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Philip D. Gingerich, Director

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UNUSUAL MAMMALIAN LIMB BONES (CETACEA?, ARCHAEOCETI?)  
FROM THE EARLY-TO-MIDDLE EOCENE  
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By

PHILIP D. GINGERICH<sup>1</sup> AND DONALD E. RUSSELL<sup>2</sup>

*Abstract*—Three unusual mammalian limb bones are described from the early-to-middle Eocene Subathu Formation of Pakistan Kashmir. The first is the distal part of a moderately large humerus from Maklorhi that has a densely ossified or osteosclerotic midshaft, and a relatively narrow elbow articulation oriented oblique to the humeral shaft. The second is a complete astragalus of an even larger animal from Kamroti with a greatly reduced head, no neck, and a tibial facet restricted to the medial eminence. The third is a pelvic fragment of a medium-sized mammal from Batala that has a flat lunate surface filling almost all of the acetabulum, precluding articulation of a weight-bearing femur. These features are all consistent with aquatic adaptation and resemble characteristics seen in later Archaeoceti. If limb bones described here represent early archaeocetes, then there was more morphological diversity than previously recognized in the early-to-middle Eocene transition of whales from land to sea.

#### INTRODUCTION

Field work in 1980 and 1981 yielded the first collection of identifiable early-to-middle Eocene mammals from bone beds in the Subathu Formation near the town of Kotli in Pakistan Kashmir. This area is about 80 km east of Islamabad and Rawalpindi. Wadia (1928) reported an "ossiferous pseudoconglomerate" here, which we attempted to relocate. Topography is rugged and travel is difficult, but several bone beds were found. Dental remains of mammals are fragmentary, but include isolated teeth or broken teeth of rodents, a hyaenodontid creodont, anthracobunid proboscideans, artiodactyls, and perissodactyls of the early-to-middle Eocene Upper Subathu fauna of Russell and Zhai (1987, p. 137).

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Postcranial elements are more common in the Subathu bone beds, and these are more interesting in some ways. The well-preserved astragalus of *Anthracobune* described by Gingerich, Russell, and Wells (1990) was found here. Long bones are generally broken, but vertebral centra, carpal and tarsal bones, and phalanges are often preserved intact. Isolated hand and foot bones are reasonably common, but most are difficult to interpret without having more elements than are known at present. One specimen, GSP-UM 1743, is a complete left calcaneum of a brontothere about the right size to represent *Eotitanops dayi* Dehm and Oettingen-Spielberg (1958) or *Mulkrajanops moghliensis* Kumar and Sahni (1985).

Wells and Gingerich (1987) reviewed the stratigraphy of the Subathu Formation in Pakistan Kashmir, which is approximately 100 m thick near Kotli. Paleoenvironmental interpretation indicates that the Kotli stratigraphic sequence involves a single cycle of marine transgression followed by regression, with the bone-bearing units all lying in the regressive sequence. The transgressive sequence at the base overlies a disconformity separating it from much older Jammu Limestone, and the regressive sequence is overlain by a paraconformity separating it from continental molasse of the Miocene Murree Formation. Evidence for a regressive low sea stand in the upper Subathu includes development of red and purple coloration indicating oxidation. However, red and purple coloration does not necessarily indicate subareal exposure, and we interpret the upper part of the Subathu Formation in Pakistan Kashmir as having been deposited in a shallow, nearshore, marginal marine rather than freshwater fluvial environment.

The regressive part of the Subathu sequence is usually interpreted (e.g., by Russell and Zhai, 1987, and by Wells and Gingerich, 1987) to represent the same regressive sequence as the late early Eocene Kuldana Formation (the low-stand wedge in sea level cycle TA3.1 of Haq et al., 1987), but it is also possible that this is a more continental correlative of the shelf-margin wedge in sea level cycle TA3.2 of Haq et al., which would make the Subathu fauna about one m.y. younger than the Kuldana fauna (about 48.5 Ma rather than 49.5 Ma on the Haq et al. time scale). The sequence of strata and paleoenvironments in the Subathu Formation in Pakistan Kashmir is very similar to that of the Subathu Formation yielding well-preserved land mammals 50 km farther to the southeast at Kalakot, Metka, and Moghla in Rajauri District in Indian Kashmir (Sahni and Srivastava, 1976; Kumar and Sahni, 1985; Kumar, 1991, 1992).

