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Dorsal fin and hump vascular anatomy in the Indo-Pacific humpback dolphin (*Sousa plumbea*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)

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A recent range-wide taxonomic evaluation of the genus *Sousa* (Mendez *et al.* 2013, Jefferson and Rosenbaum 2014) has confirmed earlier morphological investigations by Jefferson and Van Waerebeek (2004), suggesting a separate species of humpback dolphin, *Sousa plumbea*, in the central and western Indian Ocean. Although *S. plumbea* is a coastal dolphin prone to anthropogenic disturbance and habitat fragmentation, as documented for other coastal dolphin species elsewhere (Allen *et al.* 2012), and their conservation status in South African waters is in urgent need of attention (Braulik *et al.* 2015, Plön *et al.*

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2015, Vermeulen *et al.* 2017), there is a general paucity of basic biological information on the species, including its anatomy (Plön *et al.* 2012, 2015). Although the shape and size of the dorsal “hump” that gives the species its name (Best 2007) appears to vary among the four species within the genus, its anatomy has to date not been elucidated.

Unlike the dorsal fin of other delphinids, the fins of humpback dolphins are small and positioned atop a slowly rising dorsal ridge, *i.e.*, hump (Fig. 1). This dorsal fin and hump are unique among odontocetes; the only structure similar in appearance can be found in humpback whales (*Megaptera novaeangliae*). Photographs of the hump have been used extensively in mark-recapture studies of individual *Sousa* (Karczmarski and Cockcroft 1998), and it was found to change color in older individuals off South Africa by turning progressively white/gray by turning progressively white/gray (Ross 1994). In addition, the structure of the dorsal fin or hump of *Sousa* appears to vary among *Sousa* species (Ross 1994). *S. teuszii* and *S. plumbea* from West Africa and the northern Indian Ocean, respectively, exhibit a pronounced hump, with a small falcate fin set dorsally atop the hump about mid-length of the body, while the fin base of *S. chinensis* is considerably shorter and slopes more smoothly into the dorsal surface of the body without an apparent hump (Ross 1994). To

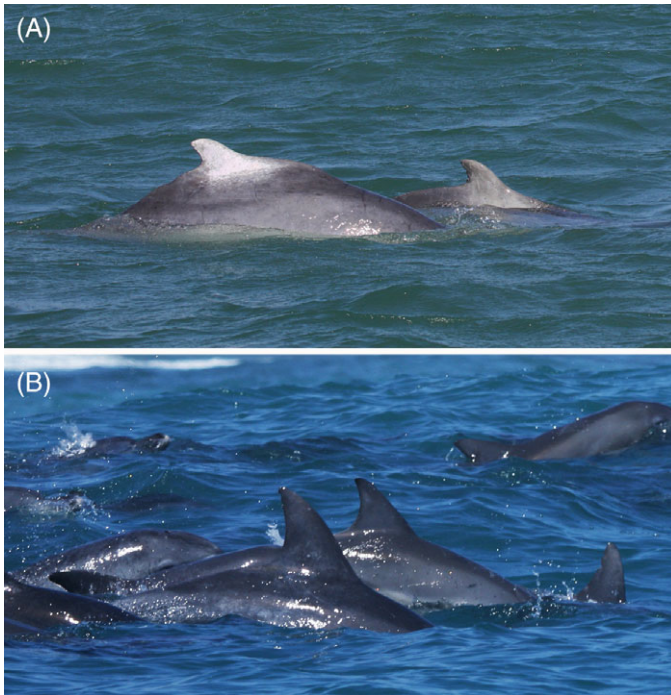


Figure 1. Dorsal fins of (A) Indian Ocean humpback dolphins (*Sousa plumbea*) and (B) Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

date no investigations have been carried out on the internal morphology of this uniquely shaped dorsal fin.

The dorsal fin in dolphins does not contain bones and is formed and supported only by connective tissue (Pabst 1996). However, the appendages of cetaceans, including the dorsal fins, present “thermal windows,” which possess deep arterio-venous counter-current heat exchangers that function to conserve heat in the body core, and superficial veins that facilitate heat loss at the skin-water interface (Pabst *et al.* 1999, Meagher *et al.* 2002, Cozzi *et al.* 2017). General features of the vascular network in cetaceans have been described by a number of authors (Fawcett 1942, Scholander and Schevill 1955, Elsner *et al.* 1972). First described by Fawcett (1942), the characteristic triad arrangement of vessels in cetacean appendages, consisting of one artery and two adjacent veins closely juxtaposed, were later described in detail by Scholander and Schevill (1955). These authors described the counter-flowing arteries and veins in the flukes and flippers of cetaceans, characteristic of counter-current heat exchangers, as peri-arterial venous retia (PAVR). Each of the major arteries is located centrally within a surrounding trabeculate venous channel, resulting in two concentric conduits, with the warm one inside (Scholander and Schevill 1955, Cozzi *et al.* 2017). Elsner *et al.* (1972) described a number of arteries, each surrounded by a PAVR, entering the base of the dorsal fin along its mid-sagittal line and running distally within that plane through the height of the fin, while superficial veins lie along the outside of the collagenous tissue, but within the columnar hypodermis.

