Morphology of the core fibrous layer of the cetacean tail fluke

William T. Gough1 | Frank E. Fish1 | Dylan K. Wainwright2 | Hilary Bart-Smith3

1Department of Biology, West Chester University, West Chester, Pennsylvania
2Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts
3Department of Mechanical and Aerospace Engineering, University of Virginia, Charlottesville, Virginia

Abstract

The cetacean tail fluke blades are not supported by any vertebral elements. Instead, the majority of the blades are composed of a densely packed collagenous fiber matrix known as the core layer. Fluke blades from six species of odontocete cetaceans were examined to compare the morphology and orientation of fibers at different locations along the spanwise and chordwise fluke blade axes. The general fiber morphology was consistent with a three-dimensional structure comprised of two-dimensional sheets of fibers aligned tightly in a laminated configuration along the spanwise axis. The laminated configuration of the fluke blades helps to maintain spanwise rigidity while allowing partial flexibility during swimming. When viewing the chordwise sectional face at the leading edge and mid-chord regions, fibers displayed a crossing pattern. This configuration relates to bending and structural support of the fluke blade. The trailing edge core was found to have parallel fibers arranged more dorso-ventrally. The fiber morphology of the fluke blades was dorso-ventrally symmetrical and similar in all species except the pygmy sperm whale (Kogia breviceps), which was found to have additional core layer fiber bundles running along the span of the fluke blade. These additional fibers may increase stiffness of the structure by resisting tension along their long spanwise axis.

KEYWORDS
cetacean, collagen fiber, fluke, morphology, tail

1 | INTRODUCTION

The primary propulsive structure of cetaceans is the fluke blades. Multiple sources have reported the general form of the fluke blades as a dorso-ventrally symmetrical, streamlined wing with a rounded leading edge and tapered trailing edge in sagittal-section (Figure 1; Lang, 1966; Webb, 1975; Vogel, 1994; Fish, 1998; Fish, Beneski, & Ketten, 2007; Fontanella, Fish, Rybczynski, Nweeia, & Ketten, 2011). The fluke blades of cetaceans are not supported by any musculature or vertebral elements (Roux, 1883; Felts, 1966; Sun, Morikawa, Ueda, Miyahara, & Nakashima, 2011). The first comprehensive anatomical analysis of the internal structure of the cetacean tail fluke blade was performed by Roux (1883). He described five unique components of the tail fluke blade: a rubbery epidermis, a blubber layer, a ligamentous fiber layer, a core of dense connective tissue, and a system of vasculature. This basic arrangement has been observed in all subsequent descriptions of the fluke blade’s internal anatomy (Felts, 1966; Purves, 1969; Purves & Pilleri, 1978; Sun et al., 2010; Sun et al., 2011). The fluke blades of cetaceans are not supported by any musculature or vertebral elements (Roux, 1883; Felts, 1966; Sun, Morikawa, Ueda, Miyahara, & Nakashima, 2011). The first comprehensive anatomical analysis of the internal structure of the cetacean tail fluke blade was performed by Roux (1883). He described five unique components of the tail fluke blade: a rubbery epidermis, a blubber layer, a ligamentous fiber layer, a core of dense connective tissue, and a system of vasculature. This basic arrangement has been observed in all subsequent descriptions of the fluke blade’s internal anatomy (Felts, 1966; Purves, 1969; Purves & Pilleri, 1978; Sun et al., 2010; Sun et al., 2011).

