

# Vertebral Anatomy in the Florida Manatee, *Trichechus manatus latirostris*: A Developmental and Evolutionary Analysis

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## ABSTRACT

The vertebral column of the Florida manatee presents an unusual suite of morphological traits. Key among these are a small precaudal count, elongate thoracic vertebrae, extremely short neural spines, lack of a sacral series, high lumbar variability, and the presence of six instead of seven cervical vertebrae. This study documents vertebral morphology, size, and lumbar variation in 71 skeletons of *Trichechus manatus latirostris* (Florida manatee) and uses the skeletons of *Trichechus senegalensis* (west African manatee) and *Dugong dugon* (dugong) in comparative analysis. Vertebral traits are used to define morphological, and by inference developmental, column modules and to propose their hierarchical relationships. A sequence of evolutionary innovations in column morphology is proposed. Results suggest that the origin of the fluke and low rates of cervical growth originated before separation of trichechids (manatees) and dugongids (dugongs). Meristic reduction in count is a later, trichechid innovation and is expressed across the entire precaudal column. Elongation of thoracic vertebrae may be an innovative strategy to generate an elongate column in an animal with a small precaudal count. Elimination of the lumbus through both meristic and homeotic reduction is currently in progress. Anat Rec 290:624–637, 2007. © 2007 Wiley-Liss, Inc.

**Key words:** vertebra; manatee; dugong; evolution; trichechid; sirenia; anatomy; morphology; lumbar

Sirenians are Afrotherian mammals (Murphy et al., 2001; Archibald, 2003) distinguished by an obligate marine lifestyle and herbivory. Most aspects of their radical morphological transition from quadrupedal terrestrial to axially locomoting aquatic animals occurred shortly after their origin in the Eocene. The two living families, Trichechidae (manatees) and Dugongidae (dugongs), have separate histories as far back as the Eocene/Oligocene boundary (Domning, 2002).

The living Florida manatee, *Trichechus manatus latirostris*, exhibits a wide range of morphological adaptations for its tropical, shallow-water, herbivorous life. Among these adaptations are an elongated streamlined body, enlarged rostrum, low-crowned rounded molars with horizontal replacement, elongated diaphragm with orientation in the frontal (dorsal) plane, fore flippers, lack of hind legs, a caudal fluke, and pronounced skeletal pachyosteosclerosis—a hydrostatic aid (Domning and

Buffrénil, 1991; Berta and Sumich, 1999; Domning, 2000; Rommel and Reynolds, 2002; Reynolds and Powell, 2002; Gray et al., 2007, this issue).

Although rarely addressed, the vertebral column of the manatee also shows the effects of dramatic evolutionary remodeling. It has large, elongated thoracic

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vertebrae, extremely short neural spines, no sacral series, and most famously, six instead of the typical seven mammalian cervical vertebrae. It also displays remarkable intraspecific variability, enough to lead the great anatomist James Murie (1872) to write, "Thus, one thing with the other, it results that the spinal column of the genus presents conflicting anomalies."

Hatt (1934) described the vertebral column of the Florida manatee in the course of his report on a specimen of *Trichechus senegalensis*. In a sample of 11 skeletons of *Trichechus manatus latirostris*, he found thoracic counts from 17 to 19 and postthoracic counts of 27 to 29. Kaiser (1974) published a photographic and x-ray atlas of the osteology of living and Recent sirenians. His treatment of the *Trichechus* column is restricted to a ventral view of the articulated anterior trunk, a discussion of pachyostosis, and descriptions of the sternum, reduced pelvis, and chevron bones. The most extensive description of the column is in a comparative analysis of marine mammal postcrania by Rommel and Reynolds (2002), who described the typical anatomy of each vertebral series. These descriptions are augmented in this study with documentation of intraspecific variability, dimensional analyses, and interspecific comparisons that allow the vertebral morphology of the Florida manatee to be placed in developmental and evolutionary context.

Recent advances in developmental biology, and the reassessment of morphology they have encouraged, provide a framework for this discussion. Underlying many previous analyses has been the assumption that each vertebra develops independently in response to a unique sequence of developmental events, a mechanism referred to as "particulate patterning" by Laubichler (2003). Recent research suggests instead that both developmental processes and morphology have hierarchical structure. The phenotype is viewed as a system of structural modules and submodules, each with a discrete genetic specification (Raff, 1996). Bolker (2000) defined a module as the product of a fundamental developmental unit that displays internal morphological integration, hierarchical organization, a particular physical location, and the ability to undergo developmental and evolutionary transformation. Selection at high hierarchical levels affects all "downstream" units; traits of individual structures may, therefore, be the "collateral byproduct" of field changes whose principal morphological consequences are selected (Lovejoy et al., 1999). Selection at low hierarchical levels allows independent transformation of submodules united at higher hierarchical levels. Such a framework anticipates that patterns of character transformation may be conserved across taxa and over time and, thus, be recognizable in comparative studies.

The vertebral column offers an ideal morphological system for the study of modularity because it is composed of discrete, easily counted and measured serially homologous units with considerable intraspecific and interspecific variability. Classically, vertebrae have been allocated to series (e.g., cervical, thoracic, lumbar) by relative position along the anterior/posterior axis, by the morphology of individual vertebrae, and by the locations of the limbs (Burke, 2000). Series boundaries are now known to be coincident with *Hox* gene expression domains (Burke et al., 1995), further supporting their identity as developmental modules. Evolutionary changes in module structure (Bateson, 1894; Carroll et al., 2001;

Polly et al., 2002) are associated with each of the three major processes of axial development. Meristic (count) changes are the product of the process of segmentation, homeotic (boundary) changes are the product of the process of regionalization, and diversifying (individualizing) changes are the product of the process of skeletogenesis. Although often assumed to be sequential, it is possible that the processes are also integrated (Polly et al., 2002).

The radical reorganization of the manatee vertebral column over evolutionary time presents an exceptional opportunity to evaluate the paradigm of column modularity. This study examines the morphology of the column of the Florida manatee using a large sample to document intraspecific variation. Comparison of the observed vertebral patterns with those of the west African manatee and the dugong is then used to reconstruct the sequence of evolutionary changes in the manatee vertebral column since separation of trichechid and dugongid lineages.

## MATERIALS AND METHODS

This study was based on the analysis of 71 skeletons of *Trichechus manatus latirostris* (Florida manatee) as well as comparative analysis of skeletons of *Trichechus senegalensis* (west African manatee) and *Dugong dugon* (dugong) that were studied at source institutions (Table 1). The Florida manatee specimens include individuals of both sexes and a wide range of body sizes. Relatively small skeletons were included only if fusion surfaces of vertebral centra and neural arches were sufficiently mature to allow vertebral order to be determined with confidence. Most of the skeletons were incomplete, lacking the distinctive terminal vertebra and one or more of the preceding caudal vertebrae.

