aquatic lifestyle, most marine mammals evolved a flipper by encasing the forelimb in soft tissue (Fig. 1). Most living marine mammals have a flipper, and flipper shape and the morphology of the underlying bony structures greatly affect the function of marine mammal forelimbs.

I. Cetaceans

From the gracile and crescent-shaped flippers of a pilot whale, to the thick and door-like flippers of right whales, cetacean flippers come in lots of shapes and sizes (Figs. 2 and 3) (Howell, 1930; Benke, 1993). Most delphinids have small and thin flippers, except the broad and thick flippers of the killer whale (*Orcinus orca*). Killer whales display sexual dimorphism in that the male flippers are larger compared to female flippers. Beaked whales and the pygmy sperm whale can tuck the flippers into an indentation in the body wall during deep dives. Bowhead and right whales have large, broad flippers, while pygmy right whales and rorqual whales have elongated and very thin flippers. Intermediate between the forelimb morphologies seen in right whales and rorqual whales, the gray whale has a broad and elongated flipper. The most unusual flipper shape is seen in humpback whales as they have longest flippers of any cetacean and the leading edge of the flipper is scallop shaped by the presence of large tubercles.

Cetacean flippers function to stabilize the body and aid in turns (Woodward *et al*., 2006). Large bowhead and right whale flippers are useful when the whale is turning at slow speeds. Gray whales make long migrations and breed in shallow lagoons, and as such their flippers have a broad surface area useful for turning at slow speeds, but the elongate flipper is also useful for generating lift while migrating. Most rorqual whales use their tiny flippers to stabilize and aid in turns. The humpback whale flipper is the exception among rorquals. The flipper is slapped on the water surface during mate displays and social touching. While swimming, the flipper moves in alternating dorsal–ventral strokes, and deforms into concave and convex arc shapes. Leading edge tubercles increase flipper area to maintain laminar flow, hinder generation of tip vortices, and allow a greater generation of lift.

All modern cetaceans have a remarkably shortened humerus, and the radius and ulna are flattened (Fig. 1A) (Howell, 1930). In most small-sized odontocetes, the carpal bones of the wrist have distinct bony articular facets, but almost all mysticetes and large-bodied odontocetes have burr-shaped carpal bones that lack articular facets and these carpals are immersed in a block of cartilage (Fig. 1A).

Cetacean metacarpals and phalanges, the bones of the digits, have unique characteristics compared to other mammals. These bones are hourglass shaped and lack all articular facets such that the dorsal and palmar, and proximal and distal surfaces are unidentifiable. Differentiating characteristics between metacarpals and phalanges are lacking, and identification of these elements can only be certain in articulated limbs. Cetaceans also have epiphyses on both the proximal and distal surfaces of the metacarpals and phalanges. Cetaceans are the only mammals to have a greater number of phalanges per digit (hyperphalangy) than the standard mammalian condition of two phalanges in the thumb, followed by three phalanges in the other digits (Table I). Odontocetes have the greatest number of phalanges in digits II and III, while mysticetes display the greatest number of phalanges in digits III and IV. Most cetaceans have five digits, but three families of mysticetes (Neobalaenidae, Eschrichtiidae, and Balaenopteridae) lack metacarpal I and all the phalanges of digit I (Fig. 1A).

Compared to other marine mammals, the cetacean flipper has a distinct lack of muscular and soft tissue structures (Howell, 1930). The triceps muscle complex is reduced with only the heads originating from the scapula being functional. The elbow is locked and the triceps