The attachment of satellite-linked radio-transmitters to small cetaceans has become a common technique for studying diving behavior, habitat selection, and movements (*e.g.*, Baird *et al.* 2010, Teilmann *et al.* 2013, Sveegaard *et al.* 2015). However, there are concerns regarding animal welfare and the sublethal effects of tags possibly causing long-term effects on the physiology and health status of the animal (Sonne *et al.* 2012, Moore *et al.* 2013, Norman *et al.* 2018, Peter-Jørgensen *et al.* 2017). Thus, information on soft tissue anatomy is not only important for the understanding of general biology of the species, but also for the development of successful and least invasive, species-specific tag design (Balmer *et al.* 2011).

Although Felts (1966) states that the vascularization in the dorsal fin of cetaceans has almost exactly the same organization as the flukes, Tomilin (1951) examined the dorsal fin of humpback whales (*M. novaeangliae*) and briefly mentioned the fact that the pattern of blood vessels differed somewhat to that found in the dorsal fins of *Tursiops truncatus* and *Phocoena phocoena*, but did not elude to any details. Therefore a systematic investigation of the *Sousa* dorsal fin is needed.

Here we examine the dorsal fins of Indo-Pacific humpback dolphins (*S. plumbea*) and the Indian Ocean bottlenose dolphins (*T. aduncus*) incidentally caught and drowned in shark nets off KwaZulu-Natal, South Africa, using magnetic resonance imaging (MRI) to investigate the vascular anatomy of the dorsal fin. During routine necropsies of dolphins incidentally caught and drowned in shark nets off KwaZulu-Natal,

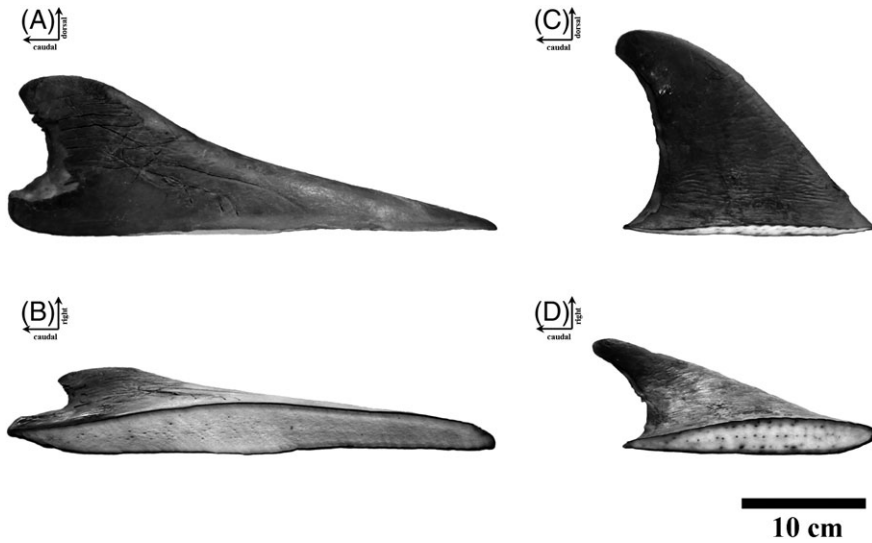


Figure 2. Dorsal fins of Indian Ocean humpback dolphin *Sousa plumbea* (left, N4693) and Indo-Pacific bottlenose dolphin *Tursiops aduncus* (right, N4681) in right lateral views (A, C) and in ventral views on the cutting surfaces (B, D).

South Africa, the dorsal fins from six specimens of *S. plumbea* (including humps, see Fig. 2) and two specimens of *T. aduncus* (Table 1) were removed together with adjacent tissues (Fig. 2) and examined. The vascular anatomy of the blood vessels was assessed by MRI scans on a Philips 1.5 Tesla Gyroscan Intera at Umhlanga Hospital (Durban, South Africa). Prior to MRI scans, several arteries in the dorsal fins were cannulated with a diluted gadolinium solution (0.1 cc gadolinium mixed with 10 cc sterile water) using 20- and 22-gauge Jelco and Venflon needles until backflow of the contrast solution from other, noncannulated vessels was observed. Using the same method, water was injected in all other visible vessels, which proved to have the same effect. A series of

Table 1. Details of specimens examined in the present study.

