A phylogenetic blueprint for a modern whale

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ABSTRACT

The emergence of Cetacea in the Paleogene represents one of the most profound macroevolutionary transitions within Mammalia. The move from a terrestrial habitat to a committed aquatic lifestyle engendered wholesale changes in anatomy, physiology, and behavior. The results of this remarkable transformation are extant whales that include the largest, biggest brained, fastest swimming, loudest, deepest diving mammals, some of which can detect prey with a sophisticated echolocation system (Odontoceti – toothed whales), and others that batch feed using racks of baleen (Mysticeti – baleen whales). A broad-scale reconstruction of the evolutionary remodeling that culminated in extant cetaceans has not yet been based on integration of genomic and paleontological information. Here, we first place Cetacea relative to extant mammalian diversity, and assess the distribution of support among molecular datasets for relationships within Artiodactyla (even-toed ungulates, including Cetacea). We then merge trees derived from three large concatenations of molecular and fossil data to yield a composite hypothesis that encompasses many critical events in the evolutionary history of Cetacea. By combining diverse evidence, we infer a phylogenetic blueprint that outlines the stepwise evolutionary development of modern whales. This hypothesis represents a starting point for more detailed, comprehensive phylogenetic reconstructions in the future, and also highlights the synergistic interaction between modern (genomic) and traditional (morphological + paleontological) approaches that ultimately must be exploited to provide a rich understanding of evolutionary history across the entire tree of Life.

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1. Introduction

The emergence of Cetacea (whales) represents one of the most striking evolutionary transitions within Mammalia (Thewissen et al., 2009; Uhen, 2010). The return to a fully aquatic mode of life required wholesale anatomical rearrangements that permit modern cetaceans to thrive in marine and freshwater habitats (Thewissen and Bajpai, 2001). In addition to the initial transformation to an obligately aquatic form, divergent subclades of Cetacea, Odontoceti (toothed whales, including dolphins and porpoises) and Mysticeti (baleen whales), have specialized still further (Figs. 1 and 2). Odontocetes have lost the olfactory sense, and utilize a sophisticated echolocation system to detect prey (Oelschläger, 1992;

Cranford et al., 2011); large relative brain size, complex social behaviors, tool use, and self-recognition indicate advanced cognitive abilities in some members of this clade (Marino et al., 2007). Mysticetes retain olfaction (Cave, 1988; Thewissen et al., 2010) but have lost their teeth and are characterized by extremely large body size and an elaborate filter-feeding apparatus that features baleen (Fitzgerald, 2006; Deméré et al., 2008).

Certain cetaceans are simply awe-inspiring, and it is difficult to imagine the long series of evolutionary changes that produced these species over the past 60 million years. The blue whale, *Balaenoptera musculus* (Fig. 1A), is perhaps the largest animal species that has ever evolved. At >90 ft in length, some specimens weigh more than 150 tons (equivalent to ~20 elephants), and are the loudest extant organisms, capable of producing low-frequency vocalizations that exceed 180 decibels (Cummings and Thompson, 1971; Nowak, 1991). In a single feeding bout, a blue whale can engulf, then filter, a volume of prey-laden water that would fill a medium-sized swimming pool (~60 m³; Pivorunas, 1979). This

remarkable batch-feeding behavior, described as the world's largest biomechanical event, is achieved via an integrated suite of behavioral and anatomical novelties (Fig. 2; Pivorunas, 1977, 1979; Lambertsen et al., 1995; Werth, 2000; Goldbogen et al., 2007). The giant sperm whale, *Physeter macrocephalus*, represents another exceptional outlier. Among the largest carnivorous organisms that have ever existed, sperm whales are capable of diving 2000 meters below the ocean's surface, holding their breath for more than an hour, and simultaneously dining on giant squid at great depths and pressures (Fig. 1B; Nowak, 1991; Watwood et al., 2006). *Physeter* also is characterized by the largest brain of any extant organism (~10 kg; Oelschläger, 2008). The phenotypic gap between these spectacular giants and their closest terrestrial relatives is huge (Fig. 1).

