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The Vertebral Column of the Hourglass Dolphin (*Lagenorhynchus cruciger*, Quoy and Gaimard, 1824), with Notes on Its Functional Properties in Relation to Its Habitat

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Abstract

Fast-swimming dolphins have a relatively stable morphological configuration, explained partially by their vertebral morphology. The hourglass dolphin (*Lagenorhynchus cruciger*), an oceanic species, is one of the least known species of small odontocetes. The aim of this paper is to describe the osteology of the vertebral column of this species, relating the main morphological characteristics to swimming performance in an oceanic habitat. We also present five new records, with meristics and measurements of the postcranial skeleton in conjunction with an exhaustive characterization of each functional region of the vertebral column through morphometric and graphical interpretations. In this species, the stability of the mid-torso is reinforced by the lumbarization and high number of vertebrae. While the morphological process indicates a mechanical advantage for the swimming muscles, the mid-torso appears to act as an "oscillatory beam" to store potential energy, working as an elastic spring. Tail displacements are mainly produced by the flexion of the peduncle, which undulates from a stable mid-region. As suggested for other fast-swimming dolphins, morphological adaptations in the hourglass dolphin fit a typical pelagic mode of life, with a highly stable column that minimizes energy consumption, increasing efficiency for prolonged swimming.

Key Words: hourglass dolphin, *Lagenorhynchus cruciger*, vertebral column, osteology, functional morphology

Introduction

The bodies of fast-swimming oceanic dolphins have a relatively stable morphological configuration (Fish, 2002). Vertebral morphology constitutes one of the passive stabilization systems of the cetacean body (Fish et al., 2003), and it varies regionally along the column (Long et al., 1997). Functional description and analysis of this variability are accomplished by the identification of structural units along the column (Buchholtz & Schur, 2004). Morphological characters such as the shape of the centrum, curvature of the faces, number of intervertebral joints, and structure and orientation of the processes can be employed to determine regions with enhanced or reduced flexibility (Slijper, 1936; Buchholtz, 2001). According to Buchholtz & Schur (2004) and Buchholtz et al. (2005), the relative centrum length (RCL) is an accurate descriptor of vertebral morphology that relates to the three variables (i.e., length, height, and width) of a centrum. A value near 1 indicates a vertebral centrum with smaller faces and less contact area between adjacent vertebrae, allowing greater angular movements and higher flexibility of the area (Long et al., 1997; Buchholtz, 2001; Buchholtz & Schur, 2004). On the other hand, lower values (RCL < 1) are associated with large, flat centrum faces; greater contact between adjacent vertebrae; long processes; and stable regions (Buchholtz, 2001; Buchholtz & Schur, 2004).

The hourglass dolphin (*Lagenorhynchus cruciger*) is an oceanic cold-water species with circumpolar distribution that is found in Antarctic and Subantarctic waters (Goodall et al., 1997; Riccialdelli et al., 2010; Dellabianca et al., 2012; Santora, 2012). Its basic biology and feeding ecology are poorly known due to its oceanic habits and the small number of specimens found dead on beaches (Fernández et al., 2003; Jefferson et al., 2008). Even though it is listed by the International Union for Conservation of Nature (IUCN) as of "least concern," it is probably one of the least known species of small odontocetes in the world (Jefferson et al., 2008). It is also included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (United Nations Environment Programme–World Conservation Monitoring Centre [UNEP-WCMC], 2011).

Since the first description of the species by Quoy & Gaimard (1824), no study has been published on the osteology of the axial skeleton of the hourglass dolphin, with only a few studies on its cranial morphology (e.g., True, 1889; Fraser, 1966; Fraser & Noble, 1968; Miyazaki & Shikano, 1997). Goodall et al. (1997) reviewed the existing literature and museum collections around the world, reporting a total of 11 specimens for the South American area, including skulls and postcranial specimens, with notes on tooth number and vertebral formulae for six of them. Miyazaki & Shikano (1997) performed a comparative analysis considering the phylogenetic relationships within the genus *Lagenorhynchus* based on cranial morphology and vertebral formula, including four specimens of hourglass dolphin. Later, Gazitúa et al. (1999) described in detail a specimen found on the coast of the Strait of Magellan, including external measurements and meristic data for the axial skeleton. They did not include quantitative data regarding the osteology, however, except for the condylobasal length and the total length of the postcranial skeleton.

