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Comparative anatomy and evolution of the odontocete forelimb

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ABSTRACT

Previous studies of the odontocete forelimb have not considered flipper anatomy in an evolutionary context. This study of 39 cetacean species (1 extinct archaeocete, 31 extant and 3 extinct odontocetes, and 4 mysticetes), provides a detailed comparative analysis of the major bones and muscles of the odontocete flipper. Differences across families in the anatomy of the deltoid, supraspinatus, coracobrachialis, and subscapularis muscles correspond directly to size and shape of forelimb elements. Specialization of the different shoulder girdle muscles allows for more maneuverability of the flipper by independent control of muscular columns. Maximum likelihood analyses helped determine the correlation of characters studied by ancestral state reconstruction, and revealed independent evolution of osteological and external characters among various lineages. Comparative Analyses by Independent Contrast (CAIC), found several contrasts between flipper area and body length for several extant odontocetes and a linear relationship was inferred. Degree of hyperphalangy and the soft tissue encasing the flipper helped determine three flipper morphologies based on aspect ratio (AR) and qualitative data. These results suggest that differences in flipper shape have an evolutionary component and are likely largely in response to ecological requirements.

Key words: cetacean, forelimb, anatomy, likelihood analyses, CAIC analyses, evolution.

The evolution of whales from terrestrial to fully aquatic mammals involved many morphological, physiological, and behavioral adaptations. The hind limb of cetaceans became vestigial in later diverging archaeocetes, such as *Basilosaurus,* having been greatly reduced during their transition to an aquatic life (Gingerich *et al*. 1990, Berta 1994). The propulsion of cetaceans in water depends mainly on caudal undulations (Fish 1998, Woodward *et al*. 2006). Conversely, one of the main transformations seen in cetaceans and other aquatic mammals was the evolution of the forelimbs into flippers by modification of bone morphology and soft tissue distribution.

A number of previous studies have described the osteology of the odontocete forelimb (Flower 1872*a*, *b*; Howell 1927; Omura *et al*. 1962; Pilleri *et al*. 1976*a*, *b*, *c*; Klima 1985; Watson *et al.* 1994; Calzada and Aguilar 1996; Sedmera *et al.* 1997; Dawson 2003; Cooper *et al.* 2007*a*, *b*). The scapula of odontocetes is almost completely flat, bears a low scapular spine, and displays a supraspinous fossa that is reduced in area relative to terrestrial artiodactyls (Benke 1993). A shortening and flattening of the humerus, radius, and ulna is also observed in odontocetes (Howell 1930*a*, Benke 1993, Dawson 2003). Most odontocetes possess five carpals, however, in some taxa such as in *Phocoena phocoena* and *Tursiops truncatus* there is a sixth carpal, the accessory (Watson *et al.* 1994, Ortega-Ortiz and Villa-Ramirez 2000). Based on previous literature, in all species the bones of the manus show a decrease in size and an increase in number of phalanges (hyperphalangy); two species also show an increase in number of digits (polydactyly) (Kukenthal 1893, Pilleri *et al.* 1976*c*, Watson *et al.* 1994, Sedmera *et al.* 1997, Ortega-Ortiz and Villa-Ramirez 2000, Bejder and Hall 2002, Cooper and Dawson 2009).

The myology of the odontocete forelimb has also been previously studied (Howell 1930*a*; Pilleri *et al.* 1976; Smith *et al.* 1976; Strickler 1978, 1980; Cooper *et al.* 2007*b*). Stability and maneuverability requirements led to various modifications of the muscles of the shoulder girdle and the manus. The shoulder girdle of physeterids and ziphiids possess a subscapularis muscle that is divided into different fiber columns separated by tendinous sheaths (Cooper 2004). Compared to delphinoids (monodontids, phocoenids, and delphinids), the shoulder of the La Plata river dolphin, *Pontoporia blainvillei*, exhibits a greater degree of muscle differentiation (specialization of muscular structures and diversity of muscular fiber architecture), and an increase in volume (Strickler 1978). The deltoid muscle in *Monodon monoceros* is characterized by being very large and showing a strong aponeurosis at the origin and a thin division overlying the main muscle mass separable only along its cranial border (Howell 1930*a*). The extensors and flexors are conserved within basal odontocetes (*i.e.*, physeterids and ziphiids), but are reduced or completely lost within later diverging species (*e.g.,* delphinids) (Cooper *et al.* 2007*b*). In *Delphinus delphis* for example, the muscles responsible for flipper extension (Pilleri *et al.* 1976) and flexion (Cooper *et al.* 2007*b*) are poorly developed.

Flippers are of prime importance in total hydrodynamics (Felts 1966), functioning as hydrofoils for controlling stability, minimizing drag, and effecting forces in roll, pitch, and yaw directions (Edel and Winn 1978). The flipper is adjustable at the shoulder through extension and flexion in the horizontal plane, abduction and adduction in the vertical plane, and rotation around its own axis (Felts 1966). The diversity of morphological shapes of the flipper has been related to swimming speed and propulsive efficiency in whales and dolphins (Fish 1998, Fish and Rohr 1999, Woodward *et al.* 2006). Functional analyses have shown that the relationship between lift and drag depends on the shape of the appendage (Hertel 1966, Alexander 1970). Previous studies have identified two flipper morphologies; fast-swimming cetaceans have an elongated flipper with a thin trailing edge capable of generating lift; while those cetaceans requiring maneuverability at slow speeds possess a broad or spatulate-shaped flipper (Benke 1993, Cooper 2004, Woodward *et al.* 2006). Paddling is associated with slow swimming and precise maneuverability (Webb 1984) and generally is used in surface swimming (Fish 1992). In either case, the flipper should have a broad surface with a relatively thin border, to swim through the water with the least amount of resistance (Howell 1930*b*).

This study provides a comparative analysis of the structure of eight muscles of the shoulder girdle responsible for flipper movement in a large sample of odontocetes. We optimize flipper osteological and external shape characters onto a composite phylogeny and reconstruct ancestral character states using likelihood analyses. We use a comparative method (Comparative Analysis by Independent Contrasts (CAIC), Purvis and Rambaut 1995) to investigate associations between flipper length and area and body length. We describe a third flipper morphology in addition to those previously identified using qualitative (*e.g.,* distal end, trailing edge) and quantitative (*i.e.*, aspect ratio, AR) data; that permits consideration of the functional implications of forelimb structure based on habitat and swimming behavior.

MATERIALS AND METHODS

Osteological specimens were examined from collections at several museums including San Diego Natural History Museum, San Diego, CA (SDNHM), Los Angeles County Museum of Natural History, Los Angeles, CA (LACM), and National Museum of Natural History, Paris, France (MNHN-Paris). Fresh specimens for dissection were acquired from NOAA Fisheries Service, Beaufort, NC; Marine Mammal Stranding Network, Newport, OR; Marine Mammal Center, Sausalito, CA; and Southwest Fisheries Science Center, La Jolla, CA. Most specimens were adult individuals. Material examined included articulated flippers, X-rays, and dissections of fresh flippers. Osteological study of the flippers employed quantitative data (*i.e.,* scapula length and width, humerus, radius, and ulna length) (Tables 1 and 2); and qualitative characters (*i.e.*, presence, shape) of several landmarks (*e.g.,* scapular spine, humeral greater tubercle, ulnar olecranon process). Hyperphalangy and polydactyly were also documented. Myology was studied by dissecting fresh specimens and analyzing differences in muscle architecture, origin and insertion, and noting arrangement of skeletal elements and connective tissue encasing the flipper. Muscle fascicles were noted as long or short and the amount of area they covered; whereas muscle bellies was noted as thick or thin. A total of 14 flippers were dissected (8 odontocete species, 11 specimens), representing three of the six odontocete families in this study (online Appendix S1).

