

Modular evolution of the Cetacean vertebral column

Emily A. Buchholtz

Department of Biological Sciences, Wellesley College, Wellesley, MA 02481, USA

Correspondence (email: ebuchholtz@wellesley.edu)

SUMMARY Modular theory predicts that hierarchical developmental processes generate hierarchical phenotypic units that are capable of independent modification. The vertebral column is an overtly modular structure, and its rapid phenotypic transformation in cetacean evolution provides a case study for modularity. Terrestrial mammals have five morphologically discrete vertebral series that are now known to be coincident with *Hox* gene expression patterns. Here, I present the hypothesis that in living Carnivora and Artiodactyla, and by inference in the terrestrial ancestors of whales, the series are themselves components of larger precaudal and caudal modular units. Column morphology in a series of fossil and living whales is

used to predict the type and sequence of developmental changes responsible for modification of that ancestral pattern. Developmental innovations inferred include independent meristic additions to the precaudal column in basal archaeocetes and basilosaurids, stepwise homeotic reduction of the sacral series in protocetids, and dissociation of the caudal series into anterior tail and fluke subunits in basilosaurids. The most dramatic change was the novel association of lumbar and anterior caudal vertebrae in a module that crosses the precaudal/caudal boundary. This large unit is defined by shared patterns of vertebral morphology, count, and size in all living whales (Neoceti).

INTRODUCTION

Cetaceans are highly modified descendants of terrestrial mammals (Gingerich et al. 2001; Thewissen et al. 2001; Thewissen and Williams 2002; Kriegs et al. 2006). In the course of their evolutionary transformation, whales evolved caudal flukes, reduced and then lost the pelvis and hind limbs, and adopted a fusiform body shape. All of these innovations required transformations of vertebral column morphology, and therefore of the developmental processes that generate morphology.

Recent advances in developmental biology provide new tools to paleontologists who hope to address the causal factors in the evolution of form. Although morphology has classically been understood as particulate (Lovejoy et al. 1999), developmental processes are now recognized as having modular organization (Raff 1996; Raff and Sly 2000; Bolker 2002). Bolker (2002) formally described modules as products of fundamental developmental units that display internal morphological integration, hierarchical organization, a particular physical location, and the ability to undergo developmental and evolutionary transformation. If development has a hierarchical and modular organization, then morphology, which is the product of development, should have modular organization as well (Raff 1996; Raff and Sly 2000).

Morphological modularity is easiest to recognize in structures with discrete serially homologous elements and several levels of organization. At least two levels of organization are immediately apparent in the vertebral column. Individual vertebrae represent the smallest units, but variation between adjacent vertebrae is irregularly distributed. Sites of marked morphological discontinuity have traditionally (e.g., Flower 1885) been used to separate the mammalian column into five series (cervical, thoracic, lumbar, sacral, caudal). The retention of these vertebral series across mammals with widely divergent column anatomy (Narita and Kuratani 2005) argues that they are both deeply embedded in mammalian development and also capable of evolutionary transformation. These series are now known to coincide with the expression fields of *Hox* and other patterning genes. In 1995, Burke et al. showed that the same morphological landmarks and *Hox* gene expression boundaries coincided in vertebrates with different vertebral counts. More recently, Cohn and Tickle (1999) showed that both the *Hox* gene expression domains and the morphology of the snake thorax are expanded anteriorly relative to their locations in other tetrapods. The possibility that the vertebral column might have higher levels of organization, with the result that changes in one series may be associated with those of another, has not received much attention (but see Todd 1922; Polly et al. 2001, and Buchholtz et al. in review).

Drawing on the work of Bateson (1894), Raff (1996), Carroll et al. (2001), and Polly et al. (2001), the most common types of evolutionary change in vertebral column morphology may be categorized:

Diversifying (sensu Carroll et al. 2001) or skeletogenetic (sensu Polly et al. 2001) changes are the result of the individualization of module members. A variety of *Hox* genes and/or growth factors may contribute to these changes (Johnson and O'Higgins 1996; McPherron et al. 1999; Oostra et al. 2005), probably acting after vertebral count and series boundaries are set.

Changes in column count (meristic changes) are the result of changes in somitogenesis, and the subdivision of the presomitic mesoderm into a variable number of discrete units. Rates of molecular oscillators appear to control somite (and therefore vertebral) number (Pourquié 2003; Sanger and Gibson-Brown 2004). Segmentation occurs early in the developmental sequence, and vertebral count is typically fixed for most of ontogeny.

Changes in regionalization (homeotic changes) are the result of changes in expression domains of genes (including the *Hox* family) that specify the identity of different axial regions. Homeotic changes typically augment count in one column series at the expense of an adjacent module and can be induced experimentally with retinoic acid (Kessel 1992) or by changes in temperature (Li et al. 1997; Li and Shiota 1999). In at least some instances, vertebral identities are set even before segmentation, as transplanted unsegmented mesoderm differentiates according to its origin, not its transplant destination (Kieny et al. 1972; Li and Shiota 1999).

Changes in module association (Raff 1996; Lovejoy et al. 1999; Polly et al. 2001) can occur at any point of the developmental sequence, constraining or freeing the development of one column series with respect to another.

A survey of mammalian vertebral anatomy such as that published by Flower in 1885 provides evidence of all of these categories of change, and also suggests that they occur with different frequencies. Vertebrae with strikingly different morphology occur in at the same axial position in different species (e.g., lumbar 4 of canid and felid carnivores, or cervical 4 of giraffes and cetaceans), and demonstrate the power and ubiquity of diversifying change. The frequency of meristic change varies by series. Cervical counts are nearly fixed across Mammalia (Galis 1999), and thoracolumbar counts are highly conserved (Todd 1922; Narita and Kuratani 2005). In contrast, caudal counts vary widely. Counts of some series (e.g., thoracic) typically increase at the “expense” of others (e.g., lumbar) suggesting higher order relationships of the series (Todd 1922) and movement of the homeotic boundary between them. Changes in modular association are very rare, but Flower lists “coalesced” series for some members of the orders Chiroptera and Edentata, and missing series for Sirenian and Cetacea.

Whales present an ideal opportunity for the study of the evolution of axial patterning over geologic time. Morphological transformation within Cetacea has been as great as in any

mammalian order, and remodeling of the overtly modular vertebral column is particularly marked. Despite the impossibility of experimentally manipulating the developmental process in extinct organisms, the cetacean fossil record is extensive and higher order phylogenetic relationships are well established (Williams 1998; Thewissen and Williams 2002; Geisler and Sanders 2003; Geisler and Uhen 2005; Geisler et al. 2005) (Fig. 1). Living cetaceans are both speciose and surprisingly diverse in body size and vertebral count, allowing interspecific comparisons (Buchholtz and Schur 2004). Below I describe patterns of axial morphology in living mammalian outgroups, fossil archaeocete cetaceans, and living neocete cetaceans, inferring their axial modular organization. I then predict the type and timing of developmental innovations that enabled transitions between these patterns during cetacean evolution.

MATERIALS AND METHODS

Two extant mammalian orders are used here as outgroups to infer the morphology and developmental hierarchy in the earliest whales, following the methodology of the Extant Phylogenetic Bracket (EPB, Witmer 1995). The Order Artiodactyla is used as the first outgroup because of its close phylogenetic relationship to Cetacea (Gingerich et al. 2001; Thewissen et al. 2001). The Order Carnivora is used as the second outgroup because it is a laurasiatherian order closely allied to Cetartiodactyla (Kriegs et al. 2006), is speciose, contains multiple experiments in secondary aquatic lifestyles, and exhibits great morphological diversity, especially with respect to column elongation. Major groups of cetaceans examined are “basal archaeocetes,” protocetids, basilosaurids, and neocetes.