Forelimb Anatomy

Lisa Noelle Cooper

Marine mammals are descended from terrestrial mammals whose forelimbs were weight-bearing appendages specialized for terrestrial locomotion. In the transition to an
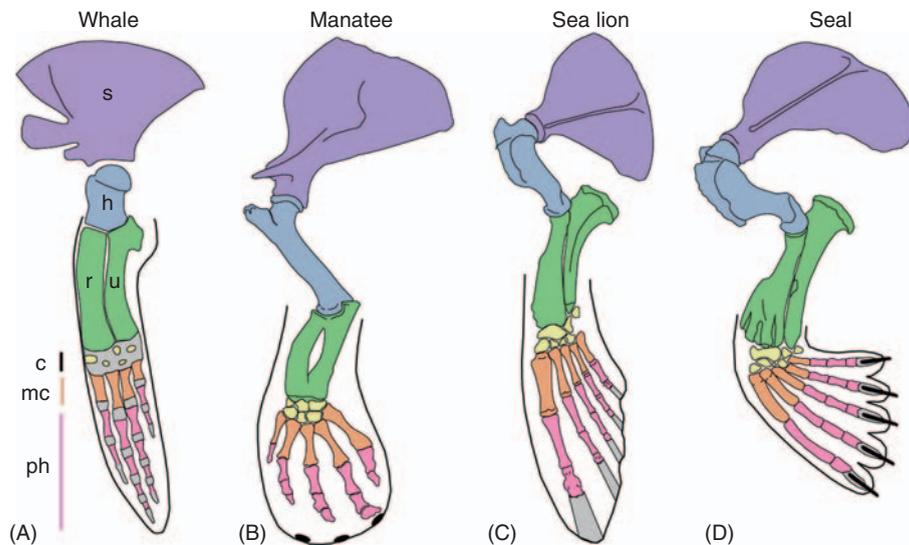
Figure 1 *Left forelimbs of marine mammals: (A) blue whale, (B) manatee, (C) sea lion, (D) seal (Howell, 1930). Cartilage indicated by gray, claws shown in black. s, scapula; h, humerus; r, radius; u, ulna; c, carpals; mc, metacarpals; ph, phalanges.*

Figure 2 *Radiographs of two members of the family Delphinidae showing variation in flipper size and shape: (A) Risso's dolphin (Grampus griseus), (B) killer whale (Orcinus orca). Scale bar 10 cm (Jacobsen, 2007).*

Figure 3 *Flipper shapes of some cetaceans. Top row representative mysticetes, bottom row representative odontocetes. The leading edge of the flipper is to the left.*

humeral heads are reduced. Flexor and extensor muscles are prominent in most mysticetes (except *Megaptera*), and sperm whales and beaked whales (physeterids, kogiids, and ziphiids), but are lacking in other families of odontocetes (monodontids, phocoenids, and delphinids). Intrinsic manus muscles (interossei, lumbricals, abductors, adductors) are absent in most cetaceans, with exceptions found in physeterids and kogiids.
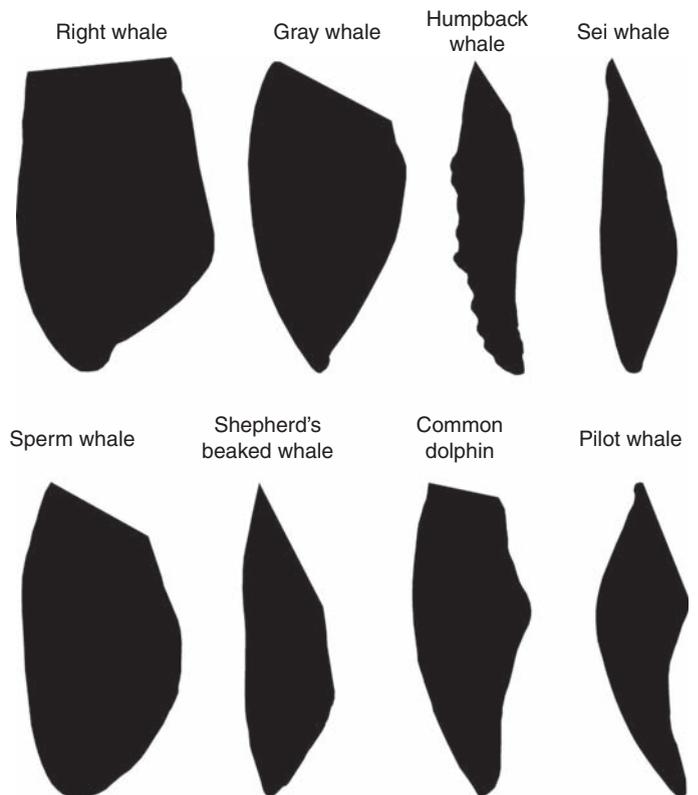
Fossil evidence indicates cetaceans increased surface area for muscles acting on the shoulder joint, immobilized the elbow and wrist, and elongated the manus (Uhen, 2004). The earliest Eocene archaeocetes used their forelimbs for terrestrial locomotion and their limbs appeared similar to those of Eocene artiodactyls. In the late Eocene, basilosaurid archaeocetes were fully aquatic and developed a wider

