

FLYING WHALES INSIGHTS INTO THE FLIPPER OF THE HUMPBACK WHALE AND ITS RELATIVES USING A NOVEL TISSUE-ILLUMINATING TECHNIQUE

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ABSTRACT

Cetaceans primarily generate thrust through dorsoventral oscillations of the caudal flukes, while their flippers are generally associated with lift generation and torque production during manoeuvring. However, the humpback whale, which possesses the largest forelimbs among extant and extinct vertebrates, has been observed performing active flipper strokes that contribute to forward propulsion. This behaviour represents a unique combination of axial swimming and underwater flight among cetaceans. In this study we investigate the anatomical correlates of this rarely observed locomotor behaviour and examine how the distinctive flipper anatomy of the humpback whale compares to that of other cetaceans. We focus in particular on the musculoskeletal and tendinous organisation of the flipper. We compared the flipper musculoskeletal anatomy of the humpback whale with that of seven other cetacean species (two mysticetes and five odontocetes). A novel protocol to acquire images during dissections involving ultraviolet (UV) light was employed to enhance the contrast between skeletal elements, musculature and connective tissues, with a particular emphasis on tendons and entheses. Although all flippers are highly vascularised, antebrachial musculature is strongly reduced across cetaceans, a condition that is especially pronounced in humpback whales and several odontocete lineages that lack antebrachial muscles. These findings suggest that active control of the flipper is primarily achieved proximally at the shoulder joint between the scapula and humerus, where the musculature is markedly developed. This proximal control pattern appears to be shared among cetaceans despite substantial differences in flipper size and external morphology. Beyond its anatomical implications this study provides photographic documentation of key flipper structures across cetacean groups and demonstrates that UV-light imaging is an effective tool for revealing internal soft-tissue anatomy. This approach is likely to be valuable for the study of other anatomical systems.

KEYWORDS: cetacea, comparative anatomy, flipper, musculoskeletal anatomy, ultraviolet imaging

1. INTRODUCTION

Cetaceans are secondarily aquatic artiodactyls (Prothero et al., 2022) that use tail-propelled axial swimming, in which thrust is generated by dorsoventral oscillations of the body and caudal flukes (Fish, 1996; Gingerich, 2003; Gutarra & Rahman, 2021; Motani & Shimada, 2023; Webb, 1988). Like their terrestrial ancestors and extant relatives, their limbs are supported by bones and enveloped in skin. However, extant cetaceans' mobility of forelimb articulations (wrist and elbow) is extremely reduced compared to that of other artiodactyls (Howell, 1930; Fish, 2002; Thewissen et al., 2009; Gatesy et al., 2013; McGowen et al., 2014). Triceps, flexors and extensors constitute the three primary muscle groups in cetacean flippers, with flexor and extensor muscles remaining well developed in mysticetes and early-diverging odontocetes (e.g. physeterids, kogiids and ziphiids), but they are markedly reduced or entirely absent in later-diverging odontocetes, including monodontids, phocoenids and delphinids (Cooper et al., 2007).

Cetaceans generate thrust primarily through dorsoventral oscillations of the caudal flukes, whereas the flippers act as paired hydrofoils that generate lift perpendicular to the oncoming flow and torque about the body axes. By modulating flipper angle of attack and orientation, cetaceans can produce differential lift between the left and right flippers to induce roll (rotation around the longitudinal axis), adjust pitch (rotation around the transverse axis) and initiate or stabilise turns through controlled yaw moments (Fish, 2002; Segre et al., 2016; Weber et al., 2009). However, the humpback whale (*Megaptera novaeangliae*) has been recorded using active flipper strokes for propulsion (Segre et al., 2017), although flukes remain the primary propulsive structure in this species, as in other cetaceans. This combination of pectoral and caudal propulsion appears to be unusual among cetaceans and may be facilitated by the exceptional length, shape and mobility of the *Megaptera* flipper. Edel and Winn (1978) described both high- and low-speed manoeuvring involving extensive three-dimensional movements of the flippers, including protraction-retraction, abduction-adduction and axial rotation. However, Krahll and Werneburg (2023) argue that active axial rotation is unlikely, though passive rotation may still occur. The humpback whale also possesses the longest limbs known among both extant and fossil vertebrates, with flippers exceeding 5 metres (approximately 5.3 metres) in the largest recorded individual, an 18.6-metre specimen (Carwardine, 2022). The exceptional lengthening of the limb of *Megaptera* provides a high aspect ratio (elongated planform in dorsal/ventral view) resulting in an excellent lift-to-drag performance (Benke, 1993; Fish & Rohr, 1999).

