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Neuromuscular Anatomy and Evolution of the Cetacean Forelimb

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ABSTRACT

The forelimb of cetaceans (whales, dolphins, and porpoises) has been radically modified during the limb-to-flipper transition. Extant cetaceans have a soft tissue flipper encasing the manus and acting as a hydrofoil to generate lift. The neuromuscular anatomy that controls flipper movement, however, is poorly understood. This study documents flipper neuromuscular anatomy and tests the hypothesis that antebrachial muscle robustness is related to body size. Data were gathered during dissections of 22 flippers, representing 15 species (7 odontocetes, 15 mysticetes). Results were compared with published descriptions of both artiodactyls and secondarily aquatic vertebrates. Results indicate muscle robustness is best predicted by taxonomic distribution and is not a function of body size. All cetaceans have atrophied triceps muscles, an immobile cubital joint, and lack most connective tissue structures and manus muscles. Forelimbs retain only three muscle groups: triceps (only the scapular head is functional as the humeral heads are vestigal), and antebrachial extensors and flexors. Well-developed flexor and extensor muscles were found in mysticetes and basal odontocetes (i.e., physeterids, kogiids, and ziphiids), whereas later diverging odontocetes (i.e., monodontids, phocoenids, and delphinids) lack or reduce these muscles. Balaenopterid mysticetes (e.g., fin and minke whales) may actively change flipper curvature, while basal odontocetes (e.g., sperm and beaked whales) probably stiffen the flipper through isometric contraction. Later diverging odontocetes lack musculature supporting digital movements and are unable to manipulate flipper curvature. Cetacean forelimbs are unique in that they have lost agility and several soft tissue structures, but retain sensory innervations. Anat Rec, 290:1121–1137, 2007. © 2007 Wiley-Liss, Inc.

Key words: cetacea; forelimb; flipper; myology; function

Cetaceans are a unique lineage of secondarily aquatic tetrapods that have greatly modified the forelimb by evolving a flipper. Compared with the ancestors of whales, terrestrial artiodactyls (i.e., even-toed hoofed mammals: pigs, hippopotamus, peccaries, camels, ruminants; Gingerich et al., 2001; Thewissen et al., 2001; Geisler and Uhen, 2003), cetaceans reconfigure the joints and soft tissue structures that typically allow terrestrial locomotion. Cetaceans immobilize the cubital

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joint and mostly immobilize the wrist and digits, develop hyperphalangy in the digits, and encase the limb in a soft tissue flipper. Flipper movement is generated at the glenohumeral joint primarily by means of the deltoid and subscapularis muscles, allowing flippers to act as stabilizers or control surfaces that function in maintaining equilibrium (Fish, 2002a), while the majority of propulsion comes from caudal undulations (Fish, 1998; Woodward et al., 2006). Although these morphologies may have evolved as a consequence of an aquatic lifestyle, fundamental comparative studies on the gross and functional anatomy of cetaceans and terrestrial artiodactyls are scarce. Herein we describe the gross neuromuscular anatomy of cetacean flippers, which may have functional and evolutionary implications.

Little is known of the brachial plexus morphology and motor and sensory innervation in cetaceans. Strickler (1978) reported the brachial plexus cranial trunk emanates from cervical spinal nerves C4, C5, and C6, while the caudal trunk arises from C6, C7, and C8. Cervical spinal nerves 4, 5, and 6 are enlarged in the porpoise (*Phocoena*), and cervical spinal nerve 5 is associated with an enlarged cetacean deltoid muscle (Harris, 1939), which moves the flipper dorsally (Benke, 1993). Terminal branches of the brachial plexus are the median, ulnar, musculocutaneous, axillary, and radial nerves. Kunze (1912) reviewed the path of these nerves in forelimbs of fetal sei and fin whales (*Balaenoptera borealis*, *B. physalus*). In odontocetes, detailed reports of these nerves focus on the La Plata river dolphin (*Pontoporia blainvillei*; Strickler, 1978), and pygmy sperm whale (*Kogia breviceps*; Schulte and Smith, 1918). However, the literature lacks a comparison between ontogenetically mature odontocete and mysticete taxa. We report the pathways of the major terminal nerve branches of the brachial plexus in three cetacean species (two mysticetes, one odontocete) of varying ages.

Although neuroanatomy of the cetacean flipper is relatively unknown, literature regarding forelimb myology is abundant. Forelimb myology has been described for balaenopterids (e.g., Carte and MacAllister, 1867; Perrin, 1870; Schulte, 1916; Schulte and Smith, 1918) and for a balaenid (Eschricht and Reinhardt, 1866); however, eschrichtiid forelimb myology remains undescribed. Odontocete forelimb descriptions include those on dolphins (Murie, 1873; Vasilevskaya, 1974; Purves and Pilleri, 1978), a pygmy sperm whale (Schulte and Smith, 1918), beaked whales (Struthers, 1873–1875; Turner, 1885–1886), a narwhal (Howell, 1930a), river dolphins (Strickler, 1978; Klima et al., 1980), and porpoises (Howell, 1927; Smith et al., 1976). This study reports the forelimb myology of 15 mysticetes and odontocetes, and we have combined our findings with data from the literature into a comprehensive database of the soft tissue anatomy of the flipper. The taxonomic diversity of this database allows for phylogenetic interpretations of the evolution of antebrachial muscles and tendons.

The objective of this study was to document soft tissue structures of the cetacean forelimb in a comparative context to test the hypothesis that large-bodied cetaceans have robust antebrachial muscles (flexors and extensors), and small-bodied cetaceans have reduced muscle morphology. This hypothesis predicts that muscle morphology is a consequence of body size and a large-bodied dolphin, such as the killer whale (*Orcinus*), would retain prominent antebrachial muscle bellies and tendons because of the mechanical loading of such a large flipper.

MATERIALS AND METHODS

Fresh cetacean forelimbs (n = 22) representing 15 species from specimens of differing ages were dissected (Table 1). From the suborder Mysticeti, specimens were dissected from all families except the monotypic Neobalaenidae. These mysticete genera include *Balaenoptera* (n = 11), *Eschrichtius* (n = 1), *Balaena* (n = 2), and *Eubalaena* (n = 1). From the suborder Odontoceti, specimens were dissected from only four families: Physeteridae (*Physeter*, n = 1), Ziphiidae (*Ziphius*, n = 1), Phocoenidae (*Phocoena*, n = 1), and Delphinidae (*Lagenorhynchus*, n = 1; *Delphinus*, n = 1; *Tursiops*, n = 1; and *Orcinus*, n = 1). Muscle origins and insertions were recorded using nomenclature and forelimb orientations following the standard Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2005) terminology. Major nerve pathways were traced from their proximal origin in the brachial plexus to their distal extent in two species of balaenopterids (fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae*) and the killer whale *Orcinus orca*.

The terms used to describe flipper orientation assume that the flipper is abducted 90 degrees away from the body and is rotated laterally so that its long axis lies in the horizontal plane (i.e., flat surfaces face up and down, the leading edge is blunt, and the trailing edge is thin). We will refer to the leading edge of the flipper as "cranial," and the trailing edge as "caudal," the region near the glenohumeral joint as "proximal," and the region around the terminal tip of the longest digit as "distal." The flat surface facing superiorly is "dorsal," and the flat surface facing inferiorly is "palmar" (or ventral). If the flipper is rotated medially and adducted (placed against the body), the dorsal surface is positioned laterally and the palmar surface is positioned medially.

This study focuses on forelimb antebrachial muscles (extensor and flexors) rather than muscles of the pectoral girdle. The term "antebrachial muscles" was used when referring to both the flexor and extensor muscles that originate near the cubital joint. Extensor muscles lie on the dorsal surface of the flipper, while flexors lie on the palmar surface. Some taxa also displayed interossei, lumbricals, and digital adductors and abductors. These muscles are collectively referred to as "intrinsic muscle of the manus." Data on musculature of fossil taxa and comparisons with extant ungulates were collated from the published accounts. The presence of antebrachial muscles was documented in fossil archaeocetes *Ambulocetus natans* (Thewissen et al., 1996; Madar et al., 2002) and *Dorudon atrox* (Uhen, 2004) based on bony landmarks of several forelimb elements. Although osteological correlates document the presence of these muscles, this study further hypothesizes that *A. natans* and *D. atrox* had well-developed antebrachial muscle bellies and tendons based on comparisons with extant terrestrial artiodactyls and cetaceans using the Extant Phylogenetic Bracket (EPB, Bryant and Russell, 1992; Witmer, 1995). By using a hypothesis of homology, the

TABLE 1. Dissected specimens including collection data and approximate ontogenetic age