The aim of this paper is to describe the osteology of the vertebral column of the hourglass dolphin, relating the main morphological characteristics to the animals' swimming performance in an oceanic habitat.

Methods

A total of nine specimens of hourglass dolphin (Table 1) were examined for physical maturity based on the fusion of the vertebral epiphyses (see Goodall et al., 1988). Vertebrae were counted, and postcranial measurements were taken with an anthropometer to the nearest cm, and with dial calipers to the nearest 0.1 mm following Perrin (1975) on five specimens available in the RNP (Rae Natalie Prosser Goodall) collection. The cervical region was analyzed qualitatively; and to quantify vertebral variation along the column, direct and indirect (photography) measurements were made on each vertebra (starting from the first thoracic vertebra) for a total of 11 osteological variables in lateral (left) and dorsal view, following Buchholtz (2001), Buchholtz & Schur (2004), and Buchholtz et al. (2005) (Figure 1; Table 2). Direct measurements were taken using a vernier caliper to the nearest 0.01 mm, as well as indirect ones employing the software *ImageJ* (*Image Processing and Analysis in Java*) (2014). Two variables, metapophyses development (MD) and RCL, were calculated based on linear measurements (Table 2). For the analyses of the processes, angular values higher than 90° were considered as anterior inclination, while values lower than 90° were considered to be posterior inclinations (Figure 1).

For functional analyses, the vertebral column was divided into five regions—(1) cervical, (2) thoracic, (3) torso, (4) caudal stock, and (5) fluke—with three subregions within the torso —(1) anterior, (2) mid, and (3) posterior—following Buchholtz & Schur (2004). The thorax was also subdivided into three areas, with five vertebrae in the first area and four vertebrae in the other two areas (Figure 2). This approach considers both vertebral morphology and the changes in direction of the neural spines.

To study differences in mean values of RCL, neural arch inclination (NAI), neural spine inclination (NSI), and transverse process inclination (TPI) between adjacent functional regions of the column, a Wilcoxon's paired test (Siegel & Castellan, 1988) was performed. For RCL, a comparison between the mid-thorax and the peduncle was also made. Mean values refer to the average values of the variables for the same vertebra in the five specimens.

Osteological variation along the column was analyzed using bivariate plots, including sets of variables. All the graphics were created with *Microsoft Excel*, and the statistical analyses were performed with *STATISTICA*, Version 7.0 (Statsoft Inc., Tulsa, OK, USA).

Results

Basic information on the nine studied specimens, the vertebral formulae, and the total count (TC) are shown in Table 1. Five specimens are new records for the species and were found in Punta Arenas, Chile (N = 1) and Tierra del Fuego, Argentina (N = 4).

The specimens were classified as subadults and adults (Classes 2 and 3, respectively) (Table 1) with most of the epiphyses fused to the centrum by Goodall et al. (1988) and Lockyer et al. (1988). Sterna were also completely fused as expected in mature animals.

While seven specimens were males, sex was unknown for the other two. Total vertebral counts

Table 1. Specimens of hourglass dolphin (*Lagenorhynchus cruciger*) included in the study. PM = physical maturity, TC = total count, Cv = cervical, Th = thoracic, L = lumbar, and Ca = caudal.

Specimen number	Sex	PM	Date found	Locality found	Vertebral formula	TC	Locality	Reference
CNPMAMM 640	M	2b	May 2001	Playa Unión, Chubut, Argentina (43° 20' S, 65° 00' W)	Cv7Th13L18Ca34	72	CENPAT	Fernández et al., 2003
CNPMAMM 641	M	3	June 2002	Playa Paraná, Chubut, Argentina (42° 49' S, 64° 53' W)	Cv7Th13L18Ca33	71	CENPAT	Fernández et al., 2003
CZIP 1007	M	3	Nov. 1998	Punta Arenas, Chile (53° 06' S, 70° 52' W)	Cv7Th13L19Ca27+	66+	IPPA	Gazitúa et al., 1999
CZIP 1080	--	3	Aug. 2003	Bahía Inútil, Tierra del Fuego, Chile (53° 33' S, 69° 45' W)	Cv7Th13L19Ca25+	65+	IPPA	This paper
RNP 1264	--	2	May 1986	Isla de los Estados, Argentina (54° 49' S, 64° 29' W)	Cv–Th14L18Ca28+	60+	AMMA	Goodall et al., 1997
RNP 2217	M	3	April 2001	Bahía San Sebastián, Tierra del Fuego, Argentina (53° 10' S, 68° 32' W)	Cv7Th13L18Ca33	71	AMMA	This paper
RNP 2366	M	3	Jan. 2005	Estancia Moat, Tierra del Fuego, Argentina (54° 57' S, 66° 45' W)	Cv7Th13L18Ca32	70	AMMA	This paper
RNP 2704	M	2b	Dec. 2010	Bahía San Sebastián, Tierra del Fuego, Argentina (53° 12' S, 68° 33' W)	Cv7Th13L18Ca34	71	AMMA	This paper
RNP 2717	M	3B	Feb. 2011	Paso Las Cholgas, Tierra del Fuego, Argentina (53° 23' S, 68° 05' W)	Cv7Th14L19Ca33	72	AMMA	This paper

