properties are measured at normal incidence, the CAF looks like a single crystal. A further implication of colloidal crystal contraction is that there must be a net attractive force at fixed interparticle distance (*2*, *4*).

The choice of AMD-MBA gels as the matrix in the intermediate step of CAF solidification is, in many respects, a good one. For low-volume fractions, the monomer does not prevent the diffusion necessary for crystal formation (*5*), and the polymerization solidifies the crystalline arrangement of polyballs with minimum perturbation. Our results show that, by a change in gel composition, the filter can be tuned to reject different wavelengths, and the addition of sucrose improves the thermal stability of the CAF. The layer structures can be further exploited by stretching of the CAF to change the rejection wavelength (*25*).

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Fossil Evidence for the Origin of Aquatic Locomotion in Archaeocete Whales

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Recent members of the order Cetacea (whales, dolphins, and porpoises) move in the water by vertical tail beats and cannot locomote on land. Their hindlimbs are not visible externally and the bones are reduced to one or a few splints that commonly lack joints. However, cetaceans originated from four-legged land mammals that used their limbs for locomotion and were probably apt runners. Because there are no relatively complete limbs for archaic archaeocete cetaceans, it is not known how the transition in locomotory organs from land to water occurred. Recovery of a skeleton of an early fossil cetacean from the Kuldana Formation, Pakistan, documents transitional modes of locomotion, and allows hypotheses concerning swimming in early cetaceans to be tested. The fossil indicates that archaic whales swam by undulating their vertebral column, thus forcing their feet up and down in a way similar to modern otters. Their movements on land probably resembled those of sea lions to some degree, and involved protraction and retraction of the abducted limbs.

The oldest cetacean, *Pakicetus*, is known from approximately 52-million-year-old river deposits in the Kuldana Formation in Pakistan (*1*, *2*). We recovered several specimens of a new genus and species of cetacean, *Ambulocetus natans* (*3*) (Fig. 1), from lower to middle Eocene beds that are stratigraphically about 120 m higher than those that yielded *Pakicetus* in the Kala Chitta Hills. The best specimen is a partly articulated skull and skeleton of *Ambulocetus*. It was found in a silt and mudstone bed, scattered over an area of approximately 1.8 m^2 (*4*).

The same bed also contains impressions of leaves and abundant *Turritella* and other marine molluscs, indicating that the carcass was buried in a shallow sea. The holotype of *Ambulocetus* provides a glimpse of the transitional morphologies between four-legged whale ancestors (*5*, *6*) and their finned descendants. Here, we focus on those morphological traits of *Ambulocetus* that have implications for locomotion in the earliest cetaceans.

Size of vertebrae, ribs, and limbs indicate that *Ambulocetus* was an archaeocete whale the size of a male of the sea lion *Otaria byronia* (approximately 300 kg). Cervical vertebrae are relatively long (centrum is 3 cm), and thoracic vertebrae have stout spinous processes and transverse processes with deeply excavated caudal sides. These depressions possibly gave rise to a strong spinal extensor muscle such as longissimus, which originates from the dorsal aspect of the transverse process in extant cetaceans (*7*, *8*). The centrum of the only preserved lumbar vertebra is wide transversely and has large transverse processes but a weak spinous process. Spinal flexors and extensors originate from the transverse processes. Little is known about the tail, but there are always many caudal vertebrae in primitive cetaceans and their relatives (*9*), whereas the length of individual elements varies widely. The only caudal vertebra known for *Ambulocetus* is elongate, suggesting that the tail was much longer than in modern cetaceans.

Ambulocetus had a robust radius and ulna. The forearm was fixed in a semipronated position, as a result of the triangular shape of the radial head. The olecranon is strong and makes up one-third of the length of the ulna. It is inclined caudally, and would have allowed powerful elbow extension by triceps. Unlike modern cetaceans, elbow, wrist, and digital joints were flexible and synovial in *Ambulocetus*. The pisiform projects 4.5 cm from the wrist, and would have permitted

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strong wrist flexion by flexor carpi ulnaris. The hand was long and broad and had five digits. The digits were strongly diverging, as is evident from the asymmetry of the metacarpo-phalangeal joint in digits II and IV. The fifth digit is most completely known: it was approximately as long as the forearm (MC V, 5.3 cm; phalanx V.1, 6.5 cm; phalanx V.2, 4.7 cm; radius, 17 cm). Metacarpals II, III, and IV are as robust as MC V, but longer (7.6, 10.5 and 10.2 cm), implying that the hand is much longer than the forearm. The thumb is short and slender (MC I, 5.2 cm; phalanx I.1, 4.3 cm), not unlike that of modern ziphiid cetaceans.