Centrum length (CL, measured ventrally), greatest centrum width (CW, measured anteriorly), and centrum height (CH, measured anteriorly) of each postaxial vertebra were measured with digital calipers and recorded to the nearest 0.1 mm. Only CL was measured for the atlas and axis; length of dens was excluded from axis length. Total measured centrum length (mTCL) is the sum of individual centrum lengths, while estimated total centrum length (eTCL) includes estimated lengths of missing vertebrae. Centrum lengths of nonterminal missing vertebrae were estimated by averaging those of the preceding and following vertebrae. The number and length of missing terminal caudal vertebrae were estimated by reference to size and caudal count of complete specimens if at least 22 caudals were present. Skeletons with fewer than 22 caudal vertebrae were excluded from eTCL calculations. Field length (FL) and field weight (FW) were recorded when available from field collection data. Skull measurements included basal skull length (BSL), occipital condyle width (OCW), foramen magnum width (FMW), and foramen magnum height (FMH). BSL was recorded with measuring tape to the nearest millimeter. OCW, FMW, and FMH were measured with digital calipers to the nearest 0.1 millimeter.

Measurements of cranial size were regressed against FL (when available from collection data) and against eTCL to address changes in cranial and postcranial dimensions during ontogeny. The same data were used to calculate the percentage of FL represented by the

**TABLE 1. Specimens examined in this study by species. The caudal count present is indicated for each specimen; the symbol “+” indicates that the caudal series was incomplete. Abbreviations as above.**

Specimen	Sex	FL cm	FW kg	mTCL mm	eTCL mm	Caudal count	BSL mm	OCW mm	Lumbar Pattern
<i>Trichechus manatus latirostris</i>									
USNM 571675	M	292		1833.2	1833.2	28	349	105.8	C
USNM 571674	M	219		1273.4	1297.5	24+		87.7	B
USNM 554180	F	230	240.4	1364.1	1381.3	24+	321	103.4	C
USNM 551672	M	320		2107.1	2158.1	22+	392	114.5	B
USNM 551671	M	279	422.7	1624.7	1659.7	22+	347	105.3	E
USNM 551670	M	217.5	192.7	1282.5	1286.5	25+	292	87.8	B
USNM 551667	M	196		1002.2	1013.2	23+	231	82.9	C
USNM 551666	M	175		932.7	956.1	23+	218	70.7	B
USNM 551663	M	307	600	2080.3	2085.3	26+	376	103.1	C
USNM 551662	F	270		1539.4	1546.4	25+	315	105.0	F
USNM 551661	F	287		2081.2	2088.7	26+	384	110.2	C
USNM 551660	M	228		1406.4	1436.9	22+	315	102.9	B
USNM 551659	M	292		1735.9	1795.0	24+		112.1	C
USNM 551657	M	273		1742.1	1749.1	26+	337	107.2	C
USNM 551656	F	258		1963.8	2012.3	24+			D
USNM 550421	F	375	527.7	2329.7	2336.7	25+	417	110.5	B
USNM 550420	M	213		1392.7	1413.7	22+	328	100.6	B
USNM 550419	F	335		1916.1	1937.1	22+	377	93.3	G
USNM 550417	U	335		1917.3		20+	389	99.2	B
USNM 550329	M	296		1831.6	1845.6	23+	343	111.8	C
USNM 550328	F	249		1536.6	1557.6	24+	310	96.2	C
USNM 550327	F	263		1640.8	1654.8	23+	315	106.6	C
USNM 550326	M	307	576	1864.3		21+	369	116.0	B
USNM 550325	M	176	90	1057.1	1069.4	23+	259	78.7	B
USNM 550324	M	147	50					66.8	
USNM 550323	F	218	136	1368.7	1382.7	23+	299	98.0	B
USNM 550322	F	305		1939.1	1967.0	23+	365	106.3	H
USNM 550321	F	322	504	2090.4	2104.4	23+		107.3	B
USNM 550320	M	248	218	1297.2	1339.0	24+	291	90.0	B
USNM 550319	F	141	52					63.6	
USNM 530329	M	271		1600.8		17+	359	103.7	B
USNM 530328	F	224		1340.0	1360.2	25+	289	94.2	C
USNM 530325	M	230		1324.8	1417.9	24+	311		B
USNM 530324	M	255		1081.2		8+	304	97.9	C
USNM 530323	F	302		1613.7		16+	354		D
USNM 530322	F	300		1863.5		20+	378	107.2	C
USNM 530316	F	275		1716.9		18+	363	109.3	C
USNM 530315	M	291					349	110.0	E
USNM 530313	M	312		1914.1		14+	407	112.3	B
USNM 530310	M	257		1297.6		10+	297	104.3	C
USNM 530299	F	355		2288.37	2315.37	22+	416	120.7	A
USNM 530297	M	263		1627.7	1668.5	23+	342	104.8	C
USNM 530294	M	315		1936.2	1957.2	25+	359	105.2	A
USNM 530292	F	257		1411.7		21+	295	97.4	C
USNM 527927	F	340		2183.5	2204.5	24+			D
USNM 527926	F	254		1395.0	1406.0	25+		95.9	C
USNM 527925	M	270		1623.1	1640.5	28+		100.5	E
USNM 527924	M	271		1758.8	1772.8	24+	343	101.7	C
USNM 527920	M	351		2246.2	2263.2	23+	398	116.6	B
USNM 527919	M	206		1434.9		19+	317	98.5	C
USNM 527916	M	300		1570.9		13+	356	102.9	B
USNM 527915	M	200		1266.9	1280.9	23+		86.4	B
USNM 527914	F	228					292	96.4	D
USNM 527913	M	167		959.8		17+	224	81.2	B
USNM 527911	F	245		1469.4		21+	314	106.1	D
USNM 527910	F	275		1716.35	1733.4	22+	337	111.2	E
USNM 527909	F	310		2031.3	2035.3	28+	387	113.9	D
USNM 527907	M	307		2021.3	2035.3	24+		117.8	D
USNM 527906	F	198		1323.4	1337.4	23+	287	89.0	E
USNM 527905	F	198		1719.8	1726.8	23+	362	93.7	C
USNM 527904	M	300		2011.7	2018.7	26+			B
USNM 527903	M	264		1618.1	1678.9	24+	341	110.7	B
USNM 527901	M	323		1909.1	1956.1	23+	358	121.7	B
USNM 527900	F	344		2047.8	2047.8	25	364	108.8	B

**TABLE 1. Specimens examined in this study by species. The caudal count present is indicated for each specimen; the symbol “+” indicates that the caudal series was incomplete. Abbreviations as above (continued).**

Specimen	Sex	FL cm	FW kg	mTCL mm	eTCL mm	Caudal count	BSL mm	OCW mm	Lumbar Pattern
USNM 238018	F	345.5		1808.6		21+	363	110.4	C
UF 24951	U			1744.6	1744.6	24			A
UF 24950	U			1886.5	1886.5	25			A
UF 20608	U			2366.3	2386.3	24+			G
UF 15205	M			1946.0	1946.0	27			C
MCZ 7295	F			2175.6		19+			C
AMNH 91096	M			2151.9	2161.9	24+			A
<i>Trichechus senegalensis</i>									
MCZ 23715				1525.8		18+	333	81.51	
BMNH 85.6.30.2				1608.9	1633.9	20+			
AMNH 53939	F			1181.1	1181.1	23			
USNM 20907				1513.9	1563.8	24			
<i>Dugong dugon</i>									
MCZ 6955				1903.0	2003.5	28	399	99.7	
UCMVZ 101162				1500.6	1502.6	29+			
BMNH 1966.9.7.1		251		1641.8	1641.8	30			
AMNH 89005				1668.6	1668.6	28			
AMNH 89004				1818.8		18+			
AMNH 105230	F			1678.8		19+			
AMNH 151789	F			1802.0	1802.2	28			
USNM 257107	F			1501.2	1571.2	27+			
USNM 197900	M			1460.5	1470.5	25+	317	86.1	