Scientific interest in the flipper anatomy of *Megaptera novaeangliae* dates back to Eschricht et al. (1866), yet detailed anatomical studies remain scarce. Notable exceptions include the extensive dissection by Struthers (1889) and the neuromuscular description by Cooper et al. (2007), the latter being the only published work to provide detailed photography of cetacean flipper anatomy. Further investigation into the locomotor mechanics of this species may deepen our understanding of the evolutionary pressures that shaped the longest forelimbs in vertebrate history.

Highlighting the structural components of flippers and, more broadly of dissected organisms, remains a challenge in natural sciences as conventional photographs are often limited to visually

contrasting elements and therefore provide only partial access to anatomical complexity. Techniques exploiting specific wavelengths, such as UV illumination, have proven valuable across palaeontology (Haug et al., 2009; Pittman et al., 2022), archaeology (Neiman, 2014), botany (Schulte et al., 2019) and forensic sciences (West & Barsley, 1992) and offer a practical alternative to costly and size-limited imaging modalities such as CT and MRI scanning, which are largely impractical for larger cetaceans. Detailed visualisation of the muscles, tendons, ligaments and osseous tissues of the flipper, made possible here through UV illumination, is essential for interpreting the biomechanics of cetacean swimming.

This study aims to: (i) generate high-contrast images of the musculoskeletal composition of eight cetacean flippers (three mysticetes and five odontocetes) acquired during dissections, using a novel UV-lighting protocol that highlights tendinous and skeletal structures; and (ii) compare the limb anatomy of humpback whales to that of other cetaceans, contextualising these morphological observations within the broader evolutionary and functional literature.

2. MATERIALS AND METHODS

2.1 VISUALISATION TECHNIQUES FOR FLIPPER ANATOMY AND OBSERVATION OF FLEXIBILITY

We produced a series of photographs of dissected cetacean forelimbs illuminated with UV light (model: A365-Mini; peak emission 365 nm) that enhanced contrast between skeletal elements, musculature, cartilage and entheses (tendons and ligaments). Images were acquired using a smartphone camera (Samsung Galaxy S8+; RGB images).

We first tested an alternative method to differentiate bone from all other tissues, by placing wires around bones (Figure 3b). However, this required additional effort and yielded only moderately satisfactory results. Another approach to differentiate bones from other tissues involved exposing the specimen to air for several days post-dissection, allowing blood to drain from the bones (Figure 3c). However, although this technique can enhance contrast between osseous and surrounding soft tissues to a level comparable to that achieved under UV illumination, it is less immediate to implement, requires a fresh specimen and demands adequate space within a low-temperature environment to prevent tissue decomposition. Despite its overall effectiveness, UV illumination proved less optimal for *Megaptera novaeangliae*. Owing to technical limitations of our equipment, the 3.50 m flipper (measured in a straight line from the humeral head to the distal tip) presented a surface area too large to be fully covered by the beam of our UV lamp. Consequently, in this case, the positions of the bones were carefully determined during dissection and subsequently mapped with precision onto the flipper image using Inkscape (Figure 3a).

Flipper flexibility was assessed qualitatively prior to dissection by manually bending the flippers in the dorsoventral plane. Manipulations were performed gently and without applying force beyond the natural resistance of the tissues. Bending was limited to the maximum range attainable without

causing visible tissue damage. No quantitative measurements of angular displacement or applied force were recorded.

2.2 SAMPLE

All specimens dissected in this study were strandings. Some were examined immediately after collection, whereas others were frozen prior to dissection. All individuals were classified as Carcass Condition Codes 1–3 (fresh to moderate decomposition) according to the international stranding classification system; see Mazzariol and Centelleghé (2007). Only adult and subadult individuals were included to limit potential bias related to ontogenetic stage. Our sampling strategy aimed to maximise phylogenetic diversity among the species available for dissection. The dataset comprises eight species of cetacean, including three mysticetes from the family Balaenopteridae (*Balaenoptera acutorostrata*, *Balaenoptera physalus* and *Megaptera novaeangliae*) and five odontocetes from four families: Delphinidae (*Delphinus delphis* and *Globicephala melas*), Kogiidae (*Kogia breviceps*), Ziphiidae (*Mesoplodon bidens*) and Phocoenidae (*Phocoena phocoena*). Age category, sex, provenance and imaging method are detailed in Table S1.