For character optimization onto the phylogeny the ingroup consisted of all odontocete taxa for which representative material was available. At least one species from six of the nine odontocete families was considered in order to infer flipper evolution with the greatest accuracy. The phylogeny used was that of May-Collado and Agnarsson (2006) based on molecular data (Fig. 1). The basilosaurid *Dorudon atrox* has an exceptionally well-preserved forelimb (Uhen 2004) and was included as the basal outgroup taxon. Mysticetes representing two families (Balaenidae and Balaenopteridae), were other outgroups employed. The recently described skeleton of *Brygmophyseter shigensis* (fossil sperm whale) (Kimura *et al.* 2006) was added to help with the assessment of archaic odontocete osteological characters. Forelimb osteology from basal fossil delphinoids, *Atocetus iquensis* and *Incacetus broggii*, described by Muizon (1988), were also included.

A total of 16 morphological characters were evaluated among 21 taxa (online Appendix S2). Character states were selected based on previous research and observation. The character state of 0 was assigned to the state found in the archaic cetacean outgroup, *D. atrox*, and thus, was considered to represent the ancestral condition. Character states one and two were assigned to the derived conditions observed in early diverging (*e.g.,* Physeteridae) *vs.* later divergent (*e.g.,* Delphinidae) taxa.

Character reconstructions were performed using likelihood analyses in Mesquite 2.5 (Maddison and Maddison 2008). Maximum likelihood analyses assumed equal

Table 1. Measurements of odontocete forelimb elements. Some measurements taken from Benke (1993). Others from the samples analyzed during this study (skeletal and X-rays). Measurements are in millimeters.

Species	Humerus length	Humerus mean	(Radius + ulna)/2 mean	(Radius + ulna)/2
D. atrox (extinct)	237.4	237.4	190.4	190.4
Odontocetes				
C. commersonii	58.0	58.0	63.5	63.5
D. capensis	62.0	62.0	64.3	64.3
D. delphis ($n = 3$)	52.0–73.19	60.2	67.7	63.0–76.74
D. leucas ($n = 2$)	125.0–128.0	126.5	95.0	92.0–98.0
G. macrorhynchus ($n = 3$)	126.1–154.5	142.2	138.2	129.5–147.1
G. melaena	142.0	142.0	128.5	128.5
G. griseus ($n = 2$)	85.0–103.0	94.0	102.5	92.5–112.5
I. geoffrensis ($n = 2$)	98.5–101.0	99.8	61.9	54.7–69.0
K. breviceps ($n = 2$)	103.0–106.0	104.5	77.1	75.6–78.5
K. simus	49.0	49.0	57.3	57.3
L. albirostris	90.0	90.0	96.0	96.0
L. obliquidens	64.0	64.0	72.5	72.5
Lagenorhynchus obscurus	55.0	55.0	70.0	70.0
L. borealis	68.0	68.0	71.5	71.5
M. bidens	137.0	137.0	142.0	142.0
M. hectori	136.0	136.0	126.0	126.0
Mesoplodon peruvianus	136.6	136.6	129.5	129.5
Mesoplodon stejnegeri	132.5	132.5	139.7	139.7
M. monoceros	150.0	150.0	118.5	118.5
N. phocoenoides	59.0	59.0	48.5	48.5
O. orca	219.0	219.0	208.0	208.0
P. dalli	59.4	59.4	56.4	56.4
P. phocoena ($n = 2$)	50.0–51.0	50.5	51.3	49.5–53.0
P. sinus ($n = 2$)	51.5–53.0	52.3	51.9	50.7–53.0
P. macrocephalus	456.0	456.0	310.5	310.5
P. crassidens ($n = 2$)	101.3–106.0	102.1	95.9	91.4–100.5
S. attenuata ($n = 2$)	46.5–53.0	49.8	52.8	50.2–55.5
Stenella coeruleoalba	58.0	58.0	67.0	67.0
S. longirostris	50.8	50.8	59.7	59.7
T. truncatus	86.0	86.0	89.0	89.0
Z. cavirostris	172.0	172.0	180.5	180.5
Mysticetes				
Balaena mysticetus	598.0	598.0	646.5	646.5
B. physalus	530.0	530.0	810.0	810.0
Eubalaena glacialis	538.0	538.0	487.5	487.5
M. novaeangliae	619.0	619.0	887.5	887.5

branch lengths because data on branch lengths was not available for all species studied and including only some of them could reduce the confidence of probabilities and increase uncertainty for deeper nodes (Schluter *et al.* 1997). Tests of the correlation between osteological characters and flipper shape were examined by running concentrated changes tests in McClade 4.0 (Maddison and Maddison 2000) for parsimony reconstructions. Character state transformations for external morphology and unavailable skeletal characters from fossil taxa were coded as "?".

Table 2. Scapula measurements of various cetaceans. Measurements are in millimeters. Some measurements taken from Benke (1993).

Species	Width ratio	Width mean	Length mean	Length ratio
D. atrox (extinct)	255.2	255.2	271.7	271.7
Odontocetes				
C. commersonii	169.0	169.0	117.0	117.0
D. capensis	160.0	160.0	88.5	88.5
D. delphis ($n = 3$)	150.0–189.0	165.7	118.2	109.0–123.5
D. leucas ($n = 2$)	285.0–337.0	311.0	197.0	190.0–204.0
Globicephala macrorhynchus ($n = 3$)	318.3–364.0	304.2	265.0	251.6–282.0
G. melaena	360.0	360.0	249.0	249.0
G. griseus ($n = 2$)	249.0–304.0	276.5	188.0	172.0–204.0
I. geoffrensis ($n = 2$)	180.0–190.0	185.0	133.5	130.0–137.0
K. breviceps ($n = 2$)	231.5–280.0	255.8	190.1	183.0–197.2
L. albirostris	280.0	280.0	194.0	194.0
L. obscurus	200.0	200.0	122.0	122.0
L. borealis	185.0	185.0	124.0	124.0
M. bidens	314.0	314.0	192.0	192.0
M. peruvianus	270.0	270.0	175.0	175.0
M. stejnegeri	175.0	175.0	120.0	120.0
M. monoceros	336.0	336.0	260.0	260.0
N. phocoenoides	101.0	101.0	73.0	73.0
O. orca	463.0	463.0	339.0	339.0
P. phocoena ($n = 2$)	116.0–118.0	117.0	85.0	85.0
P. sinus	122.0	122.0	88.0	88.0
P. dalli	148.0	148.0	146.6	146.6
P. macrocephalus	623.0	623.0	840.0	840.0
P. crassidens ($n = 2$)	246.0–280.0	263.0	194.5	189.0–200.0
S. attenuata ($n = 2$)	106.4–170.0	138.4	107.0	98.0–116.0
S. coeruleoalba ($n = 2$)	172.0–209.0	190.5	122.5	115.0–130.0
S. longirostris	141.7	141.7	104.8	104.8
T. truncatus	266.0	266.0	174.0	174.0
Z. cavirostris	405.0	405.0	284.0	284.0
Mysticetes				
B. mysticetus	1,125.0	1, 125.0	1, 063.0	1,063.0
B. physalus	1,383.0	1, 383.0	775.0	775.0
E. glacialis	1,150.0	1, 150.0	925.0	925.0
M. novaeangliae	1,275.0	1, 275.0	913.0	913.0

The most common state found in a single species was used when polymorphic states were present because Mesquite does not support polymorphic or ambiguous states.

