Vertebral osteology in Delphinidae (Cetacea)

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Vertebral anatomy in delphinid cetaceans exhibits marked heterogeneity. Description and functional interpretation of this variability is facilitated by the recognition of structural units along the column whose boundaries transgress those of the classical mammalian series. Vertebral anatomy of the killer whale (*Orcinus orca*) and the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) lie near the ends of an anatomical continuum. Primitive columns resemble those of living delphinapterid delphinoids in exhibiting minimal intervertebral variation, low counts and spool-shaped vertebrae. Derived columns are more regionalized, displaying traits that limit mobility in the anterior torso, enhance flexibility at the point of neural spine syncliny and increase dorsoventral displacement of prefluke vertebrae. Reconstruction of the historical sequence of anatomical innovations identifies syncliny as an early and critical step in delphinid column evolution. Trait distribution supports evolutionary isolation of *Pseudorca* and *Orcinus* from remaining delphinids, inclusion of *Feresa* and *Peponocephala* among delphinine delphinids, and subdivision of delphinines on the basis of centrum dimensions, neural spine inclination and count. Details of vertebral anatomy can also be used to place fragmentary postcranial material, particularly that of fossils, in functional and evolutionary context. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **140**, 383–401.

ADDITIONAL KEYWORDS: anatomy – evolution – postcranium – vertebrae.

INTRODUCTION

Cetaceans are obligate marine mammals with an Eocene ancestry among terrestrial ungulates. Taxonomic diagnosis is made primarily on the basis of tympanic and dental specializations (Thewissen, 1994; Luo, 1998; Berta & Sumich, 1999), but among living mammals, whales are easily recognized by the radical transformations of the skull, limbs and axial skeleton required for life in the water.

Monophyly of the odontocete superfamily Delphinoidea has been recognized on the basis of both molecular (Milinkovich, Orti & Meyer, 1993, 1994; Hasegawa, Adachi & Milinkovitch, 1997) and morphological (Heyning, 1989; Fordyce & Barnes, 1994) evidence. Relationships of its three extant families (Monodontidae, Phocoenidae, Delphinidae), however, are disputed (Mead, 1975; Heyning, 1989; Arnold & Heinsohn, 1996; Waddell *et al.*, 2000). Delphinids are characterized by lack of the posterior sac of the nasal passage (Fordyce, 1994) and by a reduced posterior end of the left premaxilla (Heyning, 1989; Fordyce & Barnes, 1994). Since its Miocene origin, this speciose (17–19 genera, 34–36 species) and geographically widespread family has undergone rapid radiation.

Within Delphinidae, relationships are poorly resolved (LeDuc, 2002); genera are commonly yet variably assigned to five or six subfamilies. Neither morphological (Kasuya, 1973; Mead, 1975; de Muizon, 1988; Perrin, 1989; Barnes, 1990) nor molecular (LeDuc, Perrin & Dizon, 1999; LeDuc, 2002) data sets fully resolve subfamilial placement of extant genera. The consensus phylogeny presented in Figure 1 draws primarily on the morphological work of Mead (1975), de Muizon (1988) and Perrin (1989), but differs in some respects from each. All three authors isolate the genus *Cephalorhynchus* at the subfamilial level, but additional monotypic subfamilies are erected for *Orcaella* (by Perrin) and for *Lissodelphis* (by both Perrin and Mead). Both de Muizon and Perrin place *Peponocephala* in the Orcininae instead of the Delphininae, the affiliation suggested by Mead. de Muizon also recognizes two delphinine subgroups

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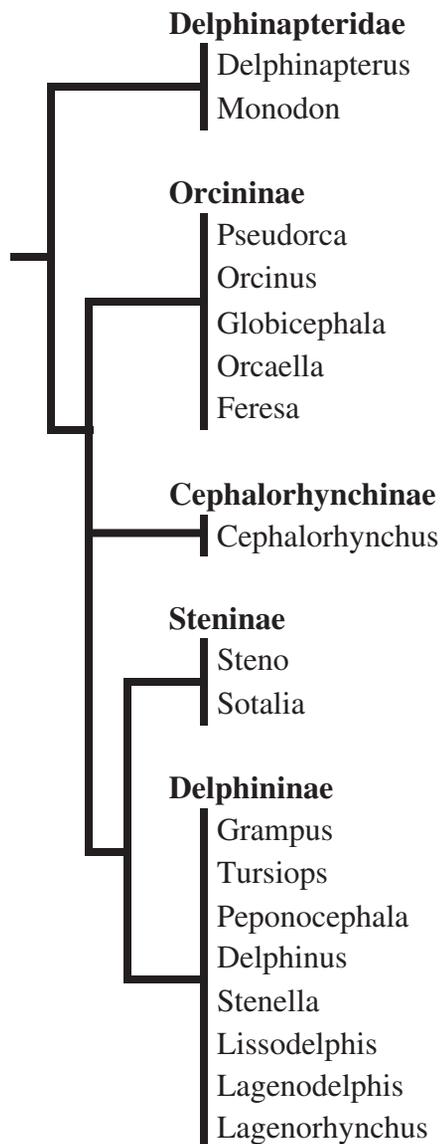
Figure 1. Consensus phylogeny of the Family Delphinidae based on the work of Mead (1975), de Muizon (1988) and Perrin (1989). The Delphinapteridae serves as the outgroup.

trum length (spool vs. disc shape). We initiated this study with the hypothesis that vertebral variation is hierarchically rather than randomly distributed, and that this distribution pattern can be used both to infer the history of trait acquisition and to contribute to the resolution of phylogenetic relationships among delphinids. Because early archeocete whales (Slijper, 1936; Thewissen, Hussain & Arif, 1994; Thewissen, Madar & Hussain, 1996; Buchholtz, 1998, 2001; Gingerich, 1998, 2003; Thewissen & Bajpai, 2001) and the delphinapterid odontocetes used as the outgroup in this project are characterized by low vertebral counts, spool-shaped centra and nearshore habitats, we identified these traits as primitive, and predicted that high counts would be associated with discoidal centra and pelagic habits.

MECHANICAL EFFECTS OF VERTEBRAL VARIATIONS

In this study we describe key aspects of vertebral osteology that differ either along the column of a single delphinid and/or among delphinid taxa. In the functional interpretation of this anatomy, we draw on previous work of general application to all vertebrates (e.g., Slijper, 1946; Filler, 1986; Gál, 1993; Walker & Liem, 1994; McGowan, 1999; Hildebrand & Goslow, 2001) as well as more specifically on previous descriptions of the cetacean vertebral column and/or musculature (e.g., Slijper, 1946, 1961; Smith, Browne & Gaskin, 1976; DeSmet, 1977; Strickler, 1980; Pabst, 1990, 1993, 1996, 2000; Rommel, 1990; Long *et al*., 1997), and especially on the monographic work of E. J. Slijper (1936).

The dolphin vertebral column has been described as a variably flexible beam (Long *et al*., 1997; Pabst, 2000). Among the factors known to affect that flexibility are muscular and ligamentous tissue, intervertebral disc composition and size, and vertebral structure and interference (Gál, 1993; Long *et al*., 1997). We acknowledge and reiterate the warning offered by Long *et al*. (1997) that skeletal features can by themselves only partially predict column function.

Tetrapod vertebrae consist of a basal centrum, typically with neural and (in caudal vertebrae) ventral (haemal) midline processes. These units may be elaborated by accessory outgrowths for muscle attachment and/or skeletal articulation. Movement between vertebrae may be sagittal (about a horizontal axis that runs across the anterior centrum face at mid height), lateral (about a vertical axis that runs through the centre of the anterior centrum face) or rotational (around the long axis of the vertebral column). As in most mammals, the dominant plane of vertebral movement in Cetacea is sagittal, and rotational movement is minimal. Variations in vertebral structure

(*Lagenorhynchus*, *Lagenodelphis* and *Lissodelphis*; *Grampus*, *Tursiops*, *Delphinus* and *Stenella*). The hierarchical placement of the subfamilies in the consensus phylogeny follows de Muizon, as both Mead and Perrin present their proposals as non-hierarchical classifications.

Despite the physical constraints of an obligate aquatic environment (see e.g., Motani, 2002), cetaceans display a considerable range of behaviour and internal morphology. This variability extends to the vertebral column of delphinids, where it is most evident in extremes of count (47–91 vertebrae) and cen-

that constrain or enhance movement between adjacent vertebrae can be grouped into considerations of centrum shape and spacing, process structure and orientation, count and accessory structures.

CENTRUM SHAPE AND SPACING

Centrum shape (face curvature, width, height) affects not only the angle through which a vertebra can rotate but also the absolute distance of displacement of a centrum's posterior face relative to its anterior face.

Face curvature. Delphinid centrum faces range from flat to gently convex in profile. Given constant intervertebral spacing, rounded faces enhance rotation by reducing interference of centrum margins on adjacent vertebrae.

Centrum length. Delphinid centra range from spool-like to discoidal in shape. Given constant angular rotation, increased centrum length increases the absolute displacement of the posterior face of a vertebra from the axis of the vertebra anterior to it.

Centrum width and height. Vertical and horizontal dimensions of delphinid centra vary both in absolute size and in relationship to each other. Interference between adjacent vertebrae separated by a given intervertebral space and rotated through a given angle increases as dimensions of the centrum faces increase.

The combined effects of extremes of centrum face curvature and centrum length are shown diagrammatically in Figure 2. Vertebrae with low curvature and short centrum length allow little intervertebral rotation or displacement, but column elasticity can be predicted as the result of the high ratio of intervertebral disc to bone. Vertebrae with high curvature and short centrum length allow intervertebral rotation with minimal absolute displacement. Vertebrae with low curvature and long centrum length produce rigid columns with minimal rotation at a restricted number of intervertebral sites, whereas those with high curvature and long centrum length enhance both rotation and absolute displacement.