3. RESULTS

3.1 COMMON ANATOMICAL FEATURES OF CETACEAN FLIPPERS

The structural components common to all cetacean flippers are the dermis, connective tissue, tendons, ligaments and bones (Figure 1). We found that UV light at 365 nm was particularly effective in maximising contrast. Under this lightning: tendons appear reddish-grey to blue (Figure 2c,e); ligaments and periosteum appear blue (Figure 2d); blood vessels appear dark red (Figures 2d, 3e); bone varies from blue to dark blue (Figure 3); cartilage appears light blue (Figure 3c–e). The skin of the cetacean flipper consists of two distinct layers (Figure 1a). The epidermis is a very thin outer layer, which peels off rapidly during the early stages of decomposition and is directly attached to the dermis, which is thicker. Along with bones, connective tissues make up most of the flipper's mass and volume. The connective tissue consists of pale, whitish fibres arranged in a disorganised pattern (Figure 1b). The most flexible regions of the flipper, particularly the tip and along the trailing edge (posterior side), consist mainly of skin with very few fibres. In contrast, the interdigital regions contain a dense accumulation of fibres, with vascularised areas observable within these tissues (Figure 1b). However, the stiffest areas are composed of bone and cartilage. Ligaments and periosteum cover the bones and can be distinguished from other connective tissues by their parallel orientation along the axis of the phalanges and long bones (Figure 1d and Figure 2d). In contrast, tendons exhibit a smoother texture and are more localised, as they do not cover the bones extensively like the periosteum (Figure 1c). All dissected flippers lack autopodial muscles, except in two species of the genus *Kogia* (*K. sima* and *K. breviceps*), which exhibit a very thin layer of the m. interosei on their medial aspect. Additionally, blood vessels were observed in all dissected flippers, both in proximal (Figures 2d, 3e) and distal areas.

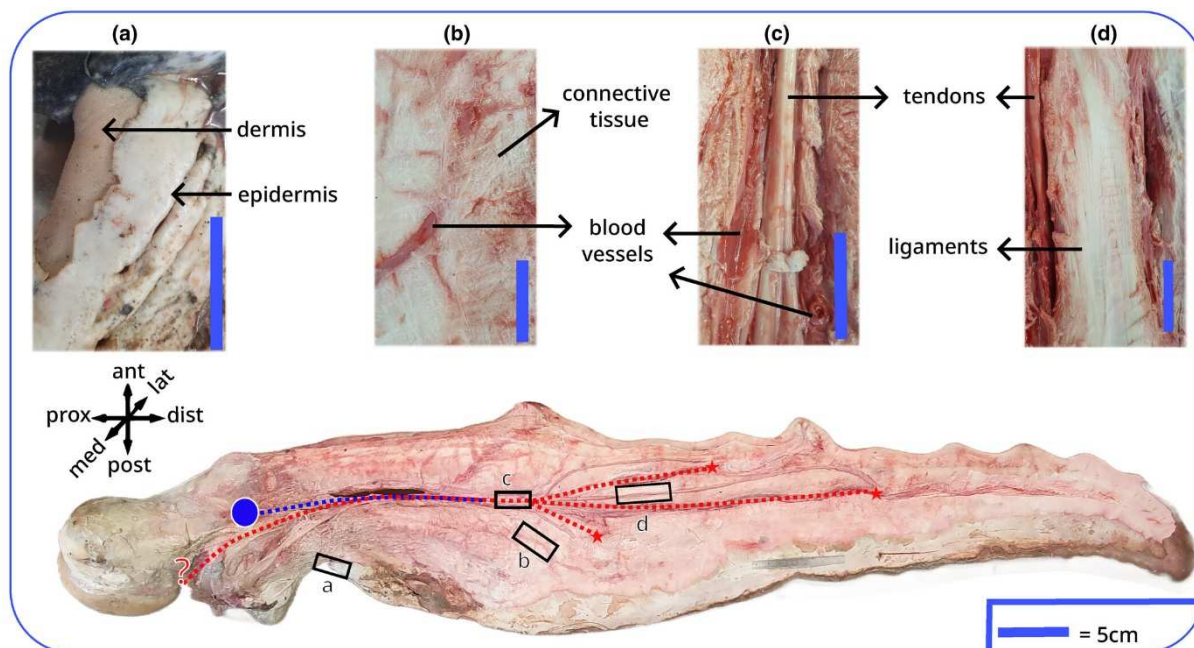


Fig. 1. Medial view of the left flipper of *Megaptera novaeangliae* (NMS.Z.2025.15.3). For better visibility, the tendons of the flexor digitorum communis have been placed adjacent to their anatomical position. The dotted red line indicates their anatomical placement, with ★ marking the functional termination of the tendon; ● muscle origin of the flexor digitorum radialis tendon; ● muscle origin of the flexor digitorum communis tendon. post: Posterior, dors: Dorsal, prox: Proximal, dist: Distal, vent: Ventral, ant: Anterior. Scale = 5 cm.