Extensive modifications, including the loss or reduction of many typical mammalian characteristics (Flower, 1883), have rendered modern representatives of Cetacea nearly unrecognizable as mammals (Fig. 2), but molecular data generally position Cetacea deep within Artiodactyla (even-toed hoofed mammals), closest to Hippopotamidae (Irwin and Arnason, 1994; Gatesy et al., 1996; Gatesy, 1997, 1998; Nikaido et al., 1999; Matthee et al., 2001; Zhou et al., 2011). Hippopotamuses and whales share some aquatic traits (Fig. 1A–C; Gatesy et al., 1996; Gatesy, 1997), but extant cetaceans are still highly derived relative to hippos across nearly all organ systems (Boisserie et al., 2011). Due to extinction, a purely molecular approach is therefore inadequate for deciphering the extended sequence of change on the lineage that led to extant whales; integration of genomic evidence with the fossil record is required (Gatesy and O'Leary, 2001). Over the past three decades, paleontologists have filled in much of the phenotypic divide between hippos and extant cetaceans, such as the blue whale, with a surprising array of extinct forms that express functionally intermediate combinations of characters (reviewed in Uhen [2010] with illustrations of skeletal anatomy). These taxa include members of Raoellidae, the putative extinct sister group to Cetacea (Fig. 3A; Thewissen et al., 2007; Cooper et al., 2011), Pakicetidae and Ambulocetidae, early "walking whales" (Fig. 3B–C; Gingerich et al., 1983; Thewissen et al., 1996, 2001; Madar et al., 2002; Madar, 2007), narrow-snouted Remingtonocetidae (Fig. 3D; Kumar and Sahni, 1986; Bajpai et al., 2011), Eocene Protocetidae that retained large external hindlimbs (Fig. 3E; Hulbert, 1998; Gingerich et al., 2001, 2009), Basilosauridae, among the first obligately aquatic cetaceans (Fig. 3F; Gingerich et al., 1990; Uhen, 2004; Martínez-Cáceres and de Muizon, 2011), and primitive mysticetes with functional dentitions (Fig. 3G–H; Fitzgerald, 2006, 2010; Deméré and Berta, 2008).

The fossil record of Cetacea offers essential information for dating and ordering key evolutionary events in deep time (e.g., Gingerich et al., 2001), and DNA sequences provide a solid phylogenetic framework with estimates of genetic divergence among living species (e.g., McGowen et al., 2009), but paleontological and neontological datasets can yield conflicting phylogenetic results (e.g., Thewissen et al., 2007; Zhou et al., 2011). By utilizing diverse data – a large concatenation of nuclear genes from across Mammalia (Meredith et al., 2011a), transposon insertions coded from the major lineages of Artiodactyla (Nikaido et al., 1999, 2001, 2006, 2007), and combined molecular plus paleontological datasets (Geisler et al., 2007, 2011; Deméré et al., 2008; Spaulding et al., 2009) – we can assemble a unified, broad-scale phylogenetic hypothesis for Cetacea. Here, in an ode to Morris Goodman, we first summarize molecular support for the phylogenetic placement of Cetacea relative to other extant mammals, and then merge trees derived from supermatrices of fossils and molecules to infer the long series of character transformations that led to modern whale species. We honor Dr. Goodman's work which included early application of rigorous cladistic methods to molecular data (e.g., Goodman et al., 1985), his prescient use of a supermatrix approach for reconstructing phylogenetic history (e.g., Miyamoto and Goodman, 1986), and his profound curiosity regarding the evolution of large-brained mammals (e.g., Goodman et al., 2009) within the context of our phylogenetic analysis of Cetacea.