The mechanical effects of variable intervertebral disc length in *Delphinus delphis* were evaluated experimentally by Long *et al.* (1997). They found that disc length was greater in caudal than in precaudal sites, and was negatively correlated with initial bending stiffness in both extension and flexion. An X-ray of an adult specimen of the dolphin *Stenella longirostris* (Crovetto, 1991: 140) indicates that intervertebral discs are noticeably longer in vertebrae near the fluke base than at adjacent sites. Unfortunately neither fresh tissue nor X-rays are consistently available for interspecific comparisons, and intervertebral disc length remains an undocumented variable in this study.
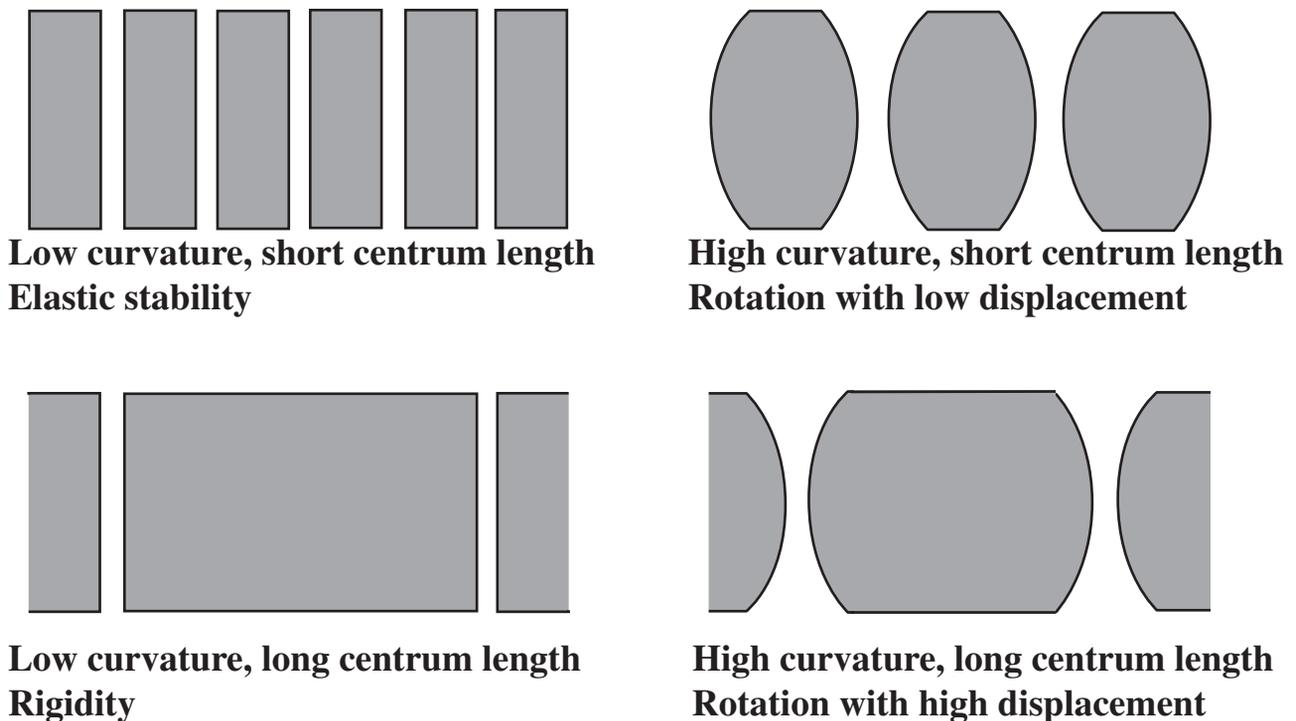

Low curvature, short centrum length
Elastic stability

High curvature, short centrum length
Rotation with low displacement

Low curvature, long centrum length
Rigidity

High curvature, long centrum length
Rotation with high displacement

Figure 2. Diagrammatic presentation of vertebral centra in lateral view to demonstrate the variations in face curvature and dimensions that affect intervertebral movement.

PROCESS STRUCTURE AND ORIENTATION

Neural, haemal and transverse processes act as sites of muscle origin and insertion. Changes in attachment sites alter the resulting torque or moment of a given muscle system. Effects of variations in process structure and orientation on sagittal rotation of a vertebra are summarized below.

Process height. Given constant muscle attachment sites and process orientations, elevation of the muscle's point of origin will increase the distance between force application and the centrum, through which the axis of vertebral rotation passes. As a result, both the length of the effective in-lever and the mechanical advantage of the associated muscle system increase (Walker, 1965; McGowan, 1999). This increase in mechanical advantage comes at the cost of a decrease in angular rotation about the axis and of the velocity ratio. Taller neural processes also reduce the amount of angular rotation possible before interference between adjacent processes occurs. Several authors (Smith *et al*., 1976; Fish & Hui, 1991; McGowan, 1999) have noted the association of tall neural processes, typical of the torso, with increased mechanical advantage in cetaceans. Long *et al*. (1997) experimentally documented the association of tall neural processes with column stability in *Delphinus delphis*. The shorter processes immediately anterior to the fluke are conversely associated with low mechanical advantage but a greater angular rotation and velocity ratio.

Process orientation. Given constant muscle attachment sites and lengths, the inclination of processes changes the line of muscle action and the effective lever arm of the system. Any change that brings the angle between force and lever arm closer to the perpendicular will increase the torque of the system (Hildebrand & Goslow, 2001).

Muscle length. Muscle length varies as the result of differences in vertebral process geometry. Given a constant proportion of length contraction and constant contraction time, longer muscles have greater contraction velocity (Kardong, 1998).

Process length. Processes also have length in the antero-posterior direction. For a given centrum length, increases in process length will minimize rotation by increasing interference between adjacent vertebrae during rotation in the plane of the process.

VERTEBRAL COUNT

Given constant vertebral length and intervertebral spacing, increased count must increase not only the total length of the column but also the number of sites for rotation and the total absolute displacement of the posterior column from the axis of the first vertebra. Somewhat counterintuitively, however, columns of high count are typical of smaller species and consistently display multiple traits associated with limited intervertebral mobility, especially in the anterior part of the column (see below).

ACCESSORY STRUCTURES

Accessory structures (metapophyses, zygapophyses, ribs) may limit or enhance muscle action and rotation between vertebrae.

Metapophyses. Metapophyses are muscle attachment sites located on the neural processes, typically at the junction of neural arch and spine. They provide mid spine insertion sites for the multifidus and longissimus muscle systems, which are the main effectors of column extension. Elevation of metapophyses increases in-lever length of attached muscles, increasing mechanical advantage. Both Lütken (1888) and Howell (1930) described metapophysis location and distribution, and Slijper (1936) used metapophyseal traits as major characters in his allocation of cetacean species to locomotor groups ('Stufen'). Absence of metapophyses indicates the absence of mid spine muscle attachment sites. Regionally, metapophyses of one vertebra may also overlap neural spines of the next cranial vertebra, constraining intervertebral movement (Long *et al*., 1997).

Zygapophyses. Zygapophyses are intervertebral articulation sites that restrict vertebral rotation in axes that intersect the plane of the zygapophyseal surface. Zygapophyses are present on only cervical and anterior thoracic vertebrae in most delphinids.

Ribs. Ribs, especially those with sternal connections, stabilize the thorax and limit rotation between the vertebrae with which they articulate (Filler, 1986).

SUMMARY

Structural variations of vertebrae may constrain or enhance intervertebral motion. As a general rule, vertebrae in flexible column areas display some combination of high centrum face curvature, relatively small centrum face dimensions, and neural processes with high angular inclination, limited height and/or short anterior–posterior length. Such vertebrae bear metapophyses, typically located close to the centrum; they lack zygapophyses and ribs. Vertebrae in more highly stabilized column areas typically have flat centrum faces with relatively large dimensions, and tall, long and erect neural processes. Metapophyses may be regionally absent; where present they are often elevated. Zygapophyses and ribs may be present.

MATERIAL AND METHODS

We have examined and measured postcranial skeletons of members of the following delphinid genera: *Cephalorhynchus*, *Delphinus*, *Feresa*, *Globicephala*, *Grampus*, *Lagenodelphis*, *Lagenorhynchus*, *Lissodelphis*, *Orcaella*, *Orcinus*, *Peponocephala*, *Pseudorca*, *Sotalia*, *Stenella*, *Steno* and *Tursiops*, as well as of the two delphinapterid genera, *Monodon* and *Delphinapterus*. For comparison, we have also measured specimens of the phocoenids *Phocoena*, *Phocoenoides* and *Neophocoena*, of the river dolphins *Inia*, *Pontoporia*, *Lipotes* and *Platanista*, and the partial skeletons of a broad sampling of fossil species. Specimen numbers and museum sources of the delphinid specimens are listed in Table 1. Complete or nearly complete individuals were measured whenever possible, although terminal caudal vertebrae were frequently missing. Individuals were adult or subadult as evaluated by the degree of epiphyseal fusion. All fossil specimens were fragmentary.

A suite of measurements was used to describe the individual vertebrae of each specimen (Fig. 3). Digital calipers were used to measure centrum length (CL, ventrally), centrum width (CW, anteriorly) and centrum height (CH, anteriorly). Dimensions and inclinations of neural processes and their component arches and spines were measured from scaled images of each vertebra. Neural process height (NPH) is the vertical distance from the tip of the neural process to the (extended) horizontal line along the dorsal centrum surface. Neural arch height (NAH) is the running distance from the metapophysis through the centre of the arch to this same centrum surface. Neural arch inclination (NAI) is the angle between this line and the horizontal. Neural spine height (NSH) is the running distance from the dorsal tip of the spine through the centre of the spine to the horizontal line at the level of the metapophysis. Neural spine inclination (NSI) is the angle between this line and the horizontal. Anterior inclinations are represented by values >90° and posterior inclinations by values <90°. A process is said to have an elevated metapophysis when NAH > NSH. Total and series counts from examined specimens are reported, and are supplemented by total counts from the literature to reflect variation due to intraspecific differences and/or specimen incompleteness.