Data for living taxa were gathered on site at museum collections (Table 1). In species for which multiple individuals were available, a single complete adult was randomly chosen to represent the species. Most fossil taxa were represented by a single species, and some by a

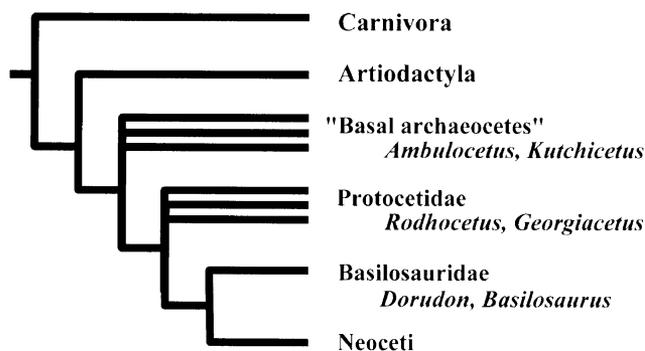


Fig. 1. Consensus phylogenetic relationships of the orders Carnivora and Artiodactyla and four families of Cetacea based on the work of Thewissen and Williams (2002), Geisler and Sanders (2003), Uhen (2004), and Geisler et al. (2005). Fossil genera addressed in this study are included. Both “Basal archaeocetes” and Protocetidae are commonly recognized as paraphyletic.

Table 1. Carnivora and Cetacea species included in this study, with specimen identification and total vertebral count (TC)

	Museum #	TC
Carnivora		
Canidae		
<i>Canis latrans</i>	MCZ 62197	50
<i>Cuon alpinus</i>	MCZ 19566	52
<i>Urocyon cinereoargenteus</i>	MCZ 57137	51
<i>Vulpes vulpes</i>	MCZ 61731	49
<i>Nyctereutes procyonoides</i>	MCZ 24860	49
Hyaenidae		
<i>Crocuta crocuta</i>	MCZ 20968	46
<i>Hyaena brumnea</i>	MCZ 57136	49
Phocidae		
	MCZ 1084	
<i>Cystophora cristata</i>	MCZ 1084	41
<i>Arctocephalus ursinus</i>	MCZ 1785	36
<i>Phoca groenlandica</i>	MCZ 28682	45
<i>Ommatophoca rossi</i>	MCZ 51852	41
Otariidae		
<i>Callorhinus ursinus</i>	MCZ 128	38
<i>Eumetopias jubatus</i>	MCZ 129	40
Odobenidae		
<i>Odobenus rosmarus</i>	MCZ 1720	39
Viverridae		
<i>Salanoia concolor</i>	MCZ 27827	56
<i>Fossa fossa</i>	MCZ 29404	53
<i>Viverricula indica</i>	MCZ 5138	55
Mustelidae		
<i>Mephitis mephitis</i>	MCZ 27881	54
<i>Melogale everetti</i>	MCZ 36114	48
<i>Lutra longicaudis</i>	MCZ 37845	55
<i>Martes pennanti</i>	MCZ 59280	43
<i>Enhydra lutris</i>	MCZ 61578	50
Ursidae		
<i>Helarctos malayanus</i>	MCZ 34152	39
<i>Ursus americanus</i>	MCZ 59938	41
Procyonidae		
<i>Bassaricyon alleni</i>	MCZ 37923	59
<i>Bassariscus astutus</i>	MCZ 42161	56
<i>Procyon lotor</i>	MCZ 62164	48
Herpestidae		
<i>Atilax paludinosus</i>	MCZ 38063	57
<i>Suricata suricata</i>	MCZ 5115	56
<i>Herpestes auropunctatus</i>	MCZ 5123	49
Felidae		
<i>Alcionyx jubatus</i>	MCZ 58142	53
<i>Caracal caracal</i>	MCZ 58305	45
<i>Felis pardalis</i>	MCZ 9351	50
<i>Panthera leo</i>	MCZ 13273	54
Cetacea		
Balaenopteridae		
<i>Balaenoptera acutorostratus</i>	MCZ 8832	47
<i>Balaenoptera borealis</i>	USNM 236680	56
<i>Balaenoptera musculus</i>	USNM 124326	63
<i>Balaenoptera physalis</i>	USNM 16045	57*
<i>Megaptera novaeangliae</i>	MCZ 6177	53

Table 1. (Contd.)

	Museum #	TC
Balaenidae		
<i>Eubalaenus glacialis</i>	USNM 23077	56
<i>Caperea marginata</i>	AMNH 36692	42*
Eschrichtiidae		
<i>Eschrichtius robustus</i>	USNM 199527	57*
Physeteridae		
<i>Physeter catodon</i>	USNM 301634	50
<i>Kogia simus</i>	USNM 550487	54
<i>Kogia brevirostris</i>	USNM 504737	52
Ziphiidae		
<i>Tasmacetus shepherdi</i>	USNM 484878	47*
<i>Ziphius cavirostris</i>	USNM 504094	45
<i>Mesoplodon europaeus</i>	USNM 504738	47
<i>Mesoplodon mirus</i>	USNM 50461	47
River dolphins		
<i>Platanista gangetica</i>	CAS, no #	49
<i>Pontoporia blainvillei</i>	USNM 501186	40
<i>Inia geoffrensis</i>	USNM 239667	42*
<i>Lipotes vexillifer</i>	AMNH 57333	44
Delphinapteridae		
<i>Delphinapterus leucas</i>	AMNH 99681	51*
<i>Monodon monoceros</i>	MCZ 2186	51
Delphinidae		
<i>Pseudorca crassidens</i>	AMNH 99681	52*
<i>Orcinus orca</i>	AMNH 34276	53
<i>Globicephala macrorhyncha</i>	USNM 22571	54
<i>Sotalia fluviatilis</i>	MCZ 7097	54
<i>Steno bredanensis</i>	USNM 550221	62
<i>Cephalorhynchus commersoni</i>	USNM 550156	63
<i>Tursiops truncatus</i>	MCZ 143	63*
<i>Grampus griseus</i>	USNM 504328	66
<i>Feresa attenuata</i>	MCZ 51458	69
<i>Stenella frontalis</i>	USNM 571139	72
<i>Stenella longirostris</i>	USNM 500017	73*
<i>Stenella coeruleoalba</i>	USNM 504350	79
<i>Delphinus delphis</i>	AMNH 130119	73
<i>Lagenorhynchus obliquidens</i>	USNM 504851	75
<i>Lagenorhynchus acutus</i>	AMNH 143513	82
<i>Lagenorhynchus albirostris</i>	USNM 550208	91
<i>Lagenodelphis hosei</i>	MCZ 52979	79*
<i>Pepenocephala electra</i>	USNM 504948	78
<i>Lissodelphis borealis</i>	USNM 484929	85
Phocoenidae		
<i>Phocoena phocoena</i>	USNM 550312	65
<i>Phocoena spinipinnis</i>	USNM 395751	69
<i>Phocoenoides dallis</i>	USNM 504969	97
<i>Neophocoena phocoenoides</i>	USNM 24002	60

AMNH, American Museum of Natural History; CAS, California Academy of Science; MCZ, Museum of Comparative Zoology, Cambridge; USNM, National Museum of Natural History, Washington, DC.
*, one or more vertebrae missing; estimated number missing included in count.

single individual. Archaeocete descriptions were taken almost exclusively from the literature. P. D. Gingerich generously provided unpublished dimensional data for nine specimens of *Basilosaurus is* used in Gingerich et al. (1990). The summary of mammalian counts was taken from Flower (1885).

In both fossil and living groups, classical morphological distinctions (e.g., Hildebrand and Goslow 2001; Rommel and Reynolds 2002) were used to identify series boundaries. Cervical vertebrae lie between the skull and the first vertebra with moveable ribs and sternal articulations. Thoracic vertebrae have moveable ribs; floating ribs, often lost in skeleton preparation, can add ambiguity to identification of the thoracic/lumbar boundary. Lumbar vertebrae lack ribs and have fused pleurapophyses. Sacral vertebrae have transverse processes that fuse with the pelvis or are fused to other vertebrae that themselves fuse with the pelvis. Caudal vertebrae include all postsacral vertebrae (terrestrial mammals, some archaeocetes) or all vertebrae posterior to the last vertebra without hemal arch facets. The diminutive size of the most anterior hemal arches can make identification of the lumbar/caudal transition difficult, and is a probable source of error. Fluke vertebrae include all posterior caudals in which centrum width exceeds centrum height. Terminal caudals are frequently missing from museum skeletons. Most of the skeletons used in this analysis were complete, as indicated by the presence of a terminal “nubbin-shaped” vertebra. When no complete skeleton was available to represent a species, number and length of missing terminal caudals were estimated. No skeleton used had more than two estimated missing caudals.