TABLE I
Phalangeal Formulas for Some Cetaceans. The Greatest Number of Phalanges Are Seen in Digits II and III in Odontocetes, and Digits III and IV in Mysticetes

Taxon	Species	Digit I	Digit II	Digit III	Digit IV	Digit V
Odontocetes						
sperm whale	*Physeter*	0–1	3–6	4–5	2–4	0–3
pygmy sperm whale	*Kogia breviceps*	1–2	7–8	6–7	5–6	3–5
Gervais' beaked whale	*Mesoplodon europaeus*	0	5–6	5–6	4	2–3
Susu	*Platanista*	1–2	3–5	3–4	3–5	3–5
Beluga	*Delphinapterus*	1	3–6	3–4	2–4	1–3
Harbor porpoise	*Phocoena phocoena*	0–2	5–9	5–8	2–4	0–2
Long-finned pilot whale	*Globicephala melas*	2–3	12–13	8	2	0–1
Atlantic white-sided dolphin	*Lagenorhynchus acutus*	1–2	7–10	5–6	2–4	0–2
Killer whale	*Orcinus*	0–2	4–6	3–4	3	0–2
Bottlenose dolphin	*Tursiops truncatus*	0–1	5–8	5–6	2–4	0–2
Mysticetes						
Bowhead whale	*Balaena*	0–2	3	4–5	3	2
Southern right whale	*Eubalaena australis*	0–2	3–4	4–5	4	3
Northern right whale	*Eubalaena glacialis*	1–2	4	4–5	2–3	2–3
Pygmy right whale	*Caperea*	Absent	2–4	3–5	3–4	1–3
Gray whale	*Eschrichtius*	Absent	2–3	4–5	3–4	2–3
Minke whale	*Balaenoptera acutorostrata*	Absent	3	6–7	5–6	3
Sei whale	*Balaenoptera borealis*	Absent	3–4	5–7	4–7	2–4
Blue whale	*Balaenoptera musculus*	Absent	3–4	5–8	5–7	3–4
Humpback whale	*Megaptera*	Absent	2	7–8	6–7	2–3

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scapula, allowing for greater areas of origin for the infraspinatus and suprspinatus muscles. Basilosaurids also developed a strong deltopectoral crest on the humerus for insertion of the deltoid muscle. This crest was lost in Oligocene cetaceans as the insertion of the deltoid muscle shifted to the distal and dorsal surface of the humerus. The elbow joint lost mobility as the distal end of the humerus evolved a v-shaped articular surface that locked the radius and ulna in place. Fossil evidence indicates elbow mobility was lost about 29 million years ago. It is currently unknown when wrist mobility was lost. Fossil evidence indicates the process of digital elongation, indicated by hyperphalangy, began at least 7–8 million years ago, although it may have started much earlier during the Oligocene.

