A new, diminutive Eocene whale from Kachchh (Gujarat, India) and its implications for locomotor evolution of cetaceans

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Our recent paleontological field work in the middle Eocene Harudi Formation of Kachchh (western India) has yielded a partial skeleton of a new species of Eocene cetaceans, here named *Kutchicetus minimus*. The new species represents a new genus in the family Remingtonocetidae and is smaller than any other Eocene whale. The skeleton includes teeth, skull fragments, limb bones and a relatively complete vertebral column. Vertebral proportions indicate that the vertebral column of the new cetacean functioned in different ways from any other known Eocene or Recent cetacean. It suggests that the mobility of the back may have approximated that of otters.

THE middle Eocene Harudi Formation of Kachchh is well known for its wealth of early cetacean fossils, including six genera in the families Remingtonocetidae, Protocetidae and Dorudontidae[1–3]. These cetaceans ranged across a wide spectrum of body shapes and locomotor modes. For instance, *Remingtonocetus* was a cetacean with powerful limb skeleton that was probably the main propulsive organ[4,5]. *Babiacetus* and *Indocetus* are protocetids for which no skeletons are available, but closely related forms such as *Georgiacetus*[6], indicate that protocetids were good swimmers that used tail-beats coupled with a fluke in some species[5]. All cetaceans from Kachchh were moderate to large, the smallest species being *Andrewsiphius minor*, which may have been similar in size to a small dolphin. Here we report on a new cetacean from Kachchh, which is significant because it extends the range of known body sizes, and because it includes limb bones and a vertebral column that is more complete than that of any other described early-middle Eocene cetacean. We propose the name *Kutchicetus minimus* for the new genus and species. The specific indication makes explicit that *K. minimus* is smaller than the smallest described remingtonocetid, *Andrewsiphius minor*. *Kutchicetus* is known at present only from its holotype: RUSB 2647, a partial skeleton, including eight fragmentary teeth, fragments of the skull, 32 vertebrae or parts thereof, a humerus, ilium, proximal femur, and tibia (Figure 1). The type locality is near Godhatad (68°39′30″E: 23°39′N), 1 km east of the village, just north of the unmetalled track to Nareda (locally known as Naredi; Figure 2). The type specimen comes from a grey limestone (often called the chocolate limestone[2]), that weathers brown and is part of the middle Eocene (Lutetian) Harudi Formation[7]. *Kutchicetus* is monotypic, and generic and specific diagnoses of the species cannot be distinguished.

The narrow snout, elongate premolars, and four-vertebrae sacrum (Figure 3) indicate that *K. minimus* is a remingtonocetid. It can be diagnosed from other remingtonocetids on the basis of its small size. It is less than half the size (in linear dimensions) of the smallest known remingtoncetid (*A. minor*), and may be the smallest Eocene cetacean in the world. *Kutchicetus* resembles *Andrewsiphius*, but differs from *Remingtonocetus* and *Dalanistes*, in having an extremely narrow snout in which the lateral wall of the upper jaw bulges laterally to accommodate alveoli. It has a tail that is stronger than that in *Remingtonocetus* or *Andrewsiphius* (RUSB 2526), and short fore- and hind-limbs.

