



Vertebral and rib anatomy in *Caperea marginata*: Implications for evolutionary patterning of the mammalian vertebral column

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ABSTRACT

The pygmy right whale, *Caperea marginata*, is a rare mysticete cetacean with an unusual suite of axial skeletal characters. Distally expanded first ribs, a long thorax with broadly overlapping vertebral transverse processes, plate-like posterior ribs, and a short tail contrast with other cetaceans and suggest unique developmental patterning. Twenty-four individuals of diverse ontogenetic age were available for analysis. Multiple, variable examples of incomplete rib fusion in dependent calves indicate that the first rib of adults is an ontogenetic fusion product of ribs 1 and 2. The composite rib articulates by way of its anterior (Rib1) component to the sternum and by way of its posterior (Rib2) component with thoracic vertebra 2. Thoracic vertebra 1 lacks rib articulations. When rib fusion is taken into account, the most frequent column formulas are $C7T18L1Cd16-17 = 42-43$ and $C7T17L1Cd16-18 = 41-43$. Thoracic and lumbar series are not reciprocal in count, arguing against their developmental linkage. Instead, parallel reduction in both lumbar and caudal counts supports the existence of neocete patterning in *Caperea*, as in all other living cetaceans. Ontogenetic vertebral column elongation is most marked in the posterior thorax, lumbos, and anterior tail. Vertebrae in these column regions are excellent predictors of total body length.

Key words: *Caperea marginata*, pygmy right whale, anatomy, vertebrae, ribs, axial, patterning.

The mammalian vertebral column is an ideal system for developmental analysis because it is composed of discrete, repeatable units organized into five highly conserved and easily recognizable series (cervical, thoracic, lumbar, sacral, caudal). Morphologies that are highly conserved across diverse environments and long geological time spans suggest bias in the generation of variation and negative pleiotropic effects when entrenched developmental sequences are disrupted. The rare species that escape entrenchment often live in extreme environments, implicating the action of strong and unusual selective pressures. The pygmy right whale, *Caperea marginata*, is an example

of such a species, and offers the opportunity to examine the developmental origins of conserved morphologies.

The paleontological record suggests that the vertebral columns of the synapsid ancestors of mammals were largely undifferentiated: each vertebra articulated with a pair of moveable ribs (Romer 1955). The transition from synapsids to mammals was marked by the progressive regionalization of the column into discrete series and by novel constraints in series counts (Rowe 1988, Bininda-Emonds *et al.* 2007, Luo 2007). Regionalized characters typical of mammals include the absence of moveable ribs on caudal vertebrae, truncation and fusion of cervical ribs, and establishment of a discrete lumbar series.

In contrast to other vertebrate classes, almost all mammals exhibit a cervical count of 7 and thoracic + lumbar (thoracolumbar) counts that total 19–21 (Todd 1922, Narita and Kuratani 2005). The cervical constraint is particularly rigid and has been in place for more than 200 million years (Jenkins 1971, Crompton and Jenkins 1973). Meristic variation reflects the developmental subdivision of the pre-somitic mesoderm into a different number of units during somitogenesis, probably caused by the changing rate of the molecular oscillators that control somite number (Hirsinger *et al.* 2000, Pourquié 2003, Sanger and Gibson-Brown 2004). Known exceptions to the cervical constraint are the arboreal tree sloths and the aquatic manatee. Enhanced (*Bradypus*) or reduced (*Choloepus*) cervical counts in tree sloths are accompanied by disruption of structures with lateral plate mesoderm (sternal ribs, sternum, sacrum) developmental histories (Buchholtz and Stepien 2009). Reduction of cervical count in the manatee (*Trichechus*) is accompanied by an extremely elongate thorax, a reduced lumbos, and absence of the sacral series (Buchholtz *et al.* 2007).

The thoracolumbar counts of mammals vary more flexibly, usually within the narrow range of 19–21. This total reaches 25 in the anomalurid rodents and 26 in the tree sloth *Choloepus*. Reciprocal variation in counts is now known to be the product of the movement of expression domain boundaries of *Hox* and other axial patterning genes (*e.g.*, Horan *et al.* 1994, Krumlauf 1994, Burke *et al.* 1995, Wellik and Capocchi 2003, Wellik 2007). It signals the developmental linkage of these column series during development, and is typical of terrestrial mammals (Buchholtz 2007). Anatomical anomalies at the thoracolumbar (T/L) and lumbocaudal (L/Cd) boundaries of whales complicate the comparison of cetacean thoracolumbar counts to those of terrestrial mammals (Slijper 1936). These anomalies include the frequent occurrence of ribs without dorsal articulations to vertebrae (floating ribs) at the T/L boundary, the lack of an ilial articulation to demarcate a sacral series, and the uncertain relationship of the first hemal arch facets to the location of the first caudal vertebra. Slijper (1936) addressed each of these complicating factors at length. Despite these uncertainties, it is clear that the range of cetacean thoracolumbar counts (16–43, Slijper 1936) is much greater than that observed in terrestrial mammals. Neocete (*i.e.*, odontocete and mysticete) cetaceans exhibit no reciprocity of thoracic and lumbar counts, a secondary dedifferentiation of lumbar and anterior caudal (*i.e.*, nonfluke) vertebrae, and parallel changes in lumbar and anterior caudal counts (Buchholtz 2007). The evolutionary origin of this neocete modular pattern, characterized by a mid-column unit that shares traits of morphology, shape, and count across the precaudal/caudal divide, can be placed at or near the Archaeoceti/Neoceti boundary (Buchholtz 2007).