We used CAIC to test for a relationship between flipper area and shape and body length. CAIC estimates contrasts for each node in the phylogeny for which there was variation in the independent variable (online Appendix 3). For this analysis, flipper shapes were divided into either broad or elongated to eliminate inaccuracy due to coding. Coding three flipper shapes (*i.e.,* zero, one, and two), would indicate that in order to transition from flipper shape "zero" to flipper shape "two," species had to develop flipper "one" first. This would be inaccurate and the results from this analysis erroneous. The data was log transformed because many programs assume

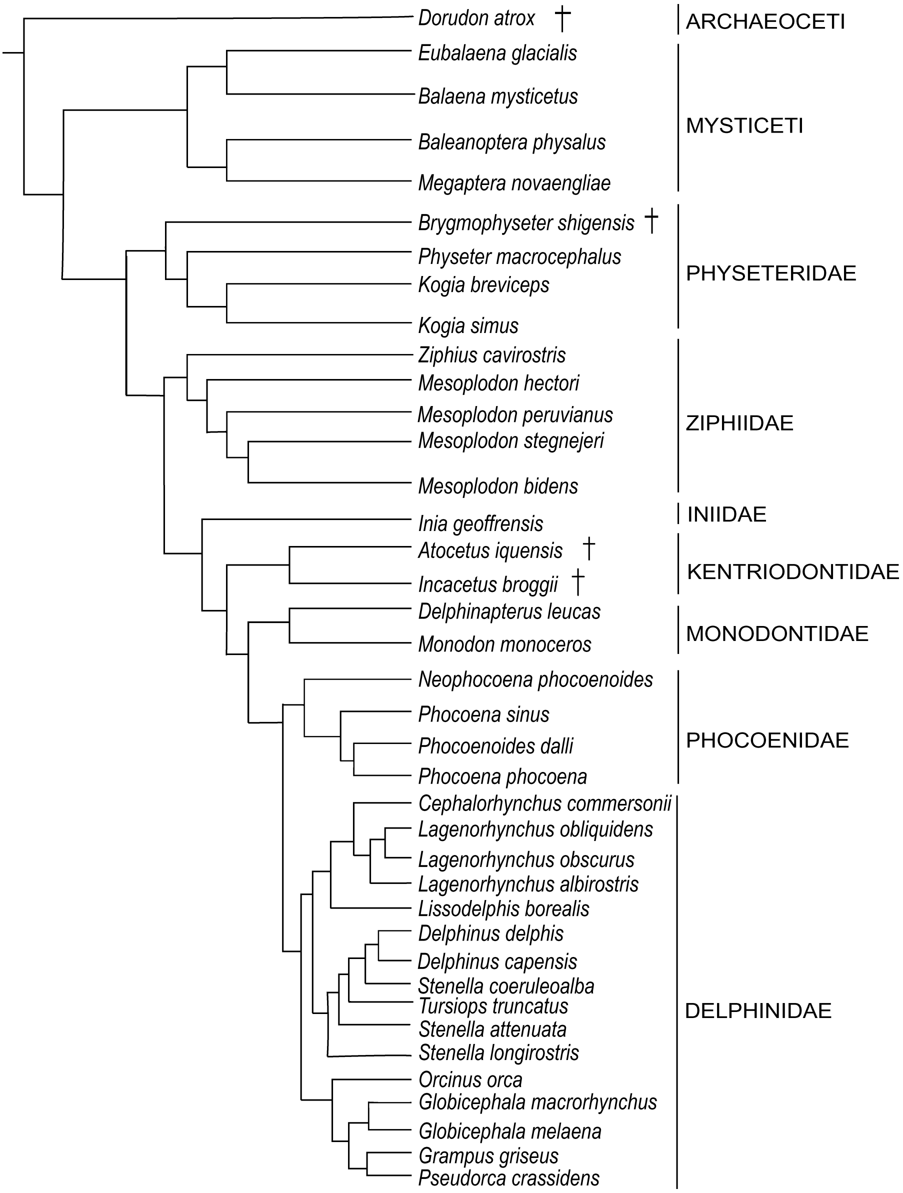

Figure 1. Composite cetacean phylogeny based on May-Collado and Agnarson (2006) used during this study. Placement of fossils follows Muizon (1988).

that variances of each sample are so similar that they ignore differences between them (Fowler and Cohen 1995). Body length data was obtained from Benke (1993). Flipper area was acquired from Benke (1993), and from fresh specimens using Image J (Abramoff *et al.* 2004).

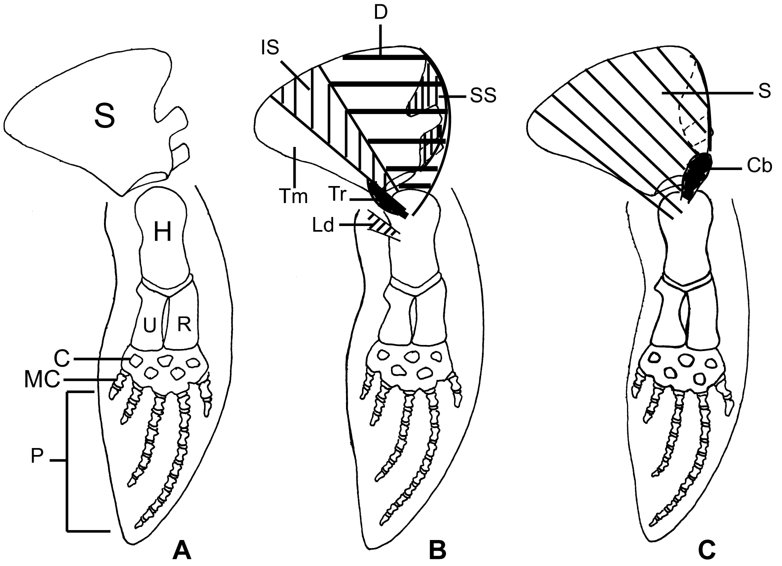

Figure 2. Generalized odontocete flipper. (A) Skeletal elements (S: scapula, H: humerus, C: carpals, MC: metacarpals, U: ulna, R: radius, P: phalanges), (B) shoulder girdle muscles in lateral view (IS: infraspinatus, D: deltoid, SS: supraspinatus, Tm: teres major, Tr: triceps, Ld: latissimus dorsi), and (C) shoulder girdle muscles in medial view (SUB: subscapularis, Cb: coracobrachialis).