Interpretation of the Subathu bone beds as having been deposited during a regressive continental or low-stand marine phase is consistent with the presence of continental mammals (washed in from land), and also helps to explain the presence of elements described here that appear to represent marine mammals, probably primitive archaeocete cetaceans. The latter are not readily identifiable to taxon, but are described and illustrated to record their unusual morphology. All come from Kotli District in Pakistan Kashmir.

#### INSTITUTIONAL ABBREVIATIONS

- GSP-UM — Geological Survey of Pakistan - University of Michigan collection, housed at GSP, Islamabad (Pakistan)
- HGSP — Howard University - Geological Survey of Pakistan collection, housed at GSP, Islamabad (Pakistan)
- USNM — U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (U.S.A.)

#### MAKLORHI HUMERUS

The Maklorhi humerus, GSP-UM 1575 shown in Figure 1, is the distal part of a moderately large left humerus including the midshaft but lacking the head and lacking greater and lesser tubercles. It was found in 1980 on a slope above the road west of the village of Maklorhi,

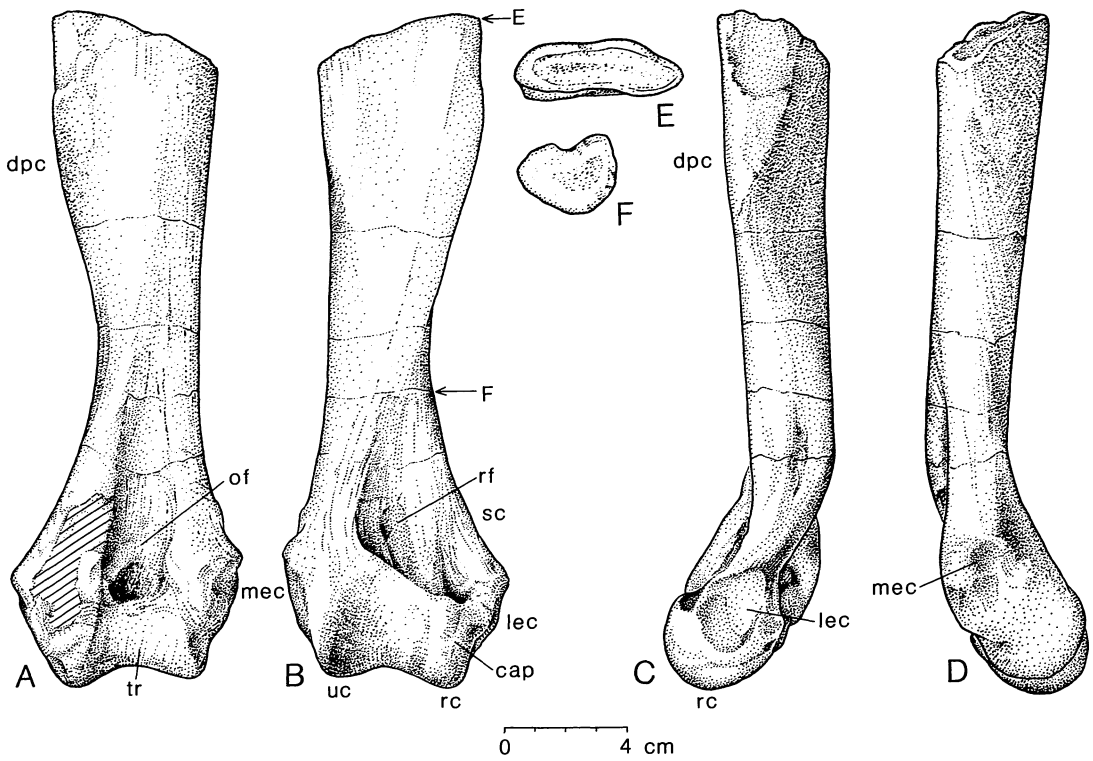


FIG. 1—Maklorhi humerus, GSP-UM 1575; left distal humerus. A, posterior view. B, Anterior view. C, lateral view. D, medial view. E, cross-section of shaft at break labeled with arrow *E* in view B. F, cross-section of shaft at break labeled with arrow *F* in view B. Note dense cortical bone throughout midshaft, relatively long shaft with a prominent deltopectoral crest, lack of an entepicondylar foramen, reduced supinator crest, and distinctly angled distal articular surface of humerus. Abbreviations: *cap*, capitulum; *dpc*, deltopectoral crest; *lec*, lateral epicondyle; *mec*, medial epicondyle; *of*, olecranon fossa; *rc*, radial condyle; *rf*, radial fossa; *sc*, supinator crest; *tr*, trochlea; *uc*, ulnar condyle.