The pygmy right whale, *Caperea marginata*, is morphologically, phylogenetically, and behaviorally isolated from other whales. Although clearly a mysticete, recent

authors variously place it as a sister group to Balaenidae (Deméré *et al.* 2005, Fitzgerald 2006, Steeman 2007) or to a balaenopterid-eschrichtiid clade (Rychel *et al.* 2004, Sasaki *et al.* 2005, Nikaido *et al.* 2006, Deméré *et al.* 2008). There is, however, broad consensus that it occupies a basal position among crown group Neoceti and has had a history separate from that of other mysticetes since the Oligocene. The vertebral anatomy of *Caperea* is unusual with respect to both series differentiation and series counts.

The thoracic series dominates the precaudal column of *Caperea* in both vertebral count and length. The lumbos is poorly defined, leaving only three unambiguous vertebral series: cervical, thoracic, and caudal (Beddard 1901; Hale 1931, 1964; Slijper 1936; Baker 1985). The apparent enhancement of the thorax at the expense of the lumbos suggests the reciprocal variation of thoracic and lumbar counts seen in terrestrial mammals and ancestral archaeocete cetaceans. The thorax is also unique in the presence of large, overlapping transverse processes and plate-like posterior ribs. Clarification of modular pattern in *Caperea* can narrow the evolutionary location of the transition from terrestrial to neocete modularity in cetaceans.

The seven cervical vertebrae of *Caperea* fuse into a single cervical mass during ontogeny. In his *Osteology of the Pigmy Whale*, Beddard (1901) reported that the unusual eighth vertebra “appears to have no rib.” This rib is key to the definition of the neck, because the first rib with a sternal articulation classically defines the anterior margin of the thorax (Turner 1847). Beddard’s observation raises the possibility that *Caperea marginata* represents an unrecognized violation of the cervical constraint in mammals. Slijper (1936) subsequently disputed Beddard’s interpretation. He described an additional adult individual with a normal cervicothoracic transition and suggested that both of Beddard’s specimens had been incorrectly mounted. This dispute has been unresolved since Slijper’s analysis.

This study documents vertebral anatomy and series boundaries in a large and ontogenetically diverse database of *Caperea* specimens. The patterns observed are used to address the timing of the transition from archaeocete to neocete column modularity in cetacean evolution and to expand recent studies of nontraditional cervicothoracic anatomy (Galis 1999, Solounias 1999, Galis *et al.* 2006, Buchholtz *et al.* 2007, Buchholtz and Stepien 2009) in mammals.

MATERIALS AND METHODS

The vertebral and costal anatomy of *Caperea marginata* was documented using osteological specimens housed at the American Museum of Natural History (AMNH), the South Australia Museum (SAM), and the Museum of New Zealand Te Papa Tongarewa (NMNZ). The skeletons include individuals of widely disparate size (Table 1), prepared over many years from accidental strandings (Kemper and Leppard 1999). The relatively small size of *Caperea* facilitates housing multiple specimens in a single museum, allowing examination of 24 complete or nearly complete individuals, a comparatively large data set for mysticete cetaceans.

Vertebral centrum length (CL), centrum width (CW), and centrum height (CH) of each vertebra were measured with digital calipers. Separated epiphyses were replaced before measurement, and the lengths of rare missing epiphyses were estimated from adjacent epiphyses. Epiphyses of the two smallest individuals were impossible to assign to individual vertebrae, although they could be assigned to series. For these specimens, the average epiphyseal length of the appropriate series was added to

Table 1. Specimens examined in this study, with sex (Male, Female, or Unknown), observed or estimated total length (TL), inferred age group, and rib fusion status. Specimens are listed by increasing TL. Asterisks identify TL values estimated from the regression of summed CL of vertebrae 14–27 on known TL values; the symbol (‡) identifies the TL value of an incomplete specimen estimated from the regression of centrum length of vertebra 25 on known TL values. Age groups follow the size categories of Kemper and Leppard (1999). A = adult, DC = dependent calf, DC(N) = neonate, SA = subadult.

Specimen	Sex	TL, mm	Age group	Ribs 1 and 2
NMNZ unregistered B	U	1,739*	DC(N)	separate
NMNZ unregistered C	U	2,000	DC(N)	composite
NMNZ 2163	U	2,601*	DC	separate
SAM M2966	M	2,667	DC	composite
SAM M17364	F	2,740	DC	partial fusion (distal, asym.)
NMNZ 2049	U	2,773*	DC	partial fusion (proximal)
NMNZ 2119	U	2,775*	DC	partial fusion (distal)
NMNZ 308	U	2,994*	DC	composite
SAM M6110	M	3,050*	DC	partial fusion (proximal)
SAM M23549	F	3,340	DC	separate
SAM M15024	M	3,382	DC	composite
NMNZ 2254	U	3,623*	SA	composite
SAM M16978	F	4,390	SA	composite
AMNH 36692	U	5,414*	SA	composite
NMNZ 2235	U	5,608*	A	composite
NMNZ 1596	U	5,630‡	A	composite
NMNZ unregistered A	U	5,846*	A	composite
SAM M15374	U	6,000	A	composite
SAM M23863	U	6,037*	A	composite
SAM M17362	F	6,080	A	composite
NMNZ 763	U	6,130*	A	composite
SAM M17363	M	6,200	A	composite
SAM M21460	F	6,290	A	composite
SAM M23548	F	6,380	A	composite

each vertebra. Centrum lengths of all individuals were graphed together to evaluate patterns of column growth.