**TABLE 2. Relationships among skull (FMH, FMW, OCW, BSL) and body (FL, eTCL, FW) dimensions in the Florida manatee. Number of individuals, correlation coefficient, and significance of each regression are given. Abbreviations as above.**

Skull dimension	Body dimension		
	FL	eTCL	FW
FMH	$y = 15.7x + 2156.4$ $r^2 = 0.03, N = 59$ NS	$y = 0.9x + 1678.9$ $r^2 = 0.00, N = 40$ NS	$\log y = 0.005x + 0.67$ $r^2 = 0.84, N = 9$ $p < 0.001$
FMW	$y = 43.7x + 369.8.0$ $r^2 = 0.43, N = 60$ $p < 0.0001$	$y = 27.3x + 249.2$ $r^2 = 0.37, N = 42$ $p < 0.0001$	$\log y = 0.04x + 0.20$ $r^2 = 0.90, N = 12$ $p < 0.0001$
OCW	$y = 35.5x - 924.9$ $r^2 = 0.68, N = 60$ $p < 0.0001$	$y = 26.2x + 986.9$ $r^2 = 0.70, N = 42$ $p < 0.0001$	$\log y = 0.3x + 0.29$ $r^2 = 0.88, N = 12$ $p < 0.0001$
BSL	$y = 9.7x - 556.2$ $r^2 = 0.81, N = 53$ $p < 0.0001$	$y = 7.5x + 836.2$ $r^2 = 0.93, N = 36$ $p < 0.0001$	$\log y = 0.05x + 0.83$ $r^2 = 0.41, N = 12$ $p < 0.05$

skull at different body sizes, and to estimate the percentage of FL represented by intervertebral disks and other soft tissues. Only a preliminary analysis of the relationship between cranial measurements and FW was possible, because FW data were available for only a small subset of the specimens. Neither skull dimensions nor vertebral sequence could be reconstructed reliably in animals with FL less than 165 cm because fusion of the multiple ossification centers was not complete.

Vertebrae of each individual were assigned to series based on classical series traits, augmented here with observations particular to sirenians (see descriptions of vertebral series below). Vertebrae that showed traits of more than one series (either a blend of traits or left/right asymmetry) were identified as transitional and scored separately. Individuals were allocated to pattern groups based upon the highly variable morphology of the lumbar vertebrae.

Axial changes in morphology, dimensions, shape, and growth rate are used here to propose boundaries of developmental modules in the manatee column. These proposed units are compared with those of the classical terrestrial mammal (cervical, thoracic, lumbar, sacral, caudal), which are assumed to be primitive. The Orders Hyracoidea and Proboscidea are used as a basis for comparison because of their recent evaluation as the outgroups most closely related to Sirenia (Murphy et al., 2001; Archibald, 2003). From this analysis, a hypothesis of modular organization and of evolutionary transformation of the manatee column is proposed.

## RESULTS

There is a significant positive relationship between skull measurements of *Trichechus manatus latirostris* and both body length (FL, eTCL) and body weight (FW)

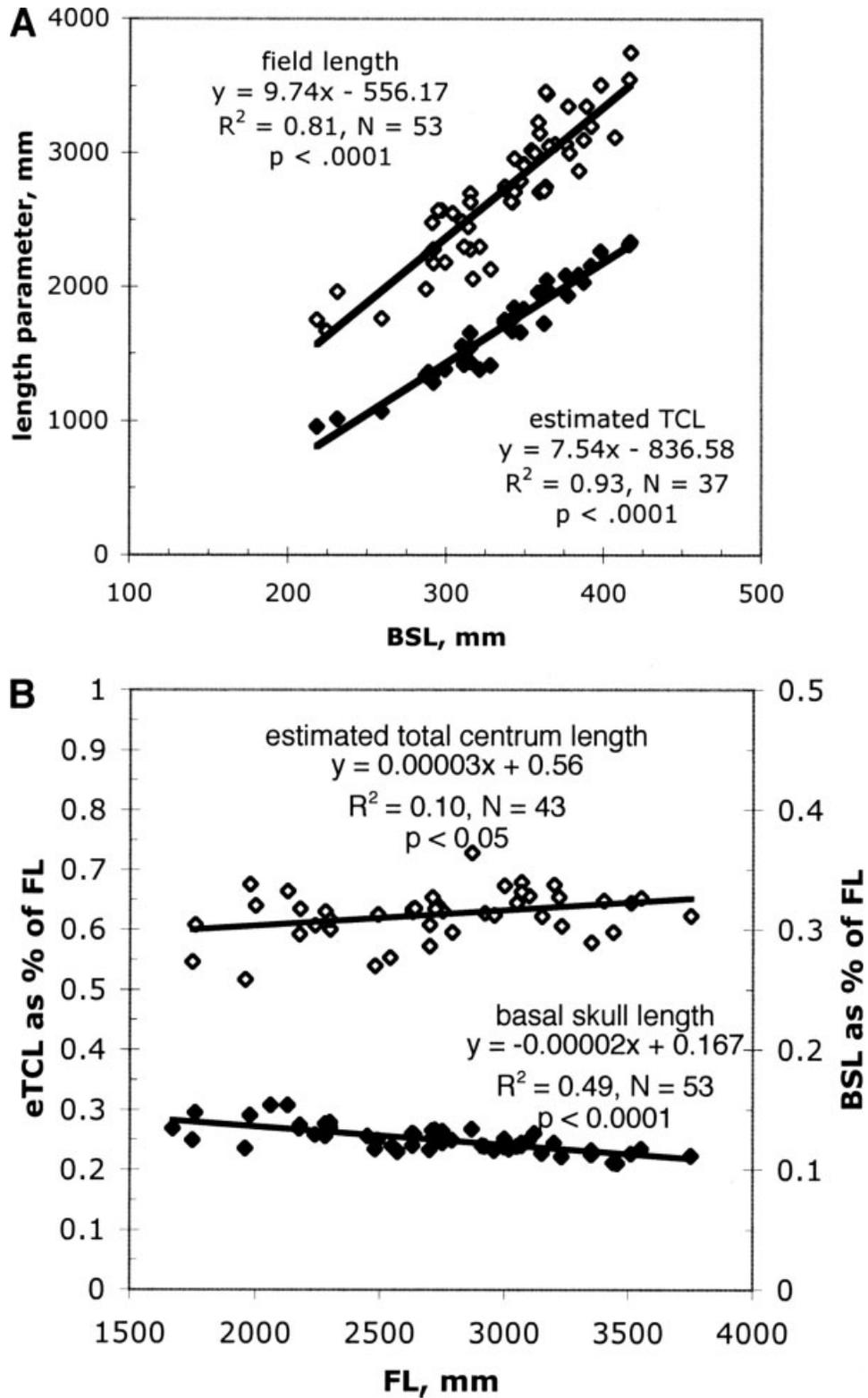


Fig. 1. Dimensional relationships of *Trichechus manatus latirostris*. **A:** Body length parameters as a function of basal skull length (BSL). **B:** Basal skull length and estimated total centrum length (eTCL) as a function of field length (FL).