Taxon	Common Name	Specimen ID	Institution	Ontogenetic Age
Mysticeti				
Balaenidae				
Balaena mysticetus	Bowhead	03B11	Barrow Arctic Science Ctr., Barrow, AK	Neonate
Balaena mysticetus	Bowhead	03B14	Barrow Arctic Science Ctr., Barrow, AK	Neonate
Eubalaena glacialis[a]	Right	NY-2680-2001	Smithsonian Institution, Washington, DC	Juvenile
Balaenopteridae				
Balaenoptera acutorostrata	Minke	None	Geology Dept., Univ. of Otago, Dunedin, NZ	Juvenile
Balaenoptera acutorostrata	Minke	COA 0207171	College of the Atlantic, Bar Harbor, ME	Neonate
Balaenoptera acutorostrata[a]	Minke	MMSC-05-121	Smithsonian Institution, Washington, DC	Mature
Balaenoptera borealis[a]	Sei	NY-2659-01	Smithsonian Institution, Washington, DC	Mature
Balaenoptera brydei	Bryde's	USNM- 578922	Smithsonian Institution, Washington, DC	Mature
Balaenoptera physalus	Fin	none	Florida Marine Research Inst., St. Petersburg, FL	Neonate
Balaenoptera physalus	Fin	USNM- 484994	Smithsonian Institution, Washington, DC	Neonate
Balaenoptera physalus	Fin	SW-03971	Sea World, San Diego, CA	Neonate
Balaenoptera physalus[a]	Fin	SYBP-0448	Smithsonian Institution, Washington, DC	Mature
Balaenoptera physalus[a]	Fin	MMSC-01-016	Smithsonian Institution, Washington, DC	Mature
Megaptera novaeangliae[a]	Humpback	NY-2700-2001	Smithsonian Institution, Washington, DC	Neonate
Eschrichtiidae				
Eschrichtius robustus	Gray	KXD-0060	SW Fisheries Science Ctr., San Diego, CA	Yearling
Odontoceti				
Physeteridae				
Physeter macrocephalus[a]	Sperm	WJW-003	Smithsonian Institution, Washington DC	Mature
Ziphiidae				
Ziphius cavirostris	Cuvier's beaked	KXD-0019	SW Fisheries Science Ctr., San Diego, CA	Neonate
Phocoenidae				
Phocoena phocoena	Harbour porpoise	X20727-01	Atlantic Veterinary College, PEI, Canada	Adult
Delphinidae				
Lagenorhynchus acutus	Atlantic white-sided dolphin	X26346-04	Atlantic Veterinary College, PEI, Canada	Juvenile
Delphinus delphis	Common dolphin	none	Dept. of Anatomy, Northeastern Ohio Univ. College of Medicine, OH	Adult
Tursiops truncatus	Bottlenose dolphin	KXD-0025	SW Fisheries Science Ctr., San Diego, CA	Adult
Orcinus orca	Killer Whale	S-946	San Diego St. Univ., San Diego, CA	Adult

[a] Specimens were originally at the Mount Sinai School of Medicine, New York, and transferred to USNM to be part of the permanent collection.

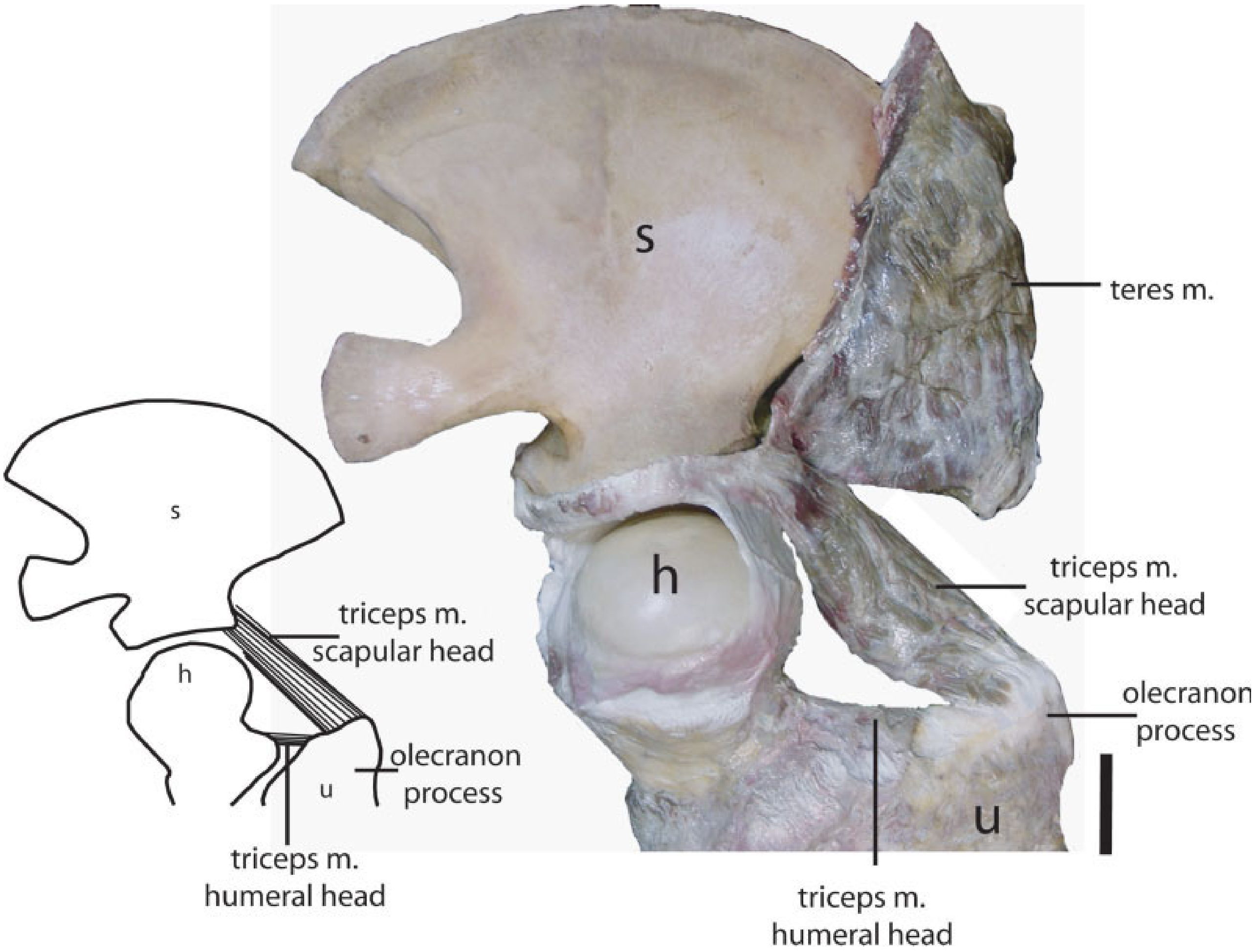

Fig. 1. Typical two-headed *m. triceps brachii* in a dissected gray whale (*Eschrichtius*) forelimb, a scapular and humeral head inserting on the olecranon process of the ulna. s, scapula; h, humerus; u, ulna. Scale bar = 10 cm.

EPB allows soft tissue reconstruction in fossil taxa based on known osteological correlates of soft tissue structures in their living relatives (Bryant and Russell, 1992; Witmer, 1995). Data used come from forelimb dissections of both the descendants of archaeocetes (extant cetaceans) and their nearest terrestrial outgroups, including pygmy hippopotamus (*Choeropsis liberiensis* Campbell, 1936; Geisler and Uhen, 2003) and pigs *Sus scrofa* (Campbell, 1936). Extant ungulates display the primitive condition of well-developed antebrachial muscles and tendons (Campbell, 1936; Fisher et al., 2005, 2007).

Hydrodynamic performance data and descriptions were gathered for each taxon from the literature. Phylogenetic implications were supplemented with locomotor characteristics: relative swimming speed (Fish, 2002a,b, 2004; Woodward et al., 2006), and level of maneuverability (cruiser vs. agile, Benke, 1993; Fish, 2002a, 2004; Woodward et al., 2006). Furthermore, Fish (2002a,b, 2004) provides locomotor data on several odontocete taxa. Some taxa lack published records of swimming speed and turning radii, and, therefore, descriptive accounts of foraging depth, swimming speed, and relative maneuverability were supplemented.

RESULTS

Dissection findings indicated cetaceans retain only three prominent intrinsic muscle groups of the forelimb, the triceps muscles, and the flexor and extensor groups. With minor exception, cetaceans lack intrinsic muscles of the manus, and corresponding motor innervations.