Osteological measurements made were centrum length (measured ventrally), centrum width (measured anteriorly), and centrum height (measured anteriorly). Measurements were made with digital calipers to the nearest 0.1 mm when size allowed or with a dendrometer (forestry tool) to the nearest millimeter when bones exceeded dimensions of the calipers.

In comparisons among taxa, each centrum length was standardized by dividing by the centrum width of the fifth thoracic vertebra of that column. The standardizing vertebra was selected because of its axial isolation from vertebrae that undergo marked changes in count or dimension during cetacean evolutionary history. Incomplete skeletons forced modification of the standardization procedure for two fossil specimens. The composite skeleton of *B. isis*, for which only centrum length data were available, was standardized to the fifth thoracic vertebra of USNM 4675, a specimen of *B. cetoides* almost identical to the composite in size (Kellogg 1936). The skeleton of *Georgiacetus vogtlenis* was standardized to the sixth thoracic vertebra, as the fifth thoracic was not preserved. Total and mean standardized series and column lengths were calculated by summing or averaging standardized centrum lengths of component vertebrae. Length of the soft tissues present in life were not estimated or included.

Developmental associations among column units of living taxa were inferred from interspecific correlations of vertebral count and standardized centrum length. Meristic changes were inferred when series counts increased without corresponding losses in adjacent series. Homeotic changes were inferred when series counts increased with corresponding losses in adjacent series. The chronological sequence of developmental innovations were predicted by mapping them onto a consensus phylogeny of cetaceans, based

here on the work of Williams (1998), Thewissen and Williams (2002), Geisler and Sanders (2003), Geisler and Uhen (2005), and Geisler et al. (2005) (Fig. 1).

Institutional abbreviations: AMNH, American Museum of Natural History, New York; CAS, California Academy of Science, San Francisco; MCZ, Museum of Comparative Zoology, Cambridge; USNM, National Museum of Natural History, Washington, DC. Morphological abbreviations: AT, anterior tail; C, cervical; Cd, caudal; CH, centrum height; CL, centrum length; CW, centrum width; F, fluke; L, lumbar; T, thoracic; TC, total count; S, sacral; StCL, standardized centrum length.

RESULTS

Analyses of modular organization by morphology, count, and centrum length are presented below for two outgroups and four major cetacean groups.

Living Artiodactyla and Carnivora

Cervical, thoracic, lumbar, sacral, and caudal vertebral series are easily identifiable in living carnivores and artiodactyls. Precaudal counts are very conservative, as they are in many mammalian orders (Flower 1885; Todd 1922; Narita and Kuratani 2005). Cervical counts are fixed at seven, total thoracolumbar counts are typically 19 or 20, and sacral counts are three or four (Table 2). Based on this data set, the “typical” precaudal count of an artiodactyl is C7 T13 L6 S4 = 30. Precaudal counts are statistically independent of the much more variable caudal counts: high total counts are the result of high caudal counts (Fig. 2, A and B). In both orders, thoracic and lumbar counts are very highly and negatively correlated (Artiodactyla, $R^2 = 0.74$; Carnivora, $R^2 = 0.93$), and cervical and sacral counts are independent of all other series counts.

Standardized CL was used as a method of evaluating vertebral shape in living Carnivora. In this order, mean precaudal CL is independent of mean caudal CL; total column length predicts very little ($R^2 = 0.26$) of precaudal but much of caudal ($R^2 = 0.86$) variation in mean CL (Fig. 2C). Total count is independent of precaudal CL, but explains 34% of the variation in caudal CL (Fig. 2D). The mean CL of each precaudal series is statistically correlated to at least the $P < 0.01$ level of probability with those of all other precaudal series with the exception of the relationship between the cervical and sacral series (Fig. 2E, $R^2 = 0.02$). Mean CLs of precaudal series are not statistically correlated with those of the caudal series with the exception of the relationship between the lumbar and caudal series (Fig. 2E, $R^2 = 0.27$).

Count and centrum length data suggest that the five terrestrial vertebral series of carnivores and artiodactyls are not uniformly associated with each other. Different patterns of elongation and segmentation support a hypothesis of different

Table 2. Counts and StCL of a cross section of species in the mammalian orders Artiodactyla and Carnivora by vertebral column unit

	C	T	L	T+L	S	PreCd	Cd
Artiodactyla (<i>N</i> = 33)							
Count mean	7	13.27	5.73	19.00	4.35	30.33	13.52
Count range	7–7	12–15	4–7	18–20	2–8	27–34	6–24
Count SD	0	0.67	0.67	0.35	0.95	1.08	5.06
Carnivora (<i>N</i> = 34)							
Count mean	7	13.91	6.09	20.00	3.18	30.18	18.26
Count range	7–7	13–15	4–7	19–21	2–6	29–33	6–29
Count SD	0	0.90	0.93	0.25	0.62	0.63	6.46
StCL mean	1.27	1.16	1.61	1.30	1.04	1.27	1.29
StCl SD	0.35	0.22	0.35	0.25	0.24	0.24	0.48

StCL values represent centrum lengths standardized to the centrum width of vertebrae T5, and are therefore dimensionless.

developmental programs in the precaudal and caudal columns. The existence of such a dichotomy is not unexpected, as these regions correspond with two discrete methods and locations (primitive streak, tail bud) of mesodermal cell origin (Tam and Tan 1992; Polly et al. 2001). The presence of only precaudal and caudal column subunits in many fish (Romer 1955; Kardong 2001) suggests that the dichotomy is also of early evolutionary origin.

Within the precaudal column, essentially fixed total count and reciprocal thoracic and lumbar counts suggest the association of thoracic and lumbar series, with homeotic movement of the boundary between them. A close relationship between the thoracic and lumbar series is supported by current understanding of their historically recent differentiation. These two series are first distinguishable as subunits of the interlimb or “dorsal” region in Triassic synapsid ancestors of mammals (Jenkins 1971), long after cervical, sacral, and caudal vertebrae were morphologically distinct.

The higher-level associations of the five mammalian series present in terrestrial mammals inferred from these data are summarized diagrammatically in Fig. 3A. Note that the associations of the cervical and sacral series within the precaudal column are ambiguous. These inferred associations closely match the historical sequence of series origins proposed by Romer (1955) from observations of the vertebrate fossil record (Fig. 3B). Based on the very conservative precaudal counts in living Artiodactyla, the precaudal count of the ancestor of whales is predicted to have been C7 T13 L6 S4 = 30. Variability among living artiodactyls makes prediction of the ancestral cetacean caudal count difficult, but it seems likely that it was within the living artiodactyl range of 6–24.

Basal archaeocetes

The earliest archaeocete cetaceans for which substantial postcranial remains exist are the early to middle Eocene ambulocetid *Ambulocetus natans* (Thewissen et al. 1996; Madar

et al. 2002) and the middle Eocene remingtonocetid *Kutchicetus minimus* (Bajpai and Thewissen 2000). Both animals were quadrupeds and their vertebrae display the distinctive regional morphologies of all five traditional mammalian series.

The precaudal count of *Ambulocetus* is estimated as C7 T16 L8 S4 = 35 (Madar et al. 2002) and of *Kutchicetus* as C7 T15 L8 S4 = 34 (Bajpai and Thewissen 2000). The increases in thoracic and lumbar count over predicted ancestral counts are not accompanied by compensating decreases in adjacent series. Standardized lengths of *Ambulocetus* thoracic (0.89) and lumbar vertebrae (1.06) vertebrae (data from Madar et al. 2002) are shorter than the means seen in living carnivores. The four sacral vertebrae are coossified and the iliosacral articulation is via S1. The sacrals are dimensionally discontinuous with both lumbar and caudals. The *Kutchicetus* column is fragmentary, but isolated lumbar and caudals meet or exceed mean StCLs of comparable carnivore vertebrae, creating two areas of vertebral elongation (lumbar and caudal) separated by short sacral vertebrae (Bajpai and Thewissen 2000).

In contrast to the pattern seen in living carnivores and artiodactyls, precaudal elongation in both *Ambulocetus* and *Kutchicetus* occurred by addition of thoracic and lumbar vertebrae. These increases are almost certainly meristic, as counts of other precaudal series are unchanged, and the parallel increases suggest a shared segmentation program for the two series. Elongation in *Kutchicetus* was also the result of increase in lumbar and caudal centrum length (a diversifying change). Basal archaeocetes display no evidence of any homeotic or associational changes from the assumed ancestral organization of the column inherited from terrestrial ancestors.