Vertebral measurements of each specimen were plotted by column location. Morphological and/or dimensional discontinuities were used to identify structural subunits of the column. Functional implications of these structural series were then proposed, and variations among delphinid genera noted. Osteological traits were evaluated for polarity using the delphinapterids *Delphinapterus leucas* and *Monodon monoceros* as primary outgroups. These polarized traits were then mapped on to the consensus phylogeny to predict the historical sequence of trait acquisition and to identify possible instances of homoplasy. Implications of trait distribution for delphinid phylogeny and for the evolutionary interpretation of the incomplete columns of extinct taxa were also addressed.

RESULTS

As the work of E. J. Slijper (1936, 1946) attests, details of dolphin postcranial anatomy vary complexly and gradationally. We have chosen to present detailed dimensional data and photographic images of the osteology of two delphinid species, *Orcinus orca* and *Lagenorhynchus acutus*, species that lie near the extremes of the morphological continuum and are known from multiple specimens. We extend this presentation with short descriptions of individual traits and then chart their distribution among the extant species studied.

DESCRIPTION OF MORPHOLOGICAL EXTREMES

Orcinus orca, the killer whale, is a large dolphin with a worldwide distribution. The vertebral count for the
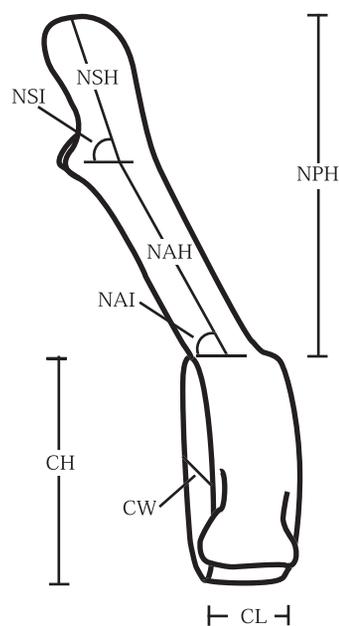

Figure 3. Left lateral view of an anterior caudal vertebra with measurements used in this study indicated. CL = centrum length; CH = centrum height; CW = centrum width; NAH = neural arch height; NAI = neural arch inclination; NPH = neural process height; NSH = neural spine height; NSI = neural spine inclination.

Table 1. Delphinid and delphinapterid cetacean specimens examined. Series counts of examined specimens are supplemented with species ranges cited in the literature. Subfamilial membership reflects that of the consensus phylogeny. TC = total count; MaxC = maximum count range for species; ME = metapophysis elevation; Syn = neural spine syncliny; 2R = secondary rise in CL/CH; TCL = average thoracic CL/CH; LCL = average lumbar CL/CH; ML = regional metapophysis loss; NPH = average lumbar neural process height. Institutional abbreviations: AMNH = American Museum of Natural History; LACM = Los Angeles County Museum; MCZ = Museum of Comparative Zoology, Harvard University; USNM = National Museum of Natural History. '+' = terminal caudal vertebrae absent. Missing data were either inaccessible or not collected

Species	Specimen	Series count	TC	MaxC	Citation for maximum count	ME	Syn	2R	TCL	LCL	ML	NPH
Delphinapteridae												
Delphinapterus leucas	USNM 571021	Cv7T11L7Cd25+	50+	49–54	Brodie (1989)	no	no	no	1.10	1.24	no	2.67
Monodon monoceros	AMNH 14156	Cv7T11L9Cd23+	50+	50–55	Hay & Mansfield (1989)	no	no	no	0.98	1.17	no	1.57
Orcininae												
Pseudorca crassidens	AMNH 99681	Cv7T10L9Cd21+	47+	47–52	Odell & McClune (1999)	no	no	no	1.05	1.36	no	1.75
Pseudorca crassidens	MCZ 30330	Cv7T9L11Cd18+	45+			no	no	no	0.98	1.26	no	2.10
Orcinus orca	USNM 23004	Cv7T11L10Cd26+	54+	50–54	Dahlheim & Heyning (1999)	yes	no	no	0.75	0.94	no	2.17
Orcinus orca	AMNH 215270	Cv7T12L9Cd11+	37+			yes	no	no	0.73	0.91	no	
Orcinus orca	AMNH 34276	Cv7T11L11Cd24	53			yes	no	no		0.97	no	2.00
Globicephala macrorhyncha	USNM 22571	Cv7T8L13Cd26	54	58–61	Bernard & Reilly (1999)	yes	yes	no	0.69	1.05	no	2.46
Orcaella brevirostris	MCZ 21929	C7T12L15Cd17+	51+	58–60	Arnold & Heinsohn (1996)	yes	yes	yes	0.91	0.84	no	1.92
Feresa attenuata	MCZ 51458	Cv7T11L17Cd34	69	67–70	Ross & Leatherwood (1994)	yes	yes	yes	0.96	0.86	yes	3.11
Cephalorhynchinae												
Cephalorhynchus commersonii	USNM 550156	Cv7T12L13Cd31	62	61–66	Goodall (1994)	yes	yes	yes	0.83	0.74	no	2.68
Steninae												
Steno bredanensis	USNM 550221	Cv7T12L15Cd28	62	65–67	Miyazaki & Perrin (1994)	yes	yes	yes	0.93	0.86	no	3.71
Sotalia fluviatilis	MCZ 7097	Cv7T12L12Cd23	56	53–55	da Silva & Best (1994)	yes	yes	yes	0.98	0.95	no	2.82
Delphinae												
Grampus griseus	USNM 504328	Cv7T12L16Cd31	66	68–69	Kruse, Caldwell & Caldwell (1999)	yes	yes	yes	0.85	0.78	yes	2.67
Tursiops truncatus	MCZ 7899	Cv7T12L16Cd27+	62+	59–67	Wells & Scott (1999)	yes	yes	yes	0.93	0.82	yes	3.18
Tursiops truncatus	AMNH 120920	Cv7T12L19Cd29+	67+			yes	yes	yes	1.00	0.83	yes	
Tursiops truncatus	USNM 550422	Cv7T10L16Cd24+	57+			yes	yes	yes	1.00	0.95	yes	2.91
Peponocephala electra	USNM 504948	Cv7T12L19Cd40	78	81–82	Perryman et al. (1994)	yes	yes	yes	0.92	0.75	yes	3.15
Delphinus delphis	AMNH 130119	Cv7T13L23Cd30	73	73–74	Evans (1994)	yes	yes	yes	0.82	0.62	yes	
Delphinus delphis	USNM 550868	Cv7T13L22Cd31+	73+			yes	yes	yes	0.80	0.61	yes	2.72
Stenella frontalis	USNM 571139	Cv7T12L20Cd33	72	67–72	Perrin, Caldwell & Caldwell (1994)	yes	yes	yes	0.81	0.68	yes	
Stenella longirostris	USNM 500017	Cv7T14L18Cd34	73	69–77	Perrin & Gilpatrick (1994)	yes	yes	yes	0.99	0.76	yes	2.82
Stenella coeruleoalba	USNM 504350	Cv7T14L20Cd38	79	71–80	Perrin, Wilson & Archer (1994)	yes	yes	yes	0.75	0.59	yes	2.96
Lissodelphis borealis	LACM 43472	Cv7T15L33Cd34	89	88–92	Jefferson et al. (1994)	no	no	yes	0.82	0.44	no	1.49
Lissodelphis borealis	USNM 484929	Cv7T15L33Cd31+	86+			no	no	yes	1.08	0.59	no	1.86
Lagenodelphis hosei	MCZ 54379	Cv7T14L24Cd33+	78+	78–81	Perrin, Leatherwood & Collet (1994)	yes	yes	yes	0.96	0.72	yes	2.86
Lagenorhynchus acutus	MCZ 62382	Cv7T14L23Cd35+	79+	77–82	Reeves et al. (1999)	yes	yes	yes	0.70	0.52	yes	2.50
Lagenorhynchus acutus	USNM 504754	Cv7T13L22Cd37	77			yes	yes	yes	0.77	0.59	yes	2.66
Lagenorhynchus acutus	MCZ 60939	Cv7T14L25Cd36	82			yes	yes	yes	0.75	0.55	yes	2.39
Lagenorhynchus acutus	MCZ 62380	Cv7T14L22Cd40	83			yes	yes	yes	0.75	0.58	yes	2.51
Lagenorhynchus albirostris	MCZ 5322	Cv7T14L24Cd46	91	88–94	Reeves et al. (1999)	yes	yes	yes	0.61	0.45	yes	2.85
Lagenorhynchus albirostris	USNM 550208	Cv7T13L24Cd47	91			yes	yes	yes	0.66	0.49	yes	2.72
Lagenorhynchus obliquidens	USNM 504851	Cv7T12L24Cd32	75	72–76	Brownell, Walker & Forney (1999)	yes	yes	yes	0.72	0.52	yes	2.72

species, Cv7,T11–13,L10–12,Cd20–24 = 50–54 (Dahlheim & Heyning, 1999), is among the lowest for any dolphin. AMNH 34276 (Fig. 4A) is a large adult animal, with a total CL of 5349 mm. All seven cervical vertebrae are fused (Fig. 5A). Thoracic, lumbar (Fig. 5B) and anterior caudal (Fig. 5C) vertebrae are relatively uniform in shape, with elongate centra and nearly circular cross-section CH ≈ CW (Fig. 4A). The longest vertebrae occur in the mid column, with CL/CH ≈ 0.92. CL decreases in the prefluke vertebrae (Fig. 5D), which are laterally compressed (CH > CW). Neural processes average 2.0 times centrum height, and all neural spines incline posteriorly – there is no reversal of spine inclination. Metapophyses are present on all lumbar vertebrae, and are elevated

(NAL > NSL) in the posterior lumbos and anterior tail. The last nine caudal vertebrae are dorsoventrally compressed, lack processes and have very short centrum length; in life they supported the fluke (Fig. 5E).