The ligamentous and core fiber layers compose the bulk of the tissue within the fluke blade (Figure 2). The ligamentous layer is a series of collagen fiber bundles oriented approximately parallel to the spanwise axis of the fluke blade (Figure 2; Purves, 1969; Sun et al., 2010; Sun et al., 2011). Felts (1966) stated that the ligamentous layer fiber bundles resist tension and maintain rigidity at the tail tips and trailing edge. Later studies performed electron microscopy on the ligamentous layer and found pleating within the fiber bundles along the ventral surface of each fluke blade (Purves, 1969; Purves & Pilleri, 1978). This pleating was thought to contribute to dorsal bending of the fluke blades during the swimming downstroke (Purves, 1969). Felts (1966) described the core layer as extremely tough and composed of bundles of collagen fibers—oriented in the horizontal, vertical, and oblique directions—set within a matrix of fat cells (Figure 2). Later studies described a similar arrangement, with bundles angled vertically and diagonally (Purves, 1969; Purves & Pilleri, 1978). These studies also noted that the fibers ran antero-posteriorly from the leading edge to the trailing edge of the fluke blades (Figure 2). Sun et al. (2010) described the core layer of a bottlenose dolphin (Tursiops truncatus) fluke blade as a series as thin, parallel laminated sheets, but did not elaborate on the orientation of individual fibers within the sheets.

The core layer is the largest component of the fluke blade (Felts, 1966). Variation in core layer morphology may be related to structural
properties of the fluke blade, swimming performance, or external shape, as has been demonstrated in other biological composites (e.g., Hamilton, Dillaman, McLellan, & Pabst, 2004; Wainwright, Biggs, Curry, & Gosline, 1982). The goal of this study was to elucidate the orientation of fibers within the core layer and determine if the internal morphology of the fluke blade is conserved across different cetacean species. This information aids in understanding the role of the core layer in the function of cetacean fluke blades, which are devoid of muscle or bone.

2 | METHODS

One set of fluke blades was obtained from bottlenose dolphin (T. truncatus; Montuga, 1821), common dolphin (Delphinus delphis; Linnaeus, 1758), white-beaked dolphin (Lagenorhynchus albirostris; Gray, 1846), Risso’s dolphin (Grampus griseus; Cuvier, 1812), harbor porpoise (Phocoena phocoena; Linnaeus, 1758), and pygmy sperm whale (Kogia breviceps; Blainville, 1838) from stranding centers at the Virginia Aquarium, New Jersey Department of Agriculture, and California Marine Mammal Stranding Center. All specimens were Code 2 on the decomposition scale and ranged in age from neonate to adult (Pugliares et al., 2007). Partial dissection and examination through visual inspection and polarized light microscopy (Zeiss, Stemi 2000-C) were performed to grossly describe anatomy. Clearing for the polarized light microscopy was performed with Hemo-De (Scientific Safety Solvents, 2017). Orientation of all tissues was confirmed at the time of dissection by cutting a small notch along the dorsal edge. If a specimen could not be dissected immediately, it was refrigerated at 4°C until dissection and analysis could be performed. All flukes were dissected within 2 weeks of arrival.

For each fluke, 2.0 mm thick sections were taken along the chordwise (anterior to posterior) axis at 10% of span (base), 40% of span (mid-span), and 70% of span (fluke tip) using a commercial deli slicer (Chef’s Choice, 667 International Professional Electric Food Slicer with 10-inch Diameter Blade) (Figure 3). Each fluke section was divided into three subsections: leading edge, mid-chord, and trailing edge. These subsections were cut perpendicular to the chordline (measured as the tip of the leading edge to the tip of the trailing edge using a ruler) of the section using a scalpel.
2.1 | Micro-computed tomography scanning