CNPMAMM = Centro Nacional Patagónico Mamíferos Marinos (CENPAT), Puerto Madryn, Chubut, Argentina; CZIP = Colección de Zoología del Instituto de la Patagonia (IPPA), Punta Arenas, Chile; and RNP = Rae Natalie Prosser Goodall Collection, Museo Acatushún de Aves y Mamíferos Marinos Australes (AMMA), Ushuaia, Tierra del Fuego, Argentina

ranged from 70 to 72. Vertebral formula was Cv7, Th13-14, L18-19, and Ca32-34 (Cv = cervical, Th = thoracic, L = lumbar, and Ca = caudal). The number of vertebrae in each functional region was determined *a posteriori* based on Buchholtz & Schur (2004) with Ta4, Tm26, Tp4, TS5, and F13 (Ta, Tm, Tp = anterior, mid-, and posterior torso; TS = tail stock; and F = fluke), with the torso having the highest number of vertebrae, especially the mid-torso (Table 1).

Postcranial meristics and measurements were taken in the five specimens available in the RNP collection (Table 3). As in other delphinids, the atlas was fused to the axis (Goodall et al., 1997). In addition, cervical vertebrae were short (low CL vs CW and CH), and the neural spines bore well-developed zygapophyses. The transverse processes were vestigial, with the exception of the atlas and the last cervical vertebrae in which they were bent toward the skull. Except for one specimen (RNP 2704), the first lumbar vertebra was found to be the widest of the skeleton (twice as wide as the first thoracic vertebra), with the extremes of the processes placed far from the body axis.

The mean values of RCL showed great variability along the vertebral column (Figure 3),

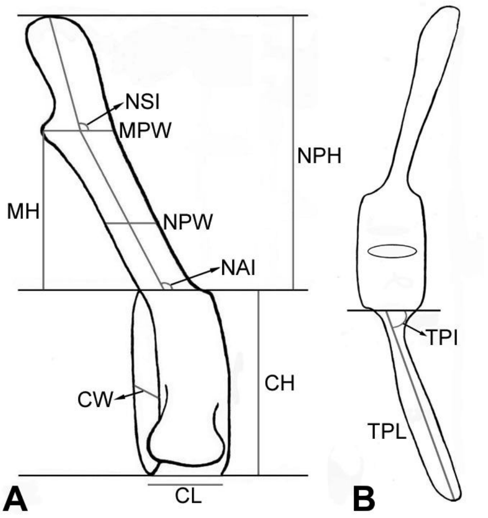

Figure 1. Vertebral parameters measured in this study for the hourglass dolphin (*Lagenorhynchus cruciger*). (A) left lateral view and (B) dorsal view. CL = centrum length, CW = centrum width, CH = centrum height, NPH = neural process height, NSI = neural spine inclination, NAI = neural arch inclination, MPW = neural process width at metapophyses, NPW = neural process width, MH = metapophyses height, TPL = transverse process length, TPI = transverse process inclination, RCL = relative centrum length, and MD = metapophyses development. Descriptions of the measurements are in Table 2.

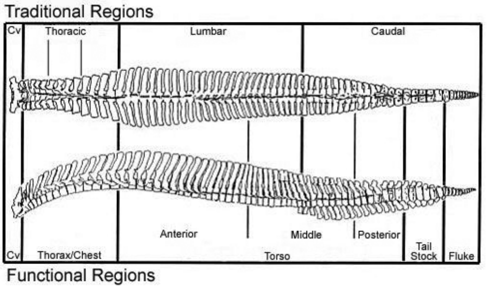

Figure 2. Vertebral series for dolphins, modified from Buchholtz & Schur (2004). Regional morphology of *L. acutus* is shown, divided according to the traditional series (above) and the functional series (below). Cv = cervical region. The image is only illustrative; it does not reflect the real number of vertebrae within each region for the hourglass dolphin.