Lagenorhynchus acutus, the Atlantic white-sided dolphin, is a mid size pelagic delphinid. Reported vertebral counts are Cv7,T14–15,L18–22,Cd38–41 = 77–82 (Reeves *et al.*, 1999), among the highest in the Delphinidae. MCZ 60939 (Fig. 4B) has 82 vertebrae and a total postcranial length of 1705 mm. The cervical vertebrae (Fig. 5F) are highly discoidal and the first four cervicals are fused. Thoracic vertebrae have posteriorly inclined spines and nearly circular cross-sections (CH ≈ CW, Fig. 4B). Anterior lumbars have erect neural arches and spines; metapophyses are absent or effectively absent on L9–19 (Fig. 5G). Posterior lumbar and anterior caudal vertebrae have anteriorly inclined neural arches and spines; they also bear elevated metapophyses (Fig. 5H). Reversal of spine orientation (syncliny) occurs in the mid caudals, at vertebra 60 (Fig. 5I). The shortest vertebrae occur in the midcolumn, immediately before the synclinal point, with CL/CH ≈ 0.40. Tail stock vertebrae are laterally compressed and longer than torso or fluke vertebrae (Fig. 5J). The last 12 caudal vertebrae are dorsoventrally compressed and supported the fluke.
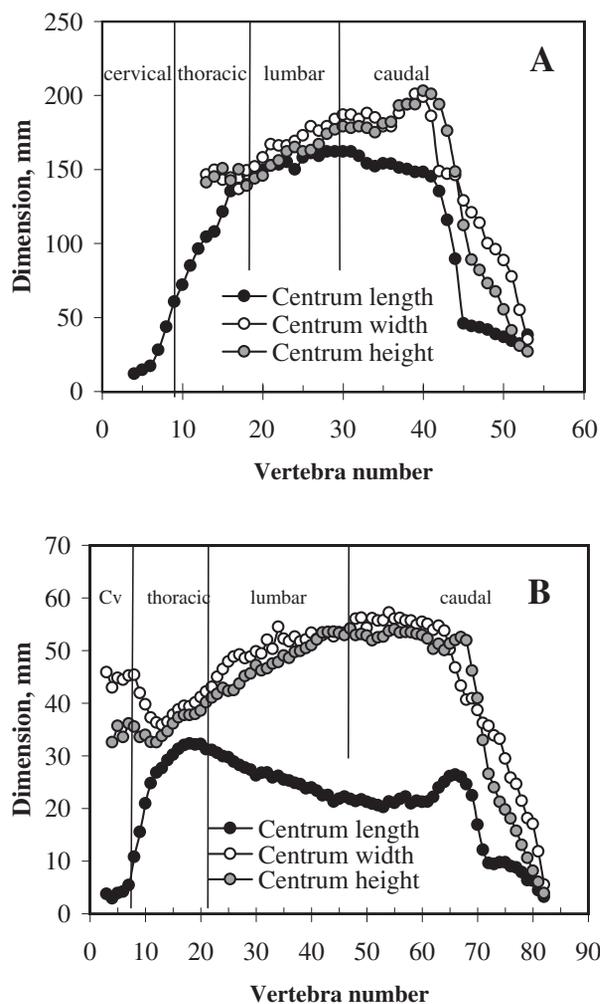
TRAIT ANALYSIS

The traits used for functional and evolutionary analysis are discussed below. In each case, trait expression is described in delphinids and compared with that in delphinapterids. Delphinapterids are broadly recognized (Heyning, 1989; Arnold & Heinsohn, 1996; Waddell *et al.*, 2000) as lying outside the Family Delphinidae but inside the Superfamily Delphinoidea, making them an appropriate outgroup.

Vertebral count. Total count in *Delphinapterus leucas* is 49–54 (Cv7,T11–12,L9,Cd22) (Brodie, 1989). Like living delphinapterids and almost all fossil odontocetes, early delphinids must have had very low total counts (≈ 50). Within the family, cervical count is fixed (at seven), and thoracic count has a very small range (8–14). Lumbar count equals or exceeds thoracic count in all genera except *Pseudorca* and *Orcinus*. Almost all increments to total count are to the lumbar and caudal series (Fig. 6A). At low and intermediate total counts (≈ 50–70) lumbar and caudal counts increase in approximately a 1 : 1 ratio. At high total counts (>70), lumbar count appears to be 'capped' (at ≈24) and all additional increase is in the caudal series. The sole exception to this pattern is *Lissodelphis*, in which the very high lumbar count may reach or even exceed the caudal count.
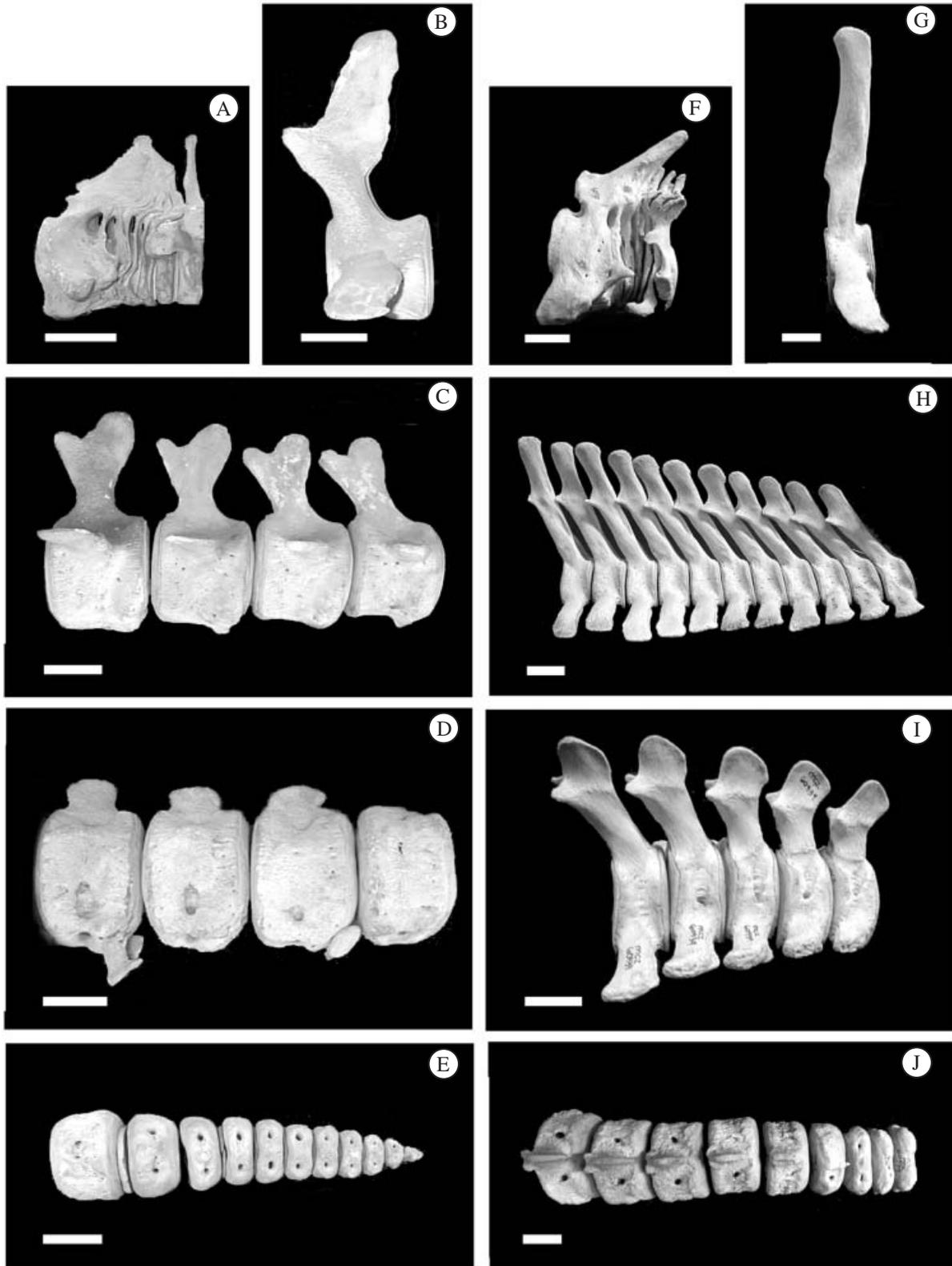
Figure 4. Vertebral dimensions in *Orcinus orca* (AMNH 34276) and *Lagenorhynchus acutus* (MCZ 60939), with classic divisions of the column. Cervical and anterior thoracic vertebrae of the *Orcinus* column are mounted, making CH and CW measurements impossible. Cv = cervical.

