP16).

Although the age of the upper Drazinda Formation is uncertain due to the late Eocene and Oligocene depositional and/or erosional hiatus, the green shales with marls and limestones at the very top of the Drazinda Formation suggest deeper-water deposition and it is conceivable that this deepening is

the high-sea stand in sea-level cycle TA3.5, which is correlated with NP17 (Haq et al., 1987).

MAGNETOSTRATIGRAPHY

We attempted to test biostratigraphic and sequence stratigraphic correlation of Sulaiman Range formations to the time scale of Haq et al. (1987) by documenting the paleomagnetic reversal stratigraphy of the Rakhi Nala stratigraphic section in Figure 3. This appeared to be a promising test because late Ypresian and Lutetian polarity reversals are few in number and widely spaced in time (Fig. 8).

A total of 389 oriented paleomagnetic samples from 103 sites were collected to document the paleomagnetic reversal stratigraphy of the Baska, Habib Rahi, Domanda, Pir Koh, and Drazinda formations (347 samples came from 93 sites in Rakhi Nala, and 42 samples came from ten sites in Takra Daab). Sixty-four limestone samples were analyzed using thermal demagnetization in a pilot investigation. Natural remanent magnetization was very weak (mean $J_0 = 0.33$ Ma/m), and characterized by nonbedding-corrected coordinates consistent with the present-day pole (Fig. 9A). Most samples were too weak to provide any stable demagnetization. Samples that did show stable behavior during demagnetization were generally characterized by low unblocking temperatures (below 400° C), and these produced nonbedding-corrected directions consistent with the present-day pole (Fig. 9B, C).

These results suggest that Eocene limestones in the Sulaiman Range carry weak present-day magnetization and little if any primary (Eocene) magnetization. Limestones represent only a small fraction of the total thickness of the Eocene section in this area, but they represent a large fraction of the total interval of time. Consequently, any magnetic polarity record that excluded limestones would be very incomplete and difficult to interpret.

SUMMARY

Taking all of the lithological and microfossil evidence together provides a coherent interpretation in terms of sea-level sequence stratigraphy. Baska gypsum is most plausibly interpreted as having been deposited during the low-sea stand at the end of the Ypresian, correlative with deposition of Bahadur Khel salt and Jatta gypsum in North-West Frontier Province, and Kuldana or Mami Khel red beds in North-West Frontier Province and northern Punjab (Meissner et al., 1975). Passage beds record some sea-level fluctuation in the transition to deeper water

of the Habib Rahi high-sea stand. The Domanda Formation represents deposition with increasing continental clastic influence in a shallowing sea completing a cycle of transgression followed by regression. The Pir Koh limestones represent a second high-sea stand. This was followed in turn by the Drazinda Formation representing deposition with increasing continental clastic influence in a shallow-

ing sea, completing a second cycle of transgression followed by regression. Harudi Formation fossils from Kutch correlate with this second cycle of transgression followed by regression. It is possible that the "Tapti" green shales and marls at the top of the Drazinda Formation reflect a third high-sea stand, with the record of everything that followed being erased by erosion.

MARINE MAMMAL FAUNAS

A total of six archaeocete faunas are recognized in Pakistan and these can be put into a temporal framework using the stratigraphic framework outlined above. The two oldest archaeocete faunas of Pakistan come from Kohat and northern Punjab: 1) the *Pakicetus* fluvial fauna comes from the lower Kuldana Formation, which we have correlated to the low-sea stand during the latest Ypresian (about 49.0 to 49.5 million years before present on the Haq et al. time scale); and 2) the *Ambulocetus* transitional-marine fauna comes from the upper Kuldana Formation and overlying Kohat Formation, which we have correlated to the earliest Lutetian (about 49.0 to 48.0 Ma). The former fauna is found in Kohat District of the North-West Frontier Province and in the Kala Chitta Range of northern Punjab (Gingerich et al., 1983), and the two faunas are found in superposition in the Kala Chitta Range of northern Punjab (Thewissen et al., 1994). The *Pakicetus* fauna includes *Ichthyolestes*, named by Dehm and Oettingen-Spielberg (1958), and *Pakicetus*, named by Gingerich and Russell (1981). *Ichthyolestes* has also been reported from Indian Kashmir (Kumar and Sahni, 1985). The *Ambulocetus* fauna includes *Ambulocetus*, named by Thewissen et al. (1994), and several additional taxa that are as yet poorly known. The *Pakicetus* fauna, as now known, is reviewed by Thewissen and Hussain (1998).