Triceps Morphology

The *m. triceps brachii* (Fig. 1; Table 2) was observed in mysticetes and the sperm whale (*Physeter*). All taxa retained a triceps humeral head (*m. triceps brachii*, *caput laterale*). A second head originating from the caudal border of the scapula (*m. triceps brachii*, *caput longum*) was found in the following odontocetes: the sperm whale (Fig. 2), pygmy sperm whale (*Kogia*), and a beaked whale (*Mesoplodon*). It was also found in all mysticetes except the bowhead (*Balaena mysticetus*). Humeral and scapular triceps heads insert on the olecranon process of the ulna, except in the sperm whale (*Physeter*). All species of dissected *Mesoplodon* are unique in displaying two triceps heads that take origin from the humerus (*caput laterale* and *caput mediale*),

TABLE 2. Origins and insertions of the various heads of the cetacean m. triceps brachii: O (origin), I (insertion), dist (distal), prox (proximal), cau (caudal), and pal (palmar)

Taxon	Heads of *m. triceps brachii*	Scapular head (*caput longum*)	Humeral head (*caput laterale* or *mediale*)	Other	Reference
Odontoceti					
P. macrocephalus	2–3	O: scapula ? I: olecranon process (dist)	O: humerus (cau, dist) I: olecranon process (prox)	O: humerus (cau) ? I: a) olecranon (dist) b) tendo *m. flexor carpi ulnaris*	This study
K. breviceps	2	O: a) post-glenoid tubercle b) scapula (cau) I: olecranon	O: humerus (cau) I: olecranon process		Schulte and Smith (1918)
Mesoplodon bidens	3	O: scapula I: olecranon process	O: humerus, shaft I: olecranon process	O: humerus, shaft I: olecranon process	Turner (1885–86)
Monodon monoceros	1		O: humerus (cau, dist) I: ulna (prox)		Howell (1930)
Pontoporia blainvillei	1		O: humerus (cau, pal) I: ulna (dist, cau)		Strickler (1978)
Neophocoena phocaenoides	1		O: humerus (tuberosity) I: olecranon process		Howell (1927)
Mysticeti					
B.mysticetus	1		O: humerus shaft (cau) I: olecranon		This study
B. borealis	2	O: glenoid cavity (cau) I: olecranon	O: humerus (cau, dist) I: olecranon (prox)		Schulte (1916)
B. physalus	2	0: scapula (cau, dist) I: olecranon (prox)	O: humerus shaft (cau) I: a) olecranon (prox) b) ulna (prox, cau)		This study
B. acutorostrata	2	O: scapula (cau, dist) I: olecranon (prox)	O: humerus shaft (cau) I: olecranon		This study
E. robustus	2	O: glenoid (cau) I: olecranon (prox, cau)	O: humeral shaft (cau) I: olecranon		This study

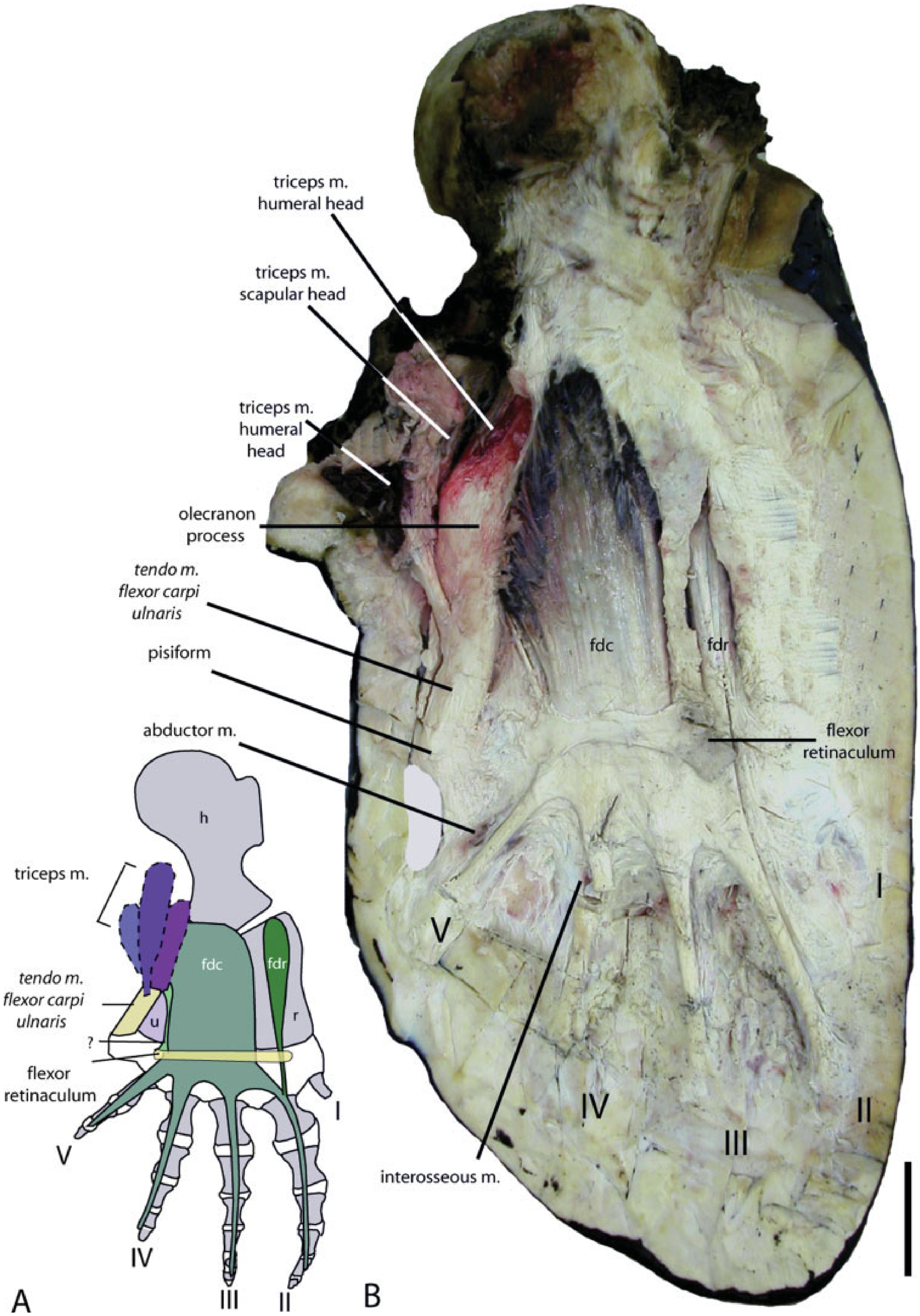
triceps m. humeral head
triceps m. scapular head
triceps m. humeral head
olecranon process
tendo m. flexor carpi ulnaris
pisiform
abductor m.
fdc
fdr
flexor retinaculum
I
V
IV
III
II
interosseous m.
h
triceps m.
fdc
fdr
tendo m. flexor carpi ulnaris
u
r
?
flexor retinaculum
V
I
IV
III
II
A
B

Figure 2.