Elongation of the precaudal column displaces the pelvis and hind limbs posteriorly. Precaudal elongation occurs in many swimming quadrupeds, including a variety of lutrine mammals (Buchholtz 1998; Bajpai and Thewissen 2000). A limb-based or a dual limb- and tail-based lutrine locomotion

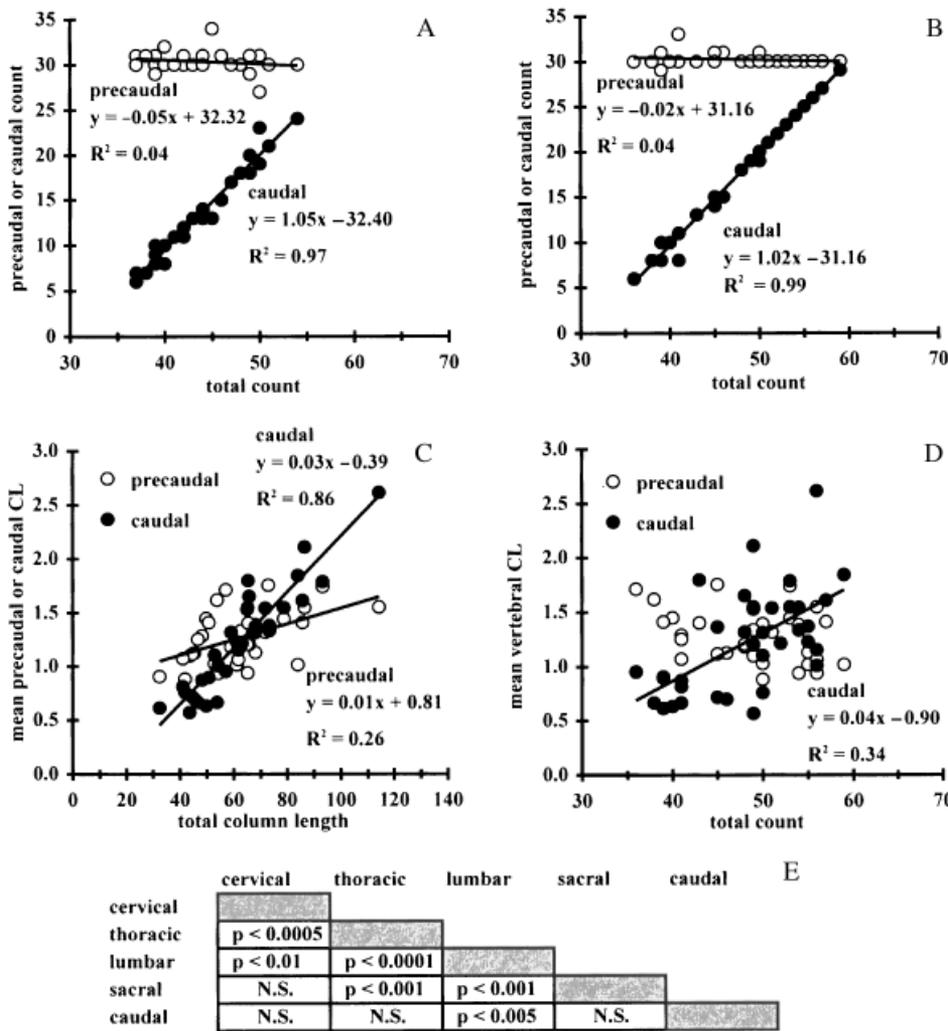


Fig. 2. Relationships of vertebral count and length in living artiodactyl and carnivore mammals. (A, B) Precaudal and caudal counts in genera of a given total count in Artiodactyla (A, $N = 33$) and Carnivora (B, $N = 34$). Note the stability of precaudal counts over a wide range of total vertebral counts. (C) Mean precaudal and caudal centrum lengths (CL) in Carnivora of different total column lengths ($N = 34$). Total column length predicts the mean centrum length of caudal, but not precaudal, vertebrae with high accuracy. (D) Mean vertebral CL in Carnivora of different total count ($N = 34$). Precaudal centrum length is independent of total count, and caudal centrum length is poorly predicted by total count. (E) Statistical correlations between mean vertebral CL in each column series in Carnivora ($N = 34$). All centrum lengths have been standardized to CW of vertebra T5 and are therefore dimensionless.

pattern has been proposed for basal archaeocetes (Thewissen and Fish 1997; Thewissen and Williams 2002).

Protocetidae

Protocetidae is a large and probably paraphyletic family of middle to late Eocene archaeocetes. Gingerich et al. (2005) subdivided protocetids into three subfamilies (Protocetinae, Makaracetinae, and Georgiacetinae) primarily on degree of adaptation to aquatic environments. The protocetine protocetid *Rodhocetus kasrani* (Gingerich et al. 1994) retains all five terrestrial vertebral series; precaudal count is C7 T13 L6? S4 = 30. The four “sacralized” vertebrae of *Rodhocetus* have fused transverse processes and the first sacral articulates with the pelvis. CLs for thoracic and lumbar vertebrae of *Rodhocetus* have not been published but no elongation is apparent from illustrations (Gingerich et al. 1994). The georgiacetine *G. vogtlensis* is used here to represent derived protocetids. Hulbert (1998) described the precaudal formula of *Georgiacetus*

as C7 T13 L8 S4 = 32. The thoracic series is interrupted, and may not be complete; only the first caudal is preserved. Hulbert distinguished sacral from lumbar vertebrae primarily on the basis of the shape and distal thickening of the transverse processes. Nevertheless, the sacral vertebrae are dimensionally continuous with the lumbar and do not fuse with each other or with the pelvis. *Georgiacetus* is interpreted here as lacking the sacral series, with a coordinated increase of four vertebrae to the lumbar series and a minimum precaudal count of C7 T13 L12 = 32. Mean standardized CLs of both thoracic (0.76) and lumbar (1.14) vertebrae (data from Hulbert 1998) of *Georgiacetus* are shorter than those of living carnivores surveyed.

The “location” of the sacral homologs in the column of living whales is an unresolved issue in cetacean anatomy. Slijper (1936) made an early contribution to this discussion by locating the roots of the pudendal plexus (whose nerves innervate urogenital structures) of a number of delphinids by dissection. Because the relationship of the pudendal plexus to

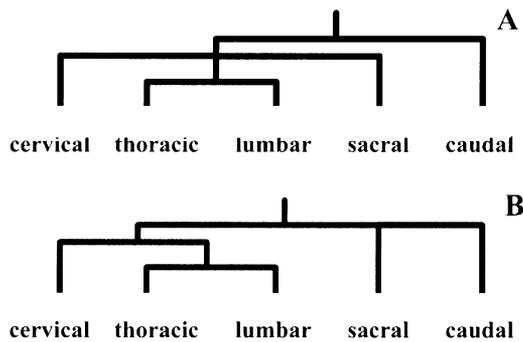


Fig. 3. Hypotheses of the higher order relationships of vertebral series of terrestrial mammals. (A) Relationships inferred from the count and shape of living artiodactyl and carnivore vertebrae. (B) Relationships inferred from the sequence of historical innovations in the vertebrate fossil record (after Romer 1955).

the sacrum is conserved in mammals, he was able to propose the existence of sacral homologs “within” the lumbar series. Although Slijper could not have known about homeotic patterning genes, his reasoning appears to be supported by more recent evidence of embryonic cetacean hind limb position (Thewissen et al. 2006) and axial gene expression in mice (Wellik and Capecchi 2003). When all *Hox11* gene expression is eliminated during mouse development, sacral vertebrae assume the morphology of lumbar vertebrae (Wellik and Capecchi 2003), suggesting a possible genetic mechanism for the apparently homeotic evolutionary transition seen in protocetids.

Fusion of a sacral vertebra to the pelvis serves an indicator of the isolation of the lumbar and caudal series, and suggests retention of a role for the limbs in early protocetid locomotion (Gingerich 2003). Evidence from the fossil record (Hulbert et al. 1998; Gingerich et al. 2005) suggests that reduction in the number of vertebrae participating in intrasacral and pelvic articulations in protocetids was a gradual, step-wise process. Loss of all sacral/pelvic articulation, seen in derived protocetids, such as *Georgiacetus*, would allow a single axial undulatory wave to travel through the entire postthoracic column.