Total body lengths (TL) from field measurements (provided by Catherine Kemper and Anton van Helden) were available for a subset of the specimens. Least squares linear regression was used to evaluate the ability of CL of vertebrae at each column position to predict known TLs. Unknown TL values were predicted from the regressions with the greatest prediction success. Known and predicted TL values were used to assign specimens to the size and life stage categories established for *Caperea* by Kemper and Leppard (1999).

Vertebral series membership was assigned using classical anatomical criteria (Turner 1847). The seven cervical vertebrae lack moveable ribs, and in cetaceans their centra are typically foreshortened. Thoracic vertebrae articulate with moveable ribs; the first thoracic vertebra has the most anteriorly occurring sternal articulation. The lack of costal articular facets on posterior ribs in *Caperea* and the possibility of ontogenetic costal fusion complicated location of the thoracic/lumbar boundary, so identification of the lumbar series used both rib counts and axial markers. These axial markers included changes in neural spine height and inclination, metapophysis

length and orientation, and transverse process shape (see below). The first vertebra that bears hemal arch facets on its posterior ventral border is identified here as the first caudal. This definition conflicts with that used by Slijper (1936), but is currently the standard in use (*e.g.*, Rommel 1990, Rommel and Reynolds 2002). The first facets are often extremely small, but the bifurcation of the ventral carina of the vertebra is a reliable indicator of their presence (Andrews 1916).

The ribs of each specimen were counted and ordered. Counts of ribs with heads were checked against counts of thoracic vertebrae with articular facets, and total rib counts were checked against total thoracic counts. Many specimens lacked one or more terminal caudal vertebrae. The number of missing vertebrae was estimated, but total vertebral count could not be firmly documented. Column series counts were used to document variation in column patterning in *Caperea*.

RESULTS

Column Dimensions and Size/Age Groups

A consistent pattern of centrum length occurs in all individuals of this data set (Fig. 1A). Centrum length values increase gradually across the thorax, and the longest vertebra occurs in the lumbos or anterior tail, often at vertebra 28. The gradual decrease in CL posterior to this point accelerates anterior to the fluke. Variations on this pattern occur in animals of different body size. Ontogenetic elongation of vertebrae is concentrated in the posterior thorax, lumbos, and anterior tail. Centrum length of the longest (typically anterior caudal) vertebra is about twice that of the first fluke vertebra in neonates, but almost three times that of the first fluke vertebra in the largest adults. Adults consequently have larger ranges of centrum length than do dependent calves, and the decreases in CL anterior to the fluke are more dramatic in adults than in calves. The relationship of centrum length to centrum width and centrum height also changes with ontogeny, with differences particularly noticeable in the anterior tail. Centrum length of the smallest calves is always less than CW and CH, but CL exceeds CW and CH at the T/L/Cd transition of larger calves (Fig. 1B). Centrum length of subadults and adults exceeds CW and CH throughout much of the column (Fig. 1C).

Centrum lengths of vertebrae at different column positions vary in their ability to predict TL (Table 2); the most accurate predictions are generated from vertebrae in the mid thorax to anterior tail. Equations for regressions of CL on total length for each vertebra are presented in Table 2, allowing TL estimates for incomplete specimens. The regression of summed CL of vertebrae 14–27 on TL ($TL = 2.69x + 262.82$, $r^2 = 0.99$) was used here to predict body lengths of specimens for which field data were unavailable. Individuals were then assigned to age groups (dependent calves, DC; subadults, SA; adults, A) following Kemper and Leppard (1999). The two smallest individuals are identified here as neonates (N) or stillbirths, as the larger of them was collected with an unhealed umbilicus attached (NMNZ field notes). Observed and estimated body lengths (Table 1) reveal a largely bimodal size distribution, with few individuals of intermediate size.

Rib Patterning

The ribs of *Caperea* are unique among mammals (Beddard 1901). Although they form an anteroposterior morphological continuum, they are roughly separable into