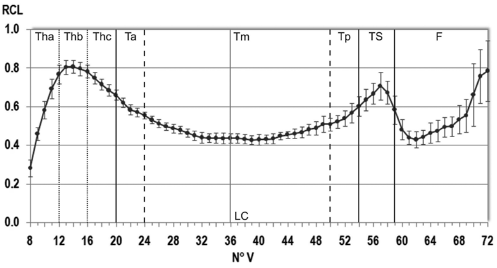

Figure 3. Mean values of relative centrum length (RCL) along the vertebral column of *L. cruciger*. Bars on each point represent standard deviation (SD). Vertical lines separate corporal regions: black lines signal the limits between functional regions: thoracic region, torso, tail stock (TS), and fluke (F); dashed lines separate subregions of the torso: anterior (Ta), mid- (Tm), and posterior (Tp); dotted lines signal the limits between the subregions of the thorax: a (Tha), b (Thb), and c (Thc); and the gray line signals the lumbo-caudal limit (LC).

evidencing different morphologies of contact surfaces between adjacent vertebrae. Two areas of maximum values were observed: the first area was between the 13th and 15th vertebrae (RCL = 0.808), while the second was in the tail stock region at the 57th vertebra. There were two areas where RCL values decreased to a minimum (RCL < 0.5), the first between the 28th and 47th vertebrae and the other at the 61st vertebra. Minimum values in these two areas were similar (mid-torso minimum RCL = 0.428; fluke minimum RCL = 0.44).

Variation in the mean values of neural process height (NPH) and transverse process length (TPL) along the vertebral column is represented in Figure 4. The neural processes reached their maximum height in the mid-region of the column (NPH = 10.6 cm). Maximum values of TPL were found in the thorax/anterior torso limit (TPL = 9.23 cm).

Metapophyses were placed high on the neural process (> 3.5 cm) in most of the vertebrae, from the 18th to the 48th vertebrae, with maximum values between the 36th and 47th vertebrae in the posterior half of the mid-torso (Figure 5). These structures were noticeable all along the skeleton, but especially in the thorax and the posterior half of the mid-torso. Metapophyses were less conspicuous between vertebrae 29 and 36.

The processes' inclination angles were highly discontinuous along the column, with high variability among different vertebral regions (Figure 6). Neural spines had two inversions of their angle of inclination: one changes from a posterior to an anterior inclination, while the other was opposite (from anterior to posterior inclination). The first change signals the anterior limit of the torso at the 24th vertebra, with maximum inclination values located around the 30th and the 47th vertebrae. The second change was between the 50th and 51st vertebrae, and it signals the synclinal point of the skeleton.

Table 2. Osteological variables measured in lateral and dorsal view on the vertebrae of hourglass dolphin specimens

Name	Code	Description
Simple measurements		
Centrum length	CL	Measured ventrally
Centrum width	CW	Measured on the anterior face
Centrum height	CH	Measured on the anterior face
Neural process height	NPH	Vertical distance from tip of neural process to a horizontal line on the dorsal surface of the vertebra
Neural spine inclination	NSI	Angle between the neural spine mid line and a horizontal line
Neural arch inclination	NAI	Angle between the neural arch mid line and a horizontal line
Neural process width at metapophyses	MPW	Length of the horizontal line that crosses the spine at the metapophyses
Neural process width	NPW	At the midpoint between the metapophyses and the vertebral centrum
Metapophyses height	MH	Vertical line from the dorsal surface of the vertebral centrum to the point of insertion of the metapophyses
Transverse process length	TPL	Length of the mid line from the vertebral centrum to the tip of the process
Transverse process inclination	TPI	Angle between the TPL mid line and a horizontal line
Calculated variables		
Relative centrum length	RCL	Following Buchholtz et al. (2001): CLi /(1/2); (CWi+CHi)
Metapophyses development	MD	Ratio MPW/NPW

Neural arches of the anterior thorax, unlike the neural spines, were inclined forward, changing their inclination angle at the 22nd vertebra (Figure 6). The posterior half of the mid-torso had NAI values similar to the values of NSI values.