Figure 5. Vertebral structure in *Orcinus orca* AMNH 34276 (A–E, scale bars = 10 cm) and *Lagenorhynchus acutus* MCZ 60939 (F–J, scale bars = 2 cm). A, left lateral view of fused neck (Cv1–7) vertebrae and first chest (T1) vertebra (truncated); B, left lateral view of mid lumbar (L5) vertebra; C, left lateral view of anterior caudal vertebrae (Cd1–4); D, left lateral view of immediate prefluke caudal vertebrae (Cd10–13); E, dorsal view of fluke vertebrae (Cd14–24). F, left lateral view of cervical vertebrae; G, left lateral view of anterior torso vertebra (L9); H, left lateral view of mid torso vertebrae (L24–25, Cd1–9) showing anterior neural arch inclination; I, left lateral view of mid torso/posterior torso transition (synclinal point) (Cd12–16); J, dorsal view of elongate tail stock vertebrae (Cd19–24) and first three fluke vertebrae (Cd25–27).
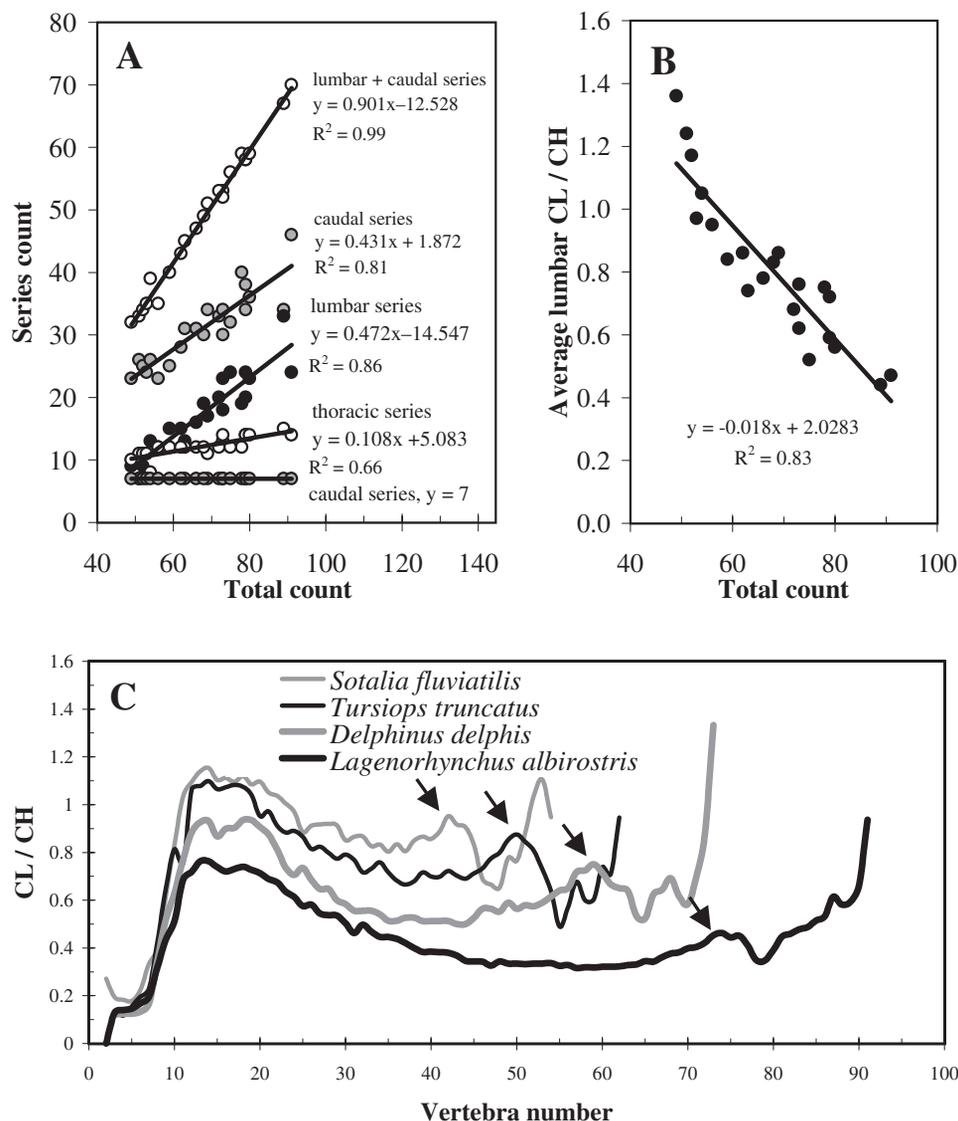

Figure 6. Vertebral count and shape in delphinids. A, relationship between total counts and series counts. B, relationship between total count and lumbar CL/CH. C, CL/CH traces for four species, each with syncliny and a secondary rise in CL (arrows). Note the progressive reduction in CL/CH with increasing total count.

Relative centrum length. Lumbar vertebral centra of delphinapterids are elongate (spool-shaped), with CL/CH ≥ 1.0. All delphinids except *Pseudorca* have lumbar vertebrae with average CL/CH < 1.0, although the extent of CL reduction varies. Shape and count are inversely associated, with more extreme reduction in lumbar CL in genera with higher counts (Fig. 6B,C). *Peponocephala*, *Delphinus*, *Stenella*, *Lagenodelphis*

and *Lagenorhynchus* all have discoidal lumbar vertebrae with average lumbar CL/CH ≤ 0.75. Species with higher counts also show extension of discoidal shape anteriorly into the thorax and posteriorly into the anterior tail. In species with very high counts (*Lagenorhynchus* spp.), as well as a few other isolated species (*Orcinus*, *Globicephala*), the average CL/CH of all thorax vertebrae is ≤ 0.75.

Orientation of neural arches and spines. Orientation of neural arches and spines is uniformly posterior in delphinapterids. At least some vertebrae bear anteriorly inclined neural arches in all delphinids, as noted by Slijper (1936). Extreme anterior inclination of the arch (here termed a 'reclining arch') displaces the tip of the neural spine anterior to the plane of the centrum face in caudal vertebrae in *Lagenorhynchus* (Fig. 5H) and other delphinids with extremely high counts (*Peponocephala*, *Delphinus*, *Stenella*, *Lagenodelphis*). In most delphinids, a region of anteriorly inclined neural spines introduces a point of divergence (syncliny) in the anterior caudal series (Fig. 5I). The synclinal point is located more posteriorly (% total postcranial length) in species with higher counts (Fig. 7). Neither *Pseudorca* nor *Orcinus* displays syncliny.

Elongation of prefluke (tailstock) vertebrae. In delphinapterids, CL peaks in the middle of the column, decreasing both anteriorly and posteriorly from a point near the lumbar/caudal transition. *Orcinus* (Fig. 4A) exhibits a similar pattern. In most delphinids, the mid column is instead the point of shortest CL (*Lagenorhynchus*, Fig. 4B). CL increases posteriorly in a 'secondary rise' to a maximum anterior to the fluke (Fig. 6C). This rise is continuous and gentle in delphinids with low counts, but is abrupt and postponed until after the synclinal point in species with high counts.

Metapophysis presence and location. Metapophyses are uniformly present on lumbar and prefluke caudals in delphinapterids, but are regionally lacking (Fig. 5G) from mid and posterior lumbars in dolphins with counts ≥ 65. Located at the transition between neural arch and neural spine, metapophyses are 'elevated' when the running distance of the arch is greater than that of the spine (NAH > NSH). Elevated metapophyses occur in posterior lumbar and anterior caudal vertebrae in all delphinids except *Pseudorca* and the highly unusual genus *Lissodelphis*.

DISCUSSION

Variations in vertebral osteology are used below to identify structural units of the delphinid column, to
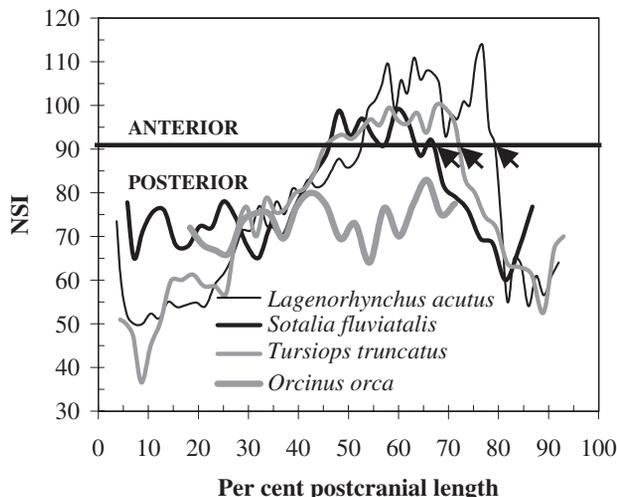

Figure 7. Neural spine inclination (NSI) at different locations along the column in four delphinid species: *Orcinus orca*, AMNH 34276, total count = 53; *Sotalia fluviatilis* (MCZ 7097, vertebral count = 54); *Tursiops truncatus* (MCZ 7899, vertebral count = 62+); *Lagenorhynchus acutus* (MCZ 60939; vertebral count = 82). Note that the position of the synclinal point (arrows) is more posterior in species with higher counts, and that *Orcinus* does not exhibit syncliny.

predict functions of these structural units, to predict the historical sequence of trait origination and to contribute to the resolution of phylogenetic relationships within the Family Delphinidae.