Four succeeding faunas come from the Sulaiman Range in southwestern Punjab: 3) the Habib Rahi Formation deep-shelf marine fauna comes from platy limestones which we have correlated to the early Lutetian (about 48.0 to 46.5 Ma), 4) the lower Domanda Formation *Rodhocetus-Takracetus* middle-shelf marine fauna comes from green clays and limestones which we have correlated to the early middle Lutetian (about 46.5 to 46.0 Ma), 5) the middle Domanda Formation *Gaviacetus-Remingtonocetus-Dalanistes* shallow shelf marine fauna comes from brown clays which we have correlated to the middle Lutetian (about 46.0 to 45.5 Ma), and

6) the middle Drazinda Formation *Babiacetus-Protosiren* shallow-shelf marine fauna comes from green clays which we have correlated to the late middle Lutetian (about 43.5 Ma). Use of a different time scale (e.g., Berggren et al., 1992; or Cande and Kent, 1992) might change the value of each calibration slightly but it will not change the geological age for any of the faunas nor the ca. 6 million-year duration of the composite sequence.

The first of the Sulaiman faunas, the Habib Rahi fauna, is rich in well-preserved fish fossils (Rahman and Dunkle, 1966), and has yielded a well-preserved, partially articulated skeleton of a new protocetid archaeocete (Gingerich, 1991; not yet studied in detail), that appears to be intermediate in morphology between earlier *Pakicetus* and later protocetids.

The best known Sulaiman faunas are those from the lower Domanda Formation (*Rodhocetus-Takracetus* fauna) and the middle Domanda Formation (*Gaviacetus-Remingtonocetus-Dalanistes* fauna). Some remains have been known for more than 50 years (Pilgrim, 1940), but these are fragmentary, were published as representing land mammals, and cannot at present be related to lower or middle parts of the Domanda Formation. Finds made in 1981, interpreted in the light of discoveries in Kutch in India (Sahni and Mishra, 1972, 1975; Satsangi and Mukhopadhyay, 1975; Kumar and Sahni, 1986), showed that the Domanda Formation has the potential to yield well-preserved archaeocetes, but these were insufficient to suggest that differences exist between lower and middle Domanda faunas.

Differences between the lower and middle Domanda faunas were perceived in 1992 when the type specimen of *Rodhocetus kasrani* was found in lower Domanda green shales (Fig. 10). This type specimen is a largely articulated axial skeleton with skull and lower jaws, cervical, thoracic, lumbar, sacral, and proximal caudal vertebrae, ribs, left and right pelvic bones, and a right femur (Fig. 11). Here the