μCT at Harvard University was used for three-dimensional visualization over a large field of view of samples from the flukes. A contrast agent (stain) was used for soft tissue discrimination (Ho & Hutmacher, 2006; Metscher, 2009; Descamps et al., 2014). Scans were made of completely stained sections using a Skyscan 1173 μCT scanner. Multiple stains, including potassium iodide, phosphomolybdic acid (PMA), and phosphotungstic acid (PTA), were tested due to their common usage in the literature (Pauwels, Van Loo, Corinlie, Brabant, & Van Hoorebeke, 2013). A 2% solution of PMA was used for all scans as it resulted in the clearest images and highest contrast between the core layer fibers and matrix material. A solution of 70% ethanol was added to each stain to inhibit microbial growth. Sections were stored in stain at room temperature for 4–8 weeks with daily agitation. All scans used X-ray settings of 100 kV and 80 μA, exposure time of 900 ms, and average rotation step was 0.63°. All scans were partial width and frame averaged. Ring artifacts and beam hardening were corrected. Slice stacks were reconstructed using NRecon. An average of 1,900 slices was used for each reconstruction and the resulting average voxel diameter of each scan was 22.2 μm. Slice stacks can be accessed through Dryad (Gough, Fish, Wainwright, and Bart-Smith, 2018, https://doi.org/10.5061/dryad.14sr463).

2.2 | Orientation analysis

All scans were analyzed in ImageJ (NIH, version 1.50i) and virtually sliced to visualize the chordwise sectional face of each fluke section. Clear, high-resolution images of each subsection were taken, resulting in nine images per specimen (Figure 4). Orientation of each image was maintained using the cut edge of the section (perpendicular to the chordline) as a vertical reference. Each image (n = 54) was analyzed manually for the orientation of individual fibers dorsal and ventral to the horizontal chordline (Figure 5). Fibers were determined
visually as lighter linear segments within the darker core layer matrix. Twenty acute measurements of fibers canted toward the leading edge and 20 acute measurements of fibers canted toward the trailing edge were taken from both the dorsal and ventral portions of each leading edge and mid-chord subsection. For trailing edge subsections, due to the reduced number of visible fibers, five acute measurements were taken from each of the dorsal and ventral portions. Each angle measurement was performed once along the entire visible length of a fiber. The orientation angle was defined on a scale from 0 to 90°. Low orientation angles denoted an arrangement of fibers oriented more horizontally along the chordwise axis, while orientation angles closer to 90° denoted an arrangement of fibers oriented more vertically along the dorso-ventral axis. Only acute angles were included to remove angle direction (forward and backward) as an additional factor in subsequent analyses.

A combined total of 1,620 acute angle measurements were taken from all flukes (n = 6). The number of measurements taken from each fluke blade (n = 270) are given for each dorso-ventral region (Table 1), spanwise location (Table 2), and chordwise subsection (Table 2).

### 2.3 Statistical analysis

All statistical analyses were run using Microsoft Excel (Microsoft, 2010) or SPSS (IBM, ver. 20.0). For each analysis, sample sizes were equal for all included sampling positions. For each species and all species combined, a series of t-tests (assuming unequal variance) were used to compare the dorsal and ventral acute angle measurements across all spanwise locations and chordwise subsections (Table 1). A series of one-way Welch’s ANOVAs (9 in total) were performed to compare the fiber orientations for each species at a single spanwise location and chordwise subsection (Table 2). A series of one-way Welch’s ANOVAs (18 in total) were performed to compare the fiber orientations for each spanwise location at a single chordwise subsection with a single species (Table 3). A series of one-way Welch’s ANOVAs (18 in total) were performed to compare the fiber orientations for each chordwise subsection at a single spanwise location within a single species (Table 3). A Games-Howell post-hoc test was performed for each Welch’s ANOVA to evaluate the relationships between the tested groups. For each analysis, Levene’s test was used to assess homogeneity of variances. Statistical significance was set at a level of p < .05.

### 3 RESULTS

When visualizing the spanwise sectional face, the core of each fluke displayed fiber sheets oriented approximately parallel along the dorso-ventral axis (Figures 2–6). When viewing across the majority of the chordwise sectional face, the pattern of parallel fiber orientation was absent.