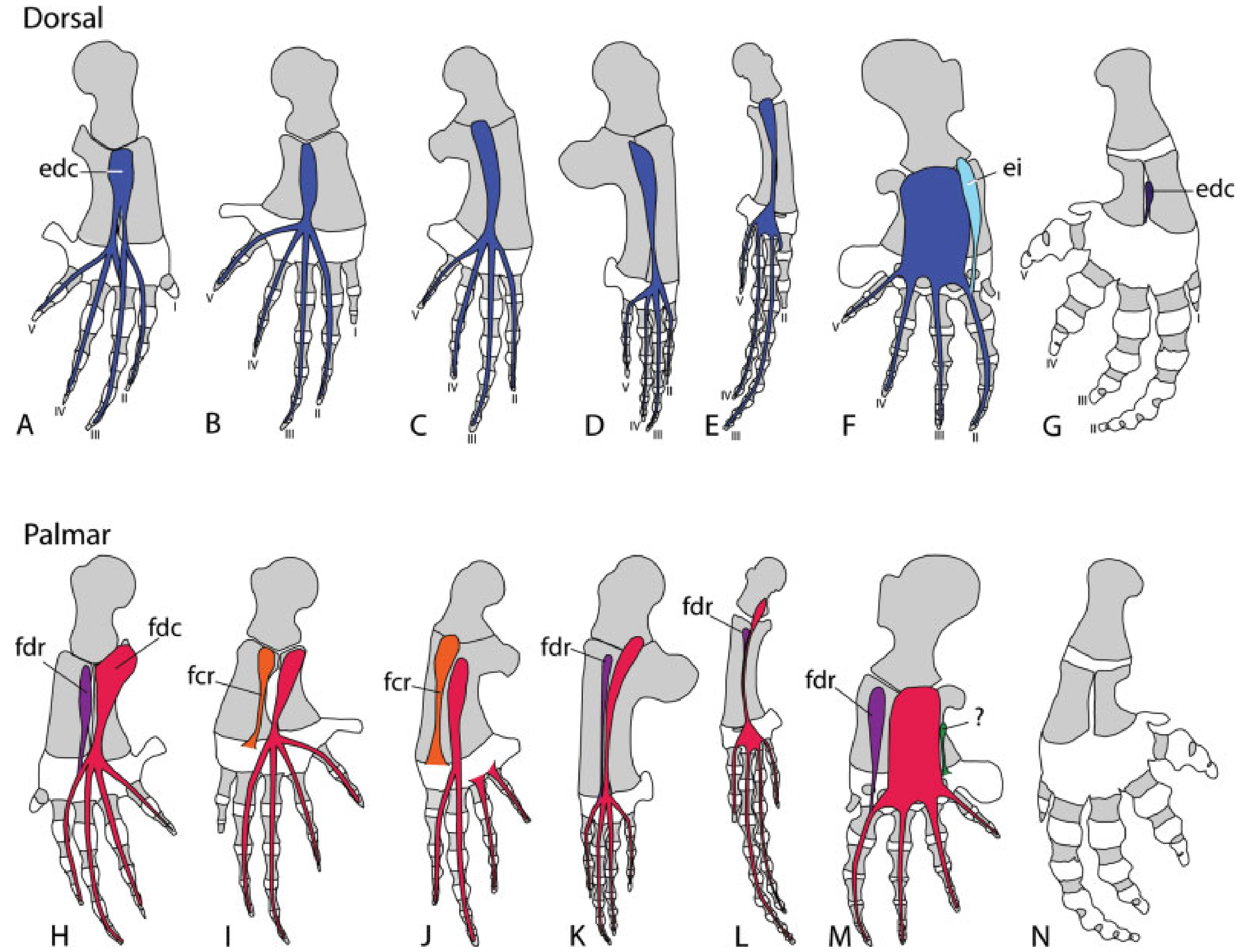

Fig. 3. Schematic of the antebrachial muscles of the cetacean forelimb. **A,H:** Bowhead whale (*B. mysticetus*). **B,I:** Northern Atlantic right whale (*E. glacialis*). **C,J:** Gray whale (*E. robustus*). **D,K:** Fin whale (*B. physalus*). **E,L:** Humpback whale (*M. novaeangliae*). **F,M:** Sperm whale (*P. macrocephalus*). **G,N:** Killer whale (*Orcinus orca*). edc, *m. extensor digitorum communis*; ei, *m. extensor indicus*; fcr, *m. flexor carpi radialis*; fdc, *m. flexor digitorum communis*; fdr, *m. flexor digitorum radialis*. Forelimbs shown in dorsal views (top row) and palmar views (bottom row).

retaining the primitive artiodactyl condition. A third triceps head, found only in *Physeter*, probably originated on the humerus, but its precise origin was unclear due to the condition of the specimen (Table 2). In *Physeter*, a scapular head (*caput longum*) of the triceps sent a tendinous band distally to the olecranon to fuse with the *tendo flexor carpi ulnaris* (Fig. 2). As the *Physeter* specimen did not have an attached scapula, this study cannot verify the muscular origin and, therefore, only tentatively describes this triceps head as originating from the scapula.

Antebrachial Muscle Morphology

Origin and insertion of antebrachial muscles are illustrated (Figs. 3, 4) and listed in Table 3. Morphology of the *m. flexor carpi ulnaris* is not included, as all taxa shared the same origin (olecranon process) and insertion along the pisiform cartilage. The main flexor, *m. flexor digitorum* was not divided as in artiodactyls into *superficialis* or *profundus* heads, and is referred to as the *m. flexor digitorum communis*.

An unambiguous insertion pattern was found in the dissected pentadactylous taxa (all odontocetes and balaenid mysticetes): the *m. flexor* and *extensor digitorum communis* inserted on digits II–V (Figs. 2, 3; Table 3). No tendons inserted on digit I. In tetradactylous taxa (nonbalaenid mysticetes), both the *m. flexor* and *extensor communis digitorum* insert on all four digits (digits II–V).

Mysticete taxa typically displayed well-developed antebrachial muscles with organized muscular bellies and thick rounded tendons on both the palmar and dorsal flipper surfaces (Fig. 3; Table 3). These muscles were

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Fig. 2. **a,b:** Palmar view of a dissected sperm whale (*Physeter*) forelimb illustrating the primitive, robust flexor muscle morphology and a three-headed *m. triceps brachii*. *m. flexor digitorum communis* (fdc), *m. flexor digitorum radialis* (fdr). Scale bar = 10 cm.

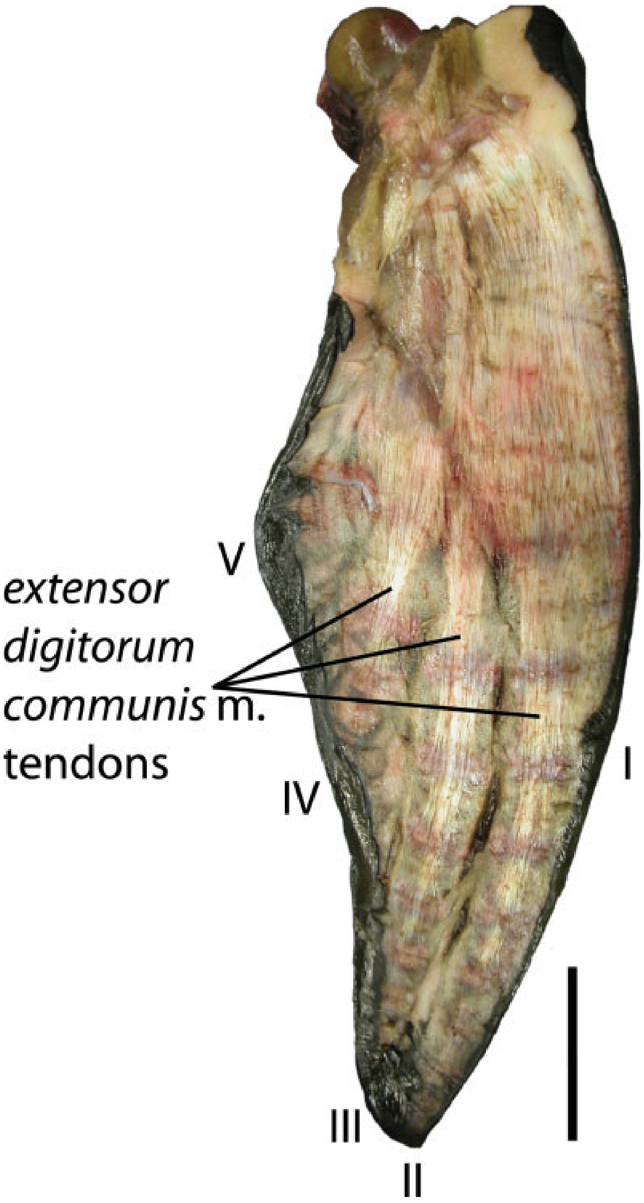

Fig. 4. Dorsal view of a dissected common dolphin (*Delphinus*) forelimb illustrating the derived, reduced antebrachial muscle morphology. Scale bar = 5 cm.

encased in a thick fascia from which the muscle fibers take origin. Unlike other mysticetes examined in this study, the humpback whale (*Megaptera*) exhibited extremely reduced muscles in which there were few muscle fibers and flattened tendons.

Odontocete taxa showed variation in antebrachial limb muscle morphology (Table 3). *Physeter* (Figs. 2, 3) and Cuvier's beaked whale (*Ziphius*), two basal odontocetes, shared the mysticete-like morphology of well-developed antebrachial muscles with organized muscular bellies on both the dorsal and palmar surfaces of the flipper. Dissection of a phocoenid and several small-bodied delphinids revealed a radical reduction in this muscular morphology; there was no gross evidence of muscle fibers of antebrachial muscles in these taxa (Fig. 4; Table 3). Instead of muscle fibers, only a thick periosteum was found covering the radius and ulna, with interwoven fibers that were mostly, but not entirely, oriented longitudinally. A single exception to the reduced delphinid muscle morphology was seen in the killer whale (*Orcinus*), in which there was evidence of a reduced extensor muscle belly in the form of a few dissociated muscle fibers (Fig. 3). No gross evidence of a flexor muscle was found in *Orcinus*.

We found no evidence of complete synovial sheaths enveloping either flexor or extensor tendons; however, two distinct morphologies were observed. Flexor tendons were clearly separated from surrounding tissues, whereas extensor tendons were more firmly attached to the underlying tissues. Flexor tendons exhibited divergent fibers along the cranial and caudal surfaces to envelope interphalangeal joints and insert on each phalanx. There was no well-defined pattern of superficial fibers wrapping around deep fibers to form a sleeve or manica flexorius, or digital annular ligaments, both typical of terrestrial artiodactyls (Table 4). Extensor tendon attachments are best developed in fin whales (*Balaenoptera physalus*), with oblique connective tissue fibers forming vinculae that fuse with the phalangeal periosteum. In *Physeter*, extensor tendons pass over the terminal phalanx, expand craniocaudally, and fan out into the connective tissue along the flipper margin.

In the phocoenid and delphinids, tendons are reduced to a thick layer of connective tissue with grossly longitudinally oriented fibers (Fig. 4). This connective tissue layer resembles antebrachial muscle tendons in the degree of fiber orientation. The tendons cannot be separated from the underlying bone and are firmly attached to all of the phalanges and metacarpals. The tendinous connective tissue overlying the metacarpals and digits is continuous with the dense connective tissue overlying the radius and ulna. Distal to the carpus, it divides into thick ribbons that overlie each phalanx.