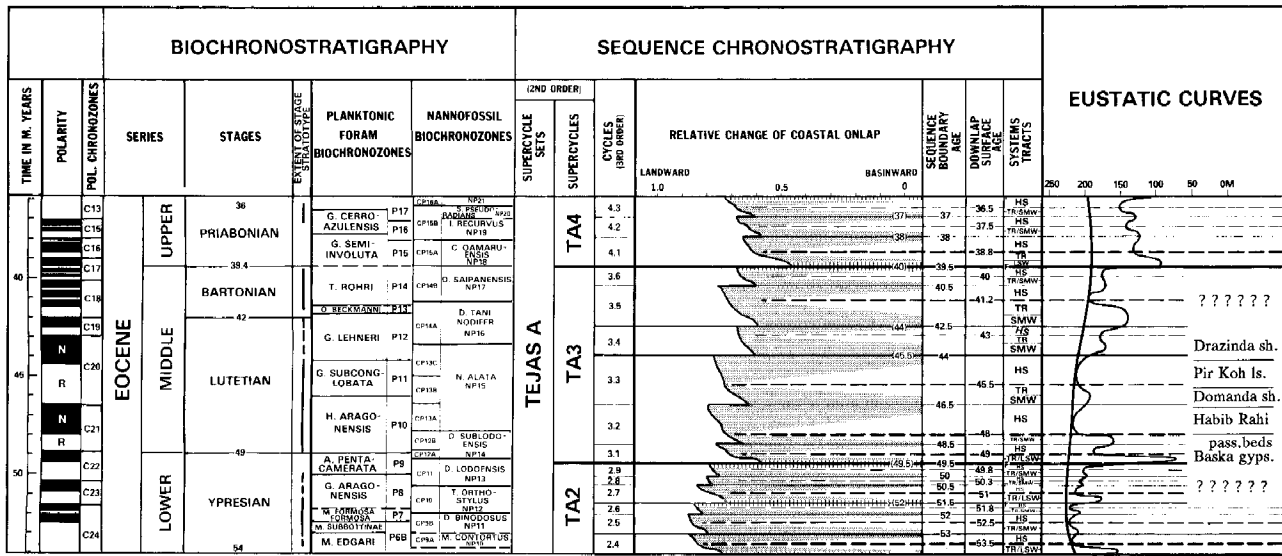


Fig. 8.—Correlation chart showing inferred ages of Baska gypsum and passage beds and Habib Rahi, Domanda, Pir Koh, and Drazinda formations in relation to sea-level sequence stratigraphy of Haq et al. (1987). Thicknesses of formations composed of different lithologies are not always proportional to temporal duration of deposition. Habib Rahi and Pir Koh limestones are relatively thin in the field but represent a considerable duration of time because they are high-stand deposits that accumulated offshore and have relatively little clastic influx; while Baska, Domanda, and Drazinda shales are relatively thick in the field but represent much less time than their thicknesses would suggest because they were deposited closer to shore and are predominantly clastic in composition. Correlation of formations studied here is shown in rightmost column of chart.

cervicals are relatively short, indicating a relatively short neck by comparison with that of *Remingtonocetus*. The sacrum has four vertebral centra, distinguished in having typical sacral articulations between pleurapophyses, but these centra are not fused together like those of land mammals and contemporary remingtonocetids. Rather, the sacra are free to move relative to each other like more-posterior caudals, indicating evolutionary “caudalization” of the sacrum and lumbus, giving them mobility like that found in later archaeocetes and required for efficient cetacean tail-powered swimming. The sacrum has auricular facets indicating direct articulation with the pelvis. The femur is short but well formed and functional, with condyles for articulation with a substantial tibia (not found). Well-developed hind limb elements suggest that *Rodhocetus* was able to support its weight and move on land, although its unfused sacrum would limit the power and range of locomotion on land. *Takracetus simus* is presently known only from a cranium with a distinctively broad palate, which was found in lower Domanda green shales. This indicates some trophic diversification of early Domanda archaeocetes but it is otherwise not very informative.

The first protocetid archaeocete found in the mid-

dle Domanda Formation was found in 1994. This form, *Gaviacetus razai*, has a distinctively narrow palate, again indicating trophic specialization. *Gaviacetus* has an associated sacral vertebra consisting of a single centrum with broad transverse processes for articulation with a pelvis (not found). The sacrum is well preserved and there is no indication of fusion to a succeeding vertebral centrum nor articulation with its pleurapophyses. Thus the sacrum included a single centrum, like that of *Protocetus*, and there was probably even more mobility in such a functionally “caudalized” vertebral column than was present in *Rodhocetus*. It seems likely that *Gaviacetus*, like *Rodhocetus* and *Protocetus*, could support its weight and move on land.