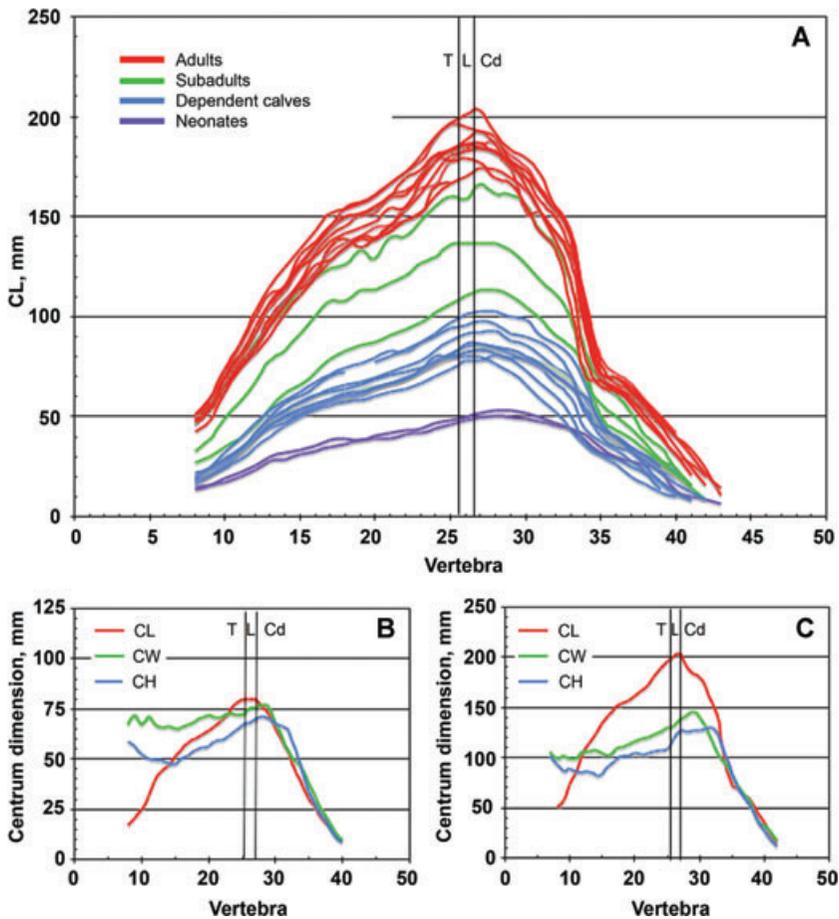


Figure 1. Vertebral dimensions in *Caperea marginata*. (A) Centrum length in all 24 specimens of the data set, separated into the age/size classes of Kemper and Leppard (1999). Three missing values have been interpolated, and epiphyseal lengths of the two smallest specimens have been estimated. Vertical lines indicate the most common locations of series boundaries. (B) Centrum length, width and height by vertebra in a dependent calf (SAM M2966). (C) Centrum length, width and height by vertebra in an adult (SAM M23548). CH = centrum height, CL = centrum length, CW = centrum width, Cd = caudal T = thoracic, L = lumbar.

three groups: the broad and arcuate first rib, a series of anterior ribs with roughly circular cross section and simple curvature that articulate via heads with anterior thoracic vertebrae, and a series of plate-like posterior ribs with complex curvature that lack articular heads.

The structure of Rib1 is central to the interpretation of *Caperea* patterning. In adult individuals this rib expands distally from a single medial head to form a triangular plate of variable width (Fig. 2A). It exhibits an anterior expansion with a distal articulation surface for the sternum, a thin intermediate region, and a second, posterior expansion. The external (lateral) surface bears subtle rugae. The first rib of some dependent calves mimics those of adults, but those of others possess medial

Table 2. Regression equations for prediction of total body length from CL of individual vertebrae or from the summed CLs of groups of vertebrae.

Vertebra	Regression of CL on TL	r^2
1–7	$y = 71.77x - 1,773.50$	0.93
8	$y = 109.43x + 902.17$	0.97
9	$y = 95.67x + 828.50$	0.96
10	$y = 76.66x + 810.76$	0.98
11	$y = 68.71x + 574.83$	0.98
12	$y = 61.00x + 436.91$	0.98
13	$y = 55.46x + 302.71$	0.98
14	$y = 52.76x + 199.03$	0.99
15	$y = 45.68x + 385.39$	0.99
16	$y = 42.45x + 394.32$	0.99
17	$y = 40.24x + 423.89$	0.98
18	$y = 38.82x + 424.66$	0.99
19	$y = 38.51x + 363.83$	0.99
20	$y = 38.60x + 274.25$	0.99
21	$y = 37.25x + 274.17$	0.99
22	$y = 35.41x + 347.73$	0.99
23	$y = 33.94x + 325.82$	0.99
24	$y = 32.83x + 265.29$	0.99
25	$y = 32.47x + 194.89$	0.99
26	$y = 32.80x + 71.02$	0.99
27	$y = 32.89x + 51.86$	0.99
28	$y = 33.54x + 55.59$	0.98
29	$y = 34.41x + 74.86$	0.98
30	$y = 35.52x + 156.68$	0.97
31	$y = 36.65x + 305.03$	0.96
32	$y = 38.14x + 420.88$	0.96
33	$y = 40.08x + 719.64$	0.87
34	$y = 50.92x + 852.50$	0.75
35	$y = 89.66x - 339.03$	0.96
36	$y = 97.83x - 210.45$	0.97
37	$y = 93.20x + 403.97$	0.97
38	$y = 98.89x + 686.91$	0.95
39	$y = 109.41x + 1,094.30$	0.94
40	$y = 122.45x + 1,436.00$	0.89
14–27	$y = 2.69x + 262.82$	0.99

gaps distally (Fig. 2B), double rami proximally (Fig. 2C), or are represented by two thin but entirely separate ribs instead of a single broad rib (Fig. 2D). The anterior ramus of all double ribs is offset distally (ventrally) relative to that of the posterior ramus; the anterior ramus does not participate in the head of the rib proper. Any articulation with the vertebral column must therefore be via the posterior ramus. When two thin ribs instead of the single broad rib occur, Rib2 bears a groove on its anterior surface that reflects the shape of Rib1.

The unusual costal anatomy of *Caperea* strongly suggests that the first rib of adult individuals is a composite ontogenetic fusion product (Rib1/Rib2) of the first two ribs of juveniles. All subadults and adults in this study have first ribs interpreted as composite. Variability in the ontogenetic timing of rib fusion can be inferred from a comparison of fusion status and total body length (Table 1). The shortest animal with