2. Materials and methods

The taxonomy of Artiodactyla and Cetacea represents an ongoing debate in the literature that reflects a desire for stability as well
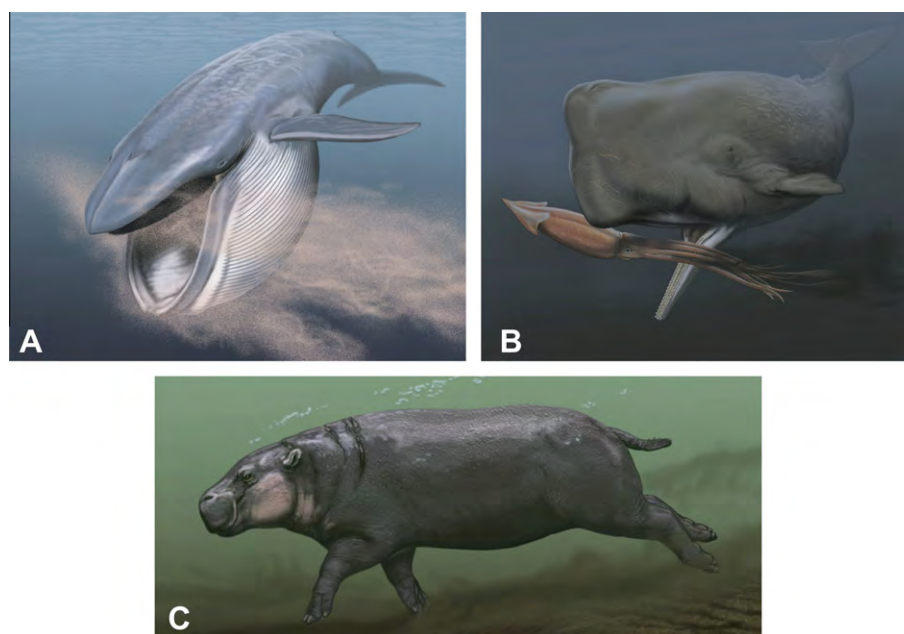

Fig. 1. Representatives of the two major clades of crown Cetacea and a member of Hippopotamidae, the extant sister group to Cetacea. The mysticete *Balaenoptera musculus* (blue whale; A) and the odontocete *Physeter macrocephalus* (giant sperm whale; B) illustrate some of the awe-inspiring specializations of modern cetaceans. Comparison to the hippopotamid *Choeropsis liberiensis* (pygmy hippo; C) shows the wide gap in anatomy between modern whales and their closest living relatives. Artwork is by Carl Buell.

as an urge to recognize only monophyletic higher-level taxa. Here, we follow the phylogenetic definition for Artiodactyla from Spaulding et al. (2009) – the last common ancestor of *Bos taurus* (cow), *Hippopotamus amphibius* (hippo), *Sus scrofa* (pig), and *Camelus dromedarius* (camel) and all of the species that descended from that common ancestor. Cetaceans are considered highly derived artiodactyls in this framework (Spaulding et al., 2009). In the present contribution, we follow the traditional delimitation of Cetacea outlined in Thewissen et al. (2007) – the clade that includes Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, Basilosauridae, Odontoceti, and Mysticeti. The five families in this list are commonly referred to as 'archaeocetes' and represent the stem groups to crown Cetacea; the family Protocetidae is a paraphyletic

grade, and Basilosauridae also may not be a natural group (Uhen, 2010; but see Fitzgerald, 2010). Crown Cetacea is composed of two monophyletic groups, Odontoceti and Mysticeti, which are sister taxa (Geisler et al., 2011).