Two associations of cranial fragments and post-cranial remains from the middle Domanda Formation were identified (misidentified) in 1992 as *Indocetus ramani* (Gingerich et al., 1993). These were later recognized as pertaining to *Remingtonocetus* cf. *R. harudiensis* by Gingerich et al. (1995a) when better comparative material was available. The most important elements of these finds are: 1) long cervical vertebrae, indicating that *Remingtonocetus* had a longer neck than contemporary protocetids; 2) a large land-mammal-like sacrum composed of four sacral vertebrae that are solidly fused together, in-

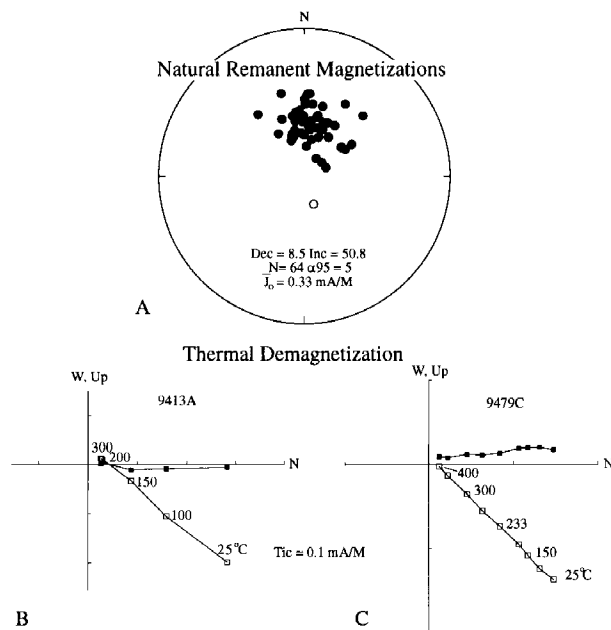


Fig. 9.—Paleomagnetic analysis of limestone samples from the Rakhi Nala section. A. Geographic coordinates (no bedding correction) of the natural remanent magnetizations (NRM) for 64 pilot samples analyzed. Samples have very low initial intensities, and directions consistent with the present-day pole. B, C. Zijderveld diagrams for two samples with stable behavior showing geographic coordinates during thermal demagnetization. Notice low unblocking temperatures, and directions consistent with the present-day pole. These results suggest the presence of a weak magnetic carrier with low unblocking temperatures bearing present-day magnetization.

dicating that *Remingtonocetus* lacked the lumbocaudal vertebral mobility of protocetids; and 3) a pelvis with auricular facets indicating direct articulation with the sacrum, and a large acetabulum, large femur, and long tibia indicating that *Remingtonocetus* retained a large hind limb capable of supporting and moving the body on land.

In 1994 a second remingtonocetid, *Dalanistes ahmedi*, was found in both lower and middle Domanda localities, but it is more common in the middle Domanda Formation. *Remingtonocetus* and *Dalanistes* have crania that are some six times longer than they are broad across the frontals, and both have preorbital rostra that are more than 60% of total skull length. Both have scapanoid or shovel-shaped frontals, relatively small orbits, ventrally convex palates, and loosely-attached exoccipitals that taper ventrally. *Dalanistes* differs from *Remingtonocetus* in being some 20% larger; having external nares open above C¹ rather than P¹; having much higher sagittal and nuchal crests, with the rostrum distinct-

ly angled downward relative to the orientation of the braincase (clinorhynch); retaining an open mandibular symphysis (synarthrosis) that ends at P₃ rather than P₄; and having mandibular canals in left and right dentaries separate throughout their length. Some other distinctive features of *Dalanistes*, like the deep ventral midline keel formed by left and right palatine-ptyergoids and the broad tympanic-paroccipital synchondrosis, may be found in *Remingtonocetus* when better specimens are known. Postcranially, *Dalanistes* has long cervical centra that are larger but otherwise seemingly identical to those of *Remingtonocetus*. The fused sacrum, pelvis, and well-developed hind limbs of *Dalanistes* appear to have been very similar to those of *Remingtonocetus*, suggesting that it too was capable of supporting the body with the hind limbs for significant locomotion on land.