Antebrachial Muscles of the Humpback Whale

In contrast to the robust muscles found in all other mysticetes, antebrachial muscles of the humpback whale (*Megaptera novaeangliae*) displayed drastically reduced origins and insertions. Muscles originated from deep within the radial and ulnar interosseous space and were represented by few and scattered muscle fibers (Table 3). These muscles gave rise to flattened tendons that were continuous with the connective tissue encasing each digit. Between the digits were regularly oriented connective tissues, interspersed with muscle-like fibers that may have been *m. interosseus* muscles.

Intrinsic Muscles of the Manus of the Sperm Whale

Two unexpected muscles were identified on the palmar surface of the manus in the *Physeter* (Fig. 2): *m. abductor digit V*, and *m. interosseus* (Table 4). Similar muscles of the manus were not identified in other dissected taxa. The *m. abductor digit V* fibers took origin from the distal carpus and proximal region of the fifth metacarpal, wrapped obliquely across the fifth metacarpal bone, and inserted on the caudal surface of digit V along the meta-

TABLE 3. Origins and insertions of the antebrachial muscles[a]

Muscle	Taxon	Origin	Insertion
m. flexor digitorum communis (fdc)	*B. mysticetus*	Ulna (prox-pal)	Digits II-V (pal)
	B. acutorostrata	Interosseous space (pal); humeral shaft (pal, cau); ulna (prox-pal)	Digits III-V or II-V (pal)
	B. borealis	Interosseous space (pal); ulna (prox-pal)	Digits II-V (pal)
	B. brydei	Interosseous space (prox-pal), ulna, (ant-prox-pal)	Carpus (pal), digits II-V(pal)
	B. physalus	Interosseous space (prox-pal); ulna, (prox-pal)	Digits II-V (pal)
	E. glacialis	Interosseous space (pal); ulna, (prox-pal)	Digits II-V (pal)
	E robustus	Interosseous space (prox-pal)	Digits II-III (pal)
	M. novaeangliae	Interosseous space, (prox-pal); humerus (pal)	Carpus (pal), digits II-V (pal)
	P. macrocephalus, Z. cavirostris	Interosseous space; humerus (dist-pal); radius and ulna (pal)	Digits II-V(pal)
	O. orca, P. phocoena, T. truncatus, D. delphis	Absent	
m. flexor digitorum radialis (fdr)	*B. mysticetus*	Interosseous space (prox-pal); radius (cau-pal)	Digit II (pal)
	B. acutorostrata	Interosseous space (prox-pal); radius (cau-pal)	Digit II (pal), joins anterior tendon of fdc
	B. borealis	Interosseous space (prox-pal); radius (cau-pal)	Digit II (pal), joins anterior tendon of fdc
	B. brydei	Interosseous space (prox-pal); radius (cau-pal)	Carpus (pal); digit II (pal)
	B. physalus	Interosseous space (cra-pal); radius (cau-pal)	Digit II (pal); joins anterior tendon of fdc
	E. glacialis, E. robustus, O. orca	Absent	
	M. novaeangliae	Interosseous space, (prox-pal); radius, (cau-pal)	Interosseous space (pal), joins tendon of fdc
	P. macrocephalus	Humerus (cra-pal); radius (pal)	Digit II (pal); joins anterior tendon of fdc
	O. orca, P. phocoena, T. truncatus, D. delphis	Absent	
m. flexor carpi radialis (fcr)	*B. acuto., B. borealis, B. brydei, B. mysticetus, B. physalus, M. novae., P. macro., O. orca, P. phoceona, T. truncatus, D. delphis*	Absent	
	E. glacialis	Interosseous space (pal); radius (cau-pal)	Carpus (cra-pal)
	E. robustus	Radius (prox-pal); humerus (dist-pal)	Scaphoid (pal)
m. extensor digitorum communis (edc)	*B. mysticetus*	Interosseous space (prox-dor)	?
	B. acutorostrata	Interosseous space (prox-dor)	Digits II-V (dor)
	B. borealis	Interosseous space (prox-dor); radius (cau-dor)	Carpus (dor), digits II-V (dor)
	B. brydei	Interosseous space (prox-dor)	Carpus (dor), digits II-V (dor)
	B. physalus	Interosseous space (prox-dor); radius (prox-dor)	Carpus (dor), digits II-V (dor)
	E. glacialis	Interosseous space (prox-dor); ulna (cra-dor)	Digits II-V (dor)
	E. robustus	Interosseous space (prox-dor); ulna (prox-dor)	Digits II-V (dor)
	M. novaeangliae	Interosseous space (prox-dor); humerus (dist-dor)	Digits II-V (dor)
	P. macrocephalus	Interosseous space (dor); humerus (dist-dor); radius and ulna (dor)	Digits II-V (dor)
	O. orca	Interosseous space (dist-dor)	Absent
	P. phocoena, T. truncatus, D. delphis	Absent	

[a] Not shown are data associated with the m. flexor carpi ulnaris (see text). Interosseous space refers to the space between the radius and ulna. cra, cranial; cau, caudal; pal, palmar; dor, dorsal; prox, proximal; dist, distal. See also Figure 1.

TABLE 4. Summary of soft tissue differences between terrestrial artiodactyls and cetacean forelimbs

Structure	Pygmy hippopotamus/pig (Campbell, 1936; Fisher et al., 2007)	*Dorudon* (Uhen, 2004)	Cetacea
Joints			
Shoulder joint	Mobile	Mobile	Mobile
Elbow joint	Mobile	Mobile, no pronation/supination	Immobile
Wrist	Mobile	Reduced mobility	Reduced mobility or immobile
Digits	Mobile	Reduced mobility	Reduced mobility or immobile
Number of phalanges per digit	Standard mammalian formula of 2/3/3/3/3 or fewer	Incomplete	Hyperphalangy in some digits
Connective tissues			
Connective tissue encasing limb	Absent	Unknown	Present
Interdigital connective tissue	Absent	Unknown	Present
Annular ligaments	-Palmar and digital ligaments present	Unknown	Absent
Retinacula	-Flexor and extensor retinacula present	Unknown	Absent, except flexor retinaculum in *Physeter*
Muscles			
m. biceps brachii	Single head	Single head	Absent
m. brachialis	Present	Present	Absent
m. triceps brachii	1 functional head (*c. mediale*)	2 functional heads	1 functional head (*c. longum*), sometimes absent
m. extensor carpi radialis	Present	Present	Absent
m. extensor digitorum communis	2 heads	Probably 1 head	-1 head well-developed in mysticetes (except *Megaptera*) and basal odontocetes -Reduced or absent in monodontids, phocoenids, and delphinids
m. flexor carpi ulnaris	Present	Present	Sometimes present
m. flexor carpi radialis	Present	Present	Sometimes present
m. flexor digitorum radialis	Present	Unknown	Sometimes present
m. flexor digitorum profundus and *superficialis*	Present	One or both heads present	Only single head present
Flexor and extensor muscle bellies	-Robust and well-developed -Act on elbow, wrist and digits	Well-developed (this study)	-Well-developed in mysticetes and basal odontocetes and probably act slightly on digits -Absent in phocoenids and delphinids (except *Orcinus*, reduced extensor belly)
Extensor muscle tendons	-Some mobility -Encased in digital synovial sheaths	Probably slightly mobile	-Reduced mobility or immobile -Encased in connective tissue
Flexor muscle tendons	-Mobile -Encased in digital synovial sheaths	Probably slightly mobile	-Reduced mobility or immobile -Encased in synovial membranes
Manus Musculature			
Abductors	Present	Unknown	Absent, except *abductor digiti V* (*Physeter*)
Interossei	Present	Present	Absent, except *Physeter* and *Kogia*
Thenar muscles	Present	Unknown	Absent
Lumbricales	Present	Unknown	Absent
m. flexor digiti V	Present	Unknown	Absent
Contrahentes	Present	Unknown	Absent