Results and Discussion

Forelimb Myology

Dissection of 11 odontocete specimens allowed the examination of eight muscles responsible for flipper movement. The origin and insertion of these muscles was consistent with previous research (Howell 1930*a*; Pilleri *et al.* 1976; Smith *et al.* 1976; Strickler 1978, 1980; Benke 1993) and only new information obtained during this study on muscle architecture is discussed below. It should be noted that there may be individual variation that was not observed in this study due to small sample size. The muscles and skeletal elements of the forelimb analyzed during this study are shown in Figure 2.

Subscapularis—This multipennate muscle is divided into several bipennate muscular columns sharing a common insertion by joining into one tendon. This division of the muscle suggests an increase in the range of flipper movement by possible independent control of each column. This study confirmed Cooper's (2004) findings for *T. truncatus* of a subscapularis muscle divided into seven columns with columns 2–5 bisected by a second layer of fibrous connective tissue. The same seven columns were found in *Kogia simus*, *Cephalorhynchus commersonii*, and *Grampus griseus*; although two extra columns were palpated but not confirmed in *K. simus*. The thickest muscle belly was observed in *T. truncatus* and *Delphinus capensis*; whereas *K. simus* and *P. phocoena* exhibited the thinnest one.

Coracobrachialis—This parallel muscle has fascicles that either remain the same width or become narrower from the origin to insertion, showing a direct relationship with the coracoid process. Thus, species with a wide coracoid process, such as *G. griseus*, also exhibited a wider origin than insertion of this muscle. In contrast, species with a small or narrow coracoid process, such as *K. simus*, presented a narrow insertion with the same width as in the origin. *C. commersonii, Phocoenoides dalli, K. simus*, and *P. phocoena* display a coracobrachialis muscle that is narrow at the origin and remains relatively the same width until it reaches the site of insertion. The thickest coracobrachialis muscle was found in *T. truncatus*; followed by *D. capensis,* which was also bulbous in shape. The two phocoenids, and *C. commersonii* displayed the flattest muscle. *G. griseus* was unique, exhibiting a muscle possessing a thick muscle belly at the origin with fibers that became thinner as they come together at the site of insertion. *K. simus* displayed the narrowest muscle of all odontocetes investigated.

Deltoid—This is a convergent muscle in which the main difference among all species studied was the scapular area covered by the muscle and the size of the muscle belly. In most species it covers one-half of the antero-lateral side of the scapula; the exceptions were the dwarf sperm whale and Risso's dolphin. In *K. simus*, this muscle covers only one-third of the scapula and in *G. griseus* it covered slightly more than one-third of the scapula. An interesting case is *K. simus,* in which this muscle follows the antero-vertebral curvature formed by the acromion process and the scapula blade; giving it a very irregular shape. The two phocoenids presented the thinnest muscle belly of all the species dissected, compared to *T. truncatus* that possessed the thickest one. Cooper (2004) also found this muscle to be bisected postero-anteriorly by a connective tissue sheet in the ziphiid, *Ziphius cavirostris*, thus making it a multipennate muscle. However this observation was not confirmed in any of the odontocetes in this study.

Supraspinatus—This is a convergent muscle that completely covers the area between the acromion and the coracoid process of the scapula. All odontocete species dissected exhibited a supraspinous muscle with fascicles that increased in breadth as they extend from the vertebral border toward the brachial region and then become narrow as they come together at the site of insertion. The widest point is the part of this muscle that passed through the acromion and coracoid processes. Thus, this muscle also showed a direct relationship with the acromion and coracoid processes. The thickest and largest tendon of insertion was found in one *D. capensis* specimen; though the second specimen and the remaining species dissected had a very short tendon or attached directly into the bone.

Infraspinatus—This muscle is located posterior to the deltoid, anterior to the teres major and below the scapular spine. The main distinction was seen in the three different areas covered by this muscle. The species *C. commersonii, D. capensis, T. truncatus,* and *P. phocoena*, possessed an infraspinatus muscle that covered one-fourth of the lateral surface of the scapula. *G. griseus* and *P. dalli* displayed a larger muscle that occupied one-third of the scapular surface. The physeterid, *K. simus,* was unique in that this muscle expanded through out most of the posterior half of the scapular surface, occupying almost one-half of the scapular blade and leaving very little space for the origin of the teres major muscle.

Teres major—This is a convergent muscle found on the posterior lateral side of the scapula, next to the infraspinatus, with some fascicles extending to the medial side, adjacent to the subscapularis muscle. In odontocetes, this muscle varied only in the amount of scapular area covered. Some species, such as *C. commersonii, D. capensis, T. truncatus, G. griseus,* and *P. phocoena,* possessed a teres major that extends through one-fourth of the scapular surface. Other species (*i.e., P. dalli*), had a smaller muscle covering only one-fifth of the scapular blade. *K. simus* exhibited a teres major

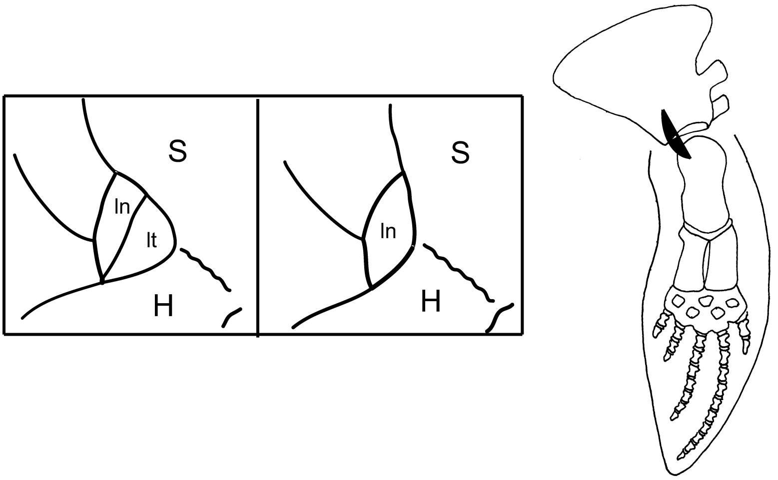

Figure 3. Long head (ln) and lateral head (lt) of the triceps muscle in *K. simus* (left image), and *P. phocoena* (right image). S: Scapula, H: Humerus. Solid black area in complete forelimb image represents the triceps location within the odontocete flipper. Anterior is to the right.

with a very small origin, due to radiation of the infraspinatus proximal fascicles, but it expanded proximo-distally and it occupied one-fourth of the scapular blade at mid-scapular region.

Triceps—In the odontocetes dissected, only one species, *K. simus*, displayed two heads of this muscle, the long head and the lateral head (Fig. 3). The remaining species exhibited a single head comparable to the triceps long head, based on the site of insertion. The long head inserted on the proximal border of the olecranon process of the ulna, whereas the lateral head inserted next to it on the antero-proximal side of the ulna. The two heads present in *K. simus* are separated by a very thin fibrous connective tissue sheet and the fascicles of both heads form an oblique angle, opposite to each other. Of the two heads observed in this species, the long head exhibits the thickest muscle belly. The long head in the remaining species was very robust and displayed longer fascicles directed antero-posteriorly at the glenohumeral joint.