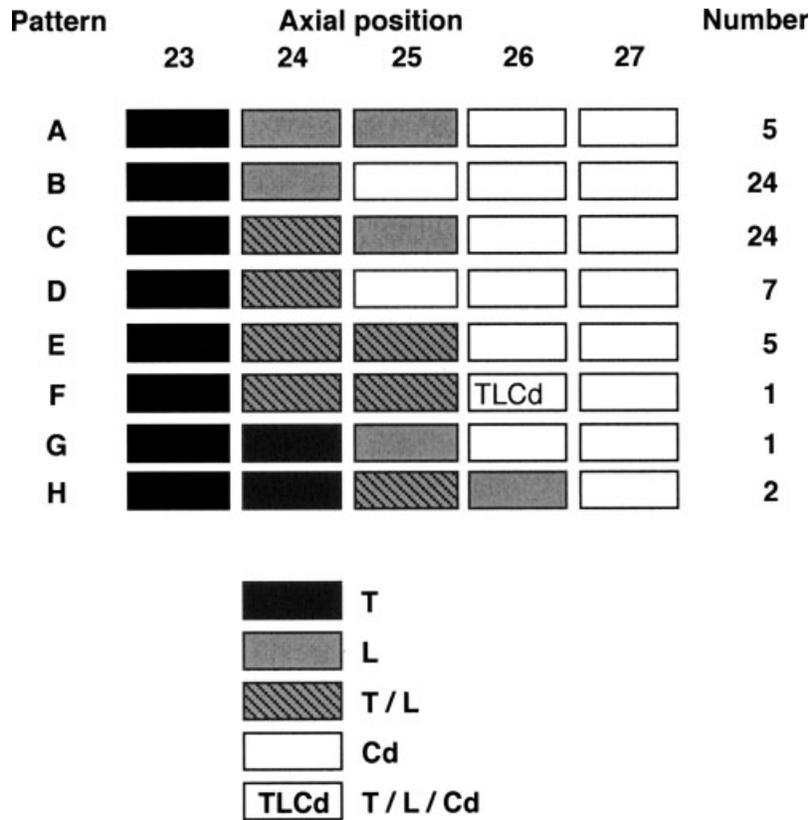


Fig. 2. Diagrammatic summary of morphological variation in the lumbar column in *Trichechus manatus latirostris*. T, thoracic vertebra; T/L, transitional thoracic/lumbar vertebra; L, "classical" lumbar vertebra; Cd, caudal vertebra; T/L/Cd, thoracic, lumbar, caudal transitional vertebra.

parameters (Table 2; Fig. 1). Basal skull length is the strongest (Fig. 1A) and foramen magnum height the weakest predictor of both field length and estimated total centrum length. There were also positive relationships between skull measurements and log of body weight, although the paucity of field measurements makes this a much smaller data set.

Over the range of FLs represented in this study, BSL becomes a smaller percentage (from  $\approx 14$  to 11%) and eTCL a larger percentage (from  $\approx 60$  to 65%) of FL as FL increases (Fig. 1B). The restriction of the data set to individuals whose skeletons could be reassembled inevitably constrains the ranges of these values, eliminating small juveniles. Despite considerable scatter, both regressions are significant. However, the relationship between FL and eTCL as a percentage of FL was relatively weak and accounted for only 10% of the variation in the data. The difference between the sum of these two units (BSL, eTCL) and FL is assumed to represent intervertebral disks plus other soft tissues, a value that decreases slightly over the size range reported here.

**General Descriptions of Manatee Vertebrae Series**

Cervical (C) vertebrae include the atlas and axis and those immediately following vertebrae that lack moveable rib articulations and/or exhibit a transverse fora-

men. Postaxial cervical vertebrae have low and very short centra and closely fitting planar zygapophyses with an oblique orientation. C6 is unusual in bearing a hemifacet for rib 1 on its posterior surface and in its frequently incomplete transverse foramen. Neural spines are very small or lacking entirely. Cervical fusion is occasional (4 of 71 individuals) and variable. All individuals in this sample have six cervical vertebrae.

Thoracic (T) vertebrae have two (anterior) or one (posterior-most in some animals) surface(s) for the articulation of large and vertically oriented, moveable ribs with rounded cross-sections. The capitular articulation surfaces are hemifacets located between adjacent centra in the anterior members of the series but are restricted to individual centra in posterior thoracics. Tubercular facets articulate with diapophyses that have origin on the neural arch. Centrum faces are vertical and planar. Zygapophyses are robust. The flat, horizontal surfaces of anterior zygapophyses become progressively more curved and vertical posteriorly; there is no discrete "diaphragmatic" vertebra. Neural spines are very short relative to centrum size and have a consistent posterior inclination. There is, thus, no anticlinal vertebra. Thoracic counts in this sample vary from 17–18; one individual has a 19th vertebra with transitional thoracic/lumbar anatomy.

"Classic" lumbar (L) vertebrae have short, planar, and orthogonal transverse processes with no or slight dorsal curvature. They lack both rib articulations and hemal

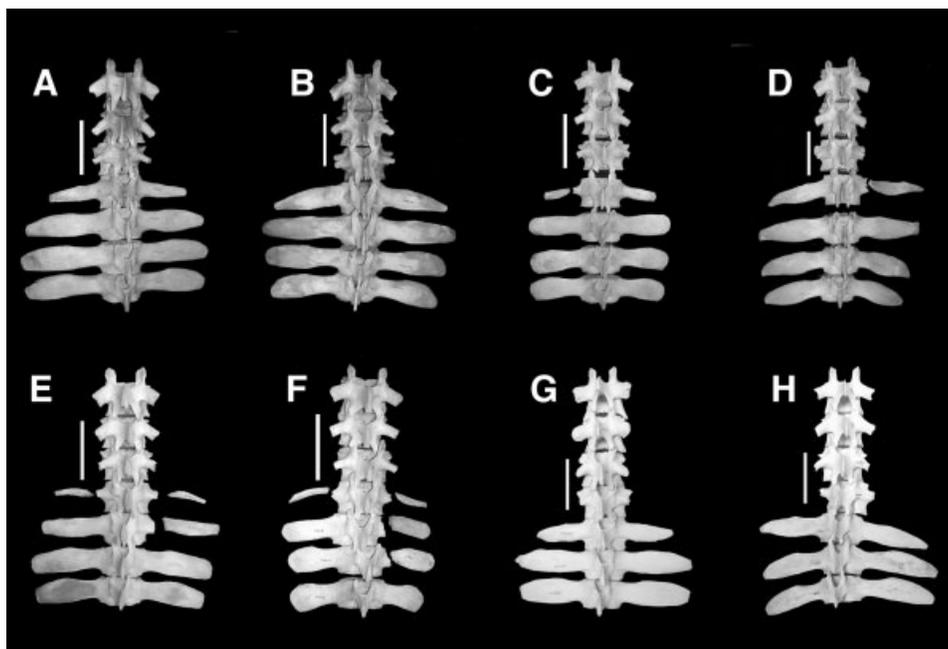


Fig. 3. Examples of morphological variation in the lumbar column of *Trichechus manatus latirostris* scaled to the same size. Scale bars = 10 cm. Pattern letters correspond to those identified in the text and in Figure 2. **A-G:** Vertebrae in axial positions 21–27. **H:** Vertebrae in axial positions 22–28.