II. Sirenians

Manatees do not use their flippers as control surfaces while the animal is swimming; instead forelimbs mostly function to orient the animal and make small corrective movements during feeding, rest, or socializing. The forelimbs are the main sources of propulsion while the animal is in contact with the sea floor, in which manatees may "walk" on the sea floor by placing flippers one in front of another, or propel themselves by paddling (Hartman, 1979). Forelimb movements are supported by abundant musculature and large, rounded tendons throughout the proximal and distal limb (Murie, 1872). Manatee digits are immersed in thick connective tissue and lack the ability to abduct and adduct, but retain intrinsic muscles of the manus (abductors and interossei).

Modern sirenians (dugongs and manatees) have a slightly modified mammalian forelimb (Howell, 1930). The elbow is mobile in sirenians, and this joint motion is stabilized by a proximally fused radius and ulna. The wrist is highly mobile and lacks a pisiform carpal bone. Dugongs have three carpal elements in the wrist, while manatees have six. The manatee manus is slightly modified as digit I lacks one phalanx, digit IV is the longest and most robust, and phalanges on the ends of the digits are irregularly shaped and flattened (Fig. 1AB). Manatees also have a number of broad and flat nails on the surface of the flipper (Fig. 1b), and some captive manatees increase the number of nails.

III Marine Carnivores

A. Pinnipeds

Pinnipeds, unlike other marine mammals, have pairs of flippers on both the forelimbs and hindlimbs. This discussion will only address the foreflippers.

Pinnipeds are unique in that their flippers are utilized mostly in aquatic locomotion and have limited utility on land. Odobenid (walrus) forelimbs act as paddles or rudders for steering (Gordon, 1981) and are used to remove sediment when searching for prey. While on land, walrus forelimbs support the trunk by placing the digits flat and bending the wrist at a right angle. This bent forelimb morphology makes terrestrial locomotion awkward. Otariid pinnipeds (English, 1976, 1977) have elongated and thin flippers that flap like

a bird wing to produce thrust underwater, and are used to support the trunk on land. Phocid forelimbs function solely in steering while underwater but are usually held flush with the body wall, and are not a significant source of propulsion. On land, most phocids do not use their forelimbs as a weight-bearing appendage.

Walrus (*Odobenus*) flippers are short compared to other pinnipeds, but are very broad and have tiny nails on the dorsal surface. Otariids have elongate and thin flippers with a slight crescent of skin at the ends of each digit. Phocid flippers are divided between some of the digits, and long thin nails extend beyond the dorsal surface of all five digits.

The digits of pinnipeds also have unique characteristics (Howell, 1930). All pinnipeds have elongated the digits by developing bars of cartilage at the ends of each digit. These cartilaginous extensions are longest in otariids, slightly shorter in the walrus and shortest in some phocids. Metacarpal I is longer and thicker than metacarpal II in all pinnipeds except phocines.

Pinnipeds also display large and complex forelimb muscles. The walrus has large and powerful muscles, with relatively the same sized muscle bellies as otariids.

Otariids isolate more than half of the forelimb musculature in the proximal portion of the forelimb. The triceps muscle complex is relatively large, and allows for elbow retraction. Muscles acting on the otariids wrist create palmar flexion, which is the main source of propulsion. Otariids also have muscles acting on the digits: interossei, digital abductors and adductors, and in some specimens a single lumbrical. Phocids have an enlarged triceps muscle complex.

The earliest fossil pinniped, *Enaliarctos mealsi*, already had forelimbs modified as flippers. No fossils indicate the transition between terrestrial carnivores and aquatic pinnipeds (Berta *et al.*, 1989).

B. Sea Otters

Sea otters (*Enhydra*) do not use their forelimbs while swimming. The forelimbs are specialized in movements requiring great dexterity: prey manipulation, grooming, and caring for young (Howard, 1973).