which is west of Tattapani, south of River Punch, near Sawar Valley, in Kotli District about 7 km NE of Kotli town. This is on Survey of Pakistan topographic sheet 43 G/14 (not seen), at approximately 33°35' N latitude and 73°58' E longitude.

GSP-UM 1575 was found as an isolated element, in several pieces, in yellow-green siltstone (unit I of Wells and Gingerich, 1987) underlying purple sediments of the upper Subathu Formation and red sandstones of the Murree Formation. The bone is partly stained red, suggesting that it might have been derived from a higher stratigraphic level, but fractures are filled with hard yellow-green siltstone indicating that the humerus was found in place. The only part that shows any weathering is the broken proximal surface where the head is missing, which indicates too that the humerus was found in place in unit I of the upper Subathu Formation.

The Maklorhi humerus is distinctive in several morphological features. First, the midshaft is composed of dense osteosclerotic bone with little porosity and no medullary cavity evident in any of the breaks where internal structure is exposed. The humeral shaft is long relative to both midshaft diameter and breadth of the distal humerus. The deltopectoral crest and deltoid tuberosity are both strongly developed and extend well down on the humeral shaft. The distal part of the humerus is relatively narrow, with small medial and lateral epicondyles bordering

a simple trochlea. There is no entepicondylar foramen. The olecranon fossa is deep but not perforated (there is no supratrochlear foramen). The trochlea is oriented at an angle of about 20-30° to the long axis of the humeral shaft, which is most clearly shown by distinct angulation of the radial fossa when examined in anterior view. The capitulum for articulation with the radius is a simple parasagittal crest bordering the trochlea, and there is hardly any trace of a lateral epicondylar or supinator crest. Taken together, these features indicate that the forearm moved in a parasagittal plane oblique to the humeral shaft, with no pronation or supination possible.

GSP-UM 1575 measures 21.5 cm in length as preserved, and it was probably 26-28 cm long when complete. Anteroposterior midshaft diameter is about 2.8 cm, and mediolateral midshaft diameter is about 3.2 cm. The distal part of the humerus measures 4.6 cm across the distal condyles and 7.2 cm across the tubercles of the medial and lateral epicondyles. The trochlea is 2.4 cm in diameter anteroposteriorly, but it does not curve smoothly and it appears to have been compressed anteroposteriorly during burial.

Osteosclerotic bone, in mammals, is highly suggestive of aquatic Sirenia (Nopcsa, 1923; Kaiser, 1960), where pachyostotic and osteosclerotic bone functions as hydrostatic ballast (Domning and Buffrénil, 1991). However, the Maklorhi humerus does not resemble any known sirenian humerus in other morphological characteristics (Domning, pers. comm.). The humerus is unusually long for its midshaft diameter, and the medial condyle or entepicondyle is small, unlike that of primitive sirenians *Protosiren* and *Eotheroides* (see Domning and Gingerich, 1994: fig. 9) where the medial epicondyle is unusually large. If the bone is not actually sirenian, it probably belonged to a mammal that was functionally sirenian-like and hence aquatic. The humerus is not known for any anthracobunid proboscidean. *Moeritherium* has a humerus with the distal trochlea oriented parallel to the humeral shaft (Andrews, 1906: pl. XI, fig. 6), or, if angled, angled in the opposite direction from angulation observed in the Maklorhi humerus, reflecting different forelimb posture.

A long shaft, prominent deltopectoral crest, narrow breadth across the distal condyles, and forearm excursion restricted to movement in a parasagittal plane oblique to the humeral shaft with no pronation or supination are features that resemble archaeocete cetaceans like "*Zeuglodon*" (Stromer, 1908) and *Zygorhiza* (Kellogg, 1936). Consequently it seems most likely, given the possibilities, that the Maklorhi humerus belongs to a primitive archaeocete. It is broader across the distal condyles and epicondyles than is seen in later archaeocetes, which we interpret as a primitive characteristic, but at the same time it has specialized functional features seen in the distal humerus of archaeocetes.