Skulls of the five archaeocetes, three protocetids and two remingtonocetids, now known from the lower and middle Domanda Formation are compared in Figure 12, which shows their differing rostral proportions and, by interpretation, trophic specializations. Among protocetids, *Takracetus* has the broadest rostrum, *Rodhocetus* has a rostrum of intermediate breadth, and *Gaviacetus* has the narrowest rostrum. The two remingtonocetids are similar in rostral proportions, but differ from all of the protocetids in being more needle-nosed. Broader-nosed archaeocetes may have fed on larger fishes, while narrower-nosed archaeocetes may have fed more selectively on smaller fishes, but details of possible specialization cannot, as yet, be suggested. When hind limb differences are considered, protocetids appear to have been more pursuit-oriented, while remingtonocetids may have been ambush-predators. There is a tendency, too, for protocetids to be found in deeper-water sediments of the lower Domanda Formation, while remingtonocetids predominate in shallower-water sediments of the middle Domanda Formation, which is consistent with the former being more efficient swimmers able to range farther offshore.

The middle Drazinda Formation *Babiacetus-Protosiren* shallow-shelf marine fauna is younger than the Domanda faunas described here, but it has not yet been sampled well enough to permit any generalization about it. The only archaeocete known to date, a protocetid skull and lower jaws described by Gingerich et al. (1995b), is evidently the same as *Babiacetus indicus*, named by Trivedy and Satsangi (1984) from Kutch in India. *Protosiren sattaensis* is found in the Drazinda Formation



Fig. 10.—Type locality of *Rodhocetus kasrani* before excavation ($30^{\circ}46'06''N$ latitude, $70^{\circ}26'37''E$ longitude). When found, all that was showing of the type specimen (Fig. 11) was the ventral margin of a dentary (white pieces of bone to left of glue bottles in foreground). This locality is in Bozmar Nadi (Fig. 1). Lithology is green clay shale of the lower Domanda Formation, with 1–5 mm-thin layers of gypsum mobilized during folding of the Zinda Pir anticlinorium. View is to the south, and the ridge in the background is a Habib Rahi Formation dip-slope at the northern plunge of the Rodho anticline. Bottles and brush give the scale in the foreground, and the collector on the ground in the right center of the photograph gives the scale in the middle distance.

(Gingerich et al., 1995b), and it, or some closely related species, is also found in Kutch (Bajpai et al., 1989). If the vertebrate fauna of the Pir Koh and Drazinda sea-level cycle is the same as that of Kutch (Sahni and Mishra, 1972, 1975; Kumar and Sahni, 1986) then we should expect to find the protocetid *Indocetus ramani* and the remingtonocetids *Remingtonocetus harudiensis* and *Andrewsiphius*

kutchensis in the Drazinda Formation in addition to *Babiocetus*.

The Drazinda Formation fauna is evidently younger than the long-known Egyptian *Protocetus*–*Protosiren* fauna of Gebel Mokattam (ca. 45.0 Ma; Gingerich, 1992), and the Indian *Indocetus*–*Remingtonocetus* fauna from Kutch probably lies in the range spanned by these two (ca. 45.0 to 43.5 Ma). *Rod-*

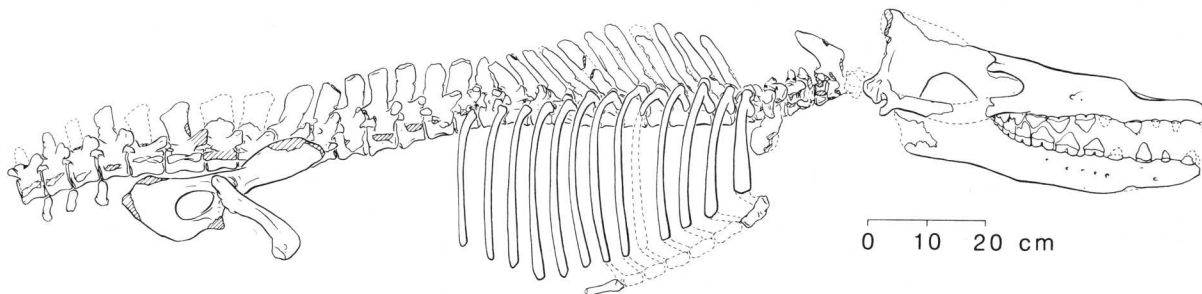


Fig. 11.—Skeleton of protocetid *Rodhocetus kasrani* (GSP-UM 3012, holotype) from the lower Domanda Formation (type locality shown in Figure 10). Note relatively short cervical vertebrae and neck, high neural spines on thoracic vertebrae, sacrum composed of four centra with pleurapophyseal articulations but no fusion, relatively large femur and pelvis articulating with sacrum, and base of heavy tail. Figure from Gingerich et al. (1994).