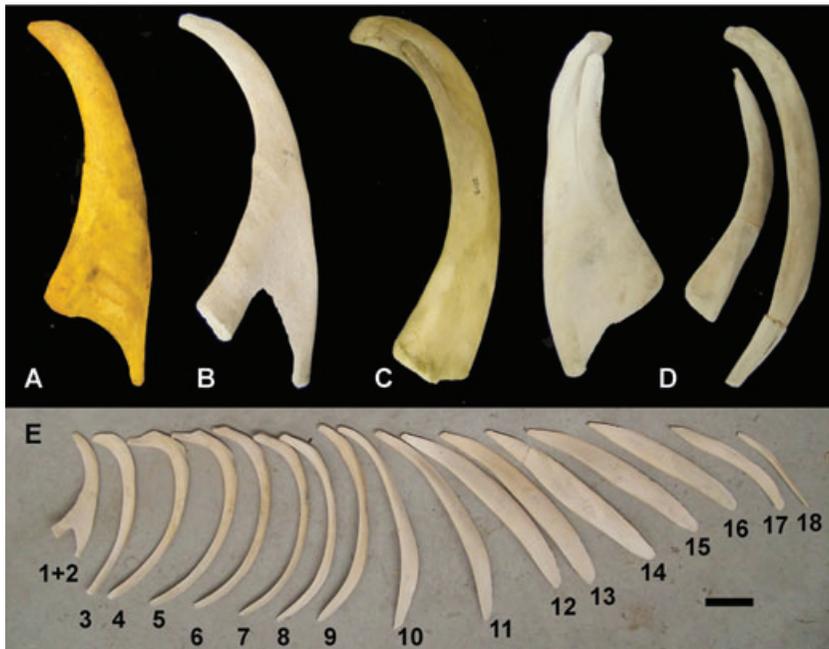


Figure 2. Rib anatomy in *Caperea marginata*. (A) A Rib1/Rib2 composite in an adult (NMNZ, unregistered). (B) Proximal fusion of Rib1/Rib2 in a juvenile (SAM M6110). (C) Proximal separation and distal fusion of Rib1/Rib2 in a juvenile (NMNZ 2119). (D) Proximal separation and distal fusion (right side) and separate ribs (left side) in a juvenile showing bilateral asymmetry (SAM M17364). (E) Left ribs of a juvenile (SAM M6110). Rib1/Rib2 is a composite, ribs 3–5 have two heads separated by a distinct neck, ribs 6–8 have two heads but no distinct neck, ribs 9–10 have a single head, and ribs 11–18 have no head. Scale bar is 10 cm in length.

a composite first rib had a reported body length of 2 m, while the longest animal with separate first and second ribs had a reported body length of 3.34 m. Rib fusion status is taken into account in the assignment of rib identifications below.

A series of 7–8 ribs with circular cross section, simple curvature, and articular heads follows the unusual first rib (Fig. 2E). The most anterior of these possess elongate, flattened necks separating capitular and tubercular heads. Rib 5 (the fourth rib in individuals with a composite Rib1/Rib2) is consistently the last rib with a flattened neck and separate heads. It is followed by 3–4 ribs with two adjacent heads, and then by 1–2 ribs with single heads. The most posterior 8–9 ribs lack heads. The anterior and posterior margins of their flattened blades appear to correspond to the lateral and medial surfaces of anterior ribs. A zone of torsion exists between the medial extremity and the main body of the blade, and the distal (ventral) extremity of the blade is often recurved posteriorly. The most posterior 3–4 ribs decrease rapidly in size, and tiny asymmetrical terminal ribs are sometimes present.

Vertebral Patterning

Secondarily similar vertebrae make determination of series boundaries difficult in all cetaceans. Series identification is further complicated in *Caperea* by the lack

of vertebral articulation facets for posterior ribs and by ontogenetic rib fusion. Nevertheless, definitive criteria for identification of cervical and caudal vertebrae leaves ambiguity only at the thoracolumbar transition, and even there axial markers allow separation with great confidence, if not certainty.

The centra of the seven cervical (C) vertebrae are fused into a single mass in every specimen, although neural arches and spines of vertebrae 6 and 7 are free in the two smallest (neonate) specimens. Most small (young) individuals show centrum gaps at C5/C6 and C6/C7, sometimes revealing the presence of epiphyses (Fig. 3A). Gaps also exist in adult specimens between adjacent cervical neural spines, increasing posteriorly in both dorsoventral and anteroposterior extent (Fig. 3B). These observations suggest that C6 and C7 are incorporated into the cervical mass later in ontogeny than C1–5. The first thoracic vertebra (T1 = vertebra 8) is incorporated into the cervical mass *via* neural spine (but not centrum) fusion in a single individual (SAM M15374). In all other individuals the anterior surface of the T1 centrum is markedly convex and articulates freely with the posterior concave surface of the C7 centrum.

Thoracic (T) vertebrae (Fig. 3E) are broadly divisible into anterior and posterior groups based on transverse process shape and the presence of costal articulations. The first thoracic vertebra (T1) lacks costal facets; its short transverse processes taper to points that are bounded laterally by those of the cervical vertebrae and the second thoracic vertebra (Fig. 3B, E) when placed into estimated life position. Articulation facets for the tuberculum of anterior ribs are always present on the transverse processes of T2–T9 and occasionally on T10. Anterior tubercular facets are arcuate in shape and strongly reinforced; those lying more posteriorly are restricted to the distal margins of the transverse processes. Capitular facets are uniformly absent, although indentations at the T2/3, T3/4, and occasionally T4/5 mid-level centrum/epiphysis junctions suggest the presence of soft tissue connections between the column and the capitular heads of the ribs (Rib 3, Rib4, Rib5) that possess elongated costal necks (Fig. 3C).

Posterior thoracic vertebrae lack rib articulation facets. Their transverse processes are extremely thin dorsoventrally and anteriorly expanded; convex lateral margins give them elliptical outlines (Fig. 3E). The posterior margin of each transverse process overlaps the anterior expansion of the process of the succeeding vertebra, even when the presence of large intervertebral discs is assumed. Transverse process expansions diminish in size posteriorly and are limited to small, anterior projections on the last thoracic vertebra.

