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Evolution

A new Eocene archaeocete (Mammalia, Cetacea) from India and the time of origin of whales

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ABSTRACT *Himalayacetus subathuensis* is a new paleocene archaeocete from the Subathu Formation of northern India. The type dentary has a small mandibular canal indicating a lack of auditory specializations seen in more advanced cetacean, and it has *Pakicetus* like molar teeth suggesting that it lived fish. *Himalayacetus* is significant because it is the oldest archaeocete known and because it was found in marine strata associated with a marine fauna. *Himalayacetus* extends the fossil record of whales about 5.5 million years back in geological time, to the middle part of the early Eocene (~52.5 million years ago (Ma)). Oxygen in the tooth enamel phosphate has an isotopic composition intermediate between values reported for freshwater and marine archaeocetes, indicating that *Himalayacetus* probably spent some time in both environments. When the temporal range of Archaeocetes is calibrated radiometrically, comparison of likelihoods constrains the time of origin of Archaeocetes and hence Cetacea to about 56–55 Ma (beginning of the Eocene), whereas their divergence from extinct terrestrial ungulates may have been as early as 61.5–57 Ma (beginning of the Cenozoic).

Pakicetus and contemporaries archaeocetes have long been the oldest whales known on Earth (1–3). All are from red beds of the lower Kuldana Formation in Pakistan and the upper Subathu Formation in India, which are intercalated in a thicker sequence of Eocene marine sediments. All were deposited in a shallow epicontinental extension of the Tethys Sea (there either that formerly separated the Indian subcontinent from the rest of Asia. These red beds yield essentially the same Kuldana and Kalabagh freshwater fish and continental vertebrate fauna of early-middle Eocene age (4, 5). When first described, *Pakicetus* was interpreted as an amphibious intermediate of whale evolution that stayed and reproduced on land and entered Tethys opportunistically to feed on fish (1).

We report here a new paleocene archaeocete from marine strata of the middle Subathu Formation of India. The new paleocene was found about 10 m lower stratigraphically and 5.5 million years older geologically than the Kuldana–Kalabagh archaeocetes. Its dentary has a single low sex sound was recognized in the early-to-middle Eocene interaction (19, 20). It was near the end of the early Eocene, *Pakicetus*-bearing red beds were thought to represent this low sea sound, and *Pakicetus* was thus thought to be late early Eocene in age.

Two low sea stands are now recognized in the early-to-middle Eocene transition (21), one late in the early Eocene and the other early in the middle Eocene (22 in Fig. 3). The *Pakicetus*-bearing interval must correspond to the higher of these, because shallow marine lower Eocene at Aquitaine gave of zone SBZ9 is reported below it in the Indian section (9). Abundant occurrences of zone SBZ4 is reported from the Kuldana Formation at its type section (21), and Orbitolites complanatus of zones SBZ3–5a is reported from the Shekhan Limestone underlying the Kuldana Formation at Panoba (13). The latter is a stratigraphic succession through the Chorabitki fossil beds where the type creation of *Pakicetus inachus* was found. This upper low sea stand is now calibrated at approximately 46 million years ago (Ma) using the time scale of Berggren *et al.* (23), meaning that *Pakicetus* is younger than previously thought.

The type specimen of *Himalayacetus* comes from interval Elbo of Michel (24) in the type section of the Subathu Formation (Fig. 3). Intervals B and D of Michel both yield Nummulites atacicus of shallow benthic zone SBZ. This constrains the age of *H. subathuensis* to between 53 and 56Ma, or above 52.5 Ma.

ENVIRONMENT OF *HIMALAYACETUS*

Himalayacetus also is significant in showing that some whales probably were partially marine very early in the course of cetacean evolution. *Himalayacetus* came from a shallow marine-bearing marine deposit, whereas *Pakicetus* and the other oldest pakicetids known previously came from continental red beds and were found in association with land mammals (1, 3).

Oxygen isotopes distinguish living freshwater from marine Cetacea (25, 26). Oxygen is in freshwater not sing is freshwater—and—enriched in light ^{18}O and depleted in heavy ^{18}O—by comparison with oxygen in marine settings that retain more heavy ^{18}O (Fig. 1). Oxygen isotopes of Eocene *Pakicetus* and *Ambulocetus* were reported to have freshwater rather than marine values, which led Thewissen *et al.* (26) to conclude that pakicetids, the geologically oldest whales, were not marine.