Latissimus dorsi—Only a small portion of this muscle at the site of insertion was preserved. In general, the odontocete latissimus dorsi muscle displayed a thick belly; however, it showed considerable differences at the site of insertion. Some species such as *D. capensis, T. truncatus,* and *C. commersonii*, exhibited a very wide muscle that becomes very narrow at site of insertion. The thickest belly was found in *T. truncatus* and the widest fascicles were found in *D. capensis*. In contrast, other species, such as *K. simus, G. griseus*, and *P. phocoena,* have a somewhat narrower muscle that does not show a significant change in width at contact with the tendon. The thinnest and narrowest muscle bellies were found in *P. phocoena*.

Forelimb Osteology and Flipper Shape

The results of the osteological and external shape examinations of odontocete flippers reflect the comparison of the state found in their most recent common

Table 3. List of characters and character states in this study.

Character	State 0	State 1	State 2
1. Scapula size	Longer than wide	Wider than long	
2. Scapula spine	Prominent/long	Reduced/absent	
3. Scapula acromion process	Present/large	Reduced/absent	
4. Scapula coracoid process	Present	Reduced/absent	
5. Length of humerus	Long	Short	
6. Humerus greater tubercle	Present	Reduced/absent	
7. Humerus lesser tubercle	Present	Reduced/absent	
8. Orientation of humeral head	Projects over ulnar edge	Does not or only slightly projects	
9. Gap between radius and ulna	Present	Absent or not significant	
10. Shape of ulna's olecranon process	Fan-shaped	Blunt	Paddle
11. Polydactyly	Absent	Branched	Interdigital
12. Elongation of manus	Absent	Hyperphalangy	
13. Arrangement of digits	Broad	Narrow	
14. Shape of flipper	Elongated	Broad triangular	Broad circular
15. Shape of leading edge	Straight/slightly curved	Significantly curved	Extremely curved
16. Tip of flipper	Rounded	Pointed	

ancestor, *D. atrox* (primitive condition), with the state found in all other species. A list of characters and characters states is provided in Table 3.

Scapular characters—Quantitative analysis allowed for the evaluation of scapular width *vs.* length (Table 2). The average measurement was used when multiple individuals were available for analysis. *D. atrox* possessed a scapula that is longer than wide (Uhen 2004). However, both mysticetes and odontocetes, evolved a scapula that is wider than long. Basal odontocetes, *Physeter macrocephalus* and *Brygmophyseter shigensis* on the other hand, retained the primitive condition.

The spine was well developed in *D. atrox* (Uhen 2004), however, although it differs in size among extant taxa, most species exhibited a small or absent spine. Physeterids, *Z. cavirostris*, monodontids, and pilot whales exhibited a very small scapular spine. The smallest spines were found in *Inia geoffrensis* and *Kogia breviceps*. It has been reported that *T. truncatus* has no trace of this spine (Klima *et al*. 1987); however, this was not supported by this study. In some cases, the scapula also exhibited smaller, secondary spines (located posterior to the cardinal spine) that presumably allowed for a greater area of muscle attachment.

The acromion and coracoid process of the scapula displayed differences in size and shape. *D. atrox* had an acromion that is very small, curved, and narrow. The basal odontocete *K. breviceps* possessed an acromion that is long, massive, and becomes wider anteriorly. In contrast, *K. simus* possessed the narrowest acromion process that becomes only slightly broader anteriorly. *Delphinapterus leucas* exhibited a very long acromion that is proximally pointed as it extends anteriorly; whereas *Globicephala macrorhynchus* exhibited a process that is short and projects antero-proximally with a pointed end. The basilosaurid *D. atrox*, also possessed a coracoid process that is very large, robust, and medially curved (Uhen 2004). *P. macrocephalus* and *I. geoffrensis* had a long and flat coracoid process. Also, the results of this study for *G. griseus* support those of Benke (1993), who noted the presence of a long, narrow, proximally extended coracoid process.

Brachial characters—The glenohumeral joint of cetaceans is a diarthroidal joint capable of circumduction. The basilosaurid, *D. atrox*, had a humerus that is longer than the average combined length of both the radius and ulna. All physeterids, *Mesoplodon hectori, I. geoffrensis*, monodontids, *Phocoena sinus*, *P. dalli*, *Neophocoena phocoenoides*, *Orcinus orca*, and both pilot whales retained this primitive condition; whereas the remaining species evolved the opposite state. This study also supports the results of Klima *et al.* (1987) that in *I. geoffrensis*, the lesser and greater tubercle are joined by a crista. This was also found for *K. breviceps* and *Lagenorhynchus obliquidens*. Both tubercles in *T. truncatus* are merged into one massive and strongly prominent tubercle (Klima *et al.* 1987). This characteristic is also exhibited by *G. griseus*, *G. macrorhynchus*, and *Stenella attenuata*.

The radius and ulna are firmly attached to the distal end of the humerus by articular cartilage. The interosseous space between these two elements might affect the shape of the flipper by expanding the internal area covered with connective tissue, making the flipper midpoint longer proximo-distally, or increasing the curvature (roundness) of the leading edge. *D. atrox* had a significant gap between these elements. This condition was retained by mysticetes, and basal odontocetes (physeterids, *Z. cavirostris*, and *Mesoplodon bidens*), but lost or not significant in remaining odontocetes. Within delphinoids, the only species displaying a significant gap are *M. monoceros*, *P. dalli*, and *Pseudorca crassidens*. In general, the radius only differs in size among cetaceans; however, the ulna greatly differs due to the shape and size of olecranon process. The olecranon process is either fan or blade-shaped as in *D. atrox* (Uhen 2004); proximo-distally rounded, paddle-shaped, as in *P. macrocephalus*; or a small protuberance that projects posteriorly as in *M. monoceros* (Cooper 2004). The fossil delphinoid, *Incacetus brogii*, all physeterids, the two *Delphinus* species, *Lagenorhynchus albirostris*, the three *Stenella* species, and *Lissodelphis borealis*, possessed an olecranon process that is paddle-shaped. The fan-shaped process was found on all ziphiids, *D. leucas*, the two most diverged phocoenids, *P. dalli* and *P. phocoena*, and many delphinoids (*P. crassidens*, *G. macrorhynchus*, *L. albirostris*, *L. obliquidens*, *T. truncatus*, *C. commersonii*, and *G. griseus)*. The blunt-shaped olecranon process was observed in the fossil delphinoid, *A. iquensis*, as well as the extant species *I. geoffrensis*, *M. monoceros*, *Phocoenoides sinus* and *N. phocoenoides*, and *Globicephala melaena*.

The results of this study also indicate that most basal odontocetes, except *M. bidens* and *Mesoplodon stegnejeri*, and *I. geoffrensis* and both monodontids displayed the primitive condition observed in the basilosaurid *D. atrox* of a broad arrangement of digits. A narrow digit arrangement is seen in the remaining delphinoids, with the exception of *P. dalli*, *P. crassidens*, *O. orca*, and *C. commersonii*.