Instead of displaying a parallel orientation when viewing the chordwise sectional face, the core layer fibers in the leading edge and mid-chord subsections showed a distinct crossing arrangement oriented approximately along the chordwise and dorso-ventral axes (Figure 7a, b). In the region of the trailing edge, fibers did not cross and were, instead, oriented along the dorso-ventral axis in an approximately parallel arrangement (Figure 7c). In K. breviceps, additional fiber bundles oriented along the spanwise axis and perpendicular to core layer fiber sheets were found dispersed throughout the core layer matrix at all three spanwise locations and within each of the three chordwise subsections of the fluke blade (Figure 8). There were no statistically significant differences found between the dorsal and ventral acute angle measurements for any of the species investigated (Table 1). A comparison of the pooled dorsal acute angle measurements (n = 810) and the pooled ventral acute angle measurements (n = 810) across all species showed no statistically significant differences (Table 1). Based on this result, subsequent analyses combined the dorsal and ventral acute angle measurements for any chordwise subsection or spanwise location into a single sample group.

The averages (mean ± SE) for each species at each spanwise location and chordwise subsection are given in Table 2. There were statistically significant differences found between the six species at eight out of the nine fluke blade areas (Table 2). There were no statistically significant differences found between the six species for the ninth fluke blade area (Table 2). The highest average acute angle

### Table 1 The average acute measures (mean ± SE) of all angles measured within the dorsal and ventral regions for each species and for all species combined

<table>
<thead>
<tr>
<th>Species</th>
<th>Dorsal (n = 135)</th>
<th>Ventral (n = 135)</th>
<th>Total (n = 270)</th>
<th>Significance Between Dorsal and Ventral</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tursiops truncatus</td>
<td>62.9 ± 1.35°</td>
<td>61.8 ± 1.26°</td>
<td>62.4 ± 0.92°</td>
<td>p = .537; df = 267</td>
</tr>
<tr>
<td>Delphinus delphis</td>
<td>59.6 ± 1.30°</td>
<td>57.1 ± 1.39°</td>
<td>58.4 ± 0.95°</td>
<td>p = .198; df = 267</td>
</tr>
<tr>
<td>Phocoena phocoena</td>
<td>60.1 ± 1.46°</td>
<td>60.0 ± 1.43°</td>
<td>60.1 ± 1.02°</td>
<td>p = .971; df = 268</td>
</tr>
<tr>
<td>Grampus griseus</td>
<td>62.9 ± 1.35°</td>
<td>59.3 ± 1.58°</td>
<td>61.1 ± 1.04°</td>
<td>p = .081; df = 262</td>
</tr>
<tr>
<td>Kogia breviceps</td>
<td>61.7 ± 1.32°</td>
<td>63.5 ± 1.36°</td>
<td>62.6 ± 0.95°</td>
<td>p = .350; df = 268</td>
</tr>
<tr>
<td>Lagenorhynchus albirostris</td>
<td>62.1 ± 1.40°</td>
<td>63.4 ± 1.23°</td>
<td>62.7 ± 0.93°</td>
<td>p = .479; df = 263</td>
</tr>
<tr>
<td>Total</td>
<td>61.6 ± 0.56°</td>
<td>60.9 ± 0.57°</td>
<td>61.2 ± 0.40°</td>
<td>p = .378; df = 1618</td>
</tr>
</tbody>
</table>

Significance values (α < 0.05 and df) are shown for each species and for all species combined.
The average acute angle measures (mean ± SE) collected at each fluke location (spanwise: 10%, 40%, 70% of span; chordwise: leading edge, mid-chord, trailing edge) for each species and for all species combined:

<table>
<thead>
<tr>
<th>Species</th>
<th>Leading Edge (n=40)</th>
<th>Mid-Chord (n=40)</th>
<th>Trailing Edge (n=40)</th>
<th>Leading Edge (n=10)</th>
<th>Mid-Chord (n=10)</th>
<th>Trailing Edge (n=10)</th>
<th>Leading Edge (n=40)</th>
<th>Mid-Chord (n=40)</th>
<th>Trailing Edge (n=40)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tursiops truncatus (n=270)</td>
<td>60.9 ± 2.32°</td>
<td>60.6 ± 2.4°</td>
<td>87.6 ± 0.88°</td>
<td>55.2 ± 2.28°</td>
<td>64.5 ± 2.51°</td>
<td>69.2 ± 2.12°</td>
<td>57.9 ± 2.15°</td>
<td>64.1 ± 2.03°</td>
<td>74.3 ± 2.57°</td>
</tr>
<tr>
<td>Delphinus delphis (n=270)</td>
<td>52.3 ± 3.0°</td>
<td>52.7 ± 1.9°</td>
<td>76.2 ± 1.37°</td>
<td>55.5 ± 1.63°</td>
<td>55.3 ± 2.34°</td>
<td>76.1 ± 3.76°</td>
<td>52.4 ± 2.38°</td>
<td>68.8 ± 1.65°</td>
<td>75.3 ± 3.17°</td>
</tr>
<tr>
<td>Phocoena phocoena (n=270)</td>
<td>48.2 ± 2.88°</td>
<td>53.5 ± 2.31°</td>
<td>75.8 ± 3.21°</td>
<td>56.3 ± 3.02°</td>
<td>63.6 ± 2.59°</td>
<td>76.6 ± 1.29°</td>
<td>63.4 ± 1.64°</td>
<td>63.5 ± 2.09°</td>
<td>75.8 ± 2.79°</td>
</tr>
<tr>
<td>Grampus griseus (n=270)</td>
<td>64.8 ± 2.34°</td>
<td>49.9 ± 1.96°</td>
<td>88.1 ± 0.66°</td>
<td>56.4 ± 2.9°</td>
<td>62.8 ± 2.22°</td>
<td>81.9 ± 1.31°</td>
<td>57.5 ± 2.52°</td>
<td>60.7 ± 2.78°</td>
<td>71.2 ± 4.62°</td>
</tr>
<tr>
<td>Kogia breviceps (n=270)</td>
<td>57.9 ± 2.35°</td>
<td>68.1 ± 1.84°</td>
<td>82.5 ± 1.74°</td>
<td>59.8 ± 2.68°</td>
<td>65.3 ± 2.15°</td>
<td>86.0 ± 0.88°</td>
<td>54.4 ± 2.06°</td>
<td>55.4 ± 1.97°</td>
<td>79.0 ± 2.21°</td>
</tr>
<tr>
<td>Lagenorhynchus a格rirostris (n=270)</td>
<td>62.1 ± 1.77°</td>
<td>54.8 ± 2.1°</td>
<td>79.3 ± 2.09°</td>
<td>63.4 ± 2.25°</td>
<td>64.1 ± 2.22°</td>
<td>82.3 ± 2.72°</td>
<td>58.9 ± 3.12°</td>
<td>61.4 ± 2.27°</td>
<td>73.0 ± 1.03°</td>
</tr>
</tbody>
</table>

Total (n=1620) 57.7 ± 1.07° 56.6 ± 0.93° 81.6 ± 0.97° 57.6 ± 1.03° 62.6 ± 0.97° 78.7 ± 1.13° 57.4 ± 0.98° 62.3 ± 0.91° 74.8 ± 1.19°

Significance values (p < 0.05 and F_{d.f.1, d.f.2}) are given for the comparison of all species at each fluke location.

There were statistically significant differences found between the three chordwise subsections for 17 out of the 18 combinations (94.4%) of species and spanwise location (Table 3). There were no statistically significant differences found between the three chordwise subsections for 1 out of the 18 combinations (5.6%) of species and spanwise location (Table 3). The average acute angle measurement was found for the three chordwise subsections (leading edge; 57.6 ± 0.59°; mid-chord; 60.5 ± 0.55°; trailing edge; 78.3 ± 0.67°) across all species and spanwise locations combined.