The transverse processes in the anterior thorax, like the neural spines, had angle values higher than 90° (Figure 6). Changes in the inclination were found around the 13th and 14th vertebrae, within the more flexible area of the thorax. TPI values reached 90° in the anterior/mid-torso, and their highest values were observed between vertebrae 38 and 42 (maximum TPI = 110.3°).

Mean values of RCL, NAI, NSI, and TPI for each region differed significantly among adjacent regions of the vertebral column (Table 4). The most remarkable results were the absence of differences in the mean values of TPI from the thorax and the anterior torso that signal the reversion of the processes, and those of the mid- and posterior torso, showing the similarity of both regions. On the contrary, the mean value of RCL from the mid-thorax was significantly different from that of the peduncle, showing some differences in the flexural capabilities of the column in these areas.

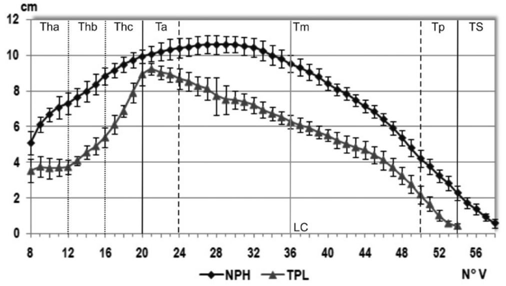

Figure 4. Mean values of neural process height (NPH) and transverse process length (TPL) (in cm) along the vertebral column of *L. cruciger*. Bars on each point represent SD. Vertical lines separate corporal regions: black lines signal the limits between functional regions: thoracic region, torso, and tail stock (TS); dashed lines separate subregions of the torso: anterior (Ta), mid- (Tm), and posterior (Tp); dotted lines signal the limits between the subregions of the thorax: a (Tha), b (Thb), and c (Thc); and the gray line signals the lumbo-caudal limit (LC).

Table 3. Postcranial meristics and measurements for five specimens of hourglass dolphin. Measurements are in mm, except for the total length of the skeleton.

	RNP 1264	RNP 2217	RNP 2366	RNP 2704	RNP 2717		
Postcranial meristics							
First vertebra with vertical foramen	50	50	46	50	49		
Last vertebra with distinct transverse process	54	54	52	53	53		
Last vertebra with distinct neural process	57	58	55	56	57		
First vertebra with chevron bone	41	39	38	38	41		
First caudal vertebra w/o chevron facet	59	60	57	60	63		
Number of chevron bones	--	20	18	21	20		
Number of fused chevron bones	--	18	17	19	16		
Widest vertebra, across lateral process	21	21	21	20	21		
First vertebra with unfused epiphyses	11	--	--	9	--		
Last vertebra with unfused epiphyses	44	--	--	42	--		
Number of cervical vertebrae fused	--	2	2	2	2		
Number of vertebral ribs, L/R	13/12+	13/13	13/13	11+/12+	14/14		
Number of sterna ribs, L/R	7+/6+	6+/7	8/8	5+/6+	8/8		
Number of floating ribs, L/R	7/7	8/8	7/7	6+/8	9/9		
Fusion of sternal bones	Total	Total	Total	Total	Total		
Postcranial measurements					Mean	SD	
Width of articulating surface of atlas; greatest diameter of face	--	76	83	79	76	78.5	3.3
Height of atlas; apex of neural channel to bottom of centrum	--	51	53	56	51	52.7	2.4
Length of the lateral process of atlas from edge of face to farthest point	--	34	30	26	24	28.5	4.4
Length of dorsal spine of atlas from top of spine to front	--	29	27	40	47	35.7	9.4
Height of first thoracic vertebrae; apex of neural channel to bottom of centrum	48	51	50	51	50	50	1.2
Width of first thoracic vertebra; maximum width across both processes	94	81	93	97	76	88.2	9.1
Length of first thoracic vertebral spine	33	33	37	42	35	36	3.7
Height of first lumbar vertebra	51	57	56	57	54	55	2.5
Width of first lumbar vertebra	213	204	223	215	212	213.4	6.8
Length of first lumbar vertebra spine	78	83	80	82	81	80.8	1.9
Maximum width of manubrium	97	109	94	89	104	98.6	7.9
Length of longest chevron bone	--	39	48	43	46	44	3.9
Width of widest vertebra	213	204	223	215	212	213.4	6.8
Length of centrum of first lumbar with epiphyses	21	21	22	22	19	21	1.2
Total length of skeleton, with skull (cm)	--	152.8	154.7	158.0	150.2	153.9	3.3