To determine the phylogenetic position of Cetacea relative to a broad array of extant mammals, and to summarize the consistency of molecular support for relationships among the major extant lineages of Artiodactyla, we reanalyzed the molecular supermatrix of Meredith et al. (2011a) and the transposon insertion data of Nikaido et al. (1999, 2001, 2006, 2007). Meredith et al. (2011a) recently sampled segments of 26 nuclear loci, 35,603 aligned basepairs, from most extant mammalian families; Bayesian and maximum likelihood analyses were highlighted in this study. Nikaido
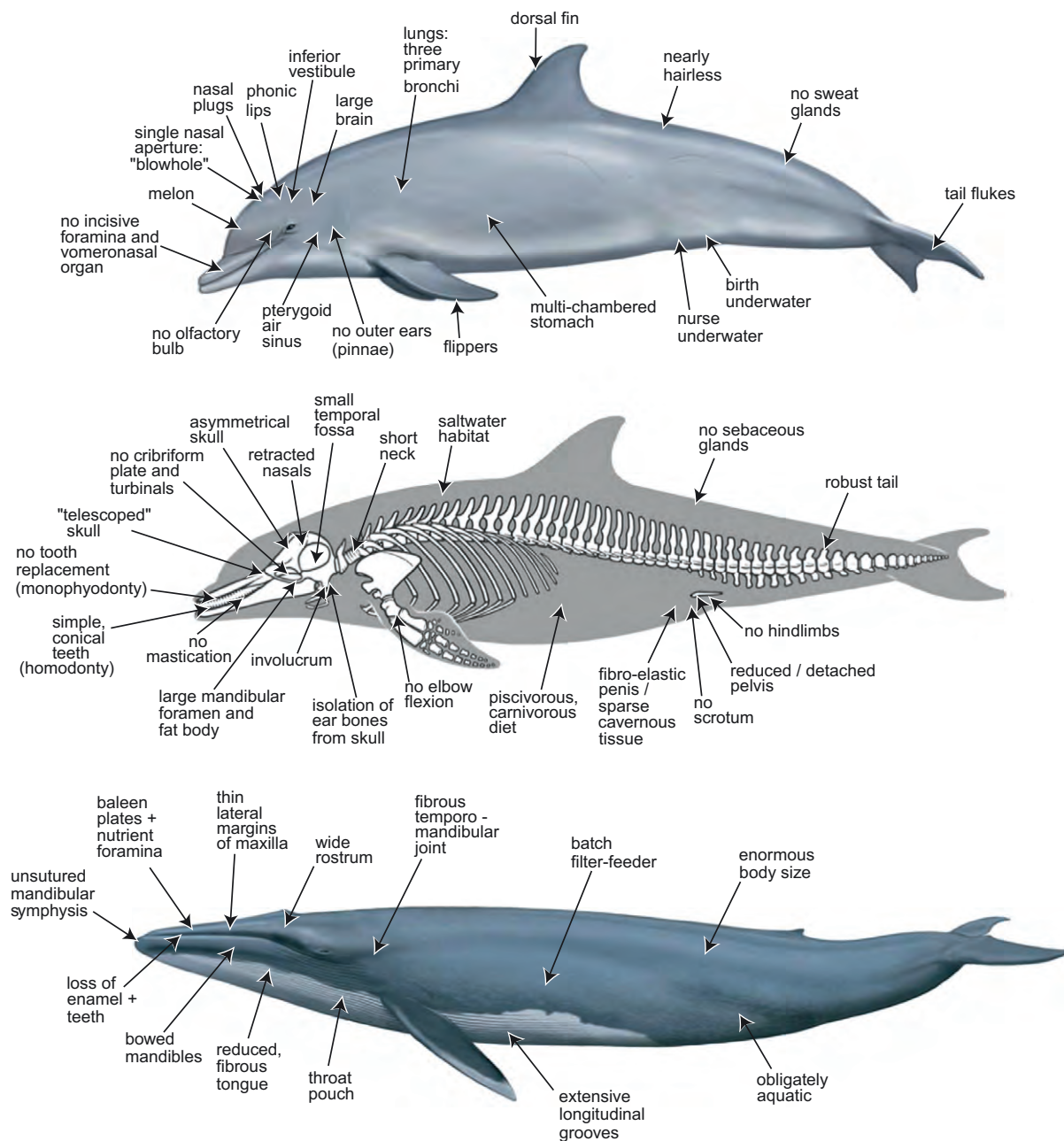