Axial indicators of the thoracic/lumbar boundary are transitional (Fig. 3F, G). The transverse processes of lumbar vertebrae have small or nonexistent anterior expansions and lack articulation surfaces for those of adjacent vertebrae. Their lateral margins are straight instead of convex and therefore resemble parallelograms, instead of ellipses, in outline. At the thoracic/lumbar transition metapophysis length shortens dramatically, and metapophysis orientation changes from vertical to horizontal. Neural spines decrease in height and increase in posterior inclination. The lumbar series is constrained anteriorly by the last rib of the thoracic series and posteriorly by the hemal arch facets of the caudal series. When so defined, no specimen in this data set had more than a single lumbar vertebra, and one individual had none.

The first caudal vertebra is identified by the bifurcation of its ventral carina (Fig. 3D). Cd 1 is commonly followed by three vertebrae with distinctive transverse process shapes and muscle scars (Fig 3F); more rarely it is coincident with the first of these (Fig. 3G). The first characteristic vertebra has parallelogram-shaped transverse processes that flare posterolaterally; a ridge marking the margin of the longissimus

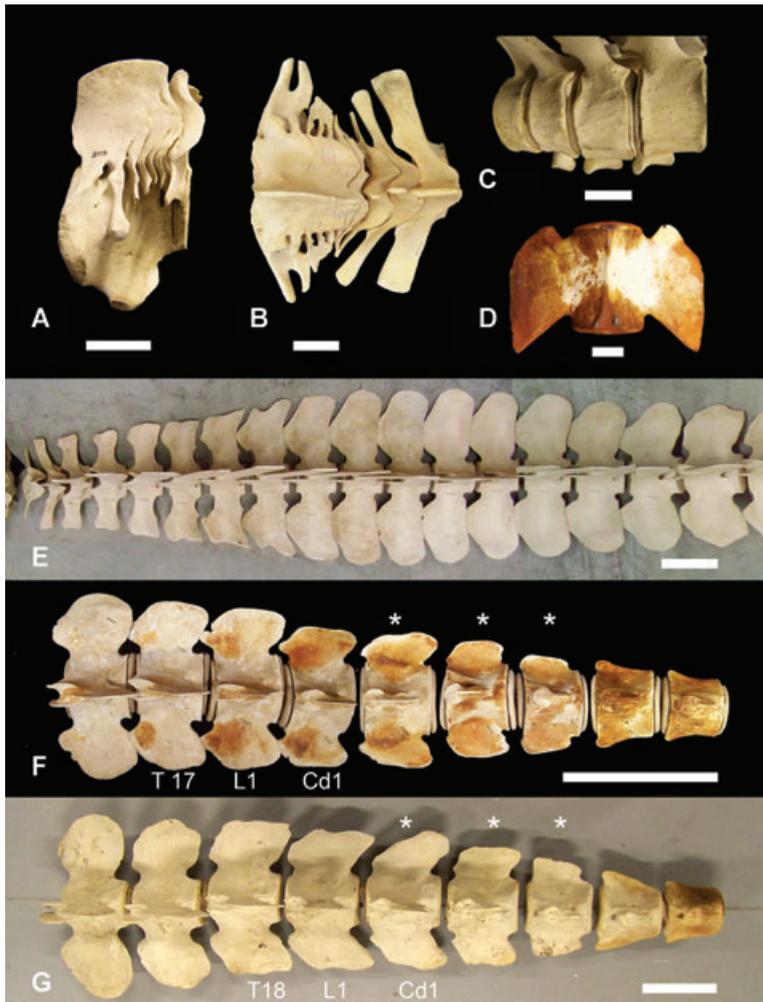


Figure 3. Vertebral morphology in *Caperea marginata*. (A) Fused cervical mass of a dependent calf (NMNZ 2119) in left lateral view showing multiple neural spine gaps and a C6/C7 centrum gap with epiphyses. (B) Vertebrae 1–10 (C1–7, T1–3) in dorsal view in a subadult (SAM M16978) showing the shape and spatial relationships of the T1 transverse processes when articulated. (C) Indentations at the C2/C3 and C3/C4 lateral centrum faces in an adult (NMNZ 2235) suggest soft tissue connections with the capitula of anterior ribs. (D) Bifurcation of the ventral carina in the first caudal vertebra in an adult (NMNZ unreg.). (A) marks the first caudal vertebra. (E) Composite photo of the thoracic series (T1–T17) of a large adult (SAM M23548) in dorsal view. (F) and (G) The thoracolumbocaudal sequence across vertebrae 23–31 in individuals with different vertebral formulas. (F) Composite photo of vertebrae in a dependent calf (SAM M23549) in which the vertebrae represent T16–17L1Cd1–6; (G) An adult (NMNZ 763) in which the vertebrae represent T16–18L1Cd1–5. Note the characteristic transverse process shapes in vertebrae 27–29 (indicated with an asterisk) in both animals despite the different series transitions as dictated by rib counts and the splitting of the ventral carina. Scale bars of A–D = 5 cm; scale bars of E–G = 20 cm.

muscle typically runs across the middle of the centrum. The second vertebra has rectangular transverse processes; the longissimus ridge rises throughout its course from the middle of the centrum to the base of the neural arch. The third vertebra has small transverse processes that flare anteriorly; the longissimus ridge is at the base of the neural arch throughout its length. Bilateral foramina for the passage of intervertebral arteries pierce most caudal centra. Their first occurrence is typically on Cd3, but may also occur on Cd2 or Cd4, often with bilateral asymmetry. These observations coincide with those of Slijper (1936), who reported ontogenetic variation in the occurrence of this foramen across cetaceans. Articulation facets for hemal arches (chevron bones) occur on anterior caudal vertebrae. The last pair of articulation facets is very small, and its left and right chevron halves are often unfused. This last pair of chevrons usually coincides with the last vertebra with a patent neural canal, a transition in shape to shorter and more rounded vertebrae, and by inference with the anterior border of the fluke. This shape transition is subtler in juveniles than in adults because the ontogenetic increase in CL of the anterior caudals has not yet occurred (see above). Prefluke caudal count is 8 or 9, as is fluke count, for a total caudal count of 16–18, unusually low among mysticetes.