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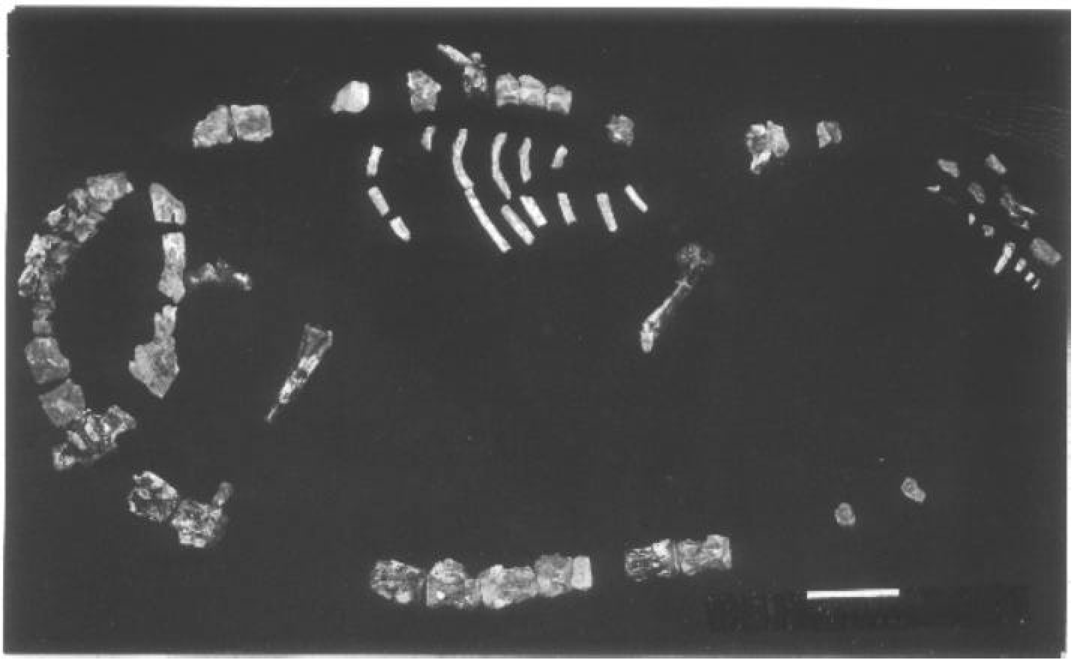

Figure 1. Skeleton of *Kutchicetus minimus*. Scale bar represents 10 cm.