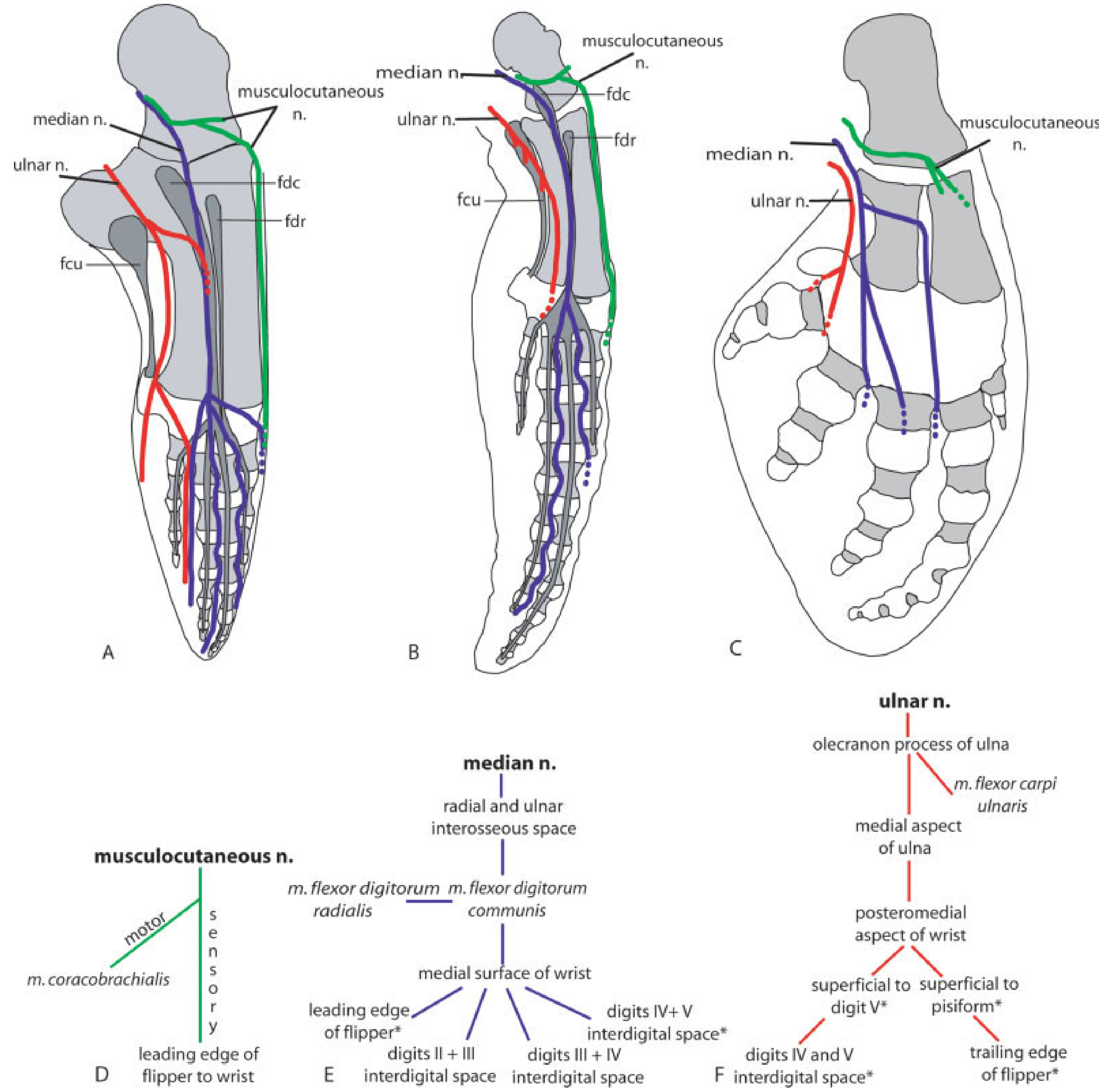

Fig. 5. Palmar views of the nerves exiting the brachial plexus. **A:** Fin whale (*Balaenoptera physalus*). **B:** Humpback whale (*Megaptera*). **C:** Killer whale (*Orcinus*). **D–F:** Schematic of nerve paths for balaenopterids, musculocutaneous nerve (D), median nerve (E), and ulnar nerve (F). Positions marked with asterisks are from Kunze (1912). Dashed lines indicate the assumed path of nerves that we were not able to trace. *m. flexor digitorum communis* (fdc), *m. flexor digitorum radialis* (fdr), *m. flexor carpi ulnaris* (fcu).

carpophalangeal joint. The *m. interossei* of digits III–V took origin from the connective tissue overlying the proximal aspect of metacarpals III–V, and inserted on the palmar and craniocaudal margins of the proximal phalanges. A tendinous slip from the *m. interosseus* inserted on the deep surface of the digital flexor tendons. In addition to these two intrinsic manus muscles, *Physeter* possessed a flexor retinaculum (Fig. 2), but this structure was not found in other taxa. The retinaculum encased the *m. flexor digitorum communis* tendon, and a small unnamed muscle, at the level of the proximal carpus. This unnamed muscle had a fleshy but small belly arising from the posteromedial aspect of the ulna, passed deep to the retinaculum, and fanned out over the connective tissue plate covering the carpus.

Neuroanatomy

Nerves of the brachial plexus followed a basic mammalian pattern but lacked several motor innervations (Fig. 5).

The musculocutaneous nerve sent a motor branch to the *m. coracobrachialis*, and its sensory branch continued along the cranial margin of the flipper (= medial cutaneous antebrachial nerve). In balaenopterids, the median and ulnar nerves were followed to the interdigital spaces, whereas in *Orcinus* the nerves along the carpus were markedly reduced in size, and their paths in the interdigital spaces remain unknown. The median nerve sent motor branches to the digital flexor muscles, continued distally in the interosseous space between the radius and ulna, and further divided to form digital nerves that travel in the interdigital spaces. The ulnar nerve has a more caudal position in the flipper relative to the median nerve. It traveled over the olecranon process before sending a motor branch to the *m. flexor carpi ulnaris*, and its sensory branches continued distally along the caudal border of the ulna (= caudal cutaneous antebrachial nerve) before dividing to supply the caudal margin of the flipper and the most caudal interdigital space.

DISCUSSION

Triceps Morphology

In contrast to the rounded distal humeral trochlea, common in mammals and the archaeocetes *Ichthyolestes* (Thewissen et al., 2001) and *Dorudon atrox* (Uhen, 2004), cetaceans have an immobilized cubital (elbow) joint with humeral articular surface facets offset in a v-shape that effectively locks the radius and ulna in place (Dwight, 1871; True, 1904; Kellogg, 1936; Fitzgerald, 1970; Barnes, 1990; Sanders and Barnes, 2002; Uhen, 2004). Cooper (2004) documented a fixed cubital joint in three fossil mysticete lineages (Aetiocetidae, Eomysticetidae, and "Cetotheriidae"), with the earliest record of a fixed cubital joint occurring in aetiocetids known from the late Oligocene (28Ma) in the North Pacific.

As the cubital joint is immobilized, and the humeral heads of the *m. triceps brachii* muscle are reduced and do not act on the flipper, this study considers these muscles vestigial. Only the *m. triceps brachii* scapular head (*caput longum*) retains a motor function. This head acts to move the flipper caudally, and lowers the leading edge of the flipper ventrally (Benke, 1993). The reduced triceps musculature of cetaceans is in strong contrast to that of the terrestrial artiodactyls (Table 4, Campbell, 1936; Dyce et al., 2002; Fisher et al., 2007), which typically have three to four functional triceps heads. In artiodactyls, there is one scapular (*caput longum*) head and two or three heads that arise from the humerus (*caput laterale*, *mediale*, and *accessorium*, Smallwood, 1992). In the pygmy hippopotamus, only the *caput mediale* arising from the humeral shaft is functional as both the scapular (*caput longum*) and humerus (*laterale*) heads are tendinous, and the *caput accessorium* is absent (Fisher et al., 2007).

Antebrachial Musculature

The hypothesis that large-bodied cetaceans would have robust antebrachial muscles (flexors and extensors), and small-bodied cetaceans have a reduced muscle morphology was shown to be incorrect. This hypothesis predicted that degree of muscle development is a consequence of body size and a large-bodied dolphin, such as *Orcinus*, would retain prominent antebrachial muscle bellies and tendons because of the mechanical loading of such a large flipper. However, our data indicate that taxonomic distribution, not body size, was the best predictor of antebrachial muscle morphology.

Those taxa with well-developed antebrachial muscles also displayed functional differences between the flexor and extensor muscles. Separating the flexor tendons from the surrounding connective tissues are synovial membranes. Extensor tendons adhere more closely to the underlying connective tissues, and lack such distinct synovial structures. The presence of synovial membranes around the flexor tendons suggests that muscular contraction may produce palmar flexion. In contrast, firm attachments of the extensors suggest a limited range of motion, and inability of the tendons to slide along the digit. Extensor muscle contraction may act to stiffen the flipper, but no evidence suggests the ability to extend the digits.

A similar distribution of synovial structures is found in artiodactyls. Extensive digital synovial sheaths surround the superficial and deep digital flexor tendons of the artiodactyl manus (Table 4). By contrast, extensor tendons have less extensive synovial sheaths and may instead have synovial bursae protecting them from the underlying bony structures (Table 4). Digital extensor tendons in the pygmy hippopotamus insert on the middle and distal phalanges (Campbell, 1936; Fisher et al., 2007), and a continuous synovial sheath would not allow any of these tendons to attach. By contrast, the deep digital flexor tendon inserts only on the distal phalanx in the pygmy hippopotamus (Fisher et al., 2007), domesticated pig, and peccary (Campbell, 1936), so an extensive synovial sheath protects it as it moves though a longer range of motion.

The antebrachial flexor and extensor muscles of the pygmy hippopotamus and domesticated pig act on the cubital joint, wrist, metacarpophalangeal, and interphalangeal joints (Fisher et al., 2007). All extant cetaceans lack the ability to move the cubital joint (see above), and movements in the wrists and digits are very slight, if present at all. Flexors and extensors of cetaceans may have evolved to act only on the joints of the manus—a pronounced reduction compared with their artiodactyl ancestors.