Basilosauridae

Basilosaurids are middle to late Eocene archaeocetes characterized by dental and hind limb features (Uhen 1998). Column morphology is particularly well known in two species, the dorudontine *Dorudon atrox* and the basilosaurine *B. isis*. Three aspects of basilosaurid postcranial morphology are noteworthy: high precaudal vertebral count, presence of a discrete fluke, and extreme vertebral elongation in some genera.

Nearly complete material of the dorudontine *D. atrox* has been meticulously described by Uhen (2004). Column count is C7 T17 L20 Cd 21 = 65. This total reflects particularly high counts for both thoracic (17) and lumbar series (20) in

an animal with a relatively low caudal count. There is no sacral series but small innominates and limb bones persist, apparently embedded in the soft tissue (Gingerich et al. 1990; Uhen 2004). Published data for *B. isis* are less complete, but count appears to be very similar to that of *D. atrox*. Column and series counts are estimated here as C7 T18 L19 Cd 22 = 66 based on a composite constructed from unpublished centrum length data provided by P. D. Gingerich for nine partial skeletons. Synchronous addition to thoracic and lumbar count in basilosaurids suggests retention of the ancestral association of these series with respect to somitogenesis. Meristic addition is not apparent in the tail.

In living cetaceans, the presence of a fluke can be identified osteologically by the reversal of CW and CH in terminal caudal vertebrae (Uhen 1991, 2004; Buchholtz 1998). This reversal is clearly recognizable in both *Dorudon* and *Basilosaurus*, but is not as marked as in living whales (Buchholtz 1998). The fluke is independent of the rest of the tail in morphology, count, and percent of total column length in Neoceti, allowing inference of the dissociation of the ancestral caudal series into two modules, here identified as anterior tail and fluke. Despite presence of the fluke, it seems unlikely that it served as the sole propulsive surface in basilosaurids. Uhen (2004) concluded that much of the *Dorudon* column was involved in dorso-ventral flexion on the basis of osteological indicators of postthoracic flexibility.

Mean StCLs of both thoracic (0.82) and lumbar (1.01) (data from Uhen 2004) vertebrae of *Dorudon* fall below those of living carnivores surveyed. In contrast, *Basilosaurus* shows extreme and nearly uniform elongation of posteriormost thoracic, lumbar, and anterior (preflume) caudal vertebrae. The mean lumbar StCL of the composite *B. isis* skeleton is over 2.5 times that of *D. atrox*, and many individual vertebrae are over three times as long (Fig. 4A). The resulting eel-like body shape, often described as serpentine (e.g., Gingerich et al. 1990), may have afforded great maneuverability but probably only low swimming speeds.

The exaggeration of vertebral length in *Basilosaurus* is important in a developmental context because it suggests a shared pattern of elongation (a diversifying change) across a long midbody unit that transgresses the precaudal/caudal boundary. Although the pattern of meristic increase suggests association of the lumbar series with the thorax in *Basilosaurus*, dimensional patterns suggest association of the lumbar series with the anterior tail. The lack of elongation in *Dorudon* makes it impossible to determine whether this dimensional association also occurred in dorudontine basilosaurids.

Neoceti

Neocetes comprise the broad and highly successful radiation of Oligocene to Recent cetaceans, including both baleen

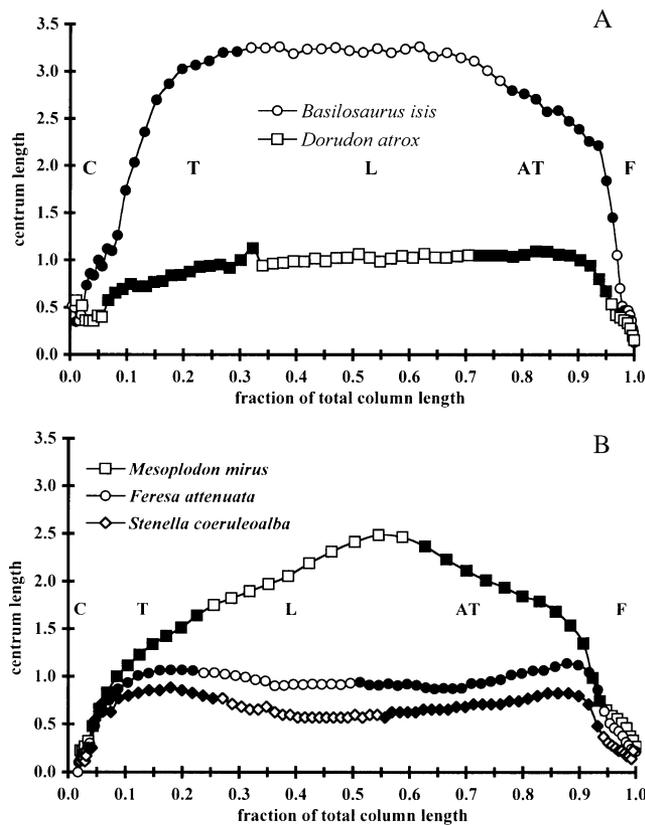


Fig. 4. Centrum length of basilosaurid and neocete cetacean vertebrae as a function of total column length. (A) The basilosaurids *Basilosaurus isis* (estimated count 66) and *Dorudon atrox* (count 65) have similar body proportions despite extreme elongation of mid-body vertebrae in *Basilosaurus*. *Basilosaurus* data are based on a composite constructed from data provided by P. D. Gingerich; *Dorudon* data are mean values from Uhen (2004). (B) The neocetes *Mesoplodon mirus* (count 47), *Feresa attenuata* (count 69), and *Stenella coeruleoalba* (count 79) have relatively shorter thoracic and lumbar series than basilosaurids, reflecting lower thoracic and lumbar counts. Note the relative stability of neocete series proportions despite large differences in count. Series boundaries are indicated by changes in symbol fill. All centrum lengths have been standardized to CW of vertebra T5 and are therefore dimensionless.

(mysticete) and toothed (odontocete) whales (Nikaïdo et al. 2001; Price et al. 2005). Neocetes are most easily distinguished from archaeocetes morphologically on the basis of cranial characters (e.g., Geisler and Sanders 2003). Cervical, thoracic, lumbar, anterior tail, and fluke vertebral series are recognizable, although the transition from lumbar to anterior tail is very subtle.

Neocete total counts range widely, from 40 (*Pontoporia blainvillei*) to almost 100 (*Phocoenoides dalli*). Basal neocetes such as sperm whales, beaked whales, and river dolphins generally have low counts, whereas derived neocetes such as dolphins and porpoises generally have high counts (Nikaïdo

et al. 2001; Buchholtz and Schur 2004). Allocation of counts to vertebral series in neocetes presents a pattern distinctly different from that of either terrestrial mammal outgroups or of archaeocete cetaceans: vertebrae are added to the precaudal and caudal regions of the column on a 1:1 basis (Fig. 5A). This correlation primarily reflects variation in lumbar and anterior tail counts, as cervical, thoracic, and fluke counts are highly conserved (Fig. 5B). Neither the reciprocal (homeotic) relationship between thoracic and lumbar counts seen in terrestrial mammals nor the coordinated (meristic) increases of archaeocete cetaceans exists: thoracic count predicts lumbar count extremely poorly ($R^2 = 0.14$).

Patterns of centrum morphology and length also suggest association of precaudal and caudal column units. In many neocetes, the morphological transition from lumbar to anterior tail vertebrae is extremely subtle, marked only by hemal arch scars ventrally. In contrast to the pattern seen in carnivores, neocete lumbar StCL predicts anterior tail centrum StCL with high accuracy ($R^2 = 0.92$, Fig. 5C). In interspecific comparisons, StCL varies most notably across posteriormost thoracic, lumbar, and anterior caudal units, a region that coincides with that of the vertebral elongation seen in *Basilosaurus*. Beaked whales (ziphiids) and dolphins (delphinids) represent extremes in this continuum (Fig. 4B) of elongation.