Interpretation is complicated because the isotopic composition of oxygen in bone and tooth phosphate of land mammals is often heavy (27), reflecting fractionation during respiration and other metabolic processes. Thus, the heavy values seen in *Ambulocetus* and at least some *Pakicetus* can be explained by respiration on land in animals that almost certainly still were amphibious. Interpretation of some heavy oxygen in marine mammals

FIG. 1. *Himalayacetus subathuensis* type specimen compared with an earlier Asian archaeocete and a later Asian archaeocete. All are left dentaries shown in medial view. (a) *Himalayacetus subathuensis* type (ex. type *Pakicetus*, holotype left p_4, anterior ↓, posterior ↑), and molar M$_1$. (Chinese Institute of Vertebrate Paleontology and Paleoanthropology, cast IVPP 10501, (b) *H. subathuensis* type, early Eocene, with M$_1$–$_2$ (Subathu Formation, Indian Geological Survey of Pakistan, 1 University of Michigan (MP 4300 Mx), drawing reversed from right side). Note similarities in overall size and extended molar profiles, suggesting similar trophic adaptation. *H. subathuensis* no more a small mandibular canal (ms) like that of earlier archaeocetes, contrasting with the large mandibular canal of *Ambulocetus* and all postpakicetid archaeocetes, and small mandibular canal produces whale like hearing in water (3).

damaged, but the lateral wall clearly narrows. The crown, as a whole, has a very weak lingual cingulid and a slightly stronger lingual cingulid M$_2$ measures 26.7 mm long and 11.1 mm wide at the base of the crown. The trigonid was about 12 mm high at the apex of the protoconid, and the talonid was about 7.0 mm high.

The crown of M$_3$ (Fig. 2b) is similar to that of M$_2$ but smaller (Measured, with the only substantial difference being of proportion. M$_3$ measures 22.1 mm long and 9.0 mm wide at the base of the crown. The trigonid is 17.5 mm high at the apex of the protoconid, and the talonid is 7.4 mm high.

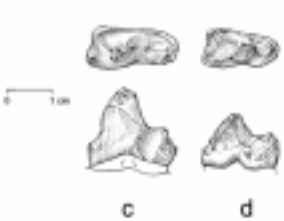

FIG. 2. Teeth of *H. subathuensis* holotype compared with those of paleocene *Pakicetus inachus* and *Pakicetus attacus*. All teeth are shown in mirror image (reversed and inverted) to ease comparison of molar morphology. (a) Crown (left) M$_1$ of *H. subathuensis*, IR 2305 (Indian Geological Survey of Pakistan 1). (b) Crown of left M$_3$ of *P. inachus* (holotype), Howard University Geological Survey of Pakistan 11 (HP 10101). (c) Crown of left M$_2$ of *P. attacus*, GSP-UM 42 (ex. Yale Peabody Museum of Natural History, type of *Pakicetus*). Differences distinguish these *Himalayacetus* molars from those of *Pakicetus*: (1) *Himalayacetus* has a larger and thicker lingual cingulid, a smaller lingual cingulid, and a smaller anteriorly projecting anterolingual cusp at the base of the trigonid.

Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls

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Modern members of the marine mammal order Cetacea (whales, dolphins and porpoises) are obligate aquatic mammals that are highly distinctive in morphology, feeding habit and hind limbs, and having flippers, flukes, and a dorsoventral body. Eocene fossils discovered much of cetaceans' land to water transition, but until now, the most primitive representative for which a skeleton was known was relatively amphibious and lived in coastal environments. We now report on the skeletons of two early Eocene pakicetid cetaceans, the 50-million-year-old *Pakicetus inachus* and the well-dated *Pakicetus attacus*. These skeletons can elucidate the relationships of cetaceans to other mammals. Morphological cladistic analyses have shown cetaceans to be most closely related to one or more mesonychians, a group of extinct, ungulate carnivores, but molecular analyses have indicated that they are the sister group to hippopotamids, the cladistic analysis indicates that cetaceans are more closely related to artiodactyls than to any mesonychian. Cetaceans are not the sister group to (one) mesonychians, our analysis stops short of identifying any particular artiodactyl family as the cetacean sister group and supports monophyly of artiodactyls.

In contrast to the debate about the cetacean sister group, the relationships among Eocene cetaceans and the origin of Cetacea itself are not controversial[1,2]. All phylogenetic studies indicate that pakicetids are most closely related to living cetaceans than to artiodactyls and mesonychians, and that pakicetids share the cetacean synapomorphies of the ear[3,4]. Pakicetids are followed by ambulocetids in the fossil record, and they have flattened and robust lower molars (and are closely related to later Eocene basilosaurids and dorudontids[5,6]). There are no fossils intermediate which show the differences between the amphibious ambulocetids and the more aquatic basilosaurids, and no transitional forms between ambulocetids and basilosaurids[7,8]. There are no fossils intermediate between the terrestrial pakicetids and the more aquatic ambulocetids, and no transitional forms between pakic