Modularity

Using the morphological markers outlined above and assuming Rib1/Rib2 composites when indicated, the 24 individuals of this data set are separable into three different vertebral patterns. The lack of variability is notable, given that previously reported. Vertebral formulas of C7T18L1Cd16–17 = 42–43 (15 individuals) and C7T17L1Cd16–18 = 41–43 (8 individuals) dominate, and differ by a single thoracic vertebra. The thoracolumbar transition occurs between vertebrae 24 and 25 in individuals with 17 thoracics, and between vertebrae 25 and 26 in individuals with 18 thoracics. Because both formulas include a single lumbar, the more posterior location of the thoracolumbar transition is accompanied by a more posterior location of the lumbocaudal boundary (between vertebrae 26 and 27) as well. A single specimen (SAM M23863) has a vertebral formula of C7T18L0Cd18 = ?43. This individual has a single tiny rib associated with T18 (its partner may have been lost during preparation) and therefore lacks lumbar vertebrae entirely. Transverse process shape changes are quite stable along the column, even in individuals with different series counts. This stability is most marked in the characteristic transition of transverse process shapes in the anterior caudal series (Fig. 3F, G).

Unfortunately, the lack of terminal caudals in many individuals makes definitive determination of full caudal counts impossible.

DISCUSSION

Column Dimensions and Size/Age Groups

Kemper and Leppard (1999) screened 32 skeletal and baleen characters and found seven that were good predictors of total body length in *Caperea*. They used curvilinear models, citing continued growth in the structures they measured after axial elongation had ceased. The excellent ability of CL to predict TL across all body sizes documented here (Table 2) suggests that growth of individual vertebrae continues until full body length is reached, albeit at different rates in different column regions. The success of TL prediction is lower in column regions where vertebrae show smaller

changes in CL during life (fused cervical mass and fluke), and higher where changes are greater (posterior thorax to anterior tail). The rather low ability of vertebrae 33–35 to predict TL almost certainly reflects individual differences in the anterior boundary of the fluke, where dimensions change rapidly.

The bimodal distribution of observed and estimated body lengths indicates that the animals in the data set are predominantly adults and dependent calves. Only three subadults were identified. This distribution supports previous suggestions that distressed mothers and calves may strand near the time of parturition and that dependent calves may strand at the time of weaning (Sergeant 1982, Kemper and Leppard 1999).

Rib Patterning

Anomalies in rib patterning appear to be common in mammals, but quantitative data are restricted to a few mammalian orders. Supernumerary cervical and lumbar ribs are the most commonly reported patterning defects, and occur spontaneously with relatively high frequency in humans, rodents, and rabbits (Chernoff and Rogers 2004). They may also be induced by maternal stress or by exposure to retinoic acid or xenobiotics during organogenesis (Kawanishi *et al.* 2003, Chernoff and Rogers 2004). Turner (1871) and Slijper (1936) documented multiple examples of supernumerary cervical ribs associated with the last cervical vertebra in both odontocete and mysticete cetaceans. The terminations of these ribs may be bluntly truncated, connected to the first thoracic rib via soft tissue, or fused with the first thoracic rib to form a double-headed rib (Fig. 4A–D).

Double-headed C7/T1 rib fusions are frequent enough in mysticete cetaceans that Gray (1870) used them as taxonomic characters, although subsequent workers

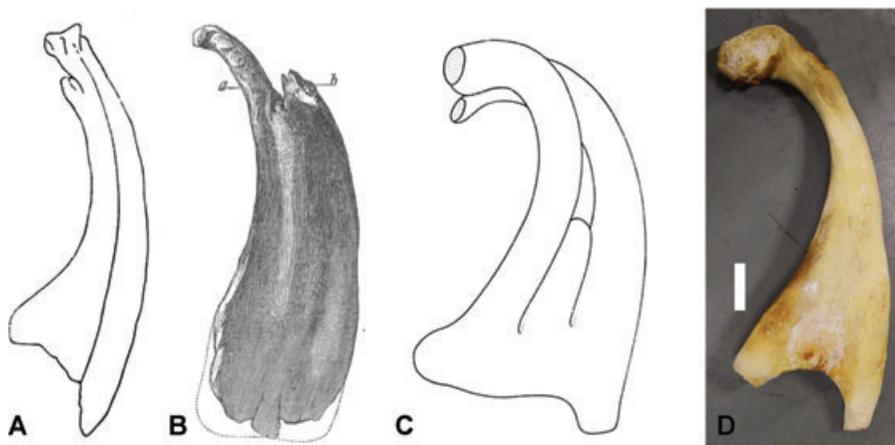


Figure 4. Costal anomalies in mysticete cetaceans. (A) A double-headed C7/T1 fused rib of *Balaenoptera musculus*, originally described as *Sibbaldius borealis* (Gray 1866); (B) A broken double-headed C7/T1 fused rib of an unknown mysticete from the Cape of Good Hope (Turner 1871); (C) A double-headed C7–T1 fused rib from the mysticete *Eschrichtius robustus* (Slijper 1936), republished from an image originally figured by van Beneden (1868) as *Rhachianectes glaucus*; (D) A single-headed T1/T2 composite rib of *Eubalaena australis* (NMNZ 2239), scale bar = 10 cm.