In what is almost certainly a unique pattern among mammals, neocetes also differ from carnivores and archaeocetes in the relationship between vertebral count and vertebral length. In Carnivora, high (caudal) count is associated with both vertebral (caudal) elongation and total column elongation. In neocetes, count bears no relationship to column length ($R^2 = 0.03$). Rather, (L+AT) count and centrum length are negatively correlated ($R^2 = 0.54$, $P < 0.0001$) with the result that neocetes have either a large number of short (L+AT) vertebrae or a small number of long (L+AT) vertebrae (Fig. 5D). With the exception of a small number of genera with very unusual anatomy (e.g., *Caperea*, *Lissodelphis*), neocete body proportions are remarkably stable over a large range of counts and body sizes (Fig. 5E).

In neocetes, very similar morphology and patterns of count and length suggest association across the precaudal/caudal boundary. Precaudal vertebral counts predict caudal counts, suggesting a shared pattern of somitogenesis. Precaudal vertebral shape predicts caudal shape, suggesting a shared pattern of diversification and growth. Most unusually, (L+AT) vertebral count shows an inverse relationship to (L+AT) vertebral length. The retention of similar body proportions despite count variation raises the possibility that regional identification of the (L + AT) mesoderm is established before its segmentation into a few long vertebrae or many short vertebrae.

As added vertebrae do not confer increased body length, elongation cannot be invoked as a functional explanation for the dramatic increase in neocete counts. A possible selective

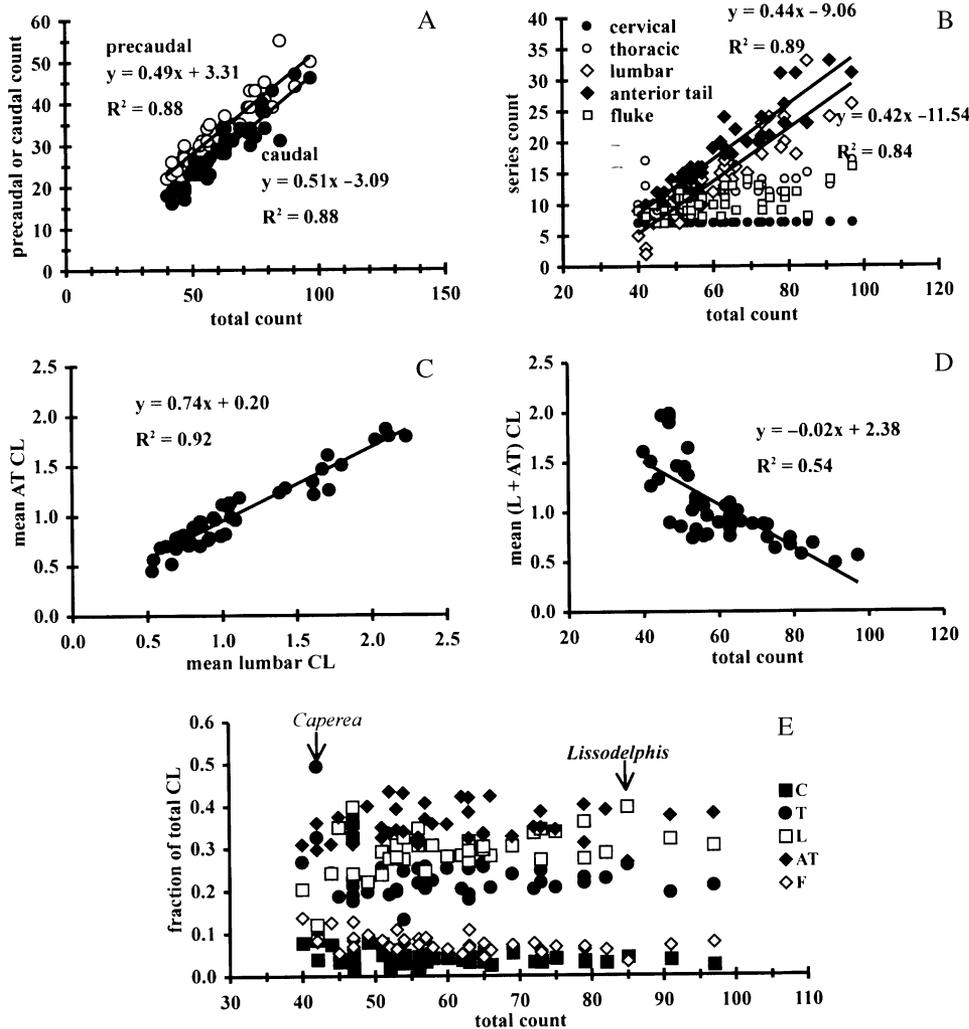


Fig. 5. Relationships of vertebral count and length in living neocete cetaceans ($N = 44$). (A) Precaudal and caudal counts in neocetes of different total count. Note the very similar slopes of precaudal and caudal increases. (B) Vertebral series counts in neocetes of different total count. Almost all of the increases in total count are due to increases in lumbar and anterior tail counts. (C) Mean anterior tail (AT) centrum lengths (CL) of neocetes with different mean lumbar centrum lengths. Lumbar CL is an excellent predictor of anterior tail centrum length. (D) Mean centrum length of (lumbar+anterior) vertebrae in neocetes of different total count. (E) The fraction of column length represented by different column series in neocetes of different total count. Series fractions are remarkably stable over a wide range of column counts and body size. Exceptions to typical neocete series proportions represented by the mysticete *Caperea marginata* and the odontocete *Lissodelphis borealis* are indicated. All centrum lengths have been standardized to CW of vertebra T5 and are therefore dimensionless.

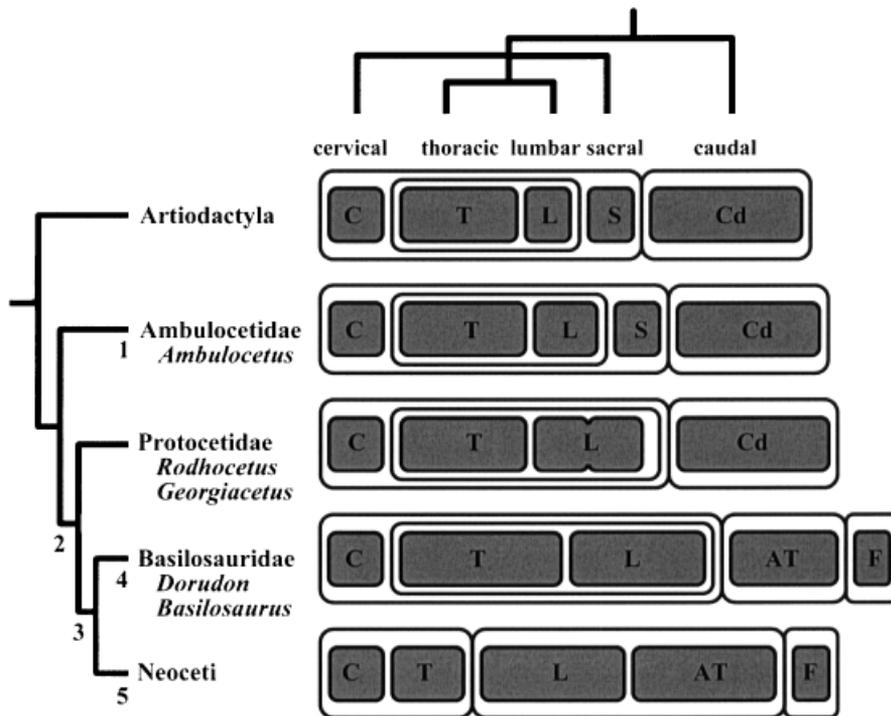
advantage of the large number of very short discoidal vertebrae seen in derived neocetes is generation of a column with a very large proportion of intervertebral disk to bone, allowing elastic energy storage during swimming.

DISCUSSION

Patterns of vertebral count and shape suggest that the five vertebral series of artiodactyls and carnivores are not uniformly associated. Patterns of count and shape in caudal vertebrae are independent of those in precaudal vertebrae, signaling different patterns of segmentation and growth. Among precaudal series, constancy of total count and negative correlation of series counts suggest that the thoracic and lumbar series have a closer association with each other than either has with the cervical or sacral series. Vertebral morphology in four large cetacean groups of documented phylogenetic relationship indicates that this ancestral column

organization underwent diversifying, meristic, homeotic, and associational changes over evolutionary time as whales adapted to aquatic environments. Inferred evolution of the modular organization of the vertebral column is presented in Fig. 6 in the form of Venn diagrams.