External flipper shape characters—Two flipper shapes have been previously described, an elongated flipper seen in fast swimming cetaceans, and broad flipper observed in those species requiring more maneuverability (Benke 1993, Cooper 2004, Woodward *et al.* 2006). We recognize here the presence of a third flipper shape and define flipper shape based on AR. An elongated flipper, described by an AR greater than 4.0 is exhibited by all delphinids, except for *C. commersonii* and *O. orca*, *P. phocoena*, *K. breviceps*, and ziphiids. A broad triangular flipper, characterized by an AR $<$ 4.0 and a pointed tip is displayed by *Kogia simus*, *I. geoffrensis*, *P. sinus*, *N. phocoenoides*, and monodontids. A newly defined broad circular paddle-shaped flipper indicated by an AR $<$ 4.0 and a circular, rounded tip was found in *P. dalli*, *O. orca*, and *C.*

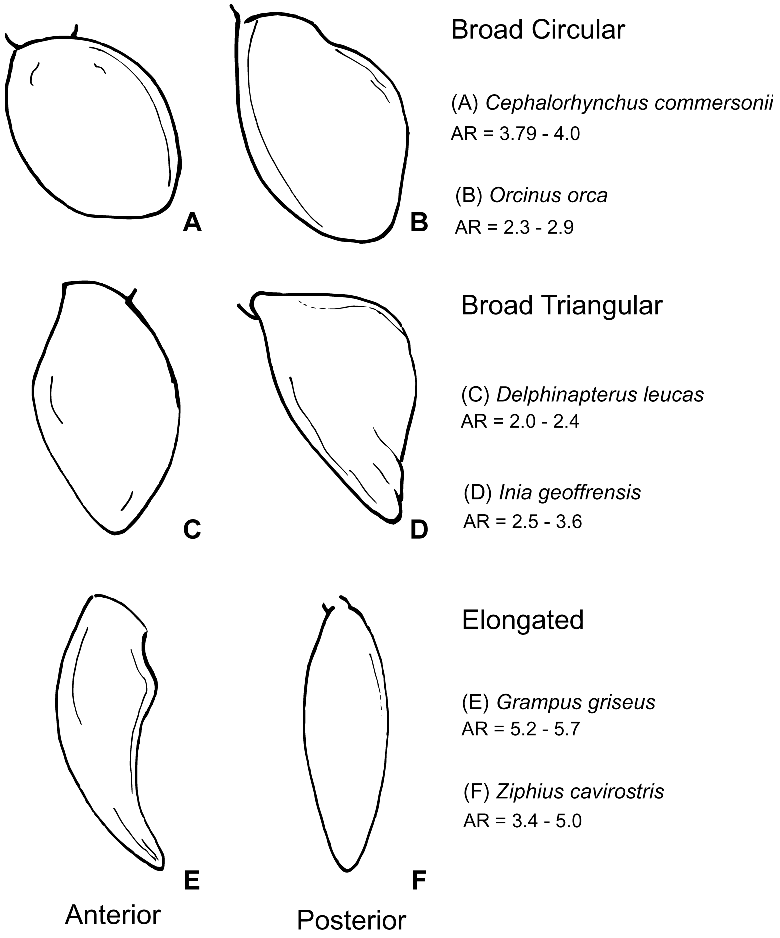

Figure 4. Three odontocete flipper shapes described during this study based on aspect ratio (AR) and shape of tip.

commersonii. *G. melaena* and *G. macrorhynchus* have the narrowest and most elongated flippers whereas *O. orca* has the most circular flipper (Fig. 4).

Character Mapping and Ancestral State Reconstructions

Optimization of characters onto a composite phylogeny was done in order to assess character state reconstructions. Each character was mapped in a "pie-model" form indicating the relative support for character states found at each node. This allowed the evaluation of character evolution among the species studied by observing the character state reconstructions shown at the ancestral nodes. Only the characters with the most significant changes are discussed. The optimization of several characters is illustrated in Figures 5 and 6.

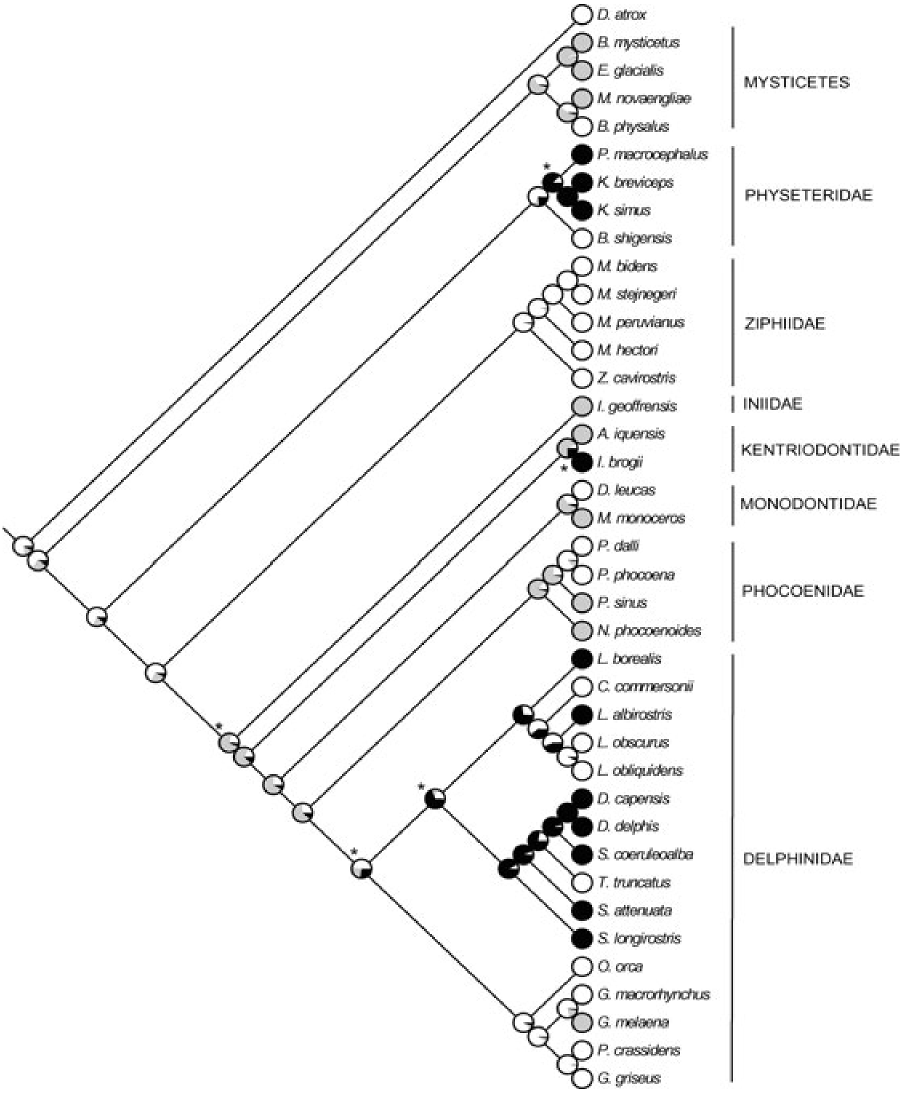

Figure 5. Optimization of character 10 (shape of olecranon process of ulna). Species with a fan-shape process are indicated by open circles. A small, blunt process is indicated by gray filled circles. Black filled circles designate paddle-shape process. Major evolutionary events are indicated by an asterisk.