**TABLE 3. Vertebral counts in sirenians and comparative taxa.**

	C	T	L	S	Cd	Total	Reference
<i>Trichechus manatus latirostris</i>	6	17–19		27–29		48–54	Hatt 1934, Husar 1978
<i>Trichechus inunguis</i>	6	15–16		22–27		43–50	Hatt 1934, Husar 1977
<i>Trichechus senegalensis</i>	6	17–18		25–26		48–50	Hatt 1934
<i>Miosiren kocki</i>	7	19	3	1	25+	55+	Sickenberg 1934
<i>Dugong dugon</i>	7	19	3	1	28–30	58–60	this data set
<i>Dusisiren jordani</i>	7	21	3	1	32	64	Domning 1978
<i>Pezosiren portelli</i>	7	20	4	4	24?	60?	Domning 2001
<i>Metaxytherium floridanum</i>	7	20	3	1	?	31+	Domning 1988
<i>Metaxytherium krahuletzki</i>	7	18–20	3	1	?	31+	Domning and Pervesler 2001
<i>Procavia habessinica</i>	7	22	7	3	6+	46+	this data set
<i>Procavia capensis</i>	7	20–21	7–9	5–7	4–8		Olds and Shoshani 1982
<i>Dendrohyrax dorsalis</i>	7	20–21	7–9	5–7	4–8		Jones 1978
<i>Loxodonta africana</i>	7	19	4	5	24+	59+	Flower 1885
<i>Elephas maximus</i>	7	19–20	3–5	3–5	24–34		Shoshani and Eisenberg 1982

arch facets. Neural spines are short and have a slight posterior inclination. Variants are common (see below) and include individuals with small, tapering cylindrical and/or sharply posteriorly oriented (unfused) pleura-physes and those with left/right asymmetry. Lumbar counts in this sample varied from 1–2.

There are no sacral vertebrae, classically defined as those vertebrae with transverse processes that articulate with the pelvis.

Caudal (Cd) vertebrae bear horizontal transverse processes, articular surfaces for hemal arches (chevrons) and very short, posteriorly oriented neural spines. Transverse processes of the most anterior caudals are constricted near the centrum and have distinctive ventral curvature. Curvature disappears by Cd4/5 and neural

spines disappear by Cd13/14. Posterior caudals lack hemal arch articular scars and transverse processes and decline progressively in size. The tiny terminal vertebrae are rarely preserved; caudal counts appear to be highly variable within a range of 24 to 29.

#### Variations in Lumbar Vertebral Patterns

All vertebrae that are evaluated as transitional exhibit at least some lumbar traits, clearly identifying the lumbus as the most variable region of the manatee column. The 69 individuals for which vertebral anatomy could be scored were sorted into eight patterns (A–H) based on variations in axial positions 24 and 25 as follows (Figs. 2, 3):

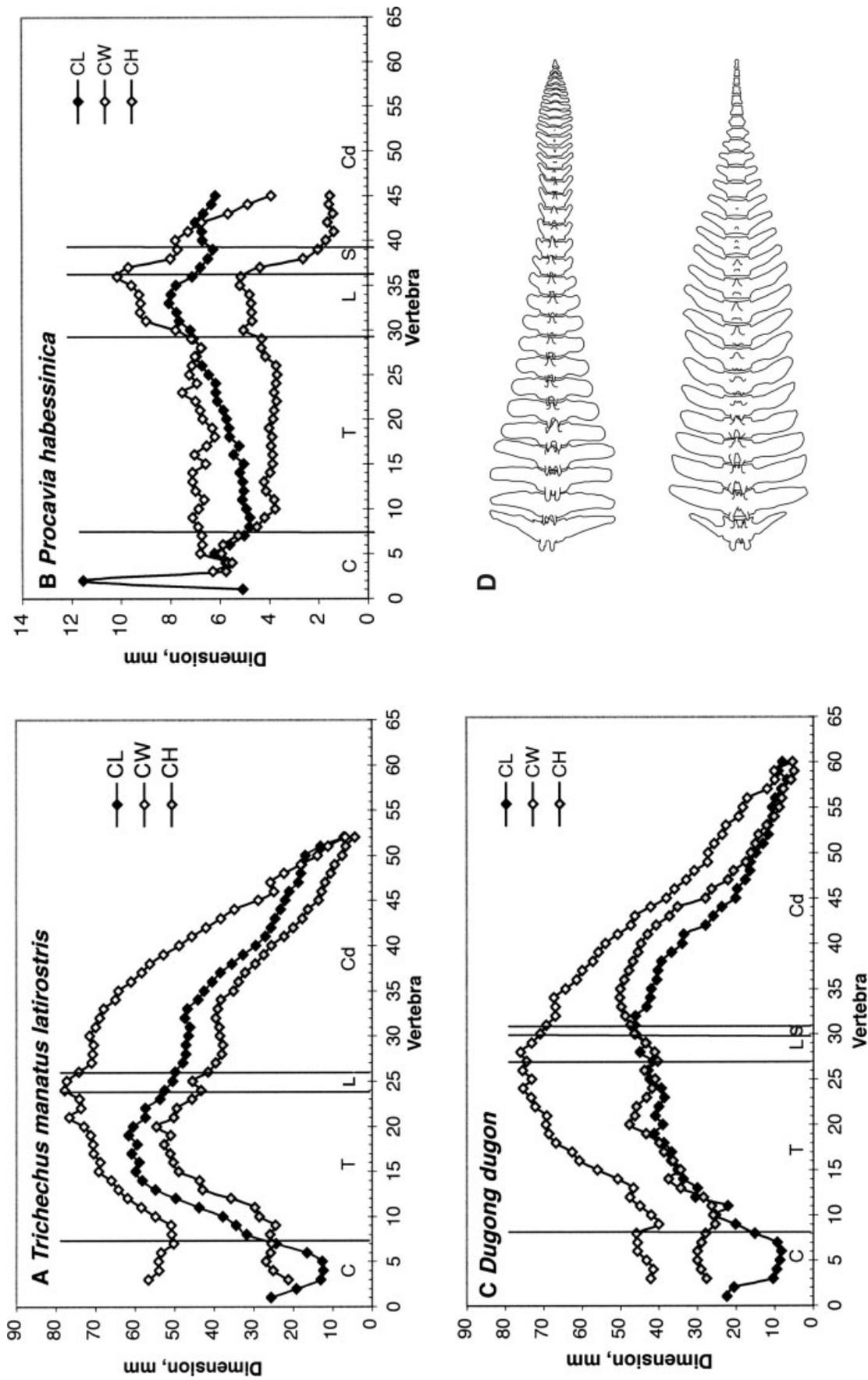


Fig. 4. **A-C:** Vertebral dimensions of A, *Trichechus manatus latirostris* UF 15205 (A); *Procavia habessinica*, MCZ 8285 (B); and *Dugong dugon* BMNH 1966.9.7.1 (C). **D:** Patterns of vertebral morphology in the tails of *T. m. l.* (above) and *D. d.* (below). CL, centrum length; CW, greatest centrum width; CH, centrum height.