Although the fossil record of “basal archaeocetes” is scant, the five terrestrial vertebral series are easily recognized in all known specimens. It seems highly likely that these animals retained the modular organization of their terrestrial ancestors. In contrast to the pattern typically seen in living artiodactyls and carnivores, *Ambulocetus* and *Kutchicetus* achieved column elongation through addition to the count of the thoracic and lumbar series. These are almost certainly meristic innovations. High counts are not present in the subsequent basal protocetids, suggesting two possible interpretations. The first is that *Ambulocetus* and *Kutchicetus* may be specialized genera off the main line of cetacean evolution. The second is that early meristic increases in basal archaeocetes were followed by secondary reductions in count.



- 1 meristic addition to the thoracic and lumbar series
- 2 homeotic loss of the sacral series
- 3 dissociation of the caudal series into anterior tail and fluke series
- 4 meristic addition to thoracic and lumbar series
elongation of lumbar and anterior tail vertebrae (some species)
- 5 association of lumbar and anterior tail series
meristic addition to lumbar and anterior tail series

Fig. 6. A hypothesis of modular organization of the vertebral column in cetacean history. Morphological innovations (numbered) are mapped onto a consensus phylogeny of Artiodactyla (as outgroup) and four groups of cetaceans. Meristic increases appear to have occurred independently in basal archaeocetes, basilosaurids, and neocetes. Neocetes inherited homeotic loss of the sacral series and dissociation of the caudal series into anterior tail and fluke from their archaeocete ancestors. Association across the precaudal/caudal boundary is a neocete innovation.

The early protocetine protocetid *Rodhocetus* displays precaudal (including sacral) counts essentially identical to those of cetacean outgroups. Later georgiacetine protocetids with more extreme aquatic adaptations increase lumbar count at the expense of sacrals, implicating homeotic movement of the lumbar/sacral boundary. Elongation of individual thoracic or lumbar vertebrae is rare in protocetids (Uhen 1999), although the lumbar vertebrae of the georgiacetine *Eocetus schweinfurthi* appear elongated (Uhen 1999).

Basilosaurids display developmental innovations interpretable as meristic, associational, and diversifying. The high thoracic and lumbar counts of the genera *Dorudon* and *Basilosaurus* suggest shared meristic additions to these two series with a history of association. Osteological markers of the fluke signal the dissociation of the caudal series into anterior tail and fluke subunits. The independence of anterior tail and fluke is demonstrable in neocetes, which show extensive additions to anterior tail count but almost none to the fluke. *Basilosaurus*, but not *Dorudon*, has exceptionally long posterior thoracic, lumbar, and anterior tail vertebrae, a diversifying change. Of the basilosaurid vertebral innovations

described here, only the fluke is shared with basal neocetes. Neither precaudal elongation by addition of vertebrae nor precaudal elongation by elongation of individual vertebrae is evident in basal neocetes. In fact, precaudal vertebral counts of the seven living basal odontocete (physeterid and ziphiid) (mean = 27.6) and 10 living mysticete (mean = 31.6) species sampled here are more similar to those of terrestrial outgroups and to protocetids than they are to those of known basilosaurids (mean = 44). These data raise the possibility that the ancestors of neocetes are to be found among still unknown fluked basilosaurids without elongate vertebrae or high precaudal counts.

Archaeocetes and neocetes have profoundly different patterns of postcranial anatomy. Archaeocetes display “terrestrial modularity.” Their columns have distinctive and independent precaudal and caudal units despite internal modifications (meristic, homeotic, subdivision into submodules). The lumbar series is most closely associated with the thoracic series, with which it shares rare meristic and frequent homeotic (reciprocal) changes in count. In contrast, all living cetaceans exhibit “neocete modularity.” Their columns are

characterized by a large (L+AT) midcolumn unit that crosses the precaudal/caudal boundary and shares traits of morphology, count, and size. The lumbar series is most closely associated with the anterior tail; these series change count on a 1:1 basis. Very few changes in count occur in the neck, thorax, or fluke. The negative correlation between vertebral count and length across the (L+AT) unit produces surprisingly similar column proportions across a neocete radiation that varies dramatically in both count and body size.

Neocete cetaceans inherited the homeotic reduction of the sacral series and the dissociation of the fluke and the anterior tail series from protocetid and basilosaurid archaeocetes. Somewhat surprisingly, the earliest neocetes show no elongation by increased count or by elongation of vertebral dimensions over that inferred in their terrestrial ancestors. Among living neocetes, high counts are instead coupled to low-vertebral lengths across a midbody unit that transgresses the precaudal/caudal boundary. The dramatic transition from the archaeocete to the neocete pattern of morphology supports a hypothesis of a historical change in developmental modularity that must have occurred near the Eocene/Oligocene boundary, when the oldest odontocete cetaceans appear in the fossil record (Barnes 2000).

Acknowledgments

I gratefully acknowledge the museum collection managers who provided access to the collections under their care, the generosity of Phil Gingerich in providing access to unpublished data, and the creativity, enthusiasm, and help of students who worked on this and associated projects: Elizabeth Wolkovich, Stephanie Schur, Courtney Stepien, Kate Webbink, and Amy Booth. Funding for this project was provided by a Faculty Grant and a Brachman Hoffman Grant from Wellesley College.