Results indicate that there is no evolutionary association between osteological characters and external traits of the flipper by visual inspection. This was confirmed by the concentrated changes tests performed in MacClade 4.0 (Maddison and Maddison 2000). Digit arrangement was the only osteological character used in these tests because based on our results it was the only character predicted to influence flipper shape. Results from these latter analyses showed a significant difference ($P = 0.2888$)

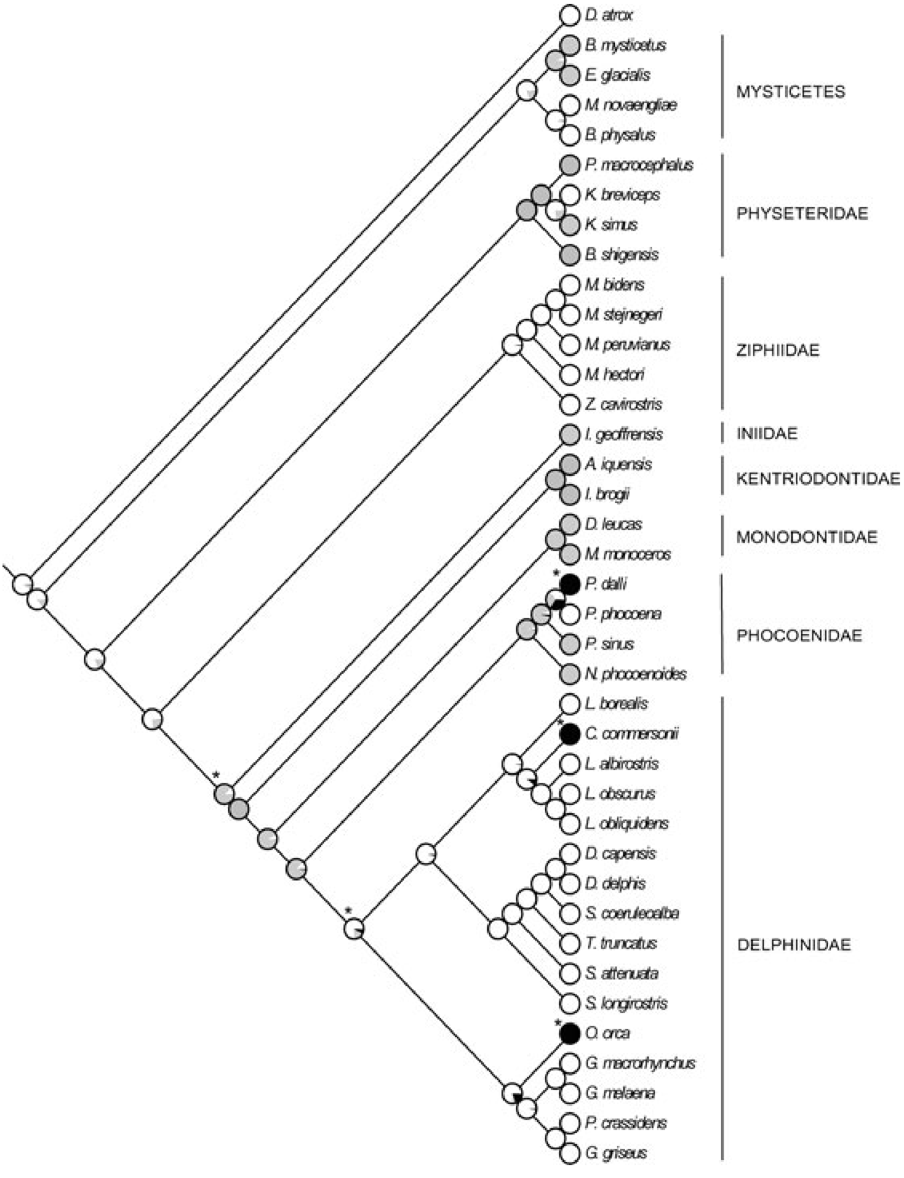

Figure 6. Optimization of character 14 (shape of flipper). Species with an elongated flipper shape are indicated by open circles. Light gray filled circles represent species that possess a broad triangular shape. Black filled circles indicate species with a broad circular shape. Major evolutionary events are indicated by an asterisk.

when comparing digit arrangement *vs.* elongated and broad flipper shapes. A significant difference ($P = 0.0644$) was also found when comparing digit arrangement *vs.* elongated and broad circular flipper shapes. In both cases, digit arrangement was used as the independent variable.

A humerus longer than the length of the radius and ulna is a characteristic shown by most cetaceans. The opposite condition is displayed among three odontocete lineages: Ziphiidae, Phocoenidae, and Delphinidae. The humerus also presents differences in the morphology of the greater and lesser tubercle. Within balaenopterid mysticetes, *Megaptera novaeangliae* and *Balaenoptera physalus* exhibit a reduced greater tubercle, although it is well developed in the common ancestor of cetaceans. Within odontocetes, the ancestral condition of a well developed greater tubercle is retained among all early diverging species (*i.e.,* physeterids, ziphiids, *I. geoffrensis*, and monodontids) with phocoenids and some delphinids displaying the derived condition. Eight delphinid species likely exhibit a reversal to the primitive condition.

The shape of the olecranon process of the ulna is one of the characters that exhibits a large number of transformations (Fig. 5). Based on maximum likelihood analyses, the fan-shaped olecranon process was likely retained by basal odontocetes and a small blunt process evolved in later divergent odontocetes (*I. geoffrensis* and delphinoids). A reversal to the primitive condition is observed in later divergent delphinids (*i.e., O. orca, G. macrorhynchus, P. crassidens*, and *G. griseus*). In contrast, the probability of a paddle-shaped olecranon process increased beginning with the early archaeocete, *D. atrox*. The development of a paddle-shaped olecranon process can be observed in many cetacean species.

Most ancestral nodes display the primitive condition of a broad arrangement of digits. The evolution of a narrow arrangement occurred convergently in mysticetes, ziphiids, and the clade containing Phocoenidae and Delphinidae. A reversal to the ancestral condition likely occurred in *P. dalli, Cephalorhynchus comersonii, O. orca*, and *P. crassidens.*

Analyzing the results from the external shape of the flipper, it is clear that the ancestral condition for all cetaceans is likely an elongated flipper, which evolved into a triangular paddle-shaped flipper during the evolution of *I. geoffrensis* and delphinoids (Fig. 6). A reversal to an elongated flipper is seen among delphinids. The circular paddle-shape is an autapomorphy for three odontocete species: *C. commersonii, P. dalli*, and *O. orca.* This latter species is the only odontocete to exhibit an extremely rounded flipper.

CAIC Analyses

The relationships between flipper shape, flipper area, and body length were also assessed for several odontocetes. Species for which complete data (*i.e.,* body length and flipper measurements) were available were analyzed using CAIC. There was no significant relationship found between flipper area and flipper shape ($n = 5$, $r^2 = 0.0812$, slope $= -0.0287$, $F = 0.3537$, $P = 0.584$), nor between body length and flipper shape ($n = 5$, $r^2 = 0.481$, slope $= -0.0723$, $F = 3.7077$, $P = 0.1265$). However, there were a total of 20 significant contrasts found between body length and flipper area ($n = 20$, $r^2 = 0.2085$, slope $= 1.0549$, $F = 5.0064$, $P = 0.0374$). This latter result indicates a direct relationship between body length and flipper area where "n" represents the number of significant contrasts found between the two variables (Fig. 7; online Appendix 3).