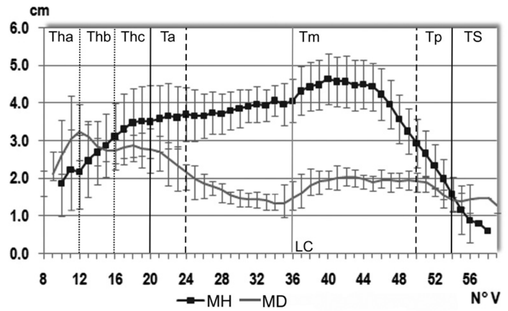

Figure 5. Mean values of metapophysis height (MH) (in cm) and trend line for metapophysis development (MD) along the vertebral column of *L. cruciger*. Bars on each point represent SD. Vertical lines separate corporal regions; see Figure 4.

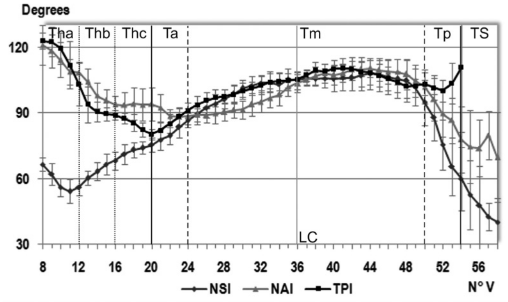

Figure 6. Mean values of inclination, in degrees, of the neural spine (NSI), the neural arches (NAI), and the transverse process (TPI) along the vertebral column of *L. cruciger*. Bars on each point represent SD. Vertical lines separate corporal regions; see Figure 4. Angles smaller than 90° indicate a posterior inclination; values larger than 90° indicate an anterior inclination.

Discussion

To date, only seven complete skeletons of hourglass dolphin have been reported worldwide, making this one of the least known extant species of small dolphins (Goodall et al., 1997; Jefferson et al., 2008). In the present work, five new records of hourglass dolphin are presented, along with meristics and measurements of the postcranial skeleton.

The hourglass dolphin has an elevated number of vertebrae in accordance with the proposition made by Buchholtz & Schur (2004) for oceanic dolphin species. Miyazaki & Shikano (1997) reported a total count of 71 vertebrae, while some specimens included in this study presented 72 as also reported by Goodall et al. (1997). The animal described by Gazitúa et al. (1999) and also studied in this paper had 70 vertebrae. Traditional vertebral formulae are highly variable for this species and differ from those given by Miyazaki & Shikano (1997). One of the specimens analyzed had an extra thoracic vertebra, and the other specimens showed differences in lumbar and caudal counts. Those differences are also obvious when comparing our results with Goodall et al. (1997). This disagreement could be explained by the difficulty of identifying the first caudal vertebra.

Table 4. *P* values obtained from the Wilcoxon's test for the differences of the mean values of relative centrum length (RCL), neural arch inclination (NAI), neural spine inclination (NSI), and transverse process inclination (TPI) between regions along the vertebral column of the hourglass dolphin. Th (a, b, and c) = thorax a, b, and c; T (a, m, and p) = anterior, mid-, and posterior torso; TS = tail stock; and F = fluke. The two nonsignificant *p* values are italicized.

	RCL	NAI	NSI	TPI
Tha-Thb	0.008	0.008	0.019	0.008
Thb-Thc	0.008	0.038	0.008	0.011
Thc-Ta	0.008	0.021	0.008	*0.066*
Ta-Tm	0.008	0.008	0.008	0.008
Tm-Tp	0.008	0.008	0.008	*0.374*
Tp-TS	0.008	0.012	0.012	
TS-F	0.008			
Thb-TS	0.008			

The vertebral columns of the genus *Lagenorhynchus* have been considered to be highly derived in relation to other delphinid genera (Buchholtz & Schur, 2004). Until now, the vertebral column of the hourglass dolphin had not been carefully examined from a functional perspective. Although vertebrae of the mammalian column are classically allocated to cervical, thoracic, lumbar, sacral, and caudal series, these series have been dramatically remodeled during evolution for aquatic locomotion (Slijper, 1936, 1946; Buchholtz, 1998, 2001; Buchholtz & Schur, 2004). The skeleton of the hourglass dolphin can be divided into functional regions such as neck (cervical region), chest (thoracic region), torso (lumbar region and the anterior portion of the caudal region), tail stock (mid-caudal region), and fluke (final caudal region).