Species	PEM number	KZN-SB number	Sex	Length (cm)	Weight (kg)
<i>Sousa plumbea</i>	N4693	RB 13002	male	207.1	95
<i>Sousa plumbea</i>	N4678	RB 12004	female	163.6	—
<i>Sousa plumbea</i>	N4679	RB 12005	female	213.5	—
<i>Sousa plumbea</i>	N5094	ZIN 15046	female	198.8	94
<i>Sousa plumbea</i>	N5102	RB 16004	female	242.2	148
<i>Sousa plumbea</i>	N5107	RB 16008	female	243.4	148
<i>Tursiops aduncus</i>	N4681	DUR 12075	female	201.0	—
<i>Tursiops aduncus</i>	N5092	UMG 15011	female	195.4	87

three-dimensional T1w sagittal scans were performed with the fins in upright position. In this way it was possible to generate sequences in all three planes (*i.e.*, transverse, sagittal, and horizontal). The resulting images were analyzed using 3D Slicer (<http://slicer.org/>). The main blood vessels were identified using the segmentation technique and measurements were made in two specimens (*S. plumbea*: N5107, 4.0 mm slice thickness, 672 pixel edge length; *T. aduncus*: N5092, 2.1 mm slice thickness, 432 pixel edge length). The images were analyzed and edited voxel by voxel on the three planes accomplished with a threshold assistance tool. Then, a 3-D model of the vessels and their surrounding tissues were generated and their volumes, surfaces, and dimensions calculated.

We were able to characterize the general arrangement of the dorsal fin vascularization in *S. plumbea* and *T. aduncus* by mapping the empty space displayed by the main blood vessels (*i.e.*, arteries and related PAVR), which is not perceived directly by the MRI scan (*i.e.*, dark coloration in Fig. 3). The vessels injected with water and those injected with contrast solution were both clearly visible in the scans. Both species presented the blood vessel with the greatest caliber, which is responsible for supplying the dorsal fin tip, at the center of each fin (Fig. 3, 4, Table 2). The main arteries coming from the body core, including the

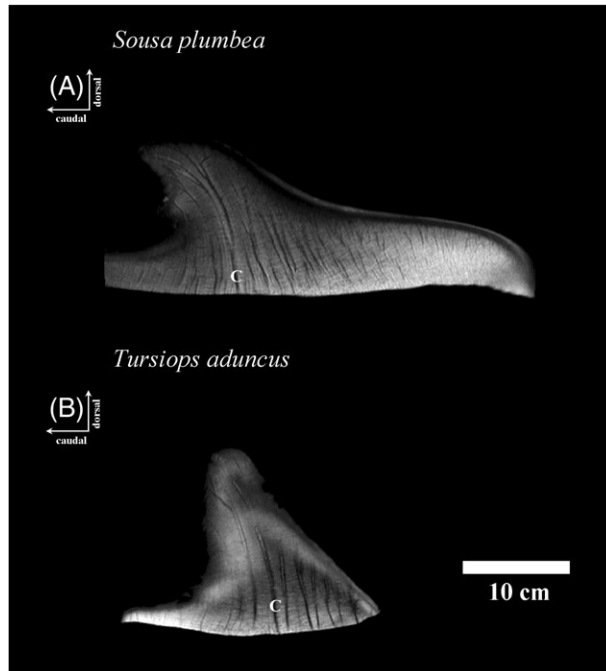


Figure 3. Magnetic resonance images of the dorsal fin of *Sousa plumbea* (N5107) and *Tursiops aduncus* (N5092) in right lateral views. C presents the central artery.

Table 2. Characteristics of the main blood vessels in the dorsal fins of *S. plumbea* and *T. aduncus* ordered from most cranial to most caudal vessels; C presents the central artery plus PAVR, which supplies the dorsal fin tip. C+ present major vessels anterior to C, while C- indicate those caudal to the central artery. The fin base was considered the line that passes horizontally through the base of the dorsal fin; negative values indicate blood vessel bifurcations below this line.