3.2 TENDINOUS STRUCTURE

Antebrachial muscles are present in all cetaceans examined, except in some derived odontocetes (e.g. delphinids, phocoenids), where a dense periosteum (also present in the other dissected cetaceans but to a lesser extent), a whitish, parallel-fibred layer, covers the bones in the region where the flexor and extensor digitorum communis tendons occur in other cetaceans (Figure 2d; Figure 3d). Conversely, *Kogia* and *Mesoplodon* retain the plesiomorphic condition, characterised by the presence of these muscles together with a well-developed tendinous system extending along the entire length of all five digits (Figure 2c,e). A similar pattern is observed in the four digits of the mysticetes, *Balaenoptera* spp. (Figure 2a, b), but not in *Megaptera novaeangliae* (Figure 1). Indeed, the specimen of *M. novaeangliae* displayed a marked tendinous development of the flexor digitorum communis (medial side), but only up to two-thirds of the flipper length, and it was restricted to digits II, III and IV, with the more distal parts becoming too thin to have any functional role. Additionally, the flexor muscle generally associated with this tendon was highly reduced in the humpback whale compared to other mysticetes. Moreover, in *Megaptera*, tendons are attached to the posterior side of the phalanges, whereas in other cetaceans they are typically positioned along the medial to medioposterior surfaces of the phalanges. In modern cetaceans this flexor muscle originates from a region between the distal part of the humerus and the proximal part of the zeugopod, depending on the cetacean species (Cooper et al., 2007). However, in our specimen of *M. novaeangliae* we were unable to identify the origin of the flexor digitorum communis. The proximal portion of the tendon was severed near the proximal region of the humerus during flipper collection. Its thickness and

compactness at the severed proximal end suggest that this tendon attaches more proximally than previously assumed, possibly on the scapula. This would indicate a unique attachment pattern among cetaceans. Even if the origin were located at the extreme proximal region of the humerus, this configuration would still differ from that reported in other cetacean species. This tendon's origin differs from that observed in the specimen illustrated in Cooper et al. (2007), in which the flexor tendons extend along all fingers up to the tip and do not originate as proximally as in our specimen.