STRUCTURAL UNITS IN THE DELPHINID COLUMN

Axial sites of marked morphological discontinuity are traditionally used to define vertebral series (e.g. Gadow, 1933). The mismatch between terrestrial mammals and cetaceans in the locations of these sites complicates interpretation of delphinid vertebral anatomy. Although cervical and thoracic series may be defined similarly in whales and in terrestrial mammals, cetacean lumbar and caudal vertebrae have been dramatically reconfigured during evolution. As a result, cetacean morphological units transgress classic series borders. This is most marked for the large lumbar series that must include, in addition to 'true' lumbars, vertebrae homologous with the sacral vertebrae of terrestrial mammals (Fig. 8A,B). Slijper (1936) tentatively identified these 'sacral lumbars' on the basis of pudendal nerve roots. He also argued for the existence of a variable number of apparent lumbars that were in fact post-sacral ('caudal lumbars') but unrecognizable as caudals because they lack haemal arch scars.
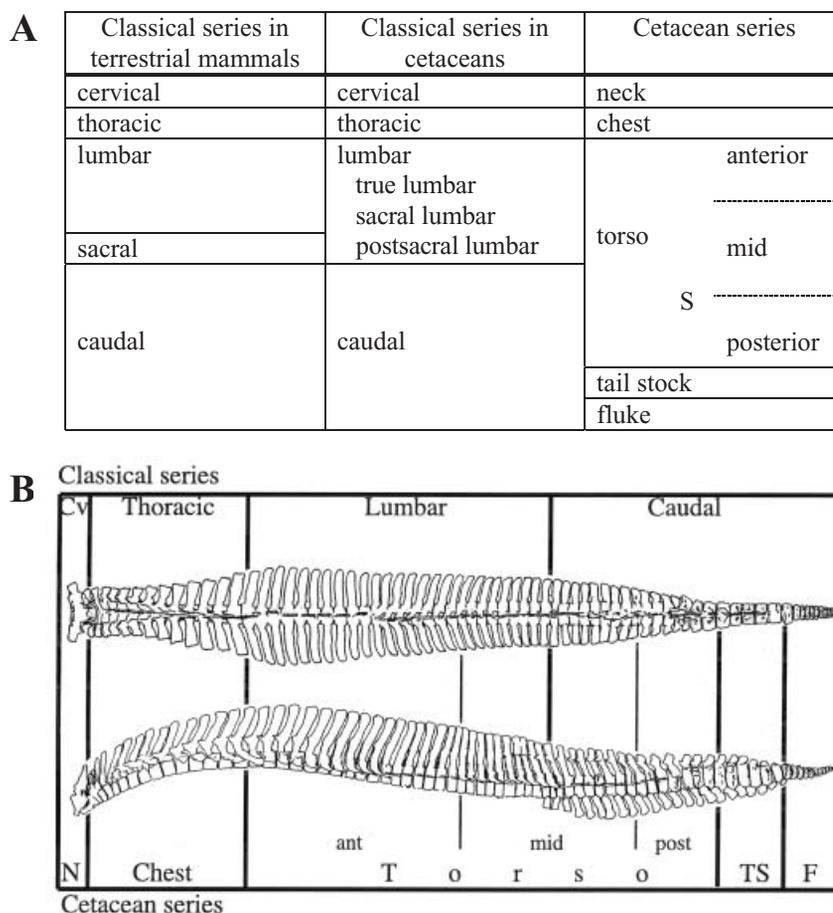
A

Classical series in terrestrial mammals	Classical series in cetaceans	Cetacean series		
cervical	cervical	neck		
thoracic	thoracic	chest		

lumbar	lumbar
	    true lumbar
	    sacral lumbar
		torso	anterior	

sacral	postsacral lumbar		mid	
caudal	caudal		S	posterior
		tail stock		
		fluke		

B

Classical series

Cetacean series

Figure 8. Two representations of the allocation of vertebrae to series in delphinid cetaceans. A, comparison of column subdivisions in terrestrial mammals, in cetaceans using terrestrial nomenclature and in cetaceans using cetacean nomenclature. Subdivision of the torso is applicable only to delphinids with syncliny. S = synclinal point. B, regional morphology of *Lagenorhynchus acutus* (MCZ 61008) by classic and cetacean column series in dorsal (above) and lateral (below) views. N = neck, TS = tail stock, F = fluke.

Alternatively, the cetacean column may be subdivided on the basis of its own structural discontinuities, which may be predicted to correspond to units of distinctive function in whales. Unambiguous subdivision of the column is possible on the basis of centrum dimensions and the presence of ribs into neck (N), chest (C), torso (T), tail stock (TS) and fluke (F) series (Fig. 8). The torso may be further subdivided in most delphinid genera (those with neural spine syncliny) into anterior, mid and posterior units on the basis of neural spine orientation. We propose recognition of the following vertebral series for delphinids, and anticipate that they may be broadly applied to other cetaceans as well:

Neck. The neck is foreshortened and supported by seven vertebrae of exceptionally short centrum length.

Anterior vertebrae are typically fused, although the number included in the fused unit varies among species, among individuals of the same species and with ontogeny in the same individual. Neural spines are very short and posteriorly inclined.

Chest. Chest vertebrae have posteriorly inclined neural spines and relatively long centra with nearly round cross-section (CW ≈ CH). Each vertebra is associated with an unfused rib that surrounds and protects the thoracic viscera. Double-headed ribs are succeeded posteriorly by single-headed and/or floating ribs.

Torso. The torso comprises numerous highly uniform, discoidal vertebrae of circular cross-section and (in most delphinids) short centrum length. Neural processes are a major site of origin for the epaxial muscles of locomotion that insert posteriorly on tail stock and

fluke vertebrae. In taxa with syncliny, torso vertebrae may be subdivided into an anterior region (with effectively erect neural arches and spines), a middle region (with anteriorly inclined arches and spines) and a posterior region (with 'bent' processes composed of anteriorly inclined arches and posteriorly inclined spines). The angular transition between spines of middle and posterior torso vertebrae marks the synclinal point (Slijper, 1936). The lumbar/caudal transition occurs within the middle torso with minimal morphological discontinuity.

Tail stock. Tail stock vertebrae are laterally compressed (CH > CW), and support the laterally compressed peduncle anterior to the fluke. Neural arches are erect or incline anteriorly, and the very short neural spines incline posteriorly. In most delphinids, tail stock vertebrae have longer centrum lengths ('secondary rise') than do adjacent torso or fluke vertebrae. The last tail stock vertebra has highly convex faces.

Fluke. The fluke is characterized by vertebrae that are dorsoventrally compressed (CW > CH), have short CL and lack processes.

FUNCTIONAL INTERPRETATION OF VERTEBRAL SERIES

Neck (cervical) and chest (thoracic) vertebral series in delphinids are defined as in terrestrial mammals and parallel them in their structural and supportive functions. The remainder of the postcranium generates the movements that propel the animal during swimming. During swimming, the post-thoracic column effects both vertical displacement and oscillation of the fluke, which is the propulsive surface (Slijper, 1961; Fish & Hui, 1991; Curren, Bose & Lien, 1994). The site of fluke oscillation is uniform and discrete; it is easily identified in osteological specimens by the convex vertebra at the end of the tail stock (Slijper, 1936; Watson & Fordyce, 1993). By contrast, vertebral morphology indicates that the axial extent of the displacing unit varies among delphinid taxa. The laterally compressed tail stock is located immediately anterior to the fluke, and is certainly part of the displacing unit in all dolphins. The torso, however, may be either unimodally (without morphological discontinuity) or bimodally (with morphological discontinuity) constructed. We propose that unimodal and bimodal torsos achieve fluke displacement differently. Vertebrae of unimodal torsos all contribute to fluke displacement, but displacement in bimodal torsos is more localized, occurring preferentially at the synclinal point.

Vertebral morphology in unimodal torsos (e.g. *Orcinus*, Figs 4, 5) is highly uniform. Count is low, centra are spool-shaped, and anterior and posterior centrum faces are gently rounded. Neural spines are relatively short and posteriorly inclined. Short spines limit the mechanical advantage of the epaxial musculature, but enhance angular rotation. The neural spines are separated from each other by the long centra that bear them, minimizing interference between adjacent vertebrae during rotation. Torso vertebrae are longer than chest or tail stock vertebrae; there is no 'secondary rise' anterior to the fluke. Similarity of structure throughout the torso signals similarity of function. We infer that all torso vertebrae are involved to at least some extent in the vertical displacement of the fluke caused by the contraction of the epaxial and hypaxial musculature.

Bimodal torsos (e.g. *Lagenorhynchus*, Figs 4, 5) have high vertebral counts and discoidal centra with flat anterior and posterior faces. Torso vertebrae are shorter than either chest or tail stock vertebrae. Anteriorly, neural spines are very tall and almost as long axially as the centra that bear them, threatening mechanical interference with minimal centrum rotation. The tall neural spines, many with elevated metapophyses, increase the distance between force application and the axis of rotation, enhancing mechanical advantage but limiting angular rotation. Metapophyses are regionally lacking in the anterior torso, inferring absence of the shorter (mid-spine) muscle fascicles that would produce greater rotation. In the mid-torso, metapophyses reappear, and neural spines shorten progressively and also incline anteriorly. At the mid-torso/posterior torso transition, neural process orientation reverses, creating a synclinal point at which angular divergence and distance between adjacent neural spines is maximized. Posterior to the synclinal point, neural spine height decreases dramatically, signalling the possibility of greater angular rotation. Centrum length increases in a 'secondary rise' that encompasses the posterior torso and tail stock. We infer from the morphology above that during swimming of bimodal animals, the anterior torso is highly stabilized. Flexibility in the posterior torso is localized at the synclinal point and displacement of the fluke is due primarily to dorsoventral movement of vertebrae posterior to that point. Elongation of these vertebrae maximizes the vertical displacement possible.

EVOLUTIONARY IMPLICATIONS OF TRAIT DISTRIBUTION

The unimodal and bimodal torsos described above represent points near the extremes of a morphological continuum. Their differences are bridged by living and fossil taxa that display some, but not all, of the traits that limit intervertebral mobility in the anterior torso and enhance it in the posterior torso. This hierarchical distribution of traits strongly suggests the stepwise acquisition of separate aspects of this anatomy in the history of the family. Used in conjunction with an established phylogeny, evolutionary transitions may

be identified by derived traits limited to progressively smaller subgroups (Fig. 9).