Although this study has not included morphometrical variables regarding the cervical region of the hourglass dolphin (only features of the atlas), based on literature and qualitative analyses, we can state that the cervical region in this species has a higher stability than the rest of the vertebral column. The high rigidity of the anterior region of the column stabilizes the pitching movements produced in response to propulsive forces generated by the final portion of the body (Buchholtz, 1998), diminishing the energy requirements necessary for swimming (Long et al., 1997; Fish et al., 2003).

In the thoracic region of the hourglass dolphin, centrum morphology was found to be highly heterogeneous, having two stable areas separated by a flexible zone with vertebral centra with small contact areas (high RCL). This zone coincides with a change in the orientation of the transverse processes that would add up to greater bending potential, at least in the horizontal plane. Traditionally, the chest (thoracic region) has been considered to be rigid. Pabst (2000) stated that the thoracic region of the bottlenose dolphin (*Tursiops truncatus*) does not undergo quantifiable bending during steady swimming. The ribs, especially those with sternal connections, stabilize the thorax and limit rotation among vertebrae (Filler, 2007); this further restricts flexural movements in the anterior region (Fish et al., 2003).

In the hourglass dolphin, the high rigidity of the thoracic region may be explained mainly by the development and morphology of the neural and transverse processes, and by the great development of the metapophyses. As in other dolphin species, the thorax-torso discontinuity is evidenced only by the development and the morphology of the processes, and by the presence of rib facets. Neural processes are tall, and transverse processes reach their maximum lengths at this limit, increasing the area of attachment for the longissimus and multifidus muscles. It is in this region (thoracic and anterior lumbar vertebrae) where the longissimus muscle develops forces of great magnitude that are transmitted to the posterior lumbar and caudal vertebrae (Pabst, 1993).

Lumbo-caudal transition occurs within the mid-torso of the hourglass dolphin without morphological discontinuities, except for the presence of chevrons, which are paired ossifications in the caudal area of many vertebrates (Rommel, 1990). Most of the paired chevrons are fused, forming the hemal channel in the caudal region. These bony elements also increase insertion surface for the hypaxial muscles involved in the ventral flexion of the tail (Rommel & Reynolds, 2008).

There is great homogeneity in centrum morphology in the torso of the hourglass dolphin, with vertebrae being noticeably discoid. This area represents a stiff segment of the column, characterized by short centra and numerous intervertebral joints but with a large diameter of the centra (Long et al., 1997). The typical lumbar series in this species is expanded by both an increased number of vertebrae and the *lumbarization* of adjacent vertebrae (Buchholtz et al., 2005), with this term referring to the fact that adjacent vertebrae have taken on centrum dimensions, neural process heights, and neural spine inclinations typical of lumbar vertebrae. This expanded midregion provides skeletal support for the muscles acting on the tail stock—the longissimus muscle and its caudal extension, the extensor caudae lateralis (Pabst, 1990). Metapophyses are regionally lacking in the anterior half of the mid-torso. According to Buchholtz & Schur (2004), this could mean an absence of the shorter (mid-spine) muscle fascicles, reducing the rotation potential of the area even more. Their reappearance in a higher position in the posterior half of the torso, just anterior to the synclinal point and the tail stock, may be related to the development of bigger and higher insertion points for the extensor caudae lateralis.

Long and strongly inclined processes along the torso of the hourglass dolphin indicate a highly stable region, which would function as a unit in the generation of propulsive forces. In this species, the position at which the processes invert their orientation results in a great number of vertebrae with their processes strongly bent forward. This feature also conditions the number of vertebrae within the mid-torso and the proportion of the skeleton this region represents, two features strongly linked to skeletal stability. Stability in the mid-body of the hourglass dolphin could reduce recoil movements, while long neural processes provide an increased mechanical advantage in order to produce forces for fast swimming.

Transition between the mid- and posterior torso is signaled by a reversion of the neural processes' inclination, creating the synclinal point at which the angular divergence between adjacent neural spines is maximum (Buchholtz & Schur, 2004). In the species studied herein, the posterior torso is short and stable, comprising only four disk-shaped vertebrae with comparatively short processes. This region represents the transition between the highly stable mid-torso and the flexible peduncle, and would be the area where the muscle forces required to change the direction of the tail are produced.