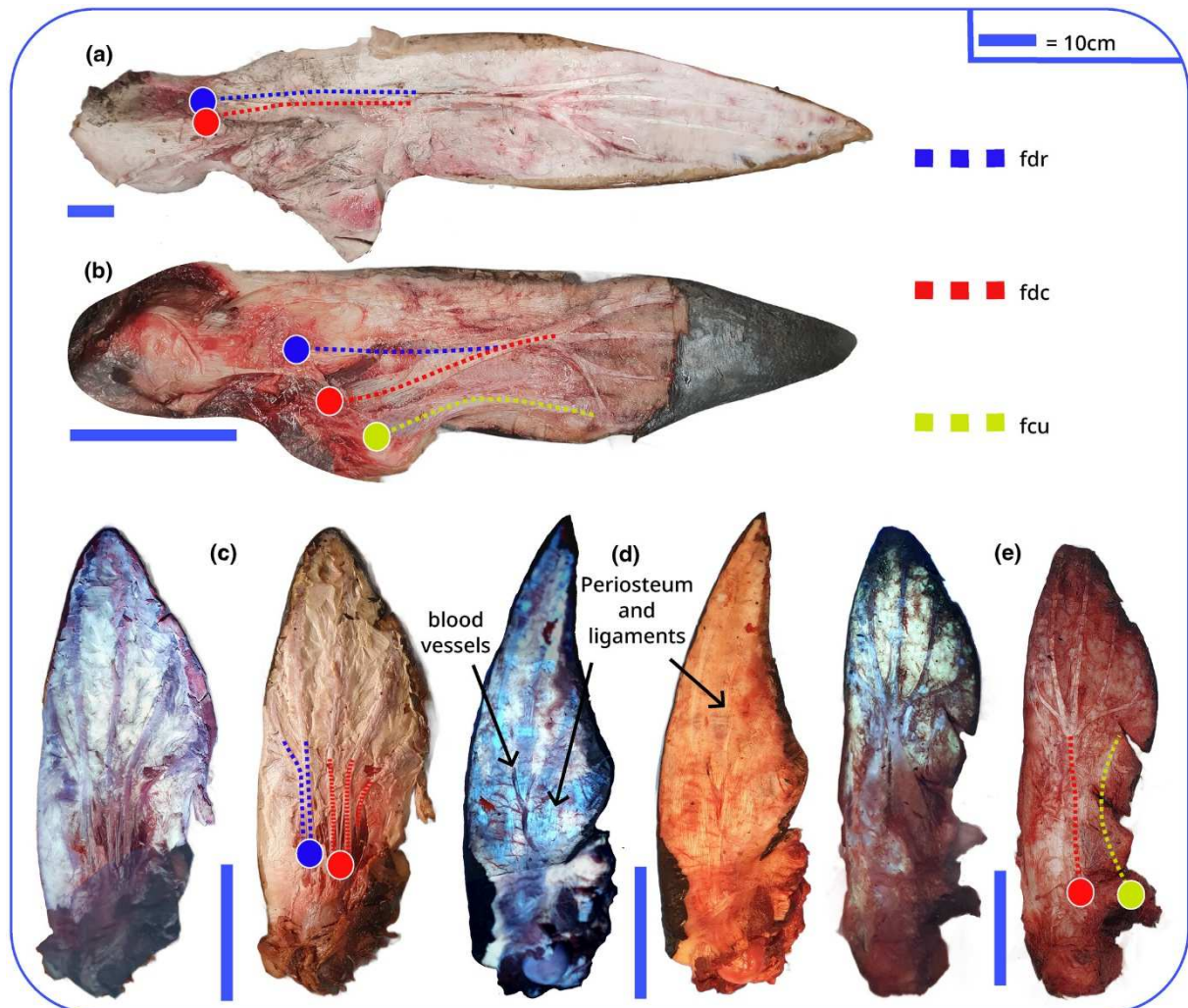


Fig. 2. A comparison of the tendinous arrangement between cetaceans. Mysticeti: A. *Balaenoptera physalus* (BAPH1AN23) right flipper in medial view (reversed), (b) *Balaenoptera acutorostrata* (NMS.Z.2020.9.1) right flipper in medial view (reversed). Odontoceti (left UV light; right normal light): C *Kogia breviceps* (IRSNB 44424) left flipper medial view, (d) *Delphinus delphis*, left flipper lateral view (reversed), (e) *Mesoplodon bidens* (12330031) left flipper medial view. ● Muscle origin of the flexor digitorum radialis tendon (fdr); ● muscle origin of the flexor digitorum communis tendon (fdc); ● muscle origin of the flexor carpi ulnaris tendon (fcu).