have regarded them as individual variants (Turner 1871, Slijper 1936). Despite occasional fusion to thoracic ribs, the previously described cervical supernumerary ribs of cetaceans do not articulate with the sternum, a key indicator of the location of the forelimb and of the cervical/thoracic transition. Their small size and lack of a ventral component suggest that they represent only the most proximal of the three costal patterning compartments identified in murine studies of rib development (Aoyama *et al.* 2005).

The composite first rib of *Caperea* differs from C7/T1 rib fusions seen in other cetaceans in several key respects. Most notably, the *Caperea* composite cannot be considered anomalous: it occurs in all adult specimens examined. Secondly, the anterior ramus of the composite bears an unambiguous ventral facet for articulation with the sole sternal facet, the classic marker of the anterior margin of the thorax. This cannot be a cervical rib. Finally, the *Caperea* composite has a single head, formed from its posterior ramus; the anterior ramus is displaced distally and has no apparent access to the short and gracile transverse processes of the first thoracic vertebra. These observations argue that the anterior ramus of the *Caperea* composite represents the first thoracic rib, and that the posterior ramus therefore represents the second thoracic rib. A search of the literature yielded no other reports of single-headed T1/T2 rib fusion in Cetacea, but a bilateral example of such a composite was identified in an individual of *Eubalaena australis* (NMNZ 2239, Fig. 4D) during the course of this study. This occurrence raises the possibility that thoracic rib fusion may be associated with aspects of cervical vertebral fusion, relatively large head size, and feeding style shared by *Caperea* and *Eubalaena*.

The functional correlates of thoracic rib fusion in *Caperea*, if any, are speculative. Rib1/Rib2 fusion suggests restriction of flexibility within the thorax, an axial region noted for its rigidity. The presence of overlapping thoracic transverse processes and the broad plate-like ribs support this interpretation. There are also several anatomical indicators of restricted movement at or near the cervicothoracic junction. The most notable of these is the deep concavo-convex articular surface of the fused cervical mass and the T1 centrum. The depth of this articulation also brings the transverse processes of C7 and T2 into closer proximity, making the articulation of a T1 rib with the short T1 transverse process unlikely if not impossible. Additionally, metapophyses of anterior thoracic vertebrae are located on the transverse processes, restricting both sagittal and lateral rotation between adjacent vertebrae. This contrasts with the condition observed in other mysticetes (*e.g.*, *Balaenoptera acutorostrata*) in which anterior thoracic metapophyses are located more medially on the neural arches, and are therefore less able to constrain rotation. The lumbos is classically a region of great column flexibility, and its near elimination in *Caperea* also indicates limited precaudal movement. These anatomical predictors of postcranial rigidity conflict with the only analysis of *Caperea* swimming style (Ross *et al.* 1975), which reports extensive flexing of the animal's entire body based on a filmed sequence.

Vertebral Patterning and Modularity

Recognition of the first rib as a Rib1/Rib2 composite affects series identifications in *Caperea*, because rib count has traditionally been used to confirm the T/L boundary in the absence of posterior thoracic rib facets. When rib fusion is taken into consideration, *Caperea* column counts are very stable, with only two dominant variants: C7T18L1Cd16–17 and C7T17L1Cd16–18. The composite rib does not affect cervical count, as axial patterning of the cervicothoracic vertebral column is

traditional and the formal criterion of the first thoracic as the vertebra associated (albeit distantly) with the first free rib with a sternal articulation is still met. *Caperea* therefore does not represent an additional exception to the mammalian constraint on cervical count.

The elongate thorax and extremely low lumbar count characteristic of *Caperea* might be viewed as support for a reciprocal relationship between the thoracic and the lumbar series in *Caperea*. Reciprocity of count is a signature of the homeotic movement of patterning gene expression borders and is a hallmark of the terrestrial modularity characteristic of most mammals and archaeocete cetaceans (Buchholtz 2007). The data reported here make this unlikely. The elongation of the *Caperea* thorax relative to that of other mysticetes is primarily the result of increased thoracic centrum length instead of count, as thoracic counts of 15 or fewer are known from fin (*Balaenoptera physaluslae*), blue (*Balaenoptera musculus*) and both northern (*Eubalaena glacialis*) and southern (*E. australis*) right whales (Slijper 1936). Additionally, with a single exception, lumbar count in *Caperea* is stable at one: it does not vary reciprocally with the (admittedly small) variations in thoracic count. Instead, developmental linkage between the lumbar and caudal series is suggested by the parallel reduction of count in these two series relative to those observed in other mysticetes. This similarity supports origin of the unusual axial anatomy of *Caperea* via homologous elongation of thoracic vertebrae and meristic reduction across the developmentally linked lumbar and caudal series. This lumbar/caudal, instead of thoracic/lumbar, linkage signals the presence of neocete rather than terrestrial modularity (Buchholtz 2007). These data therefore support the presence of neocete modularity in all living cetaceans and locate the first occurrence of neocete modularity before the Oligocene common ancestry of living mysticetes.

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