Intrinsic Muscles of the Manus in the Sperm Whale

Intrinsic muscles of the manus were found in *Physeter* (Fig. 1), and identified as the *m. abductor digiti V* and *m. interosseus*. Similar muscles were not identified in other dissected cetaceans, but the *m. interosseus* was previously reported in *Kogia* (Schulte and Smith; 1918). This reduction in musculature is in strong contrast to the muscle morphologies in terrestrial artiodactyls (Table 4, Campbell, 1936), which possess other muscles of the manus, including the *m. lumbricales*, thenar muscles, *m. flexor digiti V*, and *m. contrahentes* (Windle and Parsons, 1901; Campbell, 1936). Identification of the *m. interosseus* muscle group in *Physeter* was based on its location, attachments, and relationship to the digital flexor tendon in each digit. In terrestrial mammals, the morphology of the *m. interossei* muscle varies, but in general they arise from the distal carpus/proximal metacarpal bones on the palmar aspect of the manus, and insert on the proximal sesamoid bones at the metacarpophalangeal joint, as well as on the extensor tendon through paired tendinous slips, which pass over the adaxial and abaxial surfaces of the joint (Dyce et al., 2002). Cetaceans lack proximal sesamoid bones, so the attachments of the *m. interosseus* muscle in *Physeter* would not be expected to be completely congruent with that of terrestrial mammals. In *Physeter*, however, the muscle takes origin from the proximal metacarpus, and inserts on the proximal phalanges. There was no direct tendinous connection from the *m. interosseus* to the extensor tendons. Instead, this muscle sent tendinous slips, which diverged from the main tendon and traveled along the adaxial and abaxial surfaces of the proximal phalanges. In ruminants, there are fibrous connections of the *m. interossei* to the superficial digital flexor tendon (Smallwood, 1992); a similar connection in *Physeter* supports identification of this muscle as the *m. interosseus*. Pygmy hippos display a full complement of *m. interossei* (Fisher et al., 2005) that function either to abduct/adduct the digits, or in those artiodactyls where the muscle is largely fibrous, they act to support the metacarpophalangeal joint. In *Physeter*, the minute size of the muscle and the large amount of blubber and connective tissue preclude the *m. interosseus* from actively moving the digit. Along with the *m. abductor digiti V*, the presence of *m. interosseus* muscles in *Physeter* appears to be a primitive character state, and later diverging odontocetes lack these muscles.

With the exception of the thin carpal flexor retinaculum in *Physeter*, tendon adnexa (including annular ligaments and other retinacula) are conspicuously absent in cetaceans (Table 4). The retinacula of artiodactyls bind tendons of the digital extensor muscles at the level of the carpus, and well-developed palmar and digital annular ligaments bind the digital flexor tendons to the metacarpus and phalanges. Although cetaceans possess connective tissue specializations in the flipper (extensive fibrous layers associated with the blubber), their tendons lack annular ligaments with transversely oriented fibers.

Humpback Whale

The flipper of *Megaptera* is of special interest as it displays many unique attributes. Most balaenopterids have a flipper to body length ratio of 1/8 or less (Mohan, 1992), whereas *Megaptera* has a flipper to body length ratio of 1/4 to 1/3 and displays the longest flipper of any cetacean (Struthers, 1889; Howell, 1930b; Tomilin, 1957; Edel and Winn, 1978; Fish and Battle, 1995; Woodward et al., 2006). This great length is achieved by elongated metacarpals, phalanges, and interphalangeal cartilages in addition to the standard cetacean presence of hyperphalangy (Cooper et al., 2007). *Megaptera* is the only mysticete that displays obvious antebrachial muscle reduction, similar to that seen in monodontid, phocoenid, and delphinid odontocetes. Our data indicate this reduction is an autapomorphy. This study dissected a single specimen and cannot address whether this finding is a common morphology. Manipulation of the *Megaptera* limb before dissection showed it was extremely mobile with the manus able to flex and extend more than any other cetacean. It is possible that *Megaptera* has reduced muscular control over the manus, which would further isolate force generation to the glenohumeral joint. The distal limb would be, therefore, able to respond to flow. Video footage of *Megaptera* swimming shows the flipper passively bowing during locomotion with a smooth and rounded flipper contour, rather than actively flexing and extending at the interphalangeal joints (Villano, 2006). It appears to flex as if a wave is passing through it, similar to the "flutter" of a flag (Villano, 2006). Photographs of *Megaptera* also show the limb bowing both during underwater maneuvers and while the limb is completely out of the water (Harrison and Bryden, 1988).

Functional Implications

The terrestrial ancestors of cetaceans retained abundant forelimb musculature associated with locomotion on land, but this ability was reduced in the Eocene archaeocetes *Ambulocetus* and *Dorudon*. *Ambulocetus natans* (Thewissen et al., 1996; Madar et al., 2002) had a cubital joint capable of a wide range of flexion and extension; however, the radius and ulna could not supinate or pronate, and the digits had a small range of flexion and extension. The authors interpreted forelimb movements of *Ambulocetus* as indicating a digitigrade posture with little dorsiflexion at the metacarpophalangeal joints (Thewissen et al., 1996). *Dorudon atrox* (Uhen, 2004) retained a broad range of motion at the glenohumeral joint and had limited mobility in the wrists and digits.

Unfortunately, few bony landmarks are preserved in fossil mysticete and odontocete forelimbs, and data indicating the transition in muscle morphology between archaeocetes and extant cetaceans are lacking. The fossil record does indicate two important transitions in the cubital joint that may have soft tissue implications. Artiodactyls have pronators and supinators that are either reduced or absent, and morphologies show individual variation (Fisher et al., 2007). Within archaeocetes, osteological articulations showed both *Ambulocetus natans* (Thewissen et al., 1996) and *Dorudon atrox* (Uhen, 2004) lacked the ability to supinate or pronate, and it may be that both taxa lacked the corresponding musculature. Extant cetaceans also lack both supinators and pronators, and it may be that the muscles controlling these movements were lost during the Eocene. The common ancestor of mysticetes and odontocetes probably lacked the ability the move the cubital joint, and within mysticetes, the immobilized cubital joint evolved at least 39–24Ma during the Oligocene. It is not known when carpus and manus mobility evolved to its current reduced state.

Data regarding antebrachial musculature allow some interpretations of forelimb mobility and its evolution within extant cetaceans. Most mysticetes retain intrinsic muscles that may actively flex the digits, but only slightly (Table 4). Dissection revealed that the flexor muscles may provide some movement, even though they are wrapped in thick layers of stiff connective tissue and skin. Manipulation of fresh, intact mysticete limbs, especially balaenopterids, showed slight movement at the wrist and sometimes in the digits, thus indicating that it may be possible for these taxa to slightly manipulate their manus. However, these observations occurred on deceased specimens, and degree of manus deformity is unknown in living balaenopterids.

Flipper movements were observed in the pilot whale (*Globicephala*) based on video footage of captive whales swimming at low speeds (see Werth, 1987). No evidence indicated active digital extension or flexion against the flow of water. Instead, the manus bowed dorsoventrally in response to movements originating near the body line, presumably at the glenohumeral joint. If the flippers were moved ventrally, the tips would curl dorsally and vice versa. The lack of active digital curling against flow is not surprising as *Globicephala* displays reduced antebrachial muscle morphology (Murie, 1873) and probably lacks the ability to move the digits. Contrary to our expectations, the manus easily and frequently deformed into crescent shapes (when viewed from head-on) and did not maintain a rigid and straight profile. The surprising ease with which the flipper deformed was probably due to the lack of a thick connective tissue encasing the limb (as in the thick dermal layers of *Orcinus* and *Physeter*), and the maintenance of cartilaginous interphalangeal joints (Lee, 1978), which may allow a greater range of mobility.

Maintaining and modulating flipper stiffness is crucial for hydrodynamic efficiency. All of the structural components of the flipper contribute to its stiffness: bone, chondroepiphyses, synovial or fibrous joints, muscle, tendon, fibrous connective tissue layers, blubber, and skin. Those taxa that retain well-developed muscles and tendons have the potential to actively adjust flipper stiffness and fine-tune its shape. The basal odontocetes *Physeter* (Fig. 2) and *Ziphius*, however, have thick layers of connective tissue covering these muscles, which would effectively preclude movement of the manus. These taxa probably use the well-developed antebrachial muscles in isometric contraction, in which the flipper stiffens from the opposing action of the two muscle groups. The later diverging delphinid and phocoenid odontocetes, which have extremely reduced antebrachial muscles and tendons (Figs. 3, 4), probably rely on structures and mechanisms other than muscular contraction to stabilize the flipper. Examining the potential elastic properties of tendons and connective tissue layers, as well as the thickness and distribution of blubber may help elucidate control mechanisms in these taxa.