Fig. 2. Modern cetaceans represent a bizarre mixture of traits, many of which are thought to be specializations that enable an obligately aquatic lifestyle. Some of the characteristic features of extant cetaceans are indicated in illustrations of the delphinid odontocete *Tursiops truncatus* (bottlenose dolphin), top and middle, and the balaenopterid mysticete *Balaenoptera musculus* (blue whale). Many of the specializations that make a whale look like a whale are evolutionary losses (e.g., hindlimbs, external ears, hair, teeth) in combination with structures that are uniquely evolved within Mammalia (e.g., dorsal fin, blowhole, melon, baleen, extremely "telescoped" and asymmetrical skull, pleated throat pouch). Artwork is by Carl Buell.

et al. (1999, 2001, 2006, 2007) surveyed multiple artiodactyl species for the presence or absence of transposons at specific genomic sites, and suggested that transposon insertions represent essentially homoplasy-free characters. Here, we executed complementary parsimony analyses of Meredith et al.'s (2011a) mammalian supermatrix in PAUP* 4.0b10 (Swofford, 2002) using equal weighting of characters and also implied weights (Goloboff et al., 2008) with the concavity of the weighting curve, *k*, set to two (the default option in PAUP*). Heuristic searches included >100 random taxon addition sequences with tree-bisection and reconnection (TBR) branch swapping, and minimum length trees were rooted by non-mammalian, vertebrate outgroups (*Gallus, Taeniopygia, Anolis, Xenopus, Danio*). Bootstrap analyses (≥200 replications) employed heuristic searches with TBR branch swapping and >5 random taxon

additions per bootstrap replicate. A more taxonomically restricted analysis focused on the distribution of molecular support for relationships among extant artiodactyl families and entailed combined analysis of 26 nuclear loci from Meredith et al. (2011a) with 101 transposon insertion characters from Nikaido et al. (1999, 2001, 2006, 2007). The parsimony search and bootstrap analysis with equal weighting of all character transformations were as described above, and trees were rooted using representatives of Perissodactyla (odd-toed ungulates). To further assess the distribution of character support, branch support (Bremer, 1994) and partitioned branch support scores (PBS; Baker and DeSalle, 1997) were calculated using TreeRot (Sorenson, 1999) and PAUP* 4.0b10 (Swofford, 2002). PBS scores for each supported node were determined for 27 partitions: *TTN, CNR1, BCHE, EDG1, RAG1, RAG2, ATP7A, TYR1,*
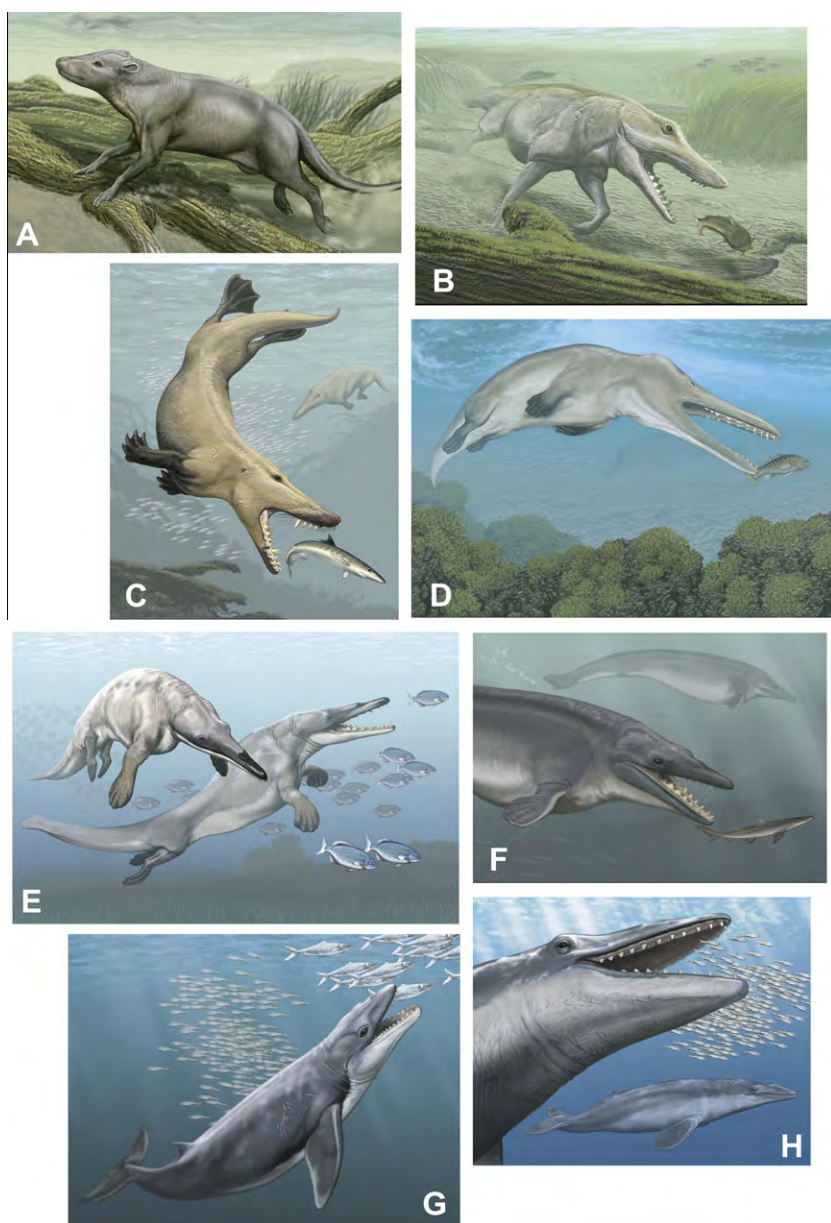