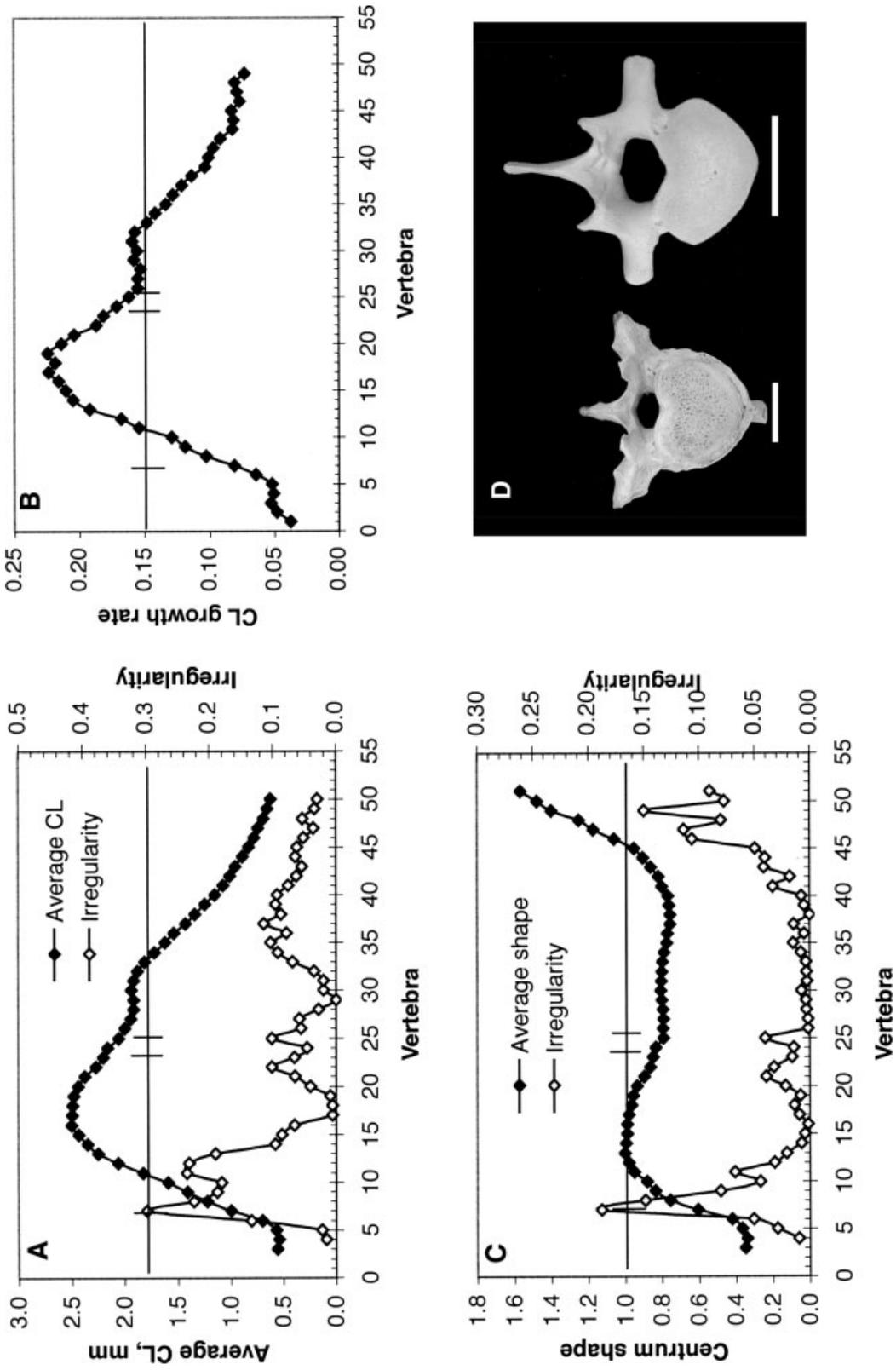


Fig. 5. A-C: Patterns of centrum length and shape in *Trichechus manatus latirostris*. **A**: Average centrum length (CL) of vertebrae in each axial position, scaled to CL of T1; n = 69. **B**: Slopes of regressions of CL on FIELD length (FL) of vertebrae in each axial position; n = 69. **C**: Average shape (=2CL/(CW + CH)) of vertebrae in each axial position; n = 69. Locations of classical series breaks are indicated by subdivided line. CW, greatest centrum width; CH, centrum height. **D**: Divergent centrum and neural spine morphology in vertebra T10 of *T. m.* (left) and *Dugong dugon* (right).

Pattern A: Two lumbar vertebrae (five individuals)—a true lumbar vertebra fills both position 24 and 25. This anatomy is considered primitive, as higher lumbar counts (when identifiable) are present in all outgroups (Table 3).

Pattern B: Reduction in lumbar count (24 individuals)—a lumbar fills position 24 and a caudal vertebra fills position 25; thoracics and caudals are, therefore, separated by a single vertebra.

Patterns C–F: “Thoracicization” (37 individuals)—position 24 is filled by a thoracic/lumbar(T/L) transitional vertebra. Three types of thoracicization are observed: (1) short lumbar “riblets” (pleurapophyses) articulate with the centrum instead of fuse with it; (2) lumbar “riblets” are fused, but show evidence of articular surfaces that were present earlier in ontogeny; and (3) one side of the vertebra has thoracic, while the other has lumbar anatomy. This transitional vertebra is followed by one of these patterns: C, position 25 is filled by a true lumbar (24 individuals); D, position 25 is filled by a caudal (7 individuals); E, position 25 is filled by a second T/L transitional vertebra (5 individuals); F, position 25 is filled by a second T/L transitional vertebra, and position 26 by a T/L/Cd vertebra with left/right asymmetry (1 individual).

Patterns G,H: Posterior translocation of T/L boundary (three individuals)—the transition from thoracic to caudal zones is still two vertebrae in length, but is translocated posteriorly by one position. Position 24 is filled by a thoracic, followed by one of these patterns: G, a lumbar in position 25 and a caudal in position 26 (2 individuals); or H, a T/L in position 25 and a lumbar in position 26 (1 individual).

### Vertebral Dimensions

Representative dimensional changes (CL, CW, CH; Fig. 4A) along the manatee column are demonstrated with those of a large complete individual. All three dimensions are essentially unimodal, and lack the distinctive dimensional signatures of lumbar (increase of CL) and sacral (decrease in CL and CH) series commonly seen in terrestrial mammals (cf. Fig. 4B). The reduction in CW so typical of the peduncular area of whales (Buchholz, 1998) and to a lesser extent of dugongs (Fig. 4C) is barely noticeable in the manatee midcaudals (Fig. 4D).