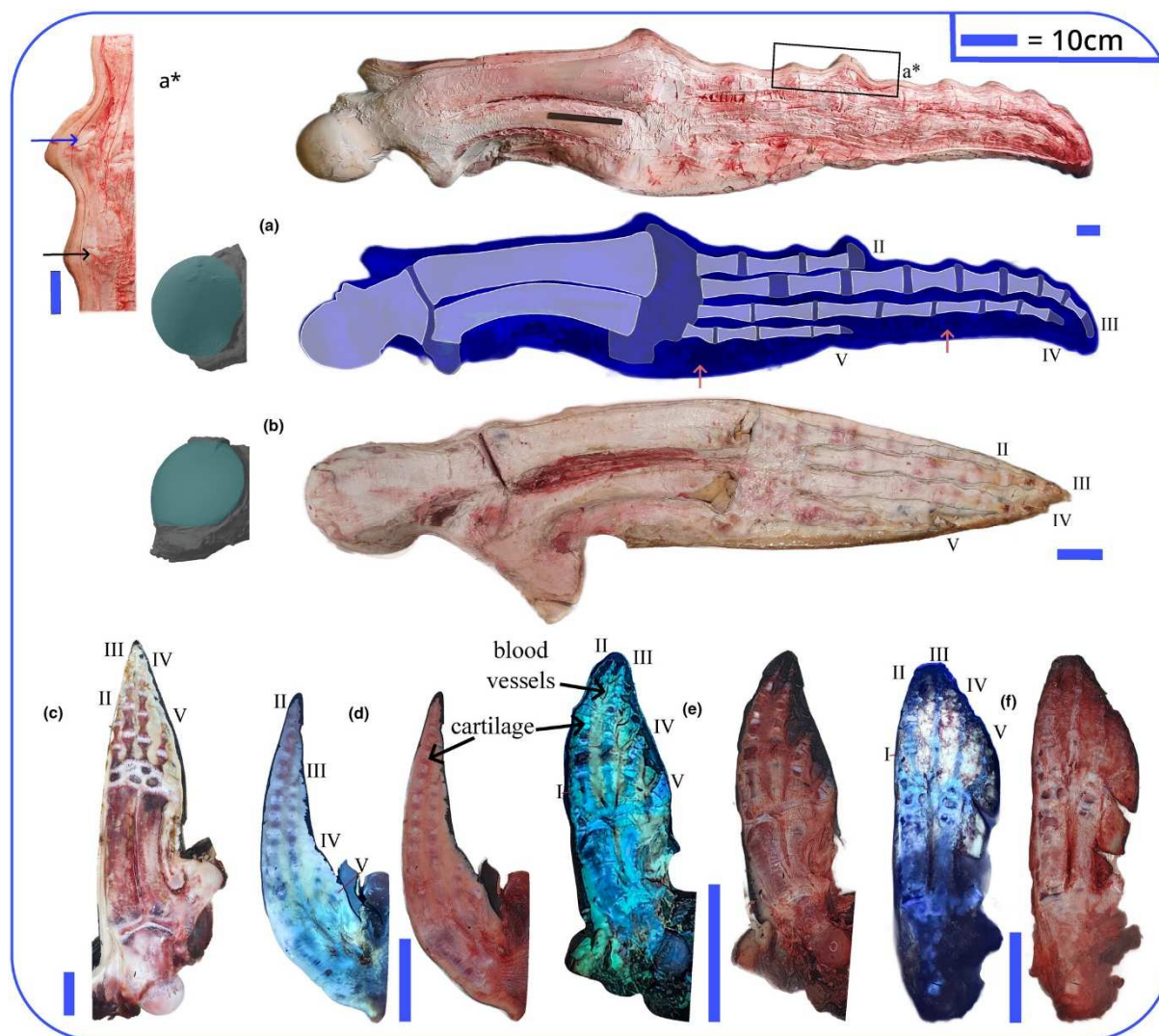


Fig. 3. Skeletal and cartilaginous structures of cetacean flippers. (a) *Megaptera novaeangliae* (NMS.Z.2025.15.3) left flipper in lateral view (mirrored), top left a*: Close-up view showing (blue arrow) the cartilage beneath the tubercle and (black arrow) the phalangeal joint beneath the tubercle; top right: Normal light; bottom left: Humeral head in posterior view with the articular surface highlighted in blue. Bottom right: UV light with bone cartography, the pink arrow indicates flexible areas lacking cartilage or bone that would otherwise stiffen the flipper. (b) *Balaenoptera physalus* (BAPH1AN23) right flipper in lateral view, a wire frame helps visualise the shape of the bones. (c) *Balaenoptera acutorostrata* (M586-18) right flipper in lateral view. (d) *Globicephala melas* (12320683) right flipper in lateral view. (e) *Phocoena phocoena* (12320761) left flipper in lateral view (mirrored). (f) *Mesoplodon bidens* (12330031) left flipper in lateral view (mirrored).

3.3 FLIPPER BONE DISTRIBUTION AND FLEXIBILITY

The leading edge of all flippers exhibits a high concentration of rigid skeletal tissues (Figure 3). The limb skeleton extends throughout most of the flipper, with digit arrangement closely linked to flipper morphology. Wider flippers display larger angles between digits (e.g. *P. phocoena*; Figure 3e), whereas elongated flippers have parallel digits (e.g. *M. novaeangliae*; Figure 3a). Other flipper morphologies fall within a spectrum of digital separation, ranging between these two extremes. The

flexibility of the limb appears to be primarily influenced by the number of digits present in the examined flipper section. Logically, the distal region of the flipper, which contains fewer digits than the proximal region, appears more flexible based on qualitative observation. The shape of the flipper, with a progressive thinning noted in both dorsoventral and anteroposterior thickness, is an additional factor contributing to increased flexibility of the distal region. Although all flippers share this general pattern, resulting in a progressive increase in flexibility along their length with the tip being the most flexible region, the degree of flexibility varies between species. *Balaenoptera acutorostrata*, *B. physalus*, *Mesoplodon bidens*, *Phocoena phocoena*, *Delphinus delphis* and *Kogia breviceps* have stiff flippers, whereas *Megaptera novaeangliae* and *Globicephala melas* have highly flexible flippers. The autopod can bend laterally by more than 30° from the axis of the zeugopod and medially by more than 45° without damaging the tissues in *Megaptera* and even more in *Globicephala* (see Data S1). Additionally, the humpback whale flipper has a slightly more flexible trailing edge, because its fifth digit and cartilage elements do not extend to the trailing edge (see pink arrows, Figure 3a) unlike in the other cetacean flippers dissected in this study.

3.4 TUBERCLES AND HUMERAL HEAD OF THE HUMPBACK WHALE FLIPPER

A unique trait of *M. novaeangliae* is the presence of tubercles along the leading edge of the flipper (Fish et al., 2011; Miklosovic et al., 2004). We observed that these tubercles correspond to the shape of the underlying phalangeal joints of the leading-edge digits, originating proximally with digit II, followed by digit III where digit II terminates and extending to the tip of the flipper (Figure 3a). Most of the apices of the tubercles align with the joints between phalanges, where the anteroposterior thickness of the phalanges is the greatest. Cartilage at the extremities of the leading-edge phalanges is more developed than in other cetaceans and supports the tubercles. Two tubercles are particularly prominent. The first is located at the distal extremity of the radius, while the second is at the tip of digit II and has a cartilaginous thickening at its distal end, which provides a rigid underlying structure for the largest tubercle on the flipper (Figure 3a *). The proximal articular surface of the humerus is notably large and rounded, covering a broad area relative to the overall bone dimensions. The humeral head is particularly prominent in *Megaptera novaeangliae*, as illustrated by comparison with that of *Balaenoptera physalus* (Figure 3a–b).