The Maklorhi humerus is the proper size to articulate with the ulna and radius of *Ambulocetus natans* described by Thewissen et al. (1994), which is approximately contemporaneous, and the Maklorhi humerus may possibly represent this genus and species (for which the humerus is not yet known).

### KAMROTI ASTRAGALUS

The Kamroti astragalus, GSP-UM 1576 shown in Figure 2, is a relatively large right astragalus that is intact except for minor defects in surface bone. It was found in 1980 at Kamroti North, which is a fossil locality just northeast of Kamroti village, in Kotli District about 13 km ESE of Kotli town. This is on Survey of Pakistan topographic sheet 43 K/3, at approximately 33°29' north latitude and 74°02' east longitude. The astragalus was found on the surface lying on green shale, but the bone itself is stained red and it probably weathered out of overlying red and purple sediments of the upper Subathu Formation (unit J of Wells and Gingerich, 1987).

GSP-UM 1576 is sufficiently different from an ordinary mammalian astragalus that it is difficult to interpret definitively without having an articulating tibia, calcaneum, navicular, or

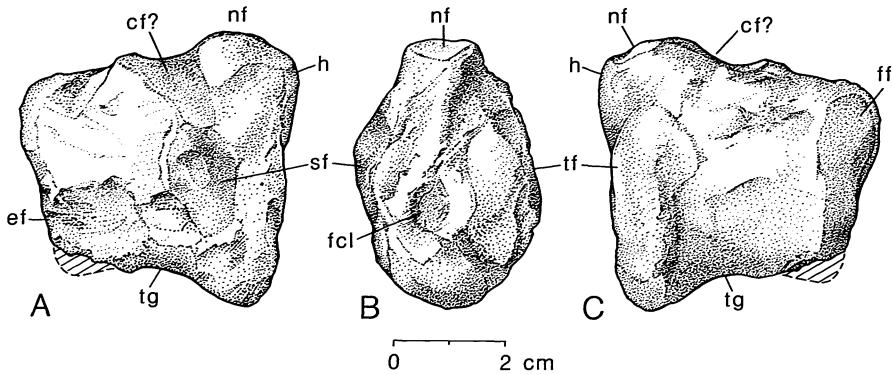


FIG. 2—Kamroti astragalus, GSP-UM 1576; right astragalus. A, plantar view. B, medial view. C, dorsal view. Note small head and virtually nonexistent neck. Abbreviations: *cf?*, cuboid facet?; *ef*, ectal facet; *fcl*, fovea for tibial collateral ligament; *ff*, fibular facet; *h*, head; *nf*, navicular facet; *sf*, sustentacular facet; *tf*, tibial facet; *tg*, trochlear groove.

cuboid. The astragalus is almost entirely body; the head is greatly reduced and the neck virtually nonexistent. There is no trace of the medial tubercle characteristic of *Anthracobune* (Gingerich, Russell, and Wells, 1990) and other proboscideans, and there is no astragalular foramen. The dorsal surface of the body is a broad shallow trochlea separating medial and lateral eminences, but the trochlea itself does not appear to have had the broad smooth surface that usually marks a tibial facet. Instead, the tibial facet was evidently confined to a smooth area on the dorsal surface of the medial eminence. There is a well marked fibular facet on the lateral surface of the lateral eminence. The trochlear groove for the digital flexors is a broad polished surface that is shallowly incised at the posterior margin of the body. The astragalular head is divided, with a projecting process supporting a relatively small navicular facet and a distinct facet that is not raised, tentatively interpreted as a cuboid facet. This facet on the front of the body is confluent with the sustentacular facet on the plantar surface of the astragalus. The ectal facet on the plantar surface is small. There is a well developed fovea on the medial surface of the astragalus for a tibial collateral ligament.

The Kamroti astragalus, GSP-UM 1576, is 4.8 cm long anteroposteriorly, as measured across the head and medial eminence. It is 3.6 cm long anteroposteriorly, as measured across the lateral eminence (slightly restored). The body is 4.4 cm wide measured across medial and lateral eminences, and 3.6 cm in maximum height. The astragalular head measures 2.2 cm wide and only 1.5 cm high.