The femur is short and stout (28 cm) and lacks strong muscular processes for extensors and flexors. It does have a deeply excavated trochanteric fossa for the lateral rotators of the hip. Distal femur, proximal tibia, and astragalus are narrow and deep, and would have allowed mainly sagittal motions in knee and ankle. The feet are enormous: the fourth metatarsal is 14.5 cm long and its toe more than 17 cm long. The fifth digit is only slightly shorter but is noticeably less robust than the fourth. Toes are terminated by a short phalanx carrying a convex hoof, as in mesonychids, the terrestrial ancestors of cetaceans (*10*).

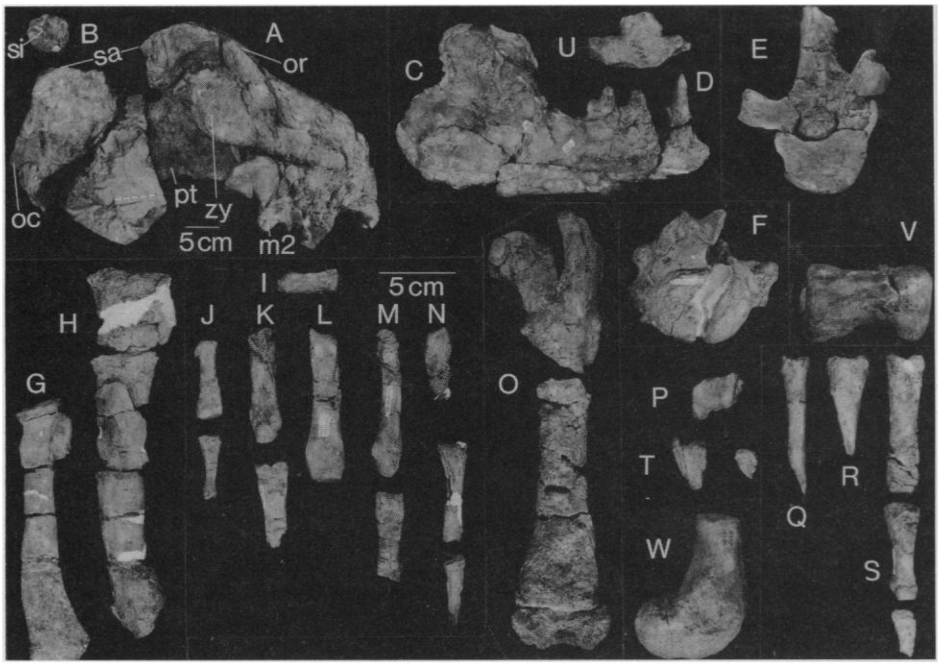

Fig. 1. Osteology of *Ambulocetus natans*. The holotype (Howard Geological Survey of Pakistan 18507) includes a skull with left P4/-M1-2/ and lacking the rostrum [(**A**) skull, right lateral view], but preserving both tympanics [(**B**) left, lateral view], right posterior mandible M/2-3 (**C**) and P/4 (**D**), cranial thoracic vertebra [(**E**) cranial view], lumbar vertebra [(**F**) caudal view], left radius [(**G**) cranial view], left ulna [(**H**) lateral view], pisiform [(**I**) distal view], metacarpal I and phalanx I, 1 [(**J**) medial view], metacarpal II and proximal phalanx II.1 [(**K**) palmar view], metacarpal III [(**L**) dorsal view], metacarpal IV and proximal phalanx IV.1 [(**M**) palmar view], proximal metacarpal V and phalanges V.1 and 2 [(**N**) dorsal view], complete femur [(**O**) caudal view], trochlea of astragalus [(**P**) dorsal view], proximal phalanx V.1 [(**Q**) dorsal view], proximal phalanx III.1 [(**R**) dorsal view], and phalanges IV.1-3 [(**S**) dorsal view], and two distal pedal phalanges [(**T**) dorsal view]. Referred material includes P/2 [HGSP 18473 (**U**), medial view], caudal vertebra [HGSP 18472 (**V**), lateral view], and distal femur [HGSP 18476 (**W**), lateral view]. Labels on (A) and (B): m2, second upper molar; oc, occipital condyle; or, orbital shield; pt, pterygoid process; sa, sagittal crest; si, sigmoid process; zy, zygomatic process of the maxilla.