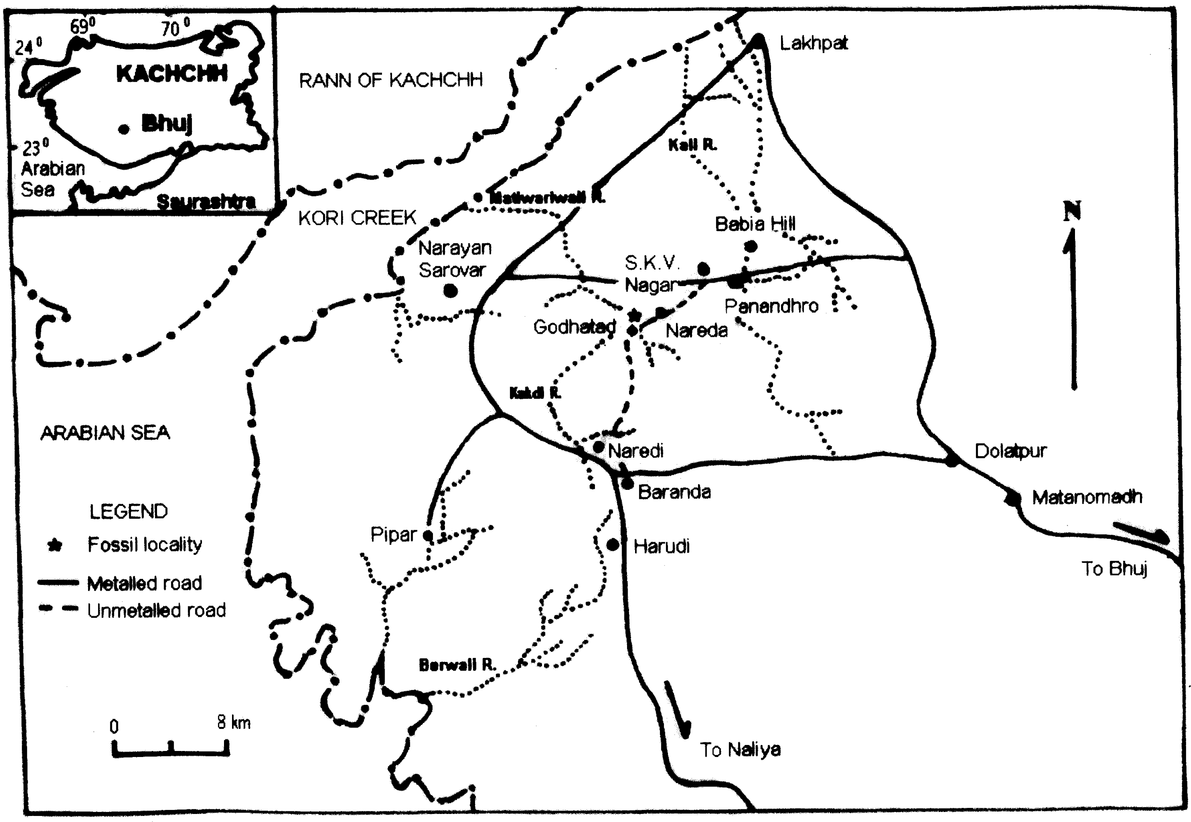

Figure 2. Location map of the type locality of *Kutchicetus*.

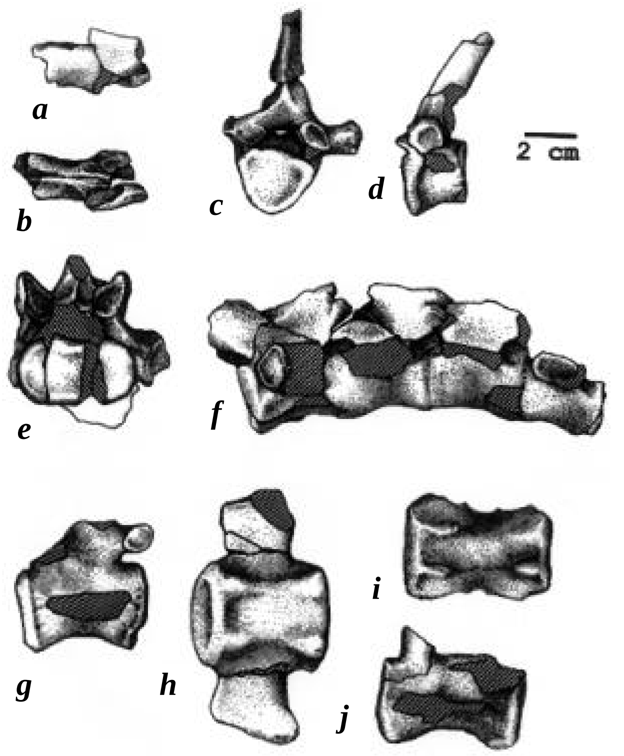

Figure 3. Osteology of *Kutchicetus minimus* (RUSB 2647). ***a***, ***b***, Premaxilla in left lateral and occlusal view, left and right alveolus for I^3; ***c***, ***d***, Thoracic vertebra in cranial and left lateral view; ***e***, ***f***, Sacrum in cranial and left lateral view; ***g***, Proximal caudal vertebra in left lateral view; ***h***, Proximal caudal vertebra in ventral view; ***i***, Mid-caudal vertebra in ventral view; ***j***, Mid-caudal vertebra in right lateral view.

Tooth crowns are rare of remingtonocetids, but the holotype of *K. minimus* includes fragments of eight teeth. Most diagnostic of these are a partial upper molar, which is dominated by a large paracone and a weak metacone. The protocone is absent. The tooth is 6 mm wide, approximately half as large as *Remingtonocetus* (RUSB 2630). The longest premolar fragment probably pertains to P3/(width 7.2 mm) and implies that this tooth was nearly twice as long as the molars, as in other remingtoncetids. Two other premolars are shorter (respective width, 10.5 and 11.2 mm). The largest unicuspid tooth was probably the canine (crown height more than 3.5 mm), and the smallest unicuspid probably represents a pointed incisor (crown height approximately 16 mm). A fragment of the rostrum shows alveoli for two left and right teeth, most likely the canine and first premolar. It also shows the diagnostic arrangement of the convergence of the edges of the palate to each other. At its midpoint between alveoli, the palate is only 6 mm wide. Dorsally this fragment shows a flat surface for articulation with the nasals.