As in other dolphin species, the tail stock in the hourglass dolphin is a region with a high degree of flexibility and rotation potential, with long vertebrae having convex vertebral facets. Interference between neural processes is reduced to a minimum given their short length and almost perpendicular inclination; transverse processes are absent. The laterally compressed peduncle cuts through the water with minimum resistance (Slijper, 1961; Fish & Hui, 1991). A great number of cetaceans swim by oscillating the third caudal portion of the body (Fish, 1993), where the column is more flexible compared to the lumbo-caudal limit (Long et al., 1997). It is in this region where the centrum elongation maximizes the vertical displacement so that the movement of the fluke is due mainly to the dorso-ventral movement of the tail stock vertebrae (Long et al., 1997; Buchholtz & Schur, 2004).

Except for the first vertebra that is ball-shaped, the vertebrae in the fluke of the hourglass dolphin have rectangular cross-sections and are immersed in the connective tissue that forms the flukes. A similar morphological pattern is observed in the bottlenose dolphin, a species with coastal and offshore forms, where the tail stock vertebrae are laterally compressed while those in the flukes are dorso-ventrally compressed (Rommel, 1990). Fettuccia & Simões-Lopes (2004) reported similar characteristics in a coastal species, the marine tucuxi (*Sotalia guianensis*). Thus, the morphology pattern of the fluke's vertebra seems to be conservative among taxa and does not appear to be related to habitat.

The tail fluke of the hourglass dolphin has an initial portion with vertebral morphology that indicates high stability. The serial configuration of a rigid anterior caudal region (mid- and posterior torso), a flexible medial region (tail stock), and the stable base of the fluke seem to be a functionally significant design that controls the flexural pattern in the body of steady-swimming vertebrates (Pabst, 2000). The greater stability of the base of the fluke is countered by the flexibility produced by intervertebral joints. The thickness of the intervertebral disks in the spinner dolphin (*Stenella longirostris*) and the common dolphin is greater in the extremes of the column than it is in the middle (Crovetto, 1991; Long et al., 1997); the hourglass dolphin has a similar variation pattern of the intervertebral disks (MCM, pers. obs.). In addition to this, in the common dolphin, the intervertebral joint at the base of the fluke is notably less rigid than any other along the column, thereby enhancing flexibility even more (Long et al., 1997). Unfortunately, there are no data regarding the physical properties of the intervertebral joints of the hourglass dolphin.

Even though all cetacean species use oscillations of the flukes to create propulsion, osteological studies have linked regional variations in vertebral morphology with differences in swimming style (Buchholtz, 2001; Buchholtz & Schur, 2004). The hourglass dolphin has discoidal vertebrae all along its column. The stability of the mid-torso is reinforced by both the lumbarization of the anterior and posterior vertebrae, and the great vertebral count of this functional region. Furthermore, process and metapophysis morphology indicate a greater mechanical advantage for the swimming muscles that are inserted in this region of the column.

At the same time, this morphology results in greater interference between processes of adjacent vertebrae, increasing the stability and limiting the rotational performance. Thus, the mid-torso would appear to act as an "oscillatory beam" in order to store potential energy, replacing in part the power of the muscles required to accelerate or decelerate the flukes, and working as an elastic spring (Pabst, 1996). In this species, tail displacements for swimming would be mainly produced by the flexion of the peduncle, which undulates from a stable mid-region. These results are in accordance with those of Fish & Rohr (1999) and Fish (2002), who suggested that animals in pelagic environments are greatly favored by a stable design. In that sense, a vertebral column designed for stability would minimize the energy consumption, increasing efficiency for prolonged swimming during migration or foraging (Fish & Rohr, 1999; Fish, 2002). This high stability of the column may also be involved in reducing the effect of external forces on direction while swimming in the turbulent waters frequented by the species.

Factors affecting cetacean locomotion and swimming techniques involve a complex interaction between the axial skeleton and its associated muscles, ligaments, and subdermal connective sheet (Long et al., 1997; Pabst, 2000; Buchholtz & Schur, 2004). Thus, only an integrative approach would allow a true characterization of the swimming technique in these aquatic animals. Nevertheless, an examination of the vertebral design provides important clues regarding the locomotor style.

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