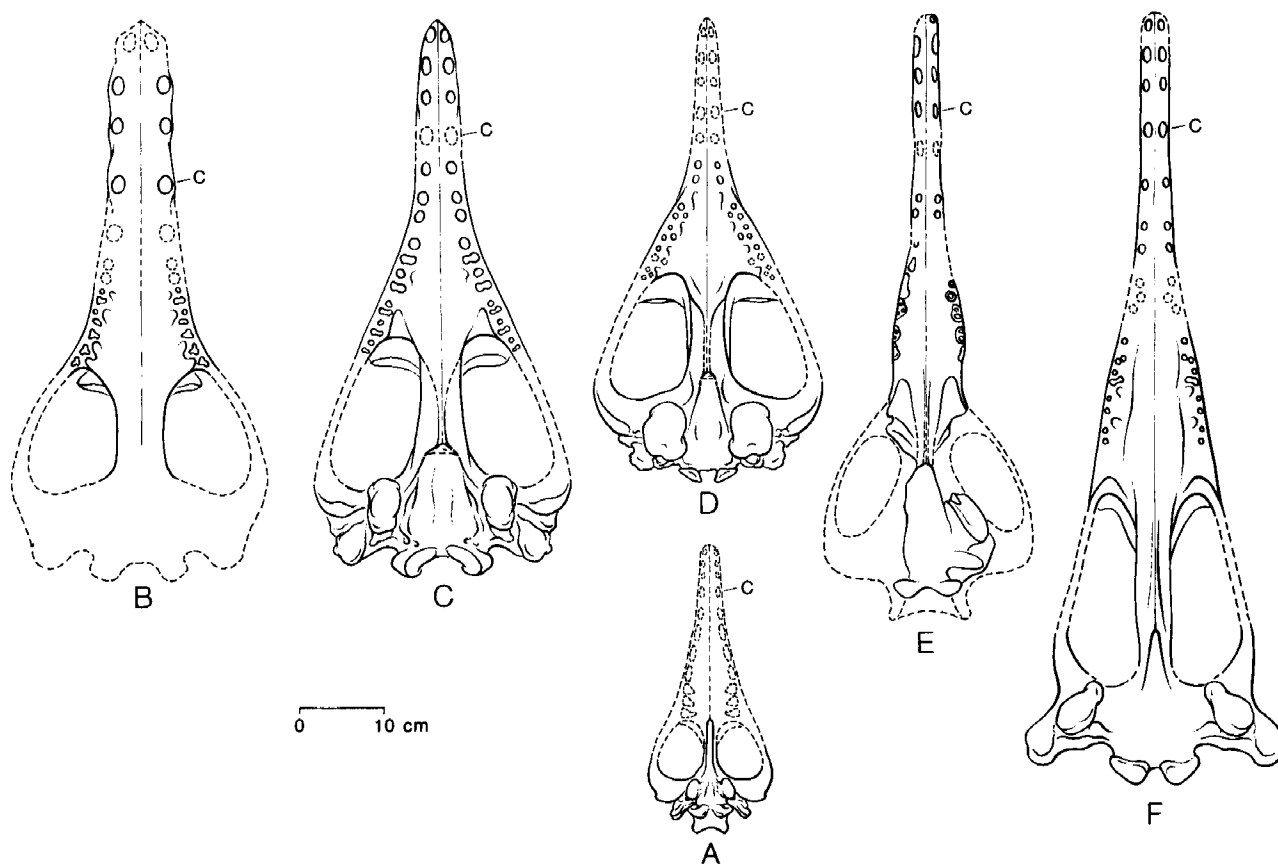


Fig. 12.—Comparison of the skull of late Ypresian *Pakicetus* (A) from the Kuldana Formation of Kohat District, North-West Frontier Province, with five skulls of later archaeocetes from the middle Lutetian Domanda Formation of the Sulaiman Range, southwestern Punjab. The five Domanda archaeocetes are the protocetids *Takracetus* (B), *Rodhocetus* (C), and *Gaviacetus* (D), and the remingtonocetids *Remingtonocetus* (E) and *Dalanistes* (F). Morphological diversity in the Sulaiman Range fauna from the Domanda Formation is greater than that known to date from any other time or place in the history of archaeocetes, but this may change as the younger Pakistan Drazinda Formation and Indian Harudi-Fulra Formation archaeocete faunas become better known. The well-known middle-to-late Eocene (latest Bartonian and Priabonian) archaeocete faunas of Egypt include a similar number of taxa, but all have very stereotyped skulls that vary little from taxon to taxon.

hocetus, *Protocetus*, and *Indocetus* are difficult to tell apart from skulls alone, but the pelves of *Rodhocetus* and *Protocetus* are very different, and it is likely that these both differ from *Indocetus* as well

(although this awaits confirmation by discovery of more nearly complete postcranial remains of *Indocetus* in Kutch).

DISCUSSION

The archaeocete faunas of Pakistan show several things about the early evolution of whales that were not evident before these were discovered. First, eastern Tethys was clearly part of the center of origin and diversification of early archaeocete whales. It may not have been the only center, and any such center or centers may have covered a broad area, but eastern Tethys has yielded more stages of early whale evolution than any other geographic region

and it must have been part of the range in which early whale diversification was taking place.

Second, there is a much broader range of cranial and postcranial morphological diversity represented in the known Pakistan archaeocetes than there is in archaeocetes found in younger deposits elsewhere (e.g., in Egypt or southeastern North America, where later archaeocetes are well sampled). This is illustrated for the Domanda Formation by the range

Table 2.—Differences distinguishing skulls and postcranial skeletons of middle Eocene Protocetidae and Remingtonocetidae (from Gingerich et al., 1995a, with additions).

Protocetidae	Remingtonocetidae
Length of cranium approximately 3× breadth across frontals	Length of cranium approximately 6× breadth across frontals