CL standardized to T1CL and averaged across all individuals with measurable vertebrae ( $n = 69$ ) is plotted in Figure 5A. Absolute values of differences between each CL value and that of the previous vertebra are plotted on the second axis to give an indication of column irregularity *sensu* McShea (1993). The shortest CL occurs in the neck, the longest in the mid- and posterior thorax. A distinctive plateau in the anterior caudals interrupts posterior reduction of CL, after which it declines steeply. Slopes of regressions of CL on FL for each vertebra are graphed by axial position in Figure 5B. The pattern of this curve closely mimics that of CL change, almost certainly a reflection of the origin of vertebrae in serially homologous and morphologically similar units.

Average values of shape ( $2CL/(CW + CH)$ ), a dimensionless variable, are presented with irregularity values in Figure 5C. Centrum shape is most distinctive in the cervicals (disc-shaped) and in the posterior caudals

(spool-shaped). Anterior caudals are relatively shorter than thoracics and highly uniform in shape. Neural spine height is extremely short along the entire manatee column, illustrated here (Fig. 5D) in a comparison of manatee and dugong T10 vertebrae scaled to the same CH.

### DISCUSSION

Dimensional relationships between skull and body parameters in the Florida manatee present few surprises. Basal skull length is a reliable predictor of field length and the skull forms a smaller percentage of body length in large than in small animals, as it does in most vertebrates (see also Domning and Beatty, 2007, this issue, for relationships between skull and tusk anatomy in dugongs).

Manatee vertebral morphology is, however, highly unusual compared with that of both terrestrial mammals and other sirenians. Key aspects of this morphology are low precaudal count (Table 3), lack of a sacral series, compressed cervical and elongated thoracic vertebrae, very short neural spine length, extreme variation and reduction of the lumbus, and the discontinuity in morphology within the caudal series. These traits are particularly intriguing because they seem to have evolved, at least in part, in response to contradictory selection regimens: precaudal elongation has occurred coincident with reduction in thoracic count and incipient deletion of the lumbar series. Morphological units of the column are demarcated below, and possible functional roles of each in aquatic locomotion are suggested. Traits unique to trichechids are identified, and a hypothesis of trait origin consistent with current developmental theory is proposed.

### Vertebral Column Subunits

Morphology of vertebral processes and transitions in vertebral size and shape support recognition of only four column units: neck, dorsum, tail base, and fluke. As demonstrated below, lumbar vertebrae do not constitute a discrete morphological unit, but two such units (tail base, fluke) exist within the classical caudal series.

**Neck (6 vertebrae).** The neck is coincident with the cervical vertebrae. Postaxis centra are extremely short, with  $CL \ll CH < CW$ . Cervical “ribs” are short and fused to centra around a transverse foramen. Zygapophyses articulate closely, centrum faces are flat, and there is a very slow rate of CL growth.

Cervical vertebrae support the head and provide attachment sites for the muscles that enable its (limited) mobility. Its short length is the result of both centrum foreshortening (relative to terrestrial species) and count reduction (relative to terrestrial species and to other sirenians). Domning (2000) suggests anterior repositioning of the flippers as the major selective advantage of a short neck, with drag reduction as a possible contributing factor.

**Dorsum (18–20 vertebrae).** Centra are large and blocky, roughly equal in CL, CW, and CH. Neural spines are short, ribs are long, rounded in cross-section, vertical or near vertical in orientation, and articulating. Zyg-

apophyses interlock, and centrum faces are both vertical and flat. CL growth rate is very high.

The dorsum comprises vertebrae classically identified as both thoracic and lumbar. The first 17 vertebrae are "typical thoracics" in all animals of this sample, and are noteworthy for their augmented length and height relative to those of other sirenians. The following one to two vertebrae display some lumbar characteristics in some animals, but the signature lumbar morphological indicators of centrum elongation and neural spine anticlivity are uniformly absent. Dorsal morphology in *T. manatus latirostris* is distinctively different from that of dugongids, which display higher dorsal (T + L) count, shorter dorsal CL, classic lumbar morphology, and also retain a recognizable sacral vertebra.

Dorsal vertebrae provide longitudinal support and stability for the trunk. Their ribs protect the viscera and provide hydrostatic ballast. Reduction in count, short neural spines, and the elongation of chest vertebrae are all interpreted here as adaptations for axial locomotion. Elongation of the body, posterior generation of propulsive force, and anterior column stability enhance axial locomotion (Domning and Buffrénil, 1991; Domning, 2000). A small(er) number of long(er) vertebrae can produce both elongation and stability if intervertebral mobility is constrained. Such constraint is suggested by the extremely short neural spines, flat centrum faces, and articulating zygapophyses of the dorsum. Precaudal stability is also enhanced by the elimination or morphological alteration of lumbar vertebrae typically specialized for dorsoventral flexion.

**Tail base (7–8 vertebrae).** Centra of tail base vertebrae are uniform in size and shape, with  $CL \approx CH < CW$ . Neural spines are short and posterior in orientation. The large transverse processes are fused and typically horizontal, centrum faces are flat. Zygapophyses articulate only in anteriormost vertebrae. Rate of CL growth is intermediate.

The tail base serves with the dorsum as the anchor for the muscles of locomotion. Transition from the tail base to the fluke is marked by a rapid decrease in centrum size, reduction in the size of neural spines and transverse processes, and an increase in posterior inclination of transverse processes (syncliny). It is also coincident with the "peduncle wrinkle" that externally marks the boundary of the broad fluke (Hansen, 1983).

**Fluke (17–22 vertebrae).** Fluke centra are small and more elongate than those of the tail base. Zygapophyses are absent, and centrum faces are emarginated dorsoventrally. Both transverse processes and hemal arch facets disappear posteriorly. Rate of CL growth is low.

Posterior caudal vertebrae support the flexible fluke, which is the propulsive surface of the tail. Movement between adjacent vertebrae is enhanced by the small size and rounded centrum faces and by the lack of zygapophyses.

### Transformation of the Trichechid Column: Shared Traits

Several of the aquatic adaptations of the Florida manatee column are shared with fossil and living dugongids, and are assumed to predate the last common ancestor of

the families in the latest Eocene. These adaptations are the following.

1. Reduction of sacral count from an original count of four. Post-Eocene sirenians have one (most species) or no (*Trichechus*) sacral vertebrae. Dugongids and trichechids retain pelvic rudiments. These lack (trichechids) or retain (dugongids) a soft tissue connection to the vertebral column.
2. Subdivision of the caudals into tail base and fluke. Both trichechids and dugongids show expanded orthogonal transverse processes on anterior caudals (tail base) for attachment of the muscles of locomotion, syncliny (divergent transverse processes) between caudal units, and a distinctive terminal fluke. Differences in midcaudal and fluke morphologies emphasize the long independent history and differing locomotor patterns in the two families.
3. Shortening of cervical vertebrae. Dugongids and trichechids both display anteroposterior foreshortening of cervical vertebrae.

### Transformation of the Trichechid Column: Derived Traits

Manatees also display at least four unique column traits that are inferred to have arisen since separation of trichechids and dugongids.