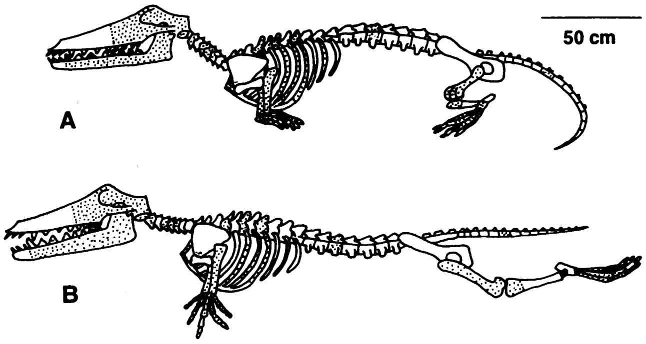

Fig. 2. Reconstruction of *Ambulocetus* while standing on land (**A**), and at the end of the power stroke during swimming (**B**).

The skeleton of *Ambulocetus* indicates that it could locomote on land and in the water. As in extant cetaceans (*11*), *Ambulocetus* swam by means of dorsoventral undulations of its vertebral column, as evidenced by the shape of the lumbar vertebra (Fig. 2B). Unlike modern cetaceans, however, *Ambulocetus* had a long tail and thus probably lacked a tail fluke. Femur and proximal tibia suggest that intrinsic hindlimb muscles were weak, which is consistent with previous findings from a middle Eocene archaeocete innominate found in Georgia (*12*). On the other hand, the foot formed a large surface that could be swung through the water when the back was flexed and extended. Therefore, the back muscles primarily powered the hindlimbs as in phocid seals (*13*). Unlike phocids, however, locomotion in water did not involve mediolateral but instead dorsoventral undulations, as in recent cetaceans; the knee and proximal ankle joint put the foot horizontal rather than vertical when the femur was retracted at the hip. The power stroke of the hindlimb flippers was thus mainly powered by extending and flexing spinal muscles, and to a lesser degree by the hindlimb muscles. Fast swimming otters (*Lutra, Enhydra*) move in this way (*13*), except that in otters the tail provides the dominant propulsive surface. The forelimbs were probably used in maneuvering and steering while swimming, as in extant cetaceans, and they lacked a major propulsive function in the water.

On land, the semipronated elbow left the hands sprawling when the shoulder was abducted and the wrist extended, resembling the posture of otariid pinnipeds (*14*). This position was necessary to accommodate the relative size of the hands with respect to the entire limb: if the feet pointed cranially, then the two limbs would interfere with each other's movements during locomotion. Lever arms of elbow and wrist for the power stroke of triceps and flexor carpi ulnaris in terrestrial locomotion are considerable. These movements were probably combined with humeral retraction during walking.

The femur was apparently held abducted and laterally rotated during land locomotion, as suggested by the strong lateral rotators of the hip inserting in the intertrochanteric fossa. Because the knee and ankle only allowed motions in one plane, this would cause the feet to sprawl. Propulsion of the hindlimbs on land may have been accomplished by extension of the back, reminiscent of the hindlimb motions of arctocephaline fur seals (*15*).

Ambulocetus is clearly a cetacean: it has an inflated ectotympanic that is poorly attached to the skull and bears a sigmoid process, reduced zygomatic arch, long narrow muzzle, broad supraorbital process, and teeth that resemble those of other archaeocetes, the paraphyletic stem group of cetaceans. Archaic archaeocete whales have been found in Africa (*16, 17*) and North America (*18, 19*), but are best known from Pakistan and India (*2, 20–22*), and it is likely that cetaceans originated near the subcontinent. Thus, the skeletal morphology of *Ambulocetus* is critical to our understanding of locomotion in early cetaceans.

The closest terrestrial relatives of whales, mesonychids, were running mammals (*10, 23*) that, when swimming, probably paddled by flexing and extending their hindlimbs alternately as in extant land mammals (*24*). At some point, cetaceans switched from unilateral paddling to bilateral (spinal) undulating (*25*) and from using the feet as a primary propulsive surface to having a tail fluke. *Ambulocetus* shows that spinal undulation evolved before the tail fluke. These fossils also test several hypotheses concerning early whale locomotion. The greatly expanded feet imply that forelimb propulsion is not primitive for cetaceans even though it may occur in other protocetids (*12*). It corroborates that cetaceans have gone through a stage that combined hindlimb paddling and spinal undulation, resembling the aquatic locomotion of fast swimming otters (*25, 26*). Unlike modern cetaceans, *Ambulocetus* certainly was able to walk on land, probably in a way similar to modern sea lions or fur seals. In water, it combined aspects of the locomotion of modern seals, otters, and cetaceans: Like modern cetaceans it swam by moving its spine up and down, but like seals, the main propulsive surface was provided by its feet. As such, *Ambulocetus* represents a critical intermediate between land mammals and marine cetaceans.