Preorbital rostrum less than 60% of total skull length	Preorbital rostrum more than 60% of total skull length
Orbits medium to large in diameter relative to rest of skull	Orbits small relative to rest of skull
Nares open above C ¹ , P ¹ , or P ²	Nares open above C ¹ or P ¹
Frontals sphyroid or hammer-shaped	Frontals scapanoid or shovel-shaped
Incisors and anterior premolars circular in cross section and robust	Incisors and anterior premolars narrow labiolingually
Upper molars generally small and broad, with two lateral roots and a distinct medial root	Upper molars generally larger and narrow, sometimes double-rooted and lacking distinct medial root
Palate flat or concave ventrally	Palate convex ventrally
Ventral palatine-ptyergoid surface flat or shallowly ridged	Ventral palatine-ptyergoid surface with deep ventral midline keel
Bulla articulation with rest of skull includes a narrow paroccipital synchondrosis	Bulla articulation with rest of skull includes a broad paroccipital synchondrosis
Exoccipitals rectangular, robustly integrated with squamosal, and solidly attached to rest of skull	Exoccipitals tapering downward, loosely attached to squamosal, and separated from basioccipital by a waisted section that often breaks
Cervical centra are shorter than they are wide or high, and shorter than anterior thoracic centra	Cervical centra are as long as they are wide or high, and as long or longer than anterior thoracic centra
Sacrum is composed of four or fewer vertebral centra, with sacral centra generally not fused to each other	Sacrum is composed of four vertebral centra, with centra of S1–S3 and generally S4 solidly fused to each other
Innominate with smooth lateral surface in front of acetabulum, with a shallow acetabular fossa and no distinct acetabular notch	Innominate with distinct depression on lateral surface in front of acetabulum, with a deep acetabular fossa and a distinct acetabular notch
Femoral head with distinct, deep fovea for round ligament	Femoral head with shallow or indistinct fovea for round ligament
Femoral shaft round; distal femur narrow relative to shaft diameter, with a narrow, raised patellar groove	Femoral shaft oval in cross section, with lateral keel for muscle insertion; distal femur broad relative to shaft diameter, with a broad, shallow patellar groove

of cranial shapes illustrated in Figure 12, but the later “Drazinda” fauna known from Kutch may include a still greater range of forms. *Babiacetus*, for example, is larger than any protocetid known from the Domanda Formation, and *Andrewsiphius*, to take another example, is a more specialized remingtonocetid than any known from the Domanda Formation.