The Kamroti astragalus cannot be compared to astragali of sirenians because none are known, but all sirenians known to date have reduced hind limbs and none is likely to have had an astragalus the size of GSP-UM 1576. This differs from the astragalus of *Anthracobune* (Gingerich, Russell, and Wells, 1990) and other proboscideans in its smaller, divided head; in lacking a medial tubercle; in lacking an astragalular foramen; and in lacking a broad, smooth, tibial facet.

None of the articular facets in the Kamroti astragalus is large, which indicates that the ankle joint must have had limited mobility in life. This is similar to the situation in later and more specialized *Basilosaurus isis*, the one archaeocete in which the tarsus is well known (Gingerich, Smith, and Simons, 1990). In *Basilosaurus*, the astragalus and navicular are fused (these are sometimes fused to the calcaneum and cuboid as well), there is limited motion at the ankle joint, and the tibia articulates with the medial eminence of the body rather than a trochlea (the trochlea is lost in *Basilosaurus*). The Kamroti astragalus is similar functionally, but it retains

its independence from other bones of the tarsus and it retains a broad trochlea (nonarticulating) on the dorsal surface of the astragalar body.

The Kamroti astragalus differs in some ways from the right astragalus (HGSP 18507.63) of *Ambulocetus natans* described by Thewissen et al. (1994): the body of the Kamroti astragalus is about 60% larger in comparable dimensions than that of *Ambulocetus*, and it has a shallower trochlea. However these astragali are similar, suggesting possible close relationship, in that both have tibial facets developed on the medial eminence that do not extend to the deepest part of the trochlea. The Kamroti astragalus clearly belonged to a larger mammal than *Ambulocetus natans*, and, judging from the astragalus, it had a more specialized ankle with less parasagittal flexion and extension than *Ambulocetus*.

### BATALA PELVIS

The Batala pelvis, GSP-UM 1591 shown in Figure 3, is a small pelvic fragment preserving the acetabulum but little of the ilium, ischium, or pubis. It was found in 1980 at Batala Nala, which is a locality northeast of Kamroti village and northeast of the Kamroti North fossil locality, in Kotli District about 13 km ESE of Kotli town. This is on Survey of Pakistan topographic sheet 43 K/3, at approximately 33°29'30" north latitude and 74°02'10" east longitude. The pelvis was found in a bone bed preserved in a hard band of yellow sediment in the upper Subathu Formation (unit I of Wells and Gingerich, 1987). The Batala Nala locality is at the bottom of a deep gully or valley below the cliff north of Kamroti (requiring a 50 minute climb to get back up to Kamroti village).

The Batala pelvic fragment preserves the acetabulum with adjoining parts of the ilium, ischium, and pubis. The lunate surface fills most of the acetabulum, with the caudal or posterior part predominating, and this is nearly flat, limiting articulation with a femoral head and meaning that the hind limb of this mammal probably was not weight-bearing. There is a distinct acetabular fissure beneath the caudal part of the lunate surface, just above the remaining border of the obturator foramen.

The Batala pelvis is 4.1 cm long as preserved, and it was probably about 10 cm long when intact. The fragment is 1.6 cm in mediolateral breadth, measured above the acetabulum, and the acetabulum itself 1.5 cm in diameter, with most of this occupied by lunate surface.

The Batala pelvis is not likely to represent an anthracobunid because no proboscideans are known that show hind limb reduction, and *Anthracobune* itself retained a relatively large, functional astragalus (Gingerich, Russell, and Wells, 1990). Among Sirenia, primitive sirenians like *Protosiren*, *Eotheroides*, and *Eosiren* have reduced hind limbs, but all retain a deep, well-formed acetabulum to receive the femoral head (see, e.g., Domning and Gingerich, 1994: fig. 11).