Conclusions

Cetaceans experienced many anatomical transformations in their forelimbs as they evolved from a terrestrial to an aquatic life. Following the loss of elbow mobility

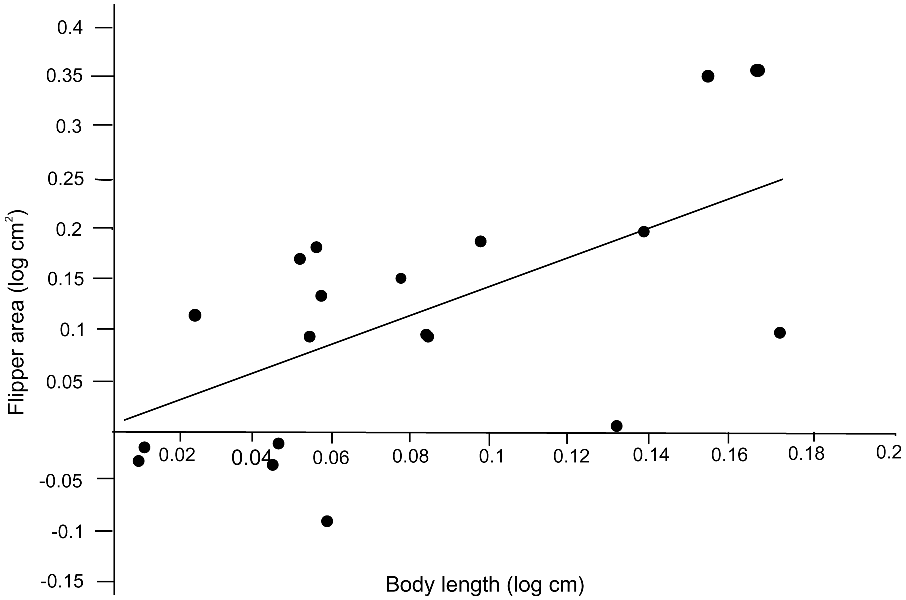

Figure 7. Plot of contrasts found between body length and flipper area, showing correlation found.

and the stiffening of the manus, there were a series of changes that adapted the odontocete flipper for hydrodynamic efficiency. These changes include osteological transformations that vary within and among the different odontocete families, as well as differences in muscle architecture, the amount and organization of soft tissue encasing the flipper, and the development of various flipper shapes.

This is the first study to examine odontocete forelimb anatomy in a comparative evolutionary context. A detailed description of the architecture of bones and muscles found in the odontocete flipper among several species is provided. Many odontocete species have modified the skeletal elements of their forelimb by developing different shapes, such as that seen in the olecranon process of the ulna. Expansion or reduction of skeletal elements is also observed, such as in the acromion and coracoid process of the scapula. The development of longer or extra bones to elongate the flipper, and the development of varying amounts of connective tissue, allowed for the evolution of different flipper morphologies.

This study suggests that muscles with thicker muscle bellies and greater degree of muscle differentiation, provide better control. Thus, a deltoid muscle with a thicker muscle belly and larger muscle fascicles allows for stronger extension and abduction of the humerus. The differentiation of the subscapularis muscle into several fairly independent columns allows for better movement control.

There is a clear relationship between muscle and bone indicating that as muscles become larger, bones also increase in size (Daly *et al.* 2004). Thus, the widening of the scapula possibly allowed for greater development of the subscapularis muscle due to a broader site for muscle attachment. Along with the stiffening of articulations within the manus (Sedmera *et al.* 1997, Cooper *et al.* 2007*a*), this study suggests that the increase in muscle mass also allowed for development of a stronger flipper that could counteract the forces exerted on the animal while swimming and assist with flipper stability and maneuverability.

The musculature of the odontocete forelimb is concentrated mainly in the shoulder girdle as muscles in the brachial region have become vestigial or absent, given the lack of mobility of the forelimb at the elbow joint. Only early diverging odontocetes such as *P. macrocephalus* (Cooper *et al.* 2007*b*) and *K. simus* possess flexor and extensor muscles that are absent in later divergent odontocetes. This is confirmed by the loss of the gap or interosseous space, a muscle attachment site, between the radius and ulna in most delphinoids. All these anatomical changes, that transform a terrestrial forelimb to an aquatic flipper, enable the flipper to assist in the stability, steering, and diving of the animal, and to generate changes in swimming directions (Benke 1993).

This is also the first study to use likelihood analysis to optimize forelimb characters onto a known cetacean phylogeny and to reconstruct ancestral character states. Concentrated changes tests confirmed the lack of correlation between the selected osteological characters and external shape of flipper. CAIC analyses were an innovative comparative method employed to examine the associations between flipper shape and area and body length. This study showed the inaccuracy of using standard statistical techniques to examine these relationships since the evolutionary history shared by all species is ignored by these methods. CAIC analyses confirmed a significant evolutionary association between flipper area and body length. However, the fact that no association was found between body length and flipper shape or between flipper area and flipper shape, supports previous studies suggesting that different flipper morphologies is likely largely the result of ecological requirements (Hertel 1966, Alexander 1970, Fitzgerald 1970, Webb 1984, Fish 1992, Benke 1993, Fish 1998, Fish and Rohr 1999). Habitat, swimming behavior, and requirements, such as stability, agility (the rapidity in which direction can be changed, Fish *et al.* 2003), and maneuverability (a controlled instability, Fish *et al.* 2003); influenced the evolution of three different flipper shapes (see Fig. 4). Thus, species that require great maneuverability and a constant motion of the flipper while slow swimming (Benke 1993, Barber *et al.* 2001), such as *I. geoffrensis* and *D. leucas*, exhibit a broad and triangular flipper shape. Species that are very agile and swim at both, shallow and deep waters, at somewhat faster speeds (Webb 1984, Benke 1993, Lescrauwaet *et al.* 2000), such as *O. orca* and *C. commersonii*, display a broad and circular flipper shape. The fastest odontocetes, the deepest divers, and the most acrobatic, requiring great stability and maneuverability, inhabit pelagic areas (Benke 1993, Davis *et al.* 1998, Fish *et al.* 2005), such as *Stenella longirostris* and *G. melaena*, possess an elongated narrow flipper.

Although this study contributes to our understanding of the anatomy, evolution, and function of the odontocete flipper, there are still many questions that remain. The study of live animals, both in captivity and in the wild, is necessary to test the functional implications derived from the analyses performed in this study. Functional aspects of the flipper need to be investigated among the three flipper shapes distinguished in this study, such as differences in hydrodynamic efficiency, strength and range of movements, and specific habitat use. This can only be done by examining the specific movements achieved by each flipper shape in extant species. Furthermore, the odontocete flipper exhibits many different shapes. This study modifies the general distinction between elongated and broad flippers (Webb 1984, Benke 1993, Cooper *et al.* 2007*a*) and introduces a third shape; however, the range of flipper shapes among odontocetes likely can be farther subdivided. There are many osteological elements that could have influenced the development of external features on the flipper, and further investigation would likely provide important data.

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SUPPORTING INFORMATION

The following supporting information is available for this article online:
Appendix S1: Specimens dissected during this study.
Appendix S2: Character matrix used in this study. †: extinct.
Appendix S3. CAIC analyses. X-value: body length, Y-value: flipper area.