Fig. 3. A gallery showing reconstructions of an Eocene raoellid (A), the extinct sister group to Cetacea, and Eocene/Oligocene cetaceans (B–H). The fossil record closes the gap in morphology between crown cetaceans and hippopotamids (Fig. 1) via a surprising array of extinct forms. *Indohyus* (Raoellidae; A), *Pakicetus* (Pakicetidae; B), *Ambulocetus* (Ambulocetidae; C), *Remingtonocetus* (Remingtonocetidae; D), *Georgiacetus* (Protocetidae; E), *Dorudon* (Basilosauridae; F), *Janjucetus* (Janjucetidae, Mysticeti; G), and *Aetiocetus* (Aetiocetidae, Mysticeti; H) are shown. Hindlimb bones have been recovered for *Indohyus, Pakicetus, Ambulocetus, Remingtonocetus,* and *Dorudon*. A well-developed acetabulum (socket for the femur) is documented in the pelvis of *Georgiacetus*. Artwork is by Carl Buell.

ADORA3, BDNF, ADRB2, PNOC, A2AB, BRCA1, BRCA2, DMP1, GHR, VWF, ENAM, APOB, IRBP, APP, BMI1, CREM, FBN1, PLCB4, and transposon insertions.

To reconstruct the evolutionary changes that led to extant cetaceans requires a reconciliation of paleontological and genomic information. The most objective approach to achieving this goal would be to generate a single concatenated dataset that includes morphological and molecular data for all taxa in our analysis. With molecular data, assembly of large supermatrices is not problematic, because DNA sequences from independent studies are easily combined by simply re-aligning the published nucleotides with newly generated data (e.g., McGowen, 2011). By contrast, morphological characters from different systematic studies usually cannot be merged successfully without major alterations of character definitions, recoding of character states, re-examination of original specimens, and scoring of additional characters to yield sufficient overlap of systematic information between taxa in matrices constructed by different researchers (e.g., O'Leary and Gatesy, 2008). Here, we chose to combine trees derived from three supermatrices to construct a composite phylogenetic hypothesis for Artiodactyla that includes both extant and extinct taxa. Parsimony analysis of a supermatrix based on data from Geisler et al. (2007) was utilized to estimate higher-level relationships among major artiodactyl clades, including the placement of stem cetaceans relative to crown Cetacea ("Artiodactyla supermatrix"). For relationships within Mysticeti (baleen whales), a slightly modified version of the supermatrix from Deméré et al. (2008) was employed ("Mysticeti supermatrix"), and for Odontoceti (toothed whales), we accepted relationships based on a recent supermatrix analysis of crown Cetacea (Geisler et al., 2011; "crown Cetacea supermatrix"). The three supermatrix-based subtrees were combined into a single composite supertree by making several assumptions of monophyly that are consistent with phylogenetic results from each of the three sub-matrices (see de Queiroz and Gatesy, 2007). We constructed this composite supertree by deleting the four crown cetaceans in the Artiodactyla supermatrix tree and then inserting subtrees for Mysticeti (Mysticeti supermatrix) and for Odontoceti (crown Cetacea supermatrix). This procedure avoided the extensive duplications of systematic evidence that have characterized published matrix representation with parsimony (MRP) supertrees of artiodactyls (see Gatesy et al., 2002) and resulted in a composite tree of 45 extant and 124 extinct taxa. As in Geisler et al. (2011), approximate divergence times in the tree were based on the first appearances of extinct taxa in the fossil record (Deméré et al., 2005, 2008; Fitzgerald, 2006, 2010; Geisler et al., 2007, 2011; Gingerich et al., 2009), extensions of ghost lineages so that first appearances of sister taxa are identical (Norell, 1992), and molecular clock estimates from the literature (outgroups and terrestrial artiodactyls: Meredith et al., 2011a; Hassanin et al., 2012, Odontoceti: McGowen et al., 2009, Mysticeti: Sasaki et al., 2005).

Relationships among higher-level artiodactyl taxa were based on an Artiodactyla supermatrix composed of a modified version of the morphological dataset employed by Geisler et al. (2007) plus molecular data compiled by Spaulding et al. (2009). Geisler et al.'s (2007) matrix includes 217 morphological characters and was formed by merging the datasets of Geisler and Uhen (2005) and Theodor and Foss (2005); 99 characters were shared in some form by both studies, 80 were unique to Geisler and Uhen (2005), and 32 were unique to Theodor and Foss (2005). Thewissen et al. (2007) used Geisler and Uhen's (2005) dataset, but added several taxa to that matrix and changed several character codings for pakicetids. For the present study, we incorporated the new data and corrections published by Thewissen et al. (2007) in our higher-level Artiodactyla supermatrix. Specifically, Geisler et al.'s (2007) dataset was updated by splitting Raoellidae into two genera (*Indohyus*, *Khirtharia*), with codings for 179 of the morphological characters