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   Ambulocetus natans, n. gen., n. sp.

   Holotype. Howard Geological Survey of Pakistan 18507: skull with left P4/-M1-2/ and lacking the rostrum, but preserving both tympanics, basihyoid, right posterior mandible with P/4, M/2-3, and left ramus with alveoli for C/1-P/3, half atlas, fragments of three other cervical vertebrae, two complete and several fragmentary thoracic and one lumbar vertebra, three complete ribs, and a sternebra. Forelimb fragments include part of the glenoid, left and right radius and ulna, all left carpals except the triquetrum, all metacarpals, and at least four proximal, two intermediate phalanges, and a fragment of one distal phalanx. Hindlimb elements include complete femur, proximal tibia, distal fibula, trochlea of astragalus, metatarsals II–V and at least two proximal, three intermediate, and three distal phalanges. The holotype was found at locality HGSP 9209 in the upper Kuldana Formation, Punjab, 3.7 km northwest of Ganda Kas (72°12′20″E, 33°39′N). *Referred material.* P/2 (HGSP 18473), P/3 (HGSP 18497), caudal vertebra (HGSP 18472), and distal femur (HGSP 18476), all from locality 9207, about 5 m above the type locality in the section. All material will be housed at the Geological Survey of Pakistan in Islamabad. *Known distribution.* Kala Chitta Hills of Pakistan, upper Kuldana Formation and transitional beds to the Kohat Formation. Lower to middle Eocene. *Differential diagnosis of genus.* P4/ of *Ambulocetus* has a single high labial cusp, unlike *Protocetus* (*16*), but lacks a protocone. M1/ and M2/ of *Ambulocetus* are similar in morphology, bearing a high and connate para- and metacone, and a protocone that is on a broad and low lingual shelf, unlike remingtonocetids where this shelf is narrow. The protocone of *Ambulocetus* is weaker than that of *Pakicetus* (*1*) and *Ichthyolestes* [R. Dehm and T. zu Oettingen-Spielberg, *Bayer. Akad. Wiss. Math. Naturwiss. Kl. Abh.* **91**, 1 (1958)], while the cusp is absent in *Protocetus*. This cusp is well set off from the labial cusps, unlike *Indocetus*. Crests are poorly developed on the teeth of *Ambulocetus*, as in their mesonychid ancestors [F. S. Szalay, *Evolution* **23**, 703 (1969)]. The lower canine is large and single rooted, whereas the four lower premolars have two roots, unlike remingtonocetids. P/4 consists of a single high cusp, unlike *Pakicetus*. The trigonid of M/2 and M/3 is much higher than the talonid, unlike *Gandakasia* and *Pappocetus* (*15*). It lacks a metaconid, unlike *Pakicetus*. *Ambulocetus* lacks the tubercles that occur rostral to the protoconid of *Pappocetus*. Few details of the talonid remain, but there seems to have been a single cusp and no basin, as in *Pakicetus*. Unlike most other archaeocetes, the pterygoid processes are enormous and their dorsoventral extent matches that of the braincase. *Etymology.* The genus name is a combination of ambulare (to walk) and cetus (whale), in recognition of a characteristic mode of locomotion in this cetacean. The species indication, natans (swimming), describes another aspect of its locomotor repertoire.
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An Inverted Double Seismic Zone in Chile: Evidence of Phase Transformation in the Subducted Slab

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Data from two microseismic field experiments in northern Chile revealed an elongated cluster of earthquakes in the subducted Nazca plate at a depth of about 100 kilometers in which down-dip tensional events were consistently shallower than a family of compressional earthquakes. This double seismic zone shows a distribution of stresses of opposite polarity relative to that observed in other double seismic zones in the world. The distribution of stresses in northern Chile supports the notion that at depths of between 90 to 150 kilometers, the basalt to eclogite transformation of the subducting oceanic crust induces tensional deformation in the upper part of the subducted slab and compressional deformation in the underlying mantle.

Since the advent of plate tectonics, intermediate and deep earthquakes have been interpreted as evidence of cold lithosphere penetrating into the mantle. At intermediate depths, most subducted lithospheres exhibit down-dip tensional faulting, which has been generally interpreted as resulting from the gravitational pull of the slab (*1–6*). The presence of a more complex state of stress in the subducted slab was observed first in Tohoku, Japan (*7*). There, a sheet of compressional earthquakes lies above a sheet of down-dip tensional events. These two seismic planes are separated by ~40 km at a depth of ~60 km, and they merge at a depth of 200 km. Similar double-planed seismic zones have subsequently been reported in other subduction zones (*7, 8*).