Cetacean antebrachial musculature surprisingly is best developed in cetaceans that are the least maneuverable. Antebrachial musculature is reduced in those taxa that are able to locomote quickly and are more agile (e.g., sharp and high-speed turns, smaller turning radii, Fish, 2002a; Woodward et al., 2006), most delphinid odontocetes and the *Megaptera*. The reduced musculature of these taxa decreased flipper thickness, created a greater aspect ratio (the ratio of proximodistal length to craniocaudal width), which would allow in turn allow more efficient generation of lift. In two cases, *Globicephala* and *Megaptera*, video footage showed flippers deforming into crescent shapes in response to hydrodynamic flow. It may be that the lack of muscular and tendinous support aids forelimb deformation during a dorsoventral paddling motion and causes lifting of the body while at slow speeds.

Behavioral data and dissection results suggest that cetacean forelimb sensory innervation retains the basic mammalian pattern of distribution. This retention is in strong contrast to the significant reduction in muscle, motor nerve, and connective tissue structures. Sensory branches of the musculocutaneous and ulnar nerves may be crucial for gathering hydrodynamic loading information on the flipper. Because pressure is greatest on the leading edge of a hydrofoil, the musculocutaneous nerve may play a crucial role in detecting leading edge forces as the angle of attack (angle of the leading edge of the flipper) is changed. Moreover, the ulnar nerve along the caudal margin of the flipper lies in a relatively thin layer of connective tissue and may be sensitive to vortices being shed along the trailing edge. Nerves along the leading and caudal margins of the flipper may play an essential role in relaying hydrodynamic information regarding hydrodynamic loading and magnitude of vortices.

Comparisons

A similar pattern of forelimb muscle and tendon reduction is also seen in the penguin forelimb. Much like cetaceans and other aquatic mammals, penguins isolate most forelimb musculature to the multiaxial shoulder joint. Correlated with this reduced musculature, joints distal to the shoulder have reduced mobility (Louw, 1992). Specifically, the distal limb is similar to monodontid, phocoenid, and delphinid odontocetes in having absent muscles or having tiny bellies and long, thin tendons (compared with flying birds, Louw, 1992). Muscles in the manus are also more reduced compared with flying birds (Louw, 1992), but are more abundant than those of the cetacean manus. A typical avian wing is made of three digits, but penguins display only two digits as digit I is fused to digit II, digit III is the principal digit, and digits IV and V are absent (Louw, 1992). Similarly, most cetaceans reduce or lack digit I and reduce digit V (Cooper et al., 2007). Penguins differ from most marine mammals in that their forelimb in cross-section is cambered, or not symmetrical about the chord line, which effectively increases lift (Fish, 2004).

Contrary to the loss of mobility and musculature in the cetacean and penguin forelimb, pinnipeds have retained agile joints and well-developed forelimb musculature. Otariids (fur seals and sea lions) have abundant forelimb muscles with complex pennation that allow for forelimb generated propulsion (English, 1976) while the hindlimbs aid in maneuvering (Gordon, 1983). In seals and sea lions, more than half of the forelimb musculature lies in the proximal aspect of the forelimb (English, 1977), and these muscles act on highly mobile shoulder and radioulnar joints. The triceps complex is relatively large in these taxa, allowing for cubital joint retraction (English, 1977), a motion that is impossible in cetaceans as the cubital joint is locked and the triceps complex is reduced in most taxa. Otariids flex the palmar surface of the manus during locomotion. This palmar flexion is created by abundant antebrachial muscles with large muscular bellies, and robust tendons (see Howell, 1930b), a combination that affords large excursion compared with cetaceans. Also contrary to cetaceans, otariids retain abundant palmar musculature, including *m. interossei*, digital abductors and adductors, and in some specimens a single lumbrical (English, 1976). Contrary to the reduced digit I in penguins and cetaceans, otariids elongate metacarpal I and digit I phalanges (Howell, 1930b).

Odobenid (walrus) forelimbs act as paddles or rudders for steering (Gordon, 1981) and are used to remove sediment when searching for prey (Levermann et al., 2003). As with other pinnipeds, penguins, and cetaceans, most walrus forelimb musculature is associated with the shoulder joint, but odobenids also retain abundant musculature distal to this joint. The antebrachial musculature displays both large muscle bellies and robust tendons, with relatively the same sized muscle bellies as the otariid, the California sea lion (English, 1976; Gordon, 1983). Like other pinnipeds, walruses also enlarge and elongate metacarpal I and digit I phalanges (Howell, 1930b).

Manatee, or sea cow, forelimbs are unique among marine mammals. Contrary to cetaceans, pinnipeds, and odobenids, manatees do not use their flippers as control surfaces while the animal is at speed; instead, the 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, 1971). The shoulder joint retains the standard ability for circumduction, the cubital joint moves during each paddle (Fish, 2004), and the wrist retains some mobility (Dart, 1974). Forelimb movements are supported by abundant musculature and large, rounded tendons throughout the proximal and distal limb (Murie, 1872; Dart, 1974; Dawson et al., 2000). Similar to cetaceans, manatee digits are immersed in thick connective tissue and lack the ability to abduct and adduct, but retain intrinsic muscles of the manus (*m. abductor* and *m. interosseus*, Murie, 1872).

Compared with other aquatic taxa with flippers, it appears that cetaceans have acquired some defining characteristics. Like most other aquatic taxa, the greatest amount of cetacean forelimb musculature is associated with the shoulder joint (Fish, 2004), and this joint is multiaxial and capable of circumduction. The cubital joint of cetaceans is immobile, while in most other aquatic taxa there is at least some flexibility at the cubital joint (penguins, seals and sea lions, and manatees; Fish, 2004). Corresponding with the loss of cubital joint mobility, cetaceans are unique in displaying atrophied muscles in the triceps complex (heads originating on the humerus). The wrist and digits of cetaceans also lack mobility, but some balaenopterid mysticetes may be able to slightly flex the digits. Most aquatic taxa retain wrist mobility, but digit mobility varies. Degree of antebrachial muscular development appears to be best predicted by taxonomic distribution, and does not correlate with body size. A lack of cetacean manus musculature appears to be correlated with a reduction or complete loss in the ability to flex and extend the digits, and the maintenance of thick interdigital tissue that restricts lateral movements of the digits. Taken together, cetaceans display a mostly immobile flipper that is rigid with the wrist and digits reinforced by dense connective tissue.

With regard to the functional and evolutionary consequences of a rigid cetacean forelimb, several hypotheses are offered. In the transition to an aquatic lifestyle, cetaceans have lost most forelimb structural complexity, and evolved a stiff forelimb distal to the shoulder. Absence of most soft tissue structures decreases flipper thickness. By decreasing thickness, aspect ratio is increased and affords cetaceans a greater ability to generate lift. Most secondarily aquatic mammals (manatees, pinnipeds, sirenians) have retained forelimb agility and remain in shallow waters to forage. Cetaceans have undergone an anatomical trade-off that has allowed them to evolve a rigid limb that may be more easily tucked against the body in deep water foragers (beaked whales), or capable of assisting high speed turns without deforming in shallow water foragers (dolphins). Deep water foragers, such as beaked whales, have an indentation in the body wall where the flipper tucks in (Mead, 1989). Without a protruding forelimb, the beaked whale has a more streamlined body and may be able to descend with less effort. If a flipper was easily deformable, it would create more drag, and it would be more energetically expensive to swim. Alternatively, in the aerobatic maneuvers of spinner dolphins, before a jump, the dolphins will begin corkscrewing in the water, and the flippers are under hydrodynamic loads in the form of torques (Fish et al., 2006). If the flippers were malleable and deformed under hydrodynamic pressure, this would increase drag and probably decrease the speed of corkscrewing.

Future Work

Functional associations of the striking differences in cetacean antebrachial muscular presence remain unknown. Retention of robust muscles by some taxa may indicate an additional functionality not directly relating to digital flexion and extension and hydrodynamic performance as proposed above. Retention of robust antebrachial musculature could be associated with thermoregulation. The belly of the *flexor digitorum communis* comes in direct contact with a large counter-current heat exchanger in the axilla of bowhead whales (*Balaena*; Cooper, unpublished data), and contraction of the muscle may generate heat that could be cooled distally in the limb. Retention of antebrachial musculature may also be associated with proprioception or mechanoreception. Cetaceans may have an abundance of muscle spindles or Golgi tendon organs in the antebrachial muscles that would allow for sensing of flipper deformation in response to hydrodynamic flow.

Functional, physiological, and muscle histochemical studies are needed to test the hypotheses presented here. Although it remains difficult to accurately observe and record mysticete forelimb movements, video footage documenting mysticete forelimb and possible digit movements provide important data. Hydrodynamic studies of cetacean flippers have focused on *Megaptera* (Fish and Battle, 1995), which has a highly derived flipper shape, but the hydrodynamic properties of other mysticetes and any odontocetes remain speculative. As more cetacean forelimbs are dissected, future investigators may address the elastic properties of the connective tissue layers encasing the forelimb, as their contribution to flipper stability and shape are currently unknown.

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