directly from Thewissen et al. (2007). We added Thewissen et al.'s (2007) data for the anthracotheriid artiodactyls, *Microbunodon* and *Siamotherium*, and supplemented Geisler et al.'s (2007) codings for an additional anthracothere, *Anthracokeryx*, with those of Thewissen et al. (2007). We also utilized Thewissen et al.'s (2007) character codes for Pakicetidae, except for a few changes as noted by Geisler and Theodor (2009). In addition to edits based on Thewissen et al. (2007), we made the following changes. We conservatively coded the protocetid whale *Maiacetus inuus* from the description of Gingerich et al. (2009), and added this taxon to the supermatrix. The character codings for the mesonychian *Hapalodectes hetangensis* in Geisler et al. (2007) were based on the holotype of this taxon, a well-preserved juvenile skull (IVPP V 5253; Ting and Li, 1987). A skull of an adult individual subsequently was described (Ting et al., 2004); thus four character codings for this taxon were changed to better reflect the adult morphology; character 32 was changed from state 1 to 0, character 36 from 0 to 2, character 66 from 0 to 1, and character 114 from ? to 2. In reviewing Geisler et al.'s (2007) morphological matrix, we found one typographic error: *Balaenoptera* was coded as having wide 2nd and 5th metatarsals, but this genus lacks hindlimbs. *Balaenoptera* was recoded as "?" for this character. Finally, six new characters were added to the morphological matrix: character 218 stomach unilocular (0) or plurilocular (1); 219 birth on land (0), on land and in water (1), or in water (2); 220 position of testes descended in scrotum (0), descended but not in scrotum (1), or not descended (2); 221 nurse on land (0), on land and in water (1), or in water (2); 222 tail flukes absent (0) or present (1); and 223 sweat glands present (0) or absent (1). Molecular data compiled by Spaulding et al. (2009), comprising 46,587 characters, were incorporated into the Artiodactyla supermatrix for the 17 extant taxa in the modified morphology dataset, and the 72 extinct taxa in this dataset were coded as missing (?) for the entire suite of molecular characters. Parsimony analysis of the higher-level Artiodactyla supermatrix in PAUP* was heuristic as described above. Multistate ordered morphological characters were weighted relative to unordered characters as in Geisler et al. (2011), and trees were rooted using the afrothere, *Orycteropus* (Meredith et al., 2011a). Branch support scores (Bremer, 1994) for nodes resolved in the strict consensus of minimum length trees were estimated by searching for topologies that were several steps beyond minimum length.

For relationships within crown Cetacea, trees for Odontoceti and Mysticeti were based on Geisler et al. (2011) and a modified version of Deméré et al.'s (2008) matrix. The crown Cetacea supermatrix (Geisler et al., 2011) includes data from 53 members of Odontoceti, as well as 16 mysticetes, two stem cetaceans, a hippopotamid, a suid, and a ruminant (304 morphological and 60,851 molecular characters; 45 extinct and 29 extant taxa). Here, we utilized the overall topology from Geisler et al. (2011) that was derived from a constrained analysis of morphological/fossil data; the backbone constraint was from Bayesian and maximum likelihood analyses of molecular data in the Geisler et al. (2011) supermatrix. The odontocete section of the crown Cetacea tree was employed in our composite phylogenetic hypothesis. Character 33 in the crown Cetacea supermatrix encodes the presence/absence of accessory cusps on posterior teeth. In Geisler et al. (2011), physeteroids were scored as "?" for this character because upper teeth are absent/vestigial. Here, *Physeter* and *Kogia* were coded as lacking accessory cusps (state 1), given that all lower teeth in these taxa do not express this feature. The Mysticeti supermatrix analyzed in the current study is an updated version of the combined dataset employed by Deméré et al. (2008; 11 extant and 20 extinct mysticetes). Several adjustments were made in the revised supermatrix. For the morphological partition, one character was adjusted for the extinct toothed mysticetes, *Janjucetus* and

Table 1
Hypotheses of characters that optimize to branches in the composite tree (Figs. 7–9). "No matrix" refers to character observations taken from the literature and not explicitly coded in the three supermatrices.

Branch	Character state
A	Artiodactyla matrix 191: large transverse contact of astragalus and cuboid (+ double trochleated astragalus) Artiodactyla matrix 203: even-toed hindfoot (equivocally optimized)
A to B	Artiodactyla matrix 216: fibro-elastic penis with sparse cavernous tissue Artiodactyla matrix 217: three primary lung bronchi Artiodactyla matrix 218: multi-chambered (plurilocular) stomach
C	Artiodactyla matrix 214: sparse hair Artiodactyla matrix 215: sebaceous glands absent Artiodactyla matrix 219: sometimes give birth in water Artiodactyla matrix 220: scrotum absent Artiodactyla matrix 221: sometimes nurse underwater No matrix: transition from terrestrial to freshwater (depositional environment, isotopes, dense bones in *Indohyus*, and hippos in freshwater; Gatesy, 1997; Thewissen et al., 2007; Cooper et al., 