No limb bone is complete, but both humerus and tibia preserve complete proximal ends and a large part of the shaft, including the distal part that flares, and is near the articular end. The humerus has a medio-laterally compressed head and a pronounced tubercle just distal to the head, that marks the proximal part of the pectoral crest. A fragment of the distal humerus shows that the trochlea was extensive antero-posteriorly and that there was no projecting medial epicondyle. The proximal femur shows that the head is directed at a low angle to the shaft of the bone and that the lesser trochanter was well-developed. There is no indication of a third trochanter. The greater trochanter projected more proximally than the head. The tibia shows that the medial condyle was concave and set more distally than the lateral condyle, as commonly seen in some seals and sealions. The tibial crest extends to approximately two-thirds of the length of the shaft.

The sacrum is composed of four solidly fused vertebrae. The first sacral vertebra shows indications of an articular facet with the innominate. This facet is set close to the centrum of the vertebra. Tail vertebrae are impressive in that they are robust and long, with paired hemal processes cranially and caudally. Their roots show that they were strong.

The vertebral column of *Kutchicetus* is more complete than that of any other described early-middle Eocene cetacean. One cervical, 8 thoracic, 4 lumbar, 4 sacral, and 12 caudal vertebrae are preserved. Its vertebral formula was probably similar to that of an Eocene cetacean from Pakistan[8], *Ambulocetus*: 7, 15, 8, 4, 20–25. The vertebral column of *Kutchicetus* is unusual in having a number of long and robust caudal vertebrae, suggesting that the animal had a powerful tail. That the tail played an important part in locomotion is further indicated by the relatively gracile humerus (approximately 140 mm long) and tibia (approximately 135 mm long), both of which are disproportionately small when compared to the caudal vertebrae. Here, we study the functional morphology of the vertebral column using the proportions of the centra of the vertebrae in a plot (Figure 4) that follows the style of Buchholtz[5]. Three conclusions can be drawn:

Firstly, the sacrum which is composed of four fused vertebrae, is of vastly different vertebral proportions than adjacent parts of the column. This is unlike all modern and described fossil cetaceans and other modern marine mammals, but is similar to several land or semiaquatic mammals (*Pachyaena*, *Lutra*[5]). This probably indicates that the sacrum of *Kutchicetus* was still weight-bearing, as are those of other remingtoncetids[9]. In this respect, *Kutchicetus* is unlike modern and other fossil cetaceans in which the sacrum is reduced and does not bear weight.

Secondly, as Figure 4 shows, there are no pronounced breaks in the height/width proportions of the preserved caudal vertebrae. Abrupt changes in these proportions occur in mammals with well-defined flukes, such as cetaceans and dugongs and are absent in mammals lack-