We use the following derived traits in reconstruction of the evolutionary history of delphinid vertebral anatomy. All delphinids display anteriorly inclined neural arches (trait 1, Fig. 9), a character that separates them from other delphinoids. With the exception of *Pseudorca* (and *Lissodelphis*, see below), all delphinids have elevated torso metapophyses (trait 2), identifying this as a very early historical innovation. The lack of syncliny (trait 5) isolates *Pseudorca* and *Orcinus* from the remaining delphinids and implies the early origin of this key step in delphinid locomotor evolution. Elongation of posterior torso and tail stock vertebrae (trait 6) occurs in most but not all animals with syncliny, signalling its subsequent origin. A smaller generic subset displays regional loss of torso metapophyses (trait 8), identifying this as a still more recent innovation.
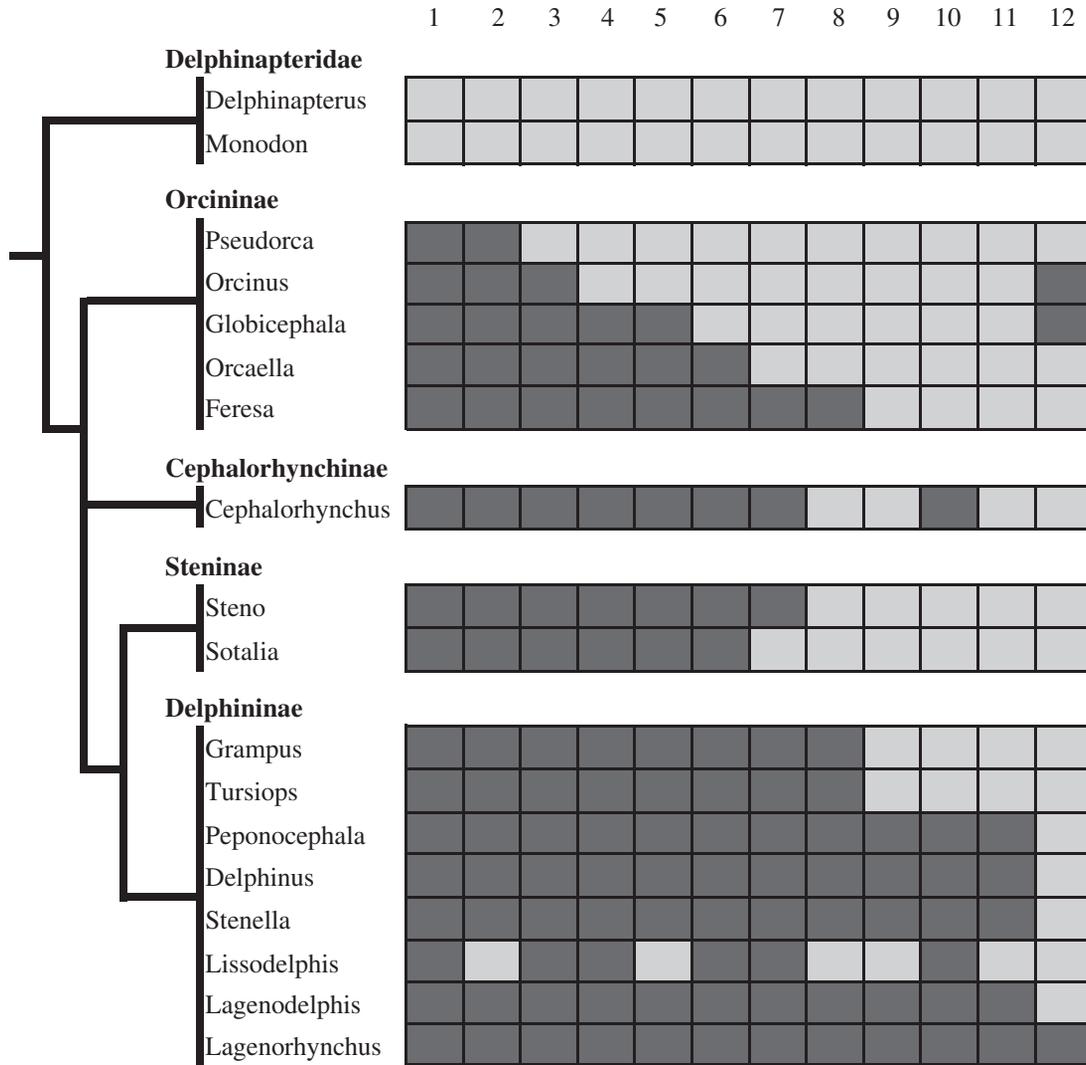
In addition to these discrete traits, others are gradational and are therefore more difficult to use in historical reconstruction. In some cases, clinal gaps provide 'steps' in these traits, allowing them to be used like discrete traits. The most notable gradational change is in vertebral count, with small counts at the primitive end of the continuum. Steps in this cline are abrupt, and may reflect evolutionary changes in *HOX* gene expression patterns. Steps occur where lumbar count exceeds thoracic count (trait 4), at total count of 60 (trait 7) and at the capping of lumbar count synchronous with total count of 70 (trait 9). Other gradational trends include the reductions in torso CL/CH below 1.0 (trait 3) and below 0.75 (trait 9), the increase in neural arch inclination that carries neural spines anterior to the centrum face (trait 11), and the anterior extension of discoidal vertebrae (RCL ≤ 0.75) into the chest (trait 12). Increase in lumbar NPH and the posteriad movement (% of postcranial length) in the position of the synclinal point (Fig. 7) are general trends but not discrete enough to allow unambiguous use.

Our interpretation of vertebral morphology suggests that the ancestors of living dolphins had relatively low vertebral counts, spool-like torso vertebrae, and relatively short neural processes without syncliny, traits possessed today by delphinapterids. We infer that the torsos of these ancestors were less regionalized and more uniformly flexible than those of most living delphinids. The cumulative functional effect of the evolutionary innovations noted above is the enhanced regionalization of the column, in particular the stabilization of the anterior column, the progressive localization of flexibility to anterior (synclinal) and posterior (fluke base) sites, and the elongation of the tail stock vertebrae responsible for fluke displacement.

Analysis of trait distribution also reveals the probable existence of homoplasy. Homoplasy is strongly implicated in the occurrence of low chest CL in taxa (*Orcinus*, *Globicephala*, *Lagenorhynchus*) widely separated by count and syncliny. Another likely occurrence of homoplasy is suggested by the reduced lumbar CL in *Cephalorhynchus*, otherwise restricted to taxa with regional metapophysis loss and counts above 70. The unusual combination of vertebral traits in the northern right whale dolphin *Lissodelphis* can be added to its anomalous lack of a dorsal fin, elongate body form and leaping style of locomotion (Jefferson *et al.*, 1994) in setting it apart from other dolphins. It combines features typical of primitive species (lack of syncliny, low torso metapophyses, short neural spines) with those of highly derived species (very high vertebral count, highly discoidal lumbar vertebrae, 'secondary rise' in posterior torso CL). These distribution patterns imply multiple origins of one or more traits, with high count and reduced CL the most likely candidates. The lability of these traits is suggested by high variation in segment count in vertebrates generally (Raff, 1996; Richardson *et al.*, 1998; Polly, Head & Cohn, 2001) and by the existence of parallel sequences of count enhancement and CL reduction in phocoenid delphinoids (Buchholtz, 2001).

Despite these considerations, we believe that vertebral anatomy provides a previously little-used source of traits that can contribute to the resolution of phylogenetic relationships within Delphinidae. Limitation of our data to a single morphological system argues against its use as a basis for the definition of new taxonomic categories. Rather, we propose the following modifications to the consensus phylogeny (Figs 1, 9):

1. Removal of genera possessing syncliny from the Orcininae into a separate ('globocephaline') subfamily, emphasizing the morphological isolation of *Pseudorca* and *Orcinus*.
2. Addition of *Sotalia*, which exhibits syncliny, a lumbar count ≈ thoracic count and metapophyses throughout the torso, to this globocephaline subfamily. Consistent with the conclusions of Arnold & Heinsohn (1996), this same combination of traits supports the inclusion of *Orcaella* in this subfamily as well.
3. Removal of *Feresa*, which lacks metapophyses regionally and has a total count of 67–70, from the Orcininae and placement of it in the Delphininae. These same traits also support Mead's (1975) placement of *Peponocephala* in the Delphininae.
4. Subdivision of the Delphininae into two subgroups on the basis of total count, lumbar count, neural arch inclination and chest CL. These subgroups include: (a) *Feresa*, *Tursiops*, *Grampus*; (b) *Pepono-*

1　2　3　4　5　6　7　8　9　10　11　12

Delphinapteridae
Delphinapterus
Monodon

Orcininae
Pseudorca
Orcinus
Globicephala
Orcaella
Feresa

Cephalorhynchinae
Cephalorhynchus

Steninae
Steno
Sotalia

Delphininae
Grampus
Tursiops
Peponocephala
Delphinus
Stenella
Lissodelphis
Lagenodelphis
Lagenorhynchus

Trait	Primitive state	Derived state
1	neural arches inclined posteriorly	regional neural arch anterior inclination
2	all metapophyses low	regional elevated metapophyses
3	lumbar vertebrae with CL / CH > 1.0	lumbar vertebrae with CL / CH ≤ 1.0
4	lumbar count < thoracic count	lumbar count ≥ thoracic count
5	neural spines inclined posteriorly	neural spine syncliny
6	torso CL > tail stock CL	secondary rise in tail stock CL
7	total count < 60	total count > 60
8	torso metapophyses uniformly present	regional absence of torso metapophyses
9	total count < 70	lumbar count capped, total count > 70,
10	lumbar vertebrae with CL / CH > 0.75	lumbar vertebrae with CL / CH ≤ 0.75
11	reclining neural arches absent in mid torso	reclining neural arches in mid torso
12	chest vertebrae with Cl / CH > 0.75	chest vertebrae with CL / CH ≤ 0.75

cephala, *Lagenodelphis*, *Delphinus*, *Stenella*, *Lagenorhynchus*.