	Vessel C + 6	Vessel C + 5	Vessel C + 4	Vessel C + 3	Vessel C + 2	Vessel C + 1	Vessel C	Vessel C - 1	Vessel C - 2	Vessel C - 3	Vessel C - 4
<i>S. plumbea</i> (N5107)											
Distance between the main bifurcation and fin base (mm)	—	-41.73	-63.69	-44.67	-39.39	-42.85	-40.09	-68.03	-61.54	-69.76	—
Width just proximal to the main bifurcation (mm)	—	1.65	1.36	2.52	3.13	1.75	5.64	2.13	1.80	1.59	—
<i>T. aduncus</i> (N5092)											
Distance between the main bifurcation and fin base (mm)	5.19	6.39	10.55	8.57	14.19	18.51	14.96	13.66	15.66	-2.47	1.56
Width just proximal to the main bifurcation (mm)	1.71	2.04	2.54	1.83	2.13	3.21	3.69	2.37	2.18	2.12	1.89

center vessel, of *S. plumbea* ($n = 8$, vessels greater than 1.36 mm width) and *T. aduncus* ($n = 12$, vessels greater than 1.71 mm) were aligned longitudinally and exhibited a main bifurcation near the base of the fin that seems to be homologous in both species (Fig. 3, 4). In *S. plumbea*, these main bifurcations were placed below a line that passes longitudinally through the base of the fin ($n = 2$) (Fig. 4, Table 2), while in *T. aduncus* only one main bifurcation was found below this line ($n = 1$). Both species presented similar branching patterns since the center vessel exhibits this main bifurcation dorsally to the other main arteries cranial and caudal to it. In *S. plumbea* the bifurcation of the center vessel was at 40.09 mm below the cranial base of the dorsal fin (Table 2).

The dorsal fin of *S. plumbea* exhibited a higher degree of branching of the vessels compared to *T. aduncus*, with the vascular orientation running perpendicular to the cut surface of the fin (Fig. 3). Vessels within the posterior third of the fin deviated (by curving slightly) in a posterior direction towards the apex, but maintained a similar branching pattern. In contrast, the arteries in the dorsal fin of *T. aduncus* extended from the base towards the tip of the fin in a gradual curve, akin to

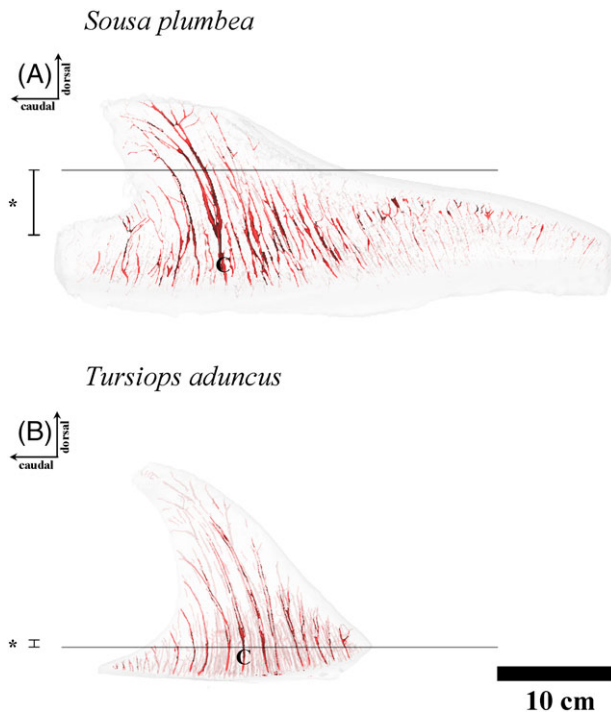


Figure 4. 3-D models of the dorsal fin vascularization in red of (A) *Sousa plumbea* (N5107) plus the hump and (B) *Tursiops aduncus* (N5092), in right lateral views. Major blood vessels between the dorsal fin limits are opaque, while small vessels are translucent. The asterisks indicate the distance of the proximal bifurcation of the center vessel (C) from the horizontal plane through the cranial base of the dorsal fin (Table 2).

orientation of feathers on a bird's wing (Fig. 3). A few peripheral orientation branches were demonstrated, but there were less branches when compared to the dorsal fin of *S. plumbea*. In addition, tiny perpendicularly orientated branch vessels were noted to arise along the length of the arteries; this configuration is also apparent in the uppermost caudal aspect of the dorsal fin.