Third, protocetids and remingtonocetids share many features characteristic of archaeocetes, but by Domanda time these two families are clearly separated in having many distinctive cranial and postcranial specializations (Table 2). Protocetids appear to have been the more active swimmers, and to have been the ancestors of basilosaurid archaeocetes and, through dorudontine basilosaurids, the ancestors of later modern cetaceans.

Fourth, the sequence of acquisition of distinctive aquatic adaptations through time indicates that the initial specialization of archaeocetes was a trophic one, with evolution of a characteristic dentition appearing first. *Pakicetus*, the oldest archaeocete known from a skull, was found in continental red

beds with an associated land-mammal fauna. It has sharply-pointed conical anterior teeth, and long, narrow posterior premolars and molars suggestive of feeding on fish (Gingerich and Russell, 1990). *Pakicetus* can have had little ability to hear directionally in water (Gingerich et al., 1983), nor even the ability to hear well in water: *Pakicetus* has a small mandibular canal, meaning that sound reached the ear drum through the external auditory meatus as in land mammals, and its incus is intermediate between land mammals and aquatic cetaceans in inflation, crural proportions, and position of the malleolar joint (Thewissen and Hussain, 1998). The postcranial skeleton of *Pakicetus* is still unknown.

The second stage of specialization of early archaeocetes involved the hearing apparatus (Luo et al., 1995). The Habib Rahi archaeocete and slightly later *Rodhocetus* (Gingerich et al., 1994) have a *Pakicetus*-like dentition with pointed anterior teeth and long, narrow posterior cheek teeth but, in addition, the auditory bullae are large and dense, and there are well-developed mandibular canals not seen in *Pakicetus* that open into a large “acoustic win-

dow" on the medial side of each dentary. These are interpreted as wave guides to aid hearing in water (Norris, 1968). There are no pterygoid fossae or accessory air sinuses associated with the bullae, so directional hearing may have been limited. Hind limbs are not yet known for the Habib Rahi archaeocete but, as stated above, *Rodhocetus* retained a sacrum, pelvis, and substantial hind limbs capable of supporting its weight on land, and the Habib Rahi archaeocete probably did also. Remingtonocetids, as far as they are known at present, appear not to have progressed beyond this second stage of aquatic specialization.

The third stage of specialization of archaeocetes involved streamlining the body by shortening the neck and reducing the hind limbs, with development of cetacean-style swimming locomotion involving "caudalization" of the lumbus and sacrum associated with dorsoventral oscillation of a heavily muscled tail. *Rodhocetus* shows clear evidence of all three: cervical vertebrae are relatively short, the femur is reduced in size, and the sacral vertebrae are

no longer fused into a solid sacrum. However, none of these shortenings, reductions, and disarticulations in *Rodhocetus* is carried as far as it is in later basilosaurids (Gingerich et al., 1990).

The observation that the initial aquatic adaptation was trophic supports the idea that archaeocetes entered Tethys to feed on fish in the late early Eocene when eastern Tethys was a highly productive shallow seaway of elevated salinity (Gingerich et al., 1983). One can easily imagine the opportunism of a succession of cursorial *Sinonyx*- or *Pachyaena*-like mesonychid "strandloopers" feeding first on fish carrion washing up on the shoreline, and then learning to catch live fish trapped in lagoonal pools or slower fish in shallow open water. There are two ways to do this: one is to ambush fish as remingtonocetids may have done, and the other is to pursue them as protocetids must have done. It is, of course, simplistic to think in terms of three discrete stages of aquatic adaptation. These clearly overlapped in development, and there must be many substages still to be recognized in the evolution of archaeocete feeding, hearing, and locomotion.

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Note added in proof:

Correlation chart (Fig. 8) in this paper is superseded by correlation chart in Gingerich et al., 1997:fig. 14.

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