1. Reduction in neural spine height. Manatee neural spines are uniformly short across all vertebral series relative to those typical of other sirenians and of mammals in general.
2. Reduction of precaudal series count. Counts of all precaudal series (C, T, L, S) are reduced (sacrals have been eliminated) relative to those of other sirenians. This reduction is almost certainly the result of a meristic change; homeotic change would generate augmented counts in adjacent series. The variability of caudal count precludes confident analysis of tail counts, but these are also low relative to other sirenians. Selection pressure for precaudal count reduction must have been very strong, as it is expressed even in the neck. Reduction of cervical count has been resisted in a wide range of mammals with short necks, and shows no variation in this data set. A reduction in count lowers the number of intervertebral flexion points. Without counteracting elongation of vertebrae, it shortens the column.
3. Elongation of dorsal vertebrae. Manatee dorsal vertebrae are elongate relative to those of other sirenians, including the trichechid *Miosiren* (data from Sickenberg, 1934). Here, elongation of dorsal vertebrae is coupled with shortening of cervical vertebrae and a reduction in count across the precaudal column, producing variable lengthening of different column units.
4. Reduction of the lumbus. Lumbar morphology is exceedingly variable; the lumbar vertebrae of most individuals display some combination of classic thoracic and lumbar traits. High variability is usually interpreted as a signature of evolutionary

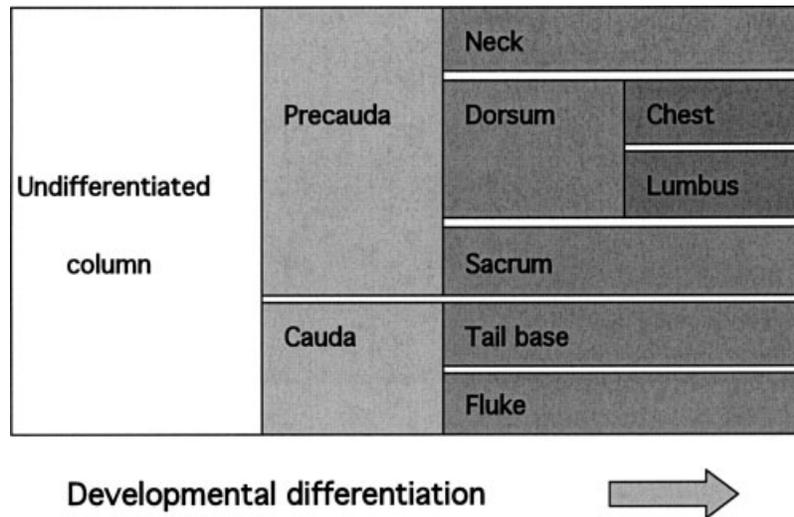


Fig. 6. Hypothesis of modular relationships among vertebral series in the manatee. Regionalization of the column increases throughout the developmental process, which proceeds from left to right in the diagram. The lumbar series is in the process of elimination through count reduction and thoracization.

transition (Bateson, 1894). The lumbar series is interpreted here as being in the process of elimination through both lumbar count reduction (meristic change) and expansion of thoracic anatomy to axial positions typically occupied by lumbar (homeotic change).

**Modularity, Development, Evolution**

The mammalian vertebral column starts development as a unified morphological unit and is subsequently regionalized by a series of developmental events with restricted axial expression. It is hypothesized here that the five ancestral column units (cervical, thoracic, lumbar, sacral, caudal) are hierarchically organized and that this organization affects patterns of evolutionary change. The data presented suggest that a sequence of evolutionary innovations modified the classic terrestrial mammalian vertebral column to generate four morphologically discrete units (neck, dorsum, tail base, and fluke) in *Trichechus manatus latirostris*.

Three hierarchical levels in the organization (Fig. 6), and by inference in the development, of the manatee column are proposed. Common developmental processes acting on serially homologous (sclerotome) units of somitic mesoderm unite the column as a whole (Kardong, 2006). Traits with broad axial distribution are viewed as the products of common developmental pathways, and are thought to have “upstream” locations relative to those with more restricted distributions.

**Primary subdivision: Precauda/cauda.** The developmentally early subdivision of the column into precaudal and caudal units is suggested by the classic stability of precaudal counts, despite high variability of tail count and morphology across many mammalian orders. The anus, a major discontinuity in morphology, also separates the two units. In manatees, remodeling of

each of these two major units proceeds without affecting the other, emphasizing their early developmental isolation.

Reduction in vertebral count occurs across all precaudal units. The reduction is meristic; there are no adjacent units with enhanced counts. Subdivision of the somitic mesoderm into a reduced number of vertebrae must occur developmentally before regionalization of the precaudal column, or it would be restricted to one or more series. The most likely selective force favoring such a change is reduction in the length of the neck. The collateral consequence, reduction in dorsum count, is apparently offset by elongation of dorsal vertebrae.

**Secondary subdivision: neck/dorsum.** Subsequent developmental subdivision of the precaudal column into neck and dorsum subunits is supported by many traits that share the same axial distribution pattern. A key trait across all mammals is the differential expression of “ribs” in the neck and the dorsum. In manatees, growth regimens (and consequent vertebral shapes) are distinctly different across this boundary: cervical vertebrae have low, and dorsal vertebrae have high, rates of CL growth with the result that centra are of markedly different size. These differing growth patterns persist late into ontogeny (Fig. 5B). There is no evidence of homeotic transfer between neck and dorsum in this data set, despite the unusual cervical count, arguing for a stable and developmentally entrenched boundary.

**Tertiary subdivision: thorax/lumbus and secondary loss of the lumbus.** Thoracic and lumbar series are morphologically distinct in most mammals, although compensating homeotic exchanges occur with high frequency (Bateson, 1894; Le Double, 1912). High variability across the T/L boundary in manatees suggests that this developmental separation is in the process of evolutionary loss. Meristic reduction in the

precauda and homeotic expansion of the thorax are eliminating the lumbus.

**Sacral vertebrae.** Living trichechids lack sacral vertebrae. Although they were almost certainly part of the precaudal unit of the column, their relationship to cervical and dorsal modules is ambiguous and not clarified by the data here.

**Secondary subdivision: tail base/fluke.** The caudal column forms a single and highly variable morphological unit in most mammals. In manatees (as in other axial locomotors, especially whales), morphological, dimensional, and functional subdivision of the tail dictates recognition of tail base and fluke modules. The presence of a fluke in dugongids places this innovation very early in sirenian evolution.

### SUMMARY

To summarize, the distribution of vertebral characters among taxa and across modular units of the column allows prediction of the historical timing and developmental "location" of morphological innovations. Subdivision of the tail and low rates of cervical growth occurred early in sirenian evolution, before the separation of trichechids and dugongids. Because these innovations have restricted axial expression, we infer that they are the products of mutations that occur relatively late in the developmental sequence. In contrast, meristic reduction in count is a trichechid innovation, so can be placed historically after the trichechid/dugongid split. However, it is expressed across the entire precaudal column, arguing for a mutation relatively early in the developmental sequence. Vertebral elongation is restricted to the dorsum and may be an offsetting strategy that allowed for column elongation, despite historically earlier and developmentally upstream reduction in count. Reduction of the lumbus is currently in progress; it appears to be the product of both developmentally early meristic mutations and developmentally late homeotic mutations.

The hypothesis presented here is preliminary, but suggests that a hierarchical understanding of vertebral column morphology and development has significant explanatory power. We anticipate that mammals with long evolutionary histories and significant vertebral column remodeling will provide rich data sets for examination of the evolution of developmental processes over time.

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