4. DISCUSSION

4.1 UV LIGHT AS A TOOL IMPROVE STRUCTURE VISUALISATION IN DISSECTIONS

The use of UV light has already proven valuable in various fields of natural sciences (Haug et al., 2009; Pittman et al., 2022; Schulte et al., 2019), and the present study demonstrates that this technique can effectively reveal the internal anatomy of cetacean flippers, particularly tendinous and skeletal structures. Its application to other anatomical regions or tetrapod groups may prove similarly informative, especially for visualising blood vessels and cartilaginous structures.

4.2 COMPARATIVE CETACEAN FLIPPER ANATOMY

Our results are consistent with the main published studies on cetacean flipper anatomy (Cooper et al., 2007; Müller, 2021; Struthers, 1889), which support a consensus regarding the absence or significant reduction of intrinsic arm and hand muscles in cetaceans. Specifically, robust flexor and extensor muscles were observed in *Kogia breviceps*, *Mesoplodon bidens*, *Balaenoptera physalus*, *B. acutorostrata* and *Megaptera novaeangliae* (i.e. early-diverging odontocetes and mysticetes), whereas in odontocetes more distantly related to mysticetes, such as *Delphinus delphis*, *Globicephala melas* and *Phocoena phocoena* (i.e. delphinoid), these muscles are either absent or strongly reduced. Therefore, robustness of muscles and tendons appears to be phylogenetically driven and does not correlate with body size in the Cooper et al. (2007) dataset, supporting the hypothesis that these structures are vestigial with minimal functional importance. Even in taxa with more developed musculature, the loss of wrist and elbow mobility severely restricts muscle-induced movement within the zeugopod and autopod. Nevertheless, the flexor digitorum tendons may contribute to passive stiffening of the flipper.

4.3 ANATOMICAL FEATURES OF FLIPPER MOBILITY IN *MEGAPTERA NOVAEANGLIAE*

Edel and Winn (1978) documented a high degree of underwater manoeuvrability in humpback whales, facilitated by three-dimensional active movements of the flippers. This range of motion is consistent with the particularly rounded humeral head described in this species (Benke, 1993), especially when compared to *B. physalus* (Figure 3a–b), suggesting enhanced glenohumeral mobility. The scapula of *Megaptera* is also markedly thicker and approximately twice as heavy as that of other balaenopterids of similar size (Struthers, 1889). One of the most distinctive osteological features of the humpback whale shoulder is the reduction of the coracoid and acromion processes to mere tubercles (Eschricht et al., 1866; Struthers, 1889; Kellogg, 1928; Clapham & Mead, 1999; Tanaka & Taruno, 2021), a condition unparalleled among cetaceans that likely represents a trade-off between joint stability and mobility (Müller, 2021). A potential compensatory mechanism may lie in the more proximal origin of the digital flexor tendons relative to those of other cetaceans, as observed in the present study. Nevertheless, these tendons become vestigial or absent beyond the distal half of the autopod (Figure 1), consistent with the narrow interosseous space and markedly reduced musculature of the zeugopodium in *Megaptera*. Previous descriptions of humpback whale flipper tendons (Cooper et al., 2007) differ from our observations of the origins and distal insertions of the flexor tendons. As only single specimens were dissected in both studies, it remains unclear whether this reflects intraspecific variation or a consistent feature of the species, particularly given the documented relaxation of genetic constraints on cetacean limb development (Telizhenko et al., 2024). Nevertheless, both Cooper et al. (2007) and the present study agree that the flexor digitorum communis originates more proximally in *Megaptera* than in other cetaceans. Myological reconstructions of archaeocetes place this origin at the very distal part of the humerus in the protocetid *Maiacetus inuus* (Müller, 2021) and the basilosaurids *Cynthiacetus peruvianus* (Martínez-Cáceres et al., 2017) and *Dorudon atrox* (Uhen, 2004), suggesting that the proximal origin of the flexor tendons may represent an autapomorphy of *Megaptera*. As in other cetaceans, voluntary mobility of

the forelimb joints was lost early in cetacean evolution and active force generation in *Megaptera* is primarily mediated by the musculature of the glenohumeral joint. Consistently, our results indicate that the intrinsic muscles of the arm and hand are too reduced to produce active rotation of the flipper, suggesting that the active three-dimensional movements documented in this species (Edel & Winn, 1978; Segre et al., 2017) are controlled more proximally. However, as our specimen only included the limb from its distal extremity to the humerus, the scapular musculature could not be examined, and further dissections targeting this region would be necessary to confirm this interpretation.