The main difference between both species consisted in the morphology of the center arteries. In *T. aduncus*, the main peripheral arteries varied in height due to the border limits of the dorsal fin and presented similar width (main blood vessel width ranging from 1.71 to 3.21 mm, mean: 2.33 mm, SD: 0.60; Table 2). In contrast, *S. plumbea* exhibited a heterogeneous arrangement of the peripheral circulation of the dorsal fin in which the centered vessel presented the greatest caliber (diameter: 5.64 mm), with all other main arteries cranial and caudal to the center vessel having smaller calibers (range: 1.36–5.64; mean: 2.40, SD: 1.33; Table 2). In addition, *S. plumbea* presented its most bifurcated plexus cranially, just at the cranial base of the fin, while in *T. aduncus* this site is supplied by the most cranial main vessel (diameter: 1.71 mm; Fig. 4).

Although more main arteries were found in *T. aduncus* ($n = 12$) vs. *S. plumbea* ($n = 8$) due to the differing fin shapes, the total surface area of blood vessels in the small dorsal fin and the surrounding hump in *S. plumbea* (dorsal fin height: 9.07 cm, blood vessel surface area: 50,264.74 mm²) was higher than in *T. aduncus* (dorsal fin height: 19.31 cm, blood vessels surface: 48,402.83 mm²). In contrast, the volume of blood vessels was much higher in *T. aduncus* (18,742.20 mm³) than in *S. plumbea* (9,957.59 mm³). This means that, in general, *S. plumbea* has more, but smaller vessels in its hump and dorsal fin than *T. aduncus*.

Our data indicate that in both species the main blood vessels were located in the dorsal fin proper, but that the hump in *Sousa* also exhibits extensive vascularization (Fig. 4). Although the small dorsal fin and hump of *Sousa* combined present a slightly greater surface area, which is reflected by the greater surface area of blood vessels measured, and thus may suggest a slightly larger thermal window (Chato 1980), counter intuitively significantly less blood vessel volume was shown for *Sousa* compared to *Tursiops*. Since the general morphology of the main blood vessels coming from the body core differs in number and caliber between both species, we expect an even more heterogeneous thermal-window for heat flux in *S. plumbea* including the well-vascularized hump than in *T. aduncus* (see Meagher *et al.* 2008). However, both species shared a similar vascular pattern with the largest vessel supplying the dorsal fin tip where the heat flux is known to be most intense (Meagher *et al.* 2008).

The counter-current heat exchanger in the dorsal fin of common bottlenose dolphins, *T. truncatus*, has been the topic of some investigation and plays an important role in the cooling of the intra-abdominal testes (Rommel *et al.* 1992, Pabst *et al.* 1995). Previous work has shown that veins from the fluke also contribute to the reproductive countercurrent heat exchanger. Our results suggest that the hump may represent a secondary extension of the thermal window due to the small number of

main blood vessels between the limits of the dorsal fin and would be a response to habitat adaptation—within the genus—for testes cooling requirements. The small testis size seen in *S. plumbea* (0.7% of total body weight) in comparison to *T. aduncus* (1.12% of total body weight) may reflect the small number of main blood vessels supplying the dorsal fin and the less volume of blood vessels (Plön *et al.* 2012). The greater surface area observed in *S. plumbea* may address the highly vascularized system, including the hump, compared to *T. aduncus*. However, further investigations are needed to verify the link of blood vessels in the hump to the reproductive countercurrent heat exchanger in this species.

Exactly how the differences in vascularization between the two species examined here affect heat flux and thermoregulation remains to be studied, and future investigations into the comparative thermoregulation of *T. aduncus* and *S. plumbea* could involve infrared thermography (Meagher *et al.* 2008, Barbieri *et al.* 2010). Since the dorsal fin of cetaceans also represents one of the control surfaces during swimming, its design and position also influences stability and maneuverability of the animal (Fish 2002). Further investigations into the hydrodynamics of the dorsal fin and hump and its role in stability (Fish *et al.* 2003) and maneuverability (McNeill Alexander 1990, Fish 2002, Fish *et al.* 2003, Lingham-Soliar 2005) may elucidate the functional significance of this structure.

Increasingly, cryptic species are being studied by attaching satellite tags (Sveegaard *et al.* 2011), but concerns have been raised regarding the invasiveness and potential sublethal effects of some of these tags (Balmer *et al.* 2011, Peter-Jørgensen *et al.* 2017). Besides the obvious advances for anatomical studies, MRI methods can contribute to the study of dorsal fin vascularization in small cetaceans (both carcasses and live specimens) and thus to the development of less invasive tag designs. We hope that this basic knowledge of the Indian Ocean humpback dolphin's hump can assist in informing potential tag design and attachment as well as address possible associated animal welfare issues (Wilson and McMahon 2006, McMahon *et al.* 2011).

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