Sea otter forelimbs are small and retractable claws extend from each of the digits (Fig. 4). The digits cannot act individually as they are connected by soft tissue webbing. Thick pads line the palmar surfaces of digits. Forelimb musculature is well developed.
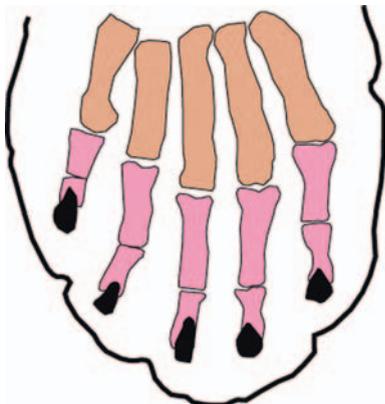

Figure 4   *Sea otter foreflipper (Howard, 1973).*

The giant extinct sea otter *Enhydritherium* was propelled by its forelimbs, but all modern sea otters are pelvic paddlers with enlarged hindlimbs.

C. Polar Bears

Polar bears are powerful swimmers but also walk on ice or land. The forelimbs are incredibly strong and are the main sources of propulsion while swimming, killing prey, fighting, and hauling out of the water. Alternating strokes of forelimb flexion generate propulsion while swimming and the hindlimbs trail and remain motionless. While fighting another, polar bears will stand on their hind limbs, wrap forelimbs around another and bite. To haul out of the water, the polar bear pulls itself mostly out of the water with its stong forelimbs, and uses the hindlimbs after most of the body mass is out of the water. While walking on ice or land, polar bears place the whole hand flat on the substrate.

Polar bear forelimbs are similar to other bears, except that the scapula has a narrow postscapular fossa. This fossa gives origin to the subscapularis muscle.

See Also the Following Article

Skeletal anatomy

References

Benke, H. (1993). Investigations on the osteology and the functional morphology of the flipper of whales and dolphins (Cetacea). *Invest. Cetacea* **24**, 9–252.

Berta, A., Ray, C. E., and Wyss, A. R. (1989). Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science* **244**, 60–62.

Cooper, L. N., Berta, A., Dawson, S. D., and Reidenberg, J. (2007). Evolution of digit reduction and hyperphalangy in the cetacean manus. *Anat. Rec.* **290**, 654–672.

Davis, D. D. (1949). The shoulder architecture of bears and other carnivores. *Field. Zool.* **31**, 285–305.

English, A. W. M. (1976). Functional anatomy of the hands of fur seals and sea lions. *Am. J. Anat.* **147**, 1–17.

English, A. W. M. (1977). Structural correlates of forelimb function in fur seals and sea lions. *J. Morphol.* **151**, 325–352.

Fish, F. E., and Battle, J. M. (1995). Hydrodynamic design of the humpback flipper. *J. Morphol.* **225**, 51–60.

Gordon, K. R. (1981). Locomotor behavior of the walrus (*odobenus*) *J. Zool. Lond*, **195**, 349–357.

Hartman, D. S. (1979). "Ecology and behavior of the manatee (*Trichechus manatus*)." American Society of Mammalogists, Special Publication No. 5.

Howard, L. D. (1973). Muscular anatomy of the forelimb of the sea otter (*Enhydra lutris*). *Proc. Cal. Acad. Sci.* **XXXIX**, 411–500.

Howell, A. B. (1930). "Aquatic mammals: Their adaptations to life in the water." Charles C. Thomas Press, Springfield.

Jacobsen, J. K. (2007). "Radiographs from the Humboldt State University Vertebrate Museum." Humboldt, California.

Murie, J. (1872). On the structure of the manatee (*Manatus americanus*). *Trans. Zool. Soc. London* **8**, 127–202.

Shulte, H.von W., and Smith, M.de F. (1918). The external characters, skeletal muscles, and peripheral nerves of *Kogia breviceps* (Blainville). *Bull. Amer. Mus. Nat. Hist.* **37**, 7–72.

Woodward, B. L., Winn, J. P., and Fish, F. E. (2006). Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *J. Morphol.* **267**, 1284–1294.

Uhen, M. D. (2004). Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the middle to late Eocene of Egypt. *Univ. Mich., Pap. Paleontol.* **34**, 1–222.