5. Isolation of *Lissodelphis*, in agreement with Mead (1975) and Perrin (1989). The vertebral morphology of this genus is enigmatic. Its lack of syncliny and retention of metapophyses argue against its placement in Delphininae, but its high count, discoidal lumbar vertebrae and 'secondary rise' prevent its placement in other, less derived, subfamilies.

INFERENCES FROM VERTEBRAL ANATOMY OF FOSSIL DELPHINIDS

The vertebral traits discussed here offer the possibility of placing partial columns or even isolated fossil vertebrae into functional and evolutionary contexts. Among the most useful traits for such evaluation is the presence of anteriorly inclined neural spines or 'bent' neural processes that indicate the presence of syncliny. Loss of metapophyses further constrains placement to a small and derived group of delphinids. Ratio of CL to CH of isolated torso vertebrae may be used as an indicator of total count (Fig. 6B) and allows at least generalized inference of phylogenetic placement. Examples of evaluation of fossil taxa are presented below.

'Odontocete indet.', CMM-V-1694, 21 vertebrae from Bed 13 (Mid Miocene) of the Calvert Formation, Calvert Co., MD, USA. Vertebrae of the torso, tail stock and even of the fluke have CL/CH $\geq$ 1.0 (Fig. 10A). No known delphinid or delphinoid has fluke vertebrae with length > width, placing this specimen outside the Delphinoidea.

Hadrodelphis calvertense, CMM-V-11, a nearly complete column of a kentriodontid from the Calvert Formation of Charles County, MD, USA, described by Dawson (1996). Neural arches lack anterior inclination. Neural spines are short, broad and lack syncliny; metapophyses are universally present and low (Fig. 10B). This vertebral profile is almost identical to that of living monodontids, which can be grouped with kentriodontids as 'non-delphinid delphinoids.'

Albireo whistleri, UCR 14589, seven neck, 13 chest and 25 torso vertebrae from a specimen described by Barnes (1984) from the Late Miocene Almejas Formation of Baja California, Mexico. Barnes erected a new family (Albireonidae) for this specimen on the basis of its unique suite of cranial characters. Mid torso vertebrae of this specimen have anteriorly inclined neural

spines, implying syncliny (Fig. 10C); metapophyses are universally present and lack elevation. This suite of characters suggests placement among basal 'synclinal' delphinids.

'*Tursiops* sp.' USNM 15727, three chest, three anterior torso and two mid torso vertebrae (previously nine in total: see Blake, 1939, 1953) from the Pleistocene Talbot Formation at Wailes Bluff, St Marys Co., MD, USA (Fig. 10D). The three most anterior torso vertebrae lack metapophyses, placing this specimen among the delphinines. Preserved chest vertebrae have CL/CH $\approx$ 1.0, probably placing the specimen outside the most derived taxa. Average CL/CH of preserved torso vertebrae = 0.72, predicting a total vertebral count of 73 using the regression equation of Figure 6B. The dimensions of the fossil specimen suggest that it falls just outside of and on the derived side of the range of total count for living *Tursiops* (Wells & Scott, 1999).

CONCLUSIONS

The delphinid vertebral column has been radically reorganized for axial locomotion in the aquatic environment. Interpretation of its structure and function is facilitated by recognition of structural discontinuities that mark the boundaries of the neck, chest, torso, tail stock and fluke. Delphinid columns show significant intrafamilial variation, with differences in vertebral count, shape and neural spine orientation being most prominent. Low counts, spool-shaped vertebrae and posterior inclination of neural spines are traits shared with living non-delphinid odontocetes and also with almost all fossil odontocete taxa; we identify them as primitive. Genera with these traits have unimodal torsos; all postthoracic vertebrae are involved to lesser or greater extent in fluke displacement. Syncliny of neural spine orientation in the mid tail was a key delphinid innovation, and signals the evolution of the bimodal torso in which prefluke flexibility is localized. Localization of caudal flexibility at the synclinal point is accompanied by traits that limit mobility in the anterior torso (increase in neural process height; regional loss of metapophyses) and enhance displacement of the tail stock (tail stock CL elongation). Bimodal torsos are typical of genera with high counts. The hierarchical distribution of vertebral traits suggests that evolution of the bimodal torso occurred step-wise, with syncliny a histori-

Figure 9. Distribution of vertebral traits in delphinid cetaceans mapped on to the consensus phylogeny. Note both the general agreement of vertebral traits with the existing phylogeny and the discordant distribution of traits in the genus *Lissodelphis*. Shading indicates primitive (light) or derived (dark) trait states.
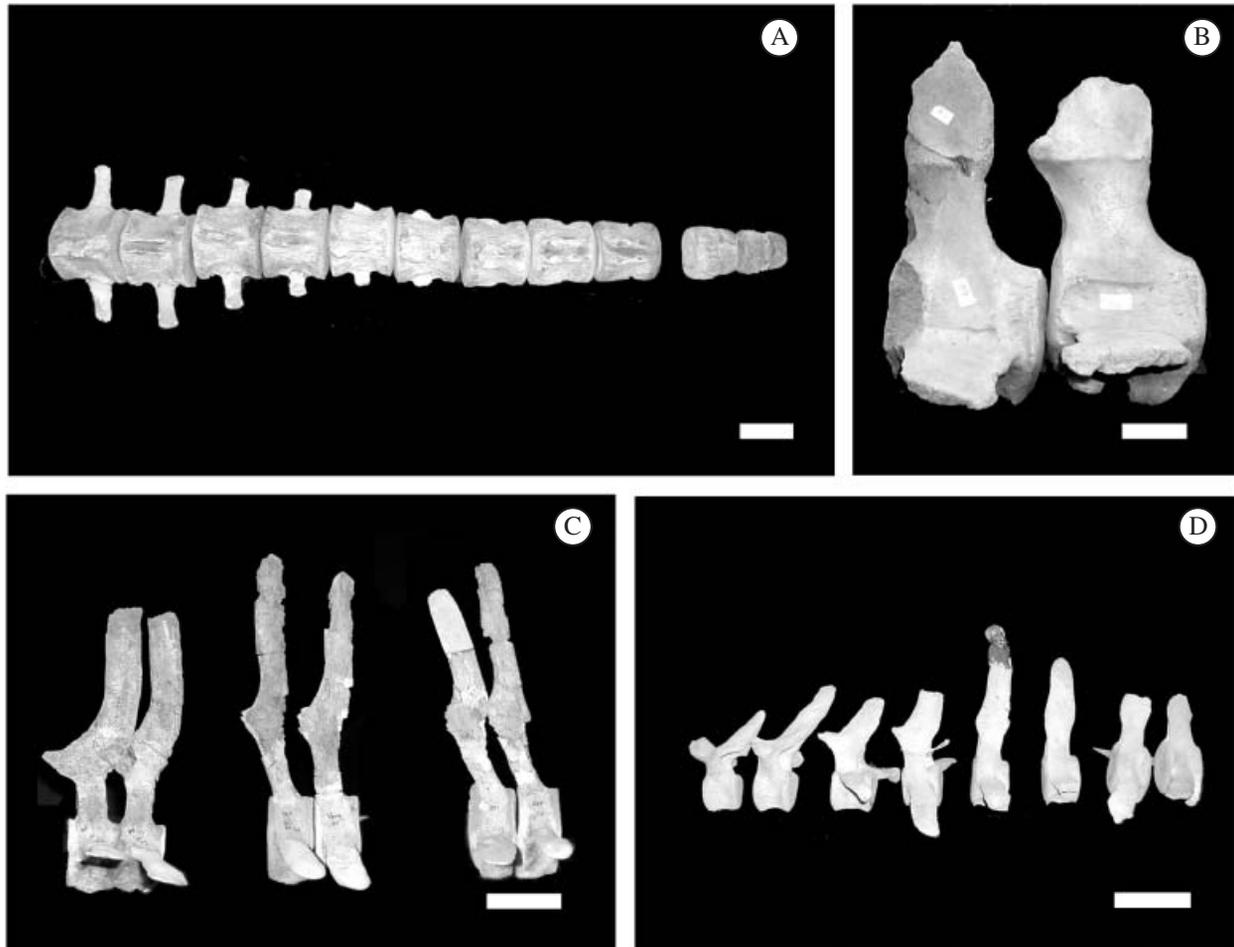
Figure 10. Isolated vertebrae from fossil cetaceans for which functional and/or evolutionary context may be predicted. A, 11 caudal vertebrae of 'Odontocete indet.' CMM-V-1694 in dorsal view, with an inferred gap in vertebral sequence. Note that the terminal (fluke) vertebrae are elongate. B, two mid torso vertebrae of *Hadrodelphis calvertense* CMM-V-11 in left lateral view. Metapophyses are present, neural processes are short and vertebrae are spool-shaped. C, six anterior and mid torso vertebrae of *Albireo whistleri* UCR 14589 in left lateral view. Metapophyses are present and low, but neural spines are very tall and centra are discoidal. D, three chest and five torso vertebrae of USNM 15727 '*Tursiops* sp.' in left lateral view. Note the lack of metapophyses on anterior torso vertebrae. All scale bars = 5 cm.

cally earlier innovation than metapophysis loss or tail stock elongation. At least some vertebral traits display homoplasy; increases in count are known in phocoenids and are also implicated in *Lissodelphis*. Vertebral trait distribution may also have phylogenetic content. Our data suggest recognition of syncliny by subfamilial separation of *Pseudorca* and *Orcinus* from remaining 'globocephaline' delphinids, placement of both *Feresa* and *Peponocephala* in the Subfamily Delphininae, and subdivision of the Delphininae. We believe that vertebral characters have great potential in the elucidation of vertebrate function and history, and encourage their inclusion in future investigations to achieve a more complete view of vertebrate evolution.

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