We observed qualitative variations in flipper flexibility associated with the proportion of osseous tissue present, consistent with the hypothesis that flippers containing a greater proportion of bony tissue are more rigid (Deblois & Motani, 2019). Their study further establishes a correlation between flapping hydrofoils in amniotes and a lower proportion of osseous tissue in the trailing edge, a relationship also supported by research on engineered hydrofoils (Katz & Weihs, 1978; Prempraneerach et al., 2003; Shyy et al., 2010; Zhao et al., 2010). Although humpback whales primarily rely on flukes for propulsion, the morphology of *Megaptera* flippers appears well-suited to supplement thrust generation during active flipper strokes. The relatively flexible trailing edge may enhance lift production (Deblois & Motani, 2019), while the tubercles on the leading edge are known to delay stall and improve hydrodynamic efficiency (Fish & Battle, 1995) during fluke-based propulsion, and likely also during flipper strokes as the flipper moves through the water. Moreover, the exceptional length of the *Megaptera* flipper confers an aspect ratio comparable to those of other lift-based aquatic amniotes (Cottureau et al., in prep.), a morphology consistent with enhanced hydrodynamic performance during flipper strokes. Furthermore, the passive flexibility observed in the present study suggests that this flipper is particularly susceptible to deformation under hydrodynamic load, and the dense connective tissue and tendinous network visualised here may facilitate elastic energy storage during such deformations.

4.4 EVOLUTIONARY AND FUNCTIONAL IMPLICATIONS OF CETACEAN TENDINOUS STRUCTURES

The reduction of intrinsic forelimb musculature observed across cetaceans suggests a shift from active muscular control towards passive mechanical regulation of flipper function. This transition likely occurred during the evolutionary shift from drag-based, semi-aquatic taxa with paddling appendages, which required joint mobility and active control of the autopodium and zeugopodium, to lift-based limbs (Fish, 1996) that rely on passive bending in response to fluid motion (Costello et al., 2023). This was accompanied by the loss of cubital joint mobility, already established during the late Eocene in mysticetes, with the earliest record of a fixed cubital joint occurring in *Mystacodon selenensis* (De Muizon et al., 2019; Lambert et al., 2017). Among odontocetes, the early-branching *Mirocetus riabinini* (Early Oligocene) shows a plesiomorphic humerus with a well-developed trochlea and capitulum, similar to those of archaeocetes (Sanders & Geisler, 2015), retaining some mobility in the forelimb. Therefore, the loss of forelimb mobility likely evolved independently at the onset of odontocete and mysticete evolution. In this context, the persistence of a tendinous network in

mysticetes and early-diverging odontocetes, and the dense periosteum and ligaments observed in delphinoids, as highlighted by UV illumination in the present study, likely reflects two evolutionary pathways through which passive mechanical regulation was achieved via flipper stiffening and elastic energy storage. Despite their structural differences, both configurations result in effective hydrodynamic control surfaces, as supported by studies on cetacean flipper performance (Cooper et al., 2008; Fish & Rohr, 1999), although the extent to which these distinct tissue architectures influence the resulting flipper flexibility and hydrodynamic properties remains to be quantitatively assessed.

5. CONCLUSION

The UV illumination protocol developed in this study provides an effective and accessible means of enhancing the visualisation of tendinous and skeletal structures during cetacean flipper dissections, offering a valuable complement to more costly imaging techniques. More broadly, the comparative dataset presented here supports the hypothesis that the progressive reduction of intrinsic forelimb musculature across cetaceans reflects an evolutionary shift towards passive mechanical regulation of flipper function. This shift appears to have been achieved through two distinct evolutionary pathways: the persistence of a tendinous network in mysticetes and early-diverging odontocetes, and the development of a dense periosteum and ligaments in derived odontocetes such as delphinoids, each contributing to flipper stiffening and elastic energy storage through different connective tissue architectures. Further quantitative investigations into flipper flexibility and scapular musculature, combined with additional dissections of *Megaptera* specimens, would be necessary to fully characterise the locomotor specialisations of this species.

AUTHOR CONTRIBUTIONS

Romain Cottureau drafted the original manuscript, performed dissections and contributed to data analysis and interpretation. Georg Hantke led data collection and carried out dissections of the NMS specimens together with Romain Cottureau; he also contributed to data analysis, interpretation and manuscript preparation. Andrew C. Kitchener contributed to data collection of the NMS specimens and critically revised the manuscript. All authors reviewed and approved the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

The data are presented in the figures of this paper; additional images and videos can be provided upon request.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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