### Significance Values (p < 0.05 and F_{d.f.1, d.f.2})

<table>
<thead>
<tr>
<th>Species</th>
<th>Leading Edge</th>
<th>Mid-Chord</th>
<th>Trailing Edge</th>
<th>10% of Span</th>
<th>40% of Span</th>
<th>70% of Span</th>
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<tr>
<td>Tursiops truncatus</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<tr>
<td>Delphinus delphis</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<tr>
<td>Phocoena phocoena</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<td>Grampus griseus</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
</tr>
<tr>
<td>Kogia breviceps</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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</tr>
<tr>
<td>Lagenorhynchus albrusris</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
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<td>p &lt; .001</td>
<td>p &lt; .001</td>
<td>p &lt; .001</td>
</tr>
</tbody>
</table>
4 | DISCUSSION

For all species, the morphology of the ligamentous layer was consistent with previous studies that reported large fiber bundles oriented approximately along the spanwise axis of the fluke blade (Roux, 1883; Felts, 1966; Purves, 1969; Purves & Pilleri, 1978; Sun et al., 2010; Sun et al., 2011). Within the literature, the cetacean tail fluke blade is described as having five unique components: an epidermis, a thin blubber layer, a ligamentous fiber layer, a core of dense connective tissue, and a system of vasculature (Roux 1883; Felts, 1966; Purves, 1969). Deep to the epidermis and thin blubber layer is the ligamentous fiber layer. The fiber bundles in this layer were traditionally described as straight (Roux, 1883; Felts, 1966), but more recent work performed on the spinner dolphin (*Stenella longirostris*) and false killer whale (*Pseudorca crassidens*) has shown pleating along the ventral surface of the flukes (Purves, 1969; Purves & Pilleri, 1978). The gross dissections of tail fluke blades performed as a portion of this study have shown similar morphologies of the ligamentous layer to what has previously been found in the literature for all included species.

Interior to the ligamentous layer is the core layer, which accounts for a large portion of the fluke volume and mass and is comprised of a latticework of collagenous fibers set within a matrix of fatty tissue (Roux, 1883; Felts, 1966). The collagenous fibers have previously been described using gross dissection or microscopy (Roux, 1883; Felts, 1966).
4.1 | Comparison of species morphology

The core layer morphology has been described generally for the bottlenose dolphin (Felts, 1966; Sun et al., 2010; Sun et al., 2011), common dolphin (Roux, 1883), harbor porpoise (Roux, 1883), beluga whale (Delphinapterus leucas) (Felts, 1966), pilot whale (Globicephala melaena) (Felts, 1966), minke whale (Balaenoptera rostrata) (Roux, 1883), spinner dolphin (S. longirostris) (Purves, 1969), and false killer whale (P. crassidens) (Purves & Pilleri, 1978). In the present study, the morphology of the core layer of all species included was found to be highly conserved. Differences were found between species, with average acute angle measurements varying over a range of 4.3°. It is unclear to what extent this slight morphological variation may affect function.

*Kogia breviceps* is distinct from the other odontocete species studied herein in terms of its core layer morphology. The addition of spanwise fiber bundles through the core layer could act to reduce bending and resist tension along the spanwise axis of the fluke blade (Felts, 1966; Alexander, 1988; Vogel, 2013). The functional significance of these spanwise fibers in relation to the animal’s ecology or behavior is unknown. Their presence may be a phylogenetic legacy, as the larger sperm whale (Physeter macrocephalus) also has spanwise fiber bundles within the fluke blade (Gough, unpublished data).

4.2 | Crossing angle and structural function

In both cetacean and non-cetacean species, crossing fibers have been shown in a number of species to impart structural support functions related to their precise crossing angle (Wainwright, Vosburgh, & Hebrank, 1978; Wainwright, Pabst, & Brodie, 1985; Alexander, 1988; Pabst, 1996). Crossing angles near 60° are optimal for bending and support of a helically wrapped structure, such as the connective tissue sheath around the body of cetaceans (Pabst, 1996) and sharks (Wainwright et al., 1978), without shortening or lengthening of fibers (Harris & Crofton, 1957; Alexander, 1987; Alexander, 1988; Vogel, 2013). This fiber morphology also resists twisting motions within the structure (Vogel, 2013).