If the Batala pelvis belongs to a whale, it is more specialized than most contemporary and even younger archaeocetes in having the acetabulum essentially all filled by the lunate surface. *Ambulocetus natans* (Thewissen et al., 1994) has a large femur with a spherical femoral head that must have articulated with a normal mammalian pelvic acetabulum. *Indocetus ramani* and *Rodhocetus kasrani* both have a normal land-mammal acetabulum (Gingerich et al., 1993, 1994). *Basilosaurus* has a shallow acetabulum, but this genus is younger geologically and has a more-completely developed acetabulum while the hind limb is greatly reduced. On balance, it seems most likely that the Batala pelvis represents a highly specialized and possibly divergently-specialized early archaeocete that was hitherto unknown. At the very minimum, such a small pelvis with a shallow, flat lunate surface of the acetabulum suggests an aquatic mammal with reduced hind limbs that could not support its weight on land.



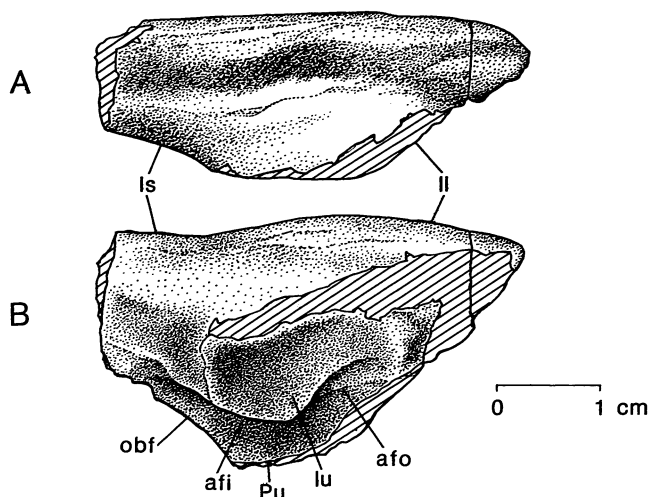


FIG. 3—Bataala pelvis, GSP-UM 1591; right pelvic fragment. A, dorsal view. B, lateral view. Note large flat lunate surface filling the acetabulum and limiting articulation with the femoral head. Abbreviations: *afi*, acetabular fissure; *afo*, acetabular fossa; *Il*, ilium; *Is*, ischium; *lu*, lunate surface of acetabulum; *obf*, intact margin of obturator foramen; *Pu*, pubis.

### DISCUSSION

The three postcranial elements described here are unusual in showing forelimb specialization (dense bone, oblique elbow articulation with limited lateral excursion), and hind limb specialization (limited excursion) and reduction (loss of weight-bearing hip) that are consistent with aquatic adaptation and are similar to reduction and specialization observed in later archaeocete whales. While exact correlation of Subathu Formation archaeocetes with those of the Kuldana Formation (late early Eocene) and Domanda Formation (early middle Eocene) is unknown, Kuldana *Ambulocetus* clearly retained a more generalized and primitive ankle articulation, and Kuldana *Ambulocetus* and Domanda *Rodhocetus* and *Indocetus* retained more generalized and primitive hip articulations. The new postcranial elements described here, if they belong to archaeocetes, indicate that there was more morphological diversity among early Archaeoceti at the early-to-middle Eocene transition from land to sea than previously recognized.

Felts and Spurrell (1965) cited paleontological studies by Nopcsa (1923) and Zangerl (1935) when they speculated that an early stage of cetacean adaptation to water involved transient development of dense "pachyostotic" (osteosclerotic) bone to achieve neutral buoyancy in water. Their own studies showed that humeri of modern cetaceans are largely filled with spongy bone of low density. Previously known archaeocete humeri exposed in cross-section, such as late Eocene USNM 4679 (*Zygorhiza kochii*, distal humerus illustrated by Kellogg, 1936, fig. 73), are essentially modern in having a thin outer layer of dense cortical bone that is entirely filled by cancellous bone. The Maklorhi humerus is much older and shows sirenian-like dense osteosclerotic bone throughout the midshaft, as Felts and Spurrell predicted. Osteosclerosis of the humerus was lost in later archaeocetes, presumably because neutral buoyancy was achieved by other means (possibly including pachyostosis of the ribs, described by Buffrénil et al., 1990)

Finally, discovery that the early-to-middle Eocene Subathu bone beds of Kashmir yield bones of such unusual morphology, probably representing primitive archaeocetes in or near the transition of whales from land to sea, gives the Subathu bone beds of Kashmir special importance for further investigation.

#### ACKNOWLEDGMENTS

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