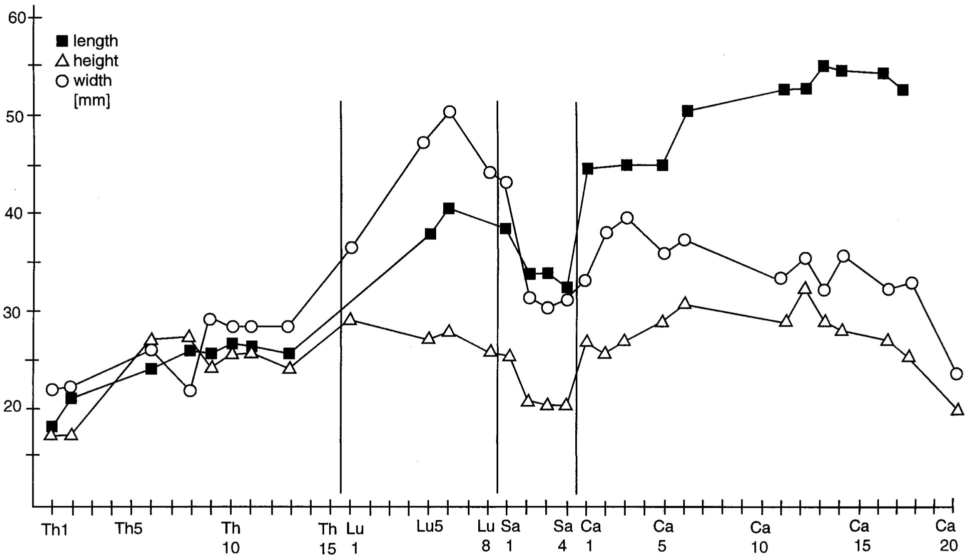

Figure 4. Vertebral dimensions of *Kutchicetus minimus*, RUSB 2647. Measurements (in mm) are plotted against inferred vertebral number of posterior thoracic, lumbar, sacral and caudal vertebrae.

ing flukes, such as manatees[5]. Buchholtz[5] used these proportions to infer that a tail-fluke was not the main propulsive organ in the Eocene cetacean *Rodhocetus*. Similarly, we argue that there is no evidence that *Kutchicetus* has a well-defined tail-fluke, although it is possible that it had a flat tail like the manatees. The very wide lumbar and proximal caudal vertebrae are consistent with a stockily built body of *Kutchicetus*, possibly not unlike a manatee. Although we do not have terminal caudal vertebrae that may give direct evidence for or against the presence of a fluke, it would be energetically inefficient to use a lift-based propulsor like a fluke on a long stalk[10], such as the proximal tail of *Kutchicetus*.

Thirdly, and most importantly, in *Kutchicetus* the pattern of change in vertebral lengths is unique among cetaceans. Two areas of the vertebral column show local maxima of vertebral length. The first maximum occurs in the lumbar column and the second in the caudal column. This pattern differs from that in all known modern and Eocene cetaceans, but is similar to the length pattern of otters (*Lutra*, *Enhydra*[5]). Buchholtz[5] interpreted this pattern as indicating a specialized mode of locomotion, where maxima in the length of the lumbar and caudal column indicate that two different maxima of excursion (called undulatory maxima) occur in the vertebral column as the animal is moving. These were also found to occur in non-mammals, such as the gavial[5]. None of the Eocene cetaceans studied by Buchholtz[5] show this pattern, and bi-modal undulatory locomotion may not have occurred in any fossil cetaceans for which the vertebral column has been described.

The similarity of the vertebral column of *Kutchicetus* to otters, and its possible implications for similarity in function are reminiscent of inferences made about the locomotor behaviour of the Eocene whale *Ambulocetus*, from Pakistan. No complete vertebral column has been described yet for this taxon, and the animal is three or four times as large as *Kutchicetus* in linear dimensions. However, based on similarities between *Ambulocetus* and otters in the limb proportions, it has been hypothesized that whales may have gone through an evolutionary stage, where their swimming mode resembled that of otters[8,11]. The vertebral column of *Kutchicetus* provides independent evidence for this hypothesis and suggests that ambulocetids and remingtonocetids swam using a transitional mode of locomotion that is not used by any other known fossil cetacean. This, in combination with its small size, implies that *Kutchicetus* is a remarkably primitive whale as far as its locomotor skeleton is concerned, certainly more primitive than any other cetacean from Kachchh. This stands in stark contrast with the limited information about the skull and dentition of *Kutchicetus*, which indicates that this whale had a very long and narrow snout, unlike any other Eocene cetacean, except for *Andrewsiphius*, to which it may have been closely related.

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