The crossing angle of the fibers within the leading edge and mid-chord subsections of the fluke blade are close to 60°, suggesting that the structure plays a role in bending and structural support. In addition to the core layer tissue, the fiber bundles of the ligamentous layer likely play a role in resisting tension and bending along their spanwise long axis (Felts, 1966; Alexander, 1988; Vogel, 2013). Together, the arrangement of fibers within the two fiber layers could limit bending to an optimal range along the spanwise and chordwise axes (Katz & Weihs, 1978; Liu & Bose, 1997; Fish, 1998; Fish, Nusbaum, Beneski, & Ketten, 2006).

In comparison to crossed fibers, fibers that are at high angles relative to the plane of bending are less resistant to shear forces or drag forces such as those created by dorso-ventral oscillation of the tail (Johnsen & Kier, 1993). This study found high crossing angles and a dorso-ventrally parallel arrangement of core layer fibers at the trailing edge, suggesting the fibers are not acting to support the structure or resist bending within this region. Deflection naturally increases toward the trailing edge of any fusiform structure due to tapering, so it is unknown what function the core layer fibers play within the complete structure of the fluke blade (Fish et al., 2006). Increased deflection of the trailing edge due to tapering is common among wing-like structures of aquatic species and helps to increase swimming efficiency (Katz & Weihs, 1978; Fish, 1998).

The core layer of the tail fluke blade is structured as a series of thin sheets of tissue tightly juxtaposed against one another to comprise a block. Biocomposites such as this are common within both plant (John & Thomas, 2008) and animal systems (Pabst, 1996; Wainwright et al., 1978; Hamilton et al., 2004; Johnsen & Kier, 1993; Lingham-Soliar, 2008). Specific biocomposite structures formed by dense weaves of collagenous or cellulosic fibers can form relatively rigid, incompressible structures by orienting fibers in ways that experience tension when loaded (Harris & Crofton, 1957; Alexander, 1987; Alexander, 1988). The similarity of fiber angles between the leading edge and mid-chord subsections of the fluke blade and other biocomposite support structures suggests that the core layer tissue is used in the absence of skeletal elements to maintain rigidity while resisting buckling and allowing for some amount of bending during swimming (Alexander, 1987; Alexander, 1988; Hamilton et al., 2004).

4.3 | Conclusion

The morphology of the tail flukes of cetaceans is similar across multiple odontocete species and consists of vasculature and four distinct layers...
of tissue: the epidermis, the blubber layer, the ligamentous layer, and the core layer. The core layer has received the least attention in the literature, but has been described grossly as a series of thin, laminated sheets comprised of collagen fibers and a fatty matrix (Roux, 1883; Felts, 1966; Sun et al., 2010; Sun et al., 2011). The crossed fibers found at the leading and mid-chord regions of each fluke are likely involved—together with the fiber bundles of the ligamentous layer—in structural support and resistance to bending. The same spanwise and chordwise morphology was found in all species, but K. breviceps displayed additional spanwise fiber bundles that could act to stiffen the fluke blades by resist tension and bending along their long axis.

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AUTHOR CONTRIBUTIONS

F.E.F conceptualized and supervised the project. H.B-S gave theoretical background and procured funding. W.T.G collected specimens and performed dissections. D.K.W performed staining and μCT scanning. W.T.G. collected and analyzed data from μCT images and ran statistical test. W.T.G and F.E.F prepared the manuscript and figures.

ORCID

William T. Gough http://orcid.org/0000-0003-2701-5299
Frank E. Fish http://orcid.org/0000-0001-5973-3282
Dylan K. Wainwright http://orcid.org/0000-0003-4964-5048

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