REFERENCES

- Bajpai, S., and Thewissen, J. G. M. 2000. A new, diminutive Eocene whale from Kachchh (Gujarat, India) and its implications for locomotor evolution of cetaceans. *Curr. Sci.* 79: 1478–1482.
- Barnes, L. G. 2000. The world's oldest known odontocete (Mammalia, Cetacea). *J. Vertebr. Paleontol.* 20: 28A.
- Bateson, W. 1894. *Materials for the Study of Variation*. Macmillan, London.
- Bolker, J. A. 2002. Modularity in development and why it matters to Evo-Devo. *Am. Zool.* 40: 770–776.
- Buchholtz, E. A. 1998. Implications of vertebral morphology for locomotor evolution in early Cetacea. In J. G. M. Thewissen (ed.). *The Emergence of Whales*. Plenum Press, New York, pp. 325–352.
- Buchholtz, E. A., and Schur, S. A. 2004. Evolution of vertebral osteology in Delphinidae (Cetacea). *Zool. J. Linn. Soc. Lond.* 140: 383–401.
- Buchholtz, E. A., Booth, A. C., and Webbink, K. E. 2007. Vertebral anatomy in the Florida manatee *Trichechus manatus latirostris*: a developmental and evolutionary analysis. *Anatomical Record* (in press).
- Burke, A. C., Nelson, C. E., Morgan, B. A., and Tabin, C. 1995. *Hox* genes and the evolution of vertebrate axial morphology. *Development* 121: 4333–4346.
- Carroll, S. B., Grenier, J. K., and Weatherbee, S. D. 2001. *From DNA to Diversity*. Blackwell Science, Malden, MA.
- Cohn, M. J., and Tickle, C. 1999. Developmental basis of limblessness and axial patterning in snakes. *Nature* 399: 474–479.
- Flower, W. H. 1885. *Osteology of the Mammalia*. Macmillan and Co., London.
- Galis, F. 1999. Why do almost all mammals have seven cervical vertebrae? Developmental constraints, *Hox* genes, and cancer. *J. Exp. Zool.* 285: 19–26.
- Geisler, J. H., and Sanders, A. E. 2003. Morphological evidence for the phylogeny of Cetacea. *J. Mammal. Evol.* 10: 23–129.
- Geisler, J. H., Sanders, A. E., and Luo, Z.-X. 2005. A new protocetid whale (Cetacea: Archaeoceti) from the late middle Eocene of South Carolina. *Am. Mus. Novit.* 3480: 1–65.
- Geisler, J. H., and Uhen, M. D. 2005. Phylogenetic relationships of extinct cetartiodactyls: results of simultaneous analyses of molecular, morphological, and stratigraphic data. *J. Mammal. Evol.* 12: 145–160.
- Gingerich, P. D. 2003. Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. *Paleobiology* 29: 429–454.
- Gingerich, P. D., Smith, B. H., and Simons, E. L. 1990. Hind limbs of Eocene Basilosaurus: evidence of feet in whales. *Science* 249: 154–157.
- Gingerich, P. D., Raza, S. M., Arif, M., Anwar, M., and Zhou, X. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* 368: 844–847.
- Gingerich, P. D., ul-Haq, M., Zalmout, I. S., Kahn, I. H., and Malkani, M. S. 2001. Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science* 293: 2239–2242.
- Gingerich, P. D., Zalmout, I. S., ul-Haq, M., and Bhatti, M. A. 2005. *Makaracetus bidens*, a new protocetid archaeocete (Mammalia, Cetacea) from the early middle Eocene of Balochistan (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* 31: 197–210.
- Hildebrand, M., and Goslow, G. E. Jr. 2001. *Analysis of Vertebrate Structure*. 5th Ed. John Wiley & Sons, New York.
- Hulbert, R. C. Jr. 1998. Postcranial osteology of the north American middle Eocene protocetid *Georgiacetus*. In J. G. M. Thewissen (ed.). *The Emergence of Whales*. Plenum Press, New York, pp. 235–268.
- Hulbert, R. C. Jr., Petkewich, R. M., Bishop, G. A., Bukry, D., and Ale-shire, D. P. 1998. A new middle Eocene protocetid whale (Mammalia: Cetacea: Archaeoceti) and associated biota from Georgia. *J. Paleontol.* 72: 907–927.
- Jenkins, F. 1971. The postcranial skeleton of African cynodonts. *Bull. Peabody Mus. Nat. Hist.* 36: 1–216.
- Johnson, D. R., and O'Higgins, P. 1996. Is there a link between changes in the vertebral “hox code” and shape of vertebrae? A quantitative study of shape change in the cervical vertebral column of mice. *J. Theor. Biol.* 183: 89–93.
- Kardong, K. V. 2001. *Vertebrates: Comparative Anatomy, Function, Evolution*. 4th Ed. McGraw Hill, Boston.
- Kellogg, R. 1936. *A Review of the Archaeoceti*. Carnegie Institute of Washington Publication Number 482. Waverly Press, Baltimore.
- Kessel, M. 1992. Respecification of vertebral identities by retinoic acid. *Development* 115: 487–501.
- Kieny, M., Mauger, A., and Sengel, P. 1972. Early regionalization of the somatic mesoderm as studied by the development of the axial skeleton of the chick embryo. *Dev. Biol.* 28: 142–161.
- Krieger, J. O., Churakov, G., Kieffmann, M., Jordan, U., Brosius, J., and Schmitz, J. 2006. Retroposed elements as archives for the evolutionary history of placental mammals. *Pub. Lib. Sci.* 4: e91.
- Li, Z.-L., Chisaka, O., Koseki, H., Akasaka, T., Ishibashi, M., and Shiota, K. 1997. Heat shock-induced homeotic transformations of the axial skeleton and associated shifts of *Hox* gene expression domains in mouse embryos. *Reprod. Toxicol.* 11: 761–770.
- Li, Z.-L., and Shiota, K. 1999. Stage-specific homeotic vertebral transformations in mouse fetuses induced by maternal hyperthermia during somitogenesis. *Dev. Dyn.* 216: 336–348.
- Lovejoy, C. O., Cohn, M. J., and White, T. D. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. *Proc. Natl. Acad. Sci. USA* 96: 13247–13252.
- Madar, S. I., Thewissen, J. G. M., and Hussain, S. T. 2002. Additional holotype remains of *Ambulocetus natans* (Cetacea, Ambulocetidae) and their implications for locomotion in early whales. *J. Vertebr. Paleontol.* 22: 405–422.

- McPherron, A. C., Lawler, A. M., and Lee, S.-J. 1999. Regulation of anterior/posterior patterning of the axial skeleton by growth/differentiation factor 11. *Nat. Genet.* 22: 260–264.
- Narita, Y., and Kuratani, S. 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. *J. Exp. Zool.* 304B: 91–106.
- Nikaido, M., et al. 2001. Retroposon analysis of major cetacean lineages: the monophyly of toothed whales and the paraphyly of river dolphins. *Proc. Natl. Acad. Sci. USA* 98: 7384–7389.
- Oostra, R.-J., Hennekam, R. C. M., de Rooij, L., and Moorman, A. F. M. 2005. Malformations of the axial skeleton in *Museum Vrolijk* I: homeotic transformations and numerical anomalies. *Am. J. Med. Genet.* 1134A: 268–281.
- Polly, P. D., Head, J. J., and Cohn, M. J. 2001. Testing modularity and dissociation: the evolution of regional proportions in snakes. In M. L. Zelditch (ed.). *Beyond Heterochrony: The Evolution of Development*. Wiley-Liss, New York, pp. 305–335.
- Pourquié, O. 2003. The segmentation clock: converting embryonic time into spatial pattern. *Science* 301: 328–330.
- Price, S. A., Bininda-Emonds, O. R. P., and Gittleman, J. L. 2005. A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla). *Biol. Rev.* 80: 445–473.
- Raff, R. A. 1996. *The Shape of Life*. The University of Chicago Press, Chicago.
- Raff, R. A., and Sly, B. J. 2000. Modularity and dissociation in the evolution of gene expression territories in development. *Evol. Dev.* 2: 102–113.
- Romer, A. S. 1955. *The Vertebrate Body*. 2nd Ed. W. B. Saunders Company, Philadelphia.
- Rommel, S. A., and Reynolds, J. E. III 2002. Skeletal anatomy. In W. F. Perrin, B. Würsig, and J. G. M. Thewissen (eds.). *Encyclopedia of Marine Mammals*. Academic Press, San Diego, pp. 1089–1103.
- Sanger, T. J., and Gibson-Brown, J. J. 2004. The developmental bases of limb reduction and body elongation in squamates. *Evolution* 58: 2103–2106.
- Slijper, E. J. 1936. *Die Cetaceen*. Capita Zoological VI–VII, reprinted 1973 by A. Asher and Co. B. V., Amsterdam.
- Tam, P. P., and Tan, S.-S. 1992. The somitogenic potential of cells in the primitive streak and the tail bud of the organogenesis-stage mouse embryo. *Development* 115: 703–715.
- Thewissen, J. G. M., Cohn, M. J., Stevens, L. S., Bajpai, S., Heyning, J., and Horton, W. E. Jr. 2006. Developmental basis for hind-limb loss in dolphins and origin of the cetacean body plan. *Proc. Natl. Acad. Sci. USA* 103: 8414–8418.
- Thewissen, J. G. M., and Fish, F. E. 1997. Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence. *Paleobiology* 23: 482–490.
- Thewissen, J. G. M., Madar, S. I., and Hussain, S. T. 1996. *Ambulocetus natans*, an Eocene cetacean (Mammalia) from Pakistan. *Courier Forschungs-Institut Senckenberg* 190: 1–86.
- Thewissen, J. G. M., Williams, E. M., Roe, L. J., and Hussain, S. T. 2001. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature* 413: 277–281.
- Thewissen, J. G. M., and Williams, E. M. 2002. The early radiations of Cetacea (Mammalia): Evolutionary pattern and developmental correlations. *Annu. Rev. Ecol. Syst.* 33: 73–90.
- Todd, T. W. 1922. Numerical significance in the thoracolumbar vertebrae of the Mammalia. *Anat. Rec.* 24: 260–286.
- Uhen, M. 1991. Vertebral proportions as indicators of locomotor style in mammals. *J. Vertebr. Paleontol.* 11: 59A.
- Uhen, M. D. 1998. Middle to Late Eocene basilosaurines and dorudontines. In J. G. M. Thewissen (ed.). *The Emergence of Whales*. Plenum Press, New York, pp. 29–61.
- Uhen, M. D. 1999. New species of protocetid archaeocete whale, *Ecetus wardii* (Mammalia: Cetacea) from the middle Eocene of North Carolina. *J. Paleontol.* 73: 512–528.
- Uhen, M. D. 2004. Form, function and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the Middle to Late Eocene of Egypt. *Univ. Mich. Pap. Paleontol.* 34: 1–222.
- Wellik, D. M., and Capocchi, M. R. 2003. *Hox10* and *Hox11* genes are required to globally pattern the mammalian skeleton. *Science* 301: 363–367.
- Williams, E. M. 1998. Synopsis of the earliest cetaceans. In J. G. M. Thewissen (ed.). *The Emergence of Whales*. Plenum Press, New York, pp. 1–28.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In J. J. Thomason (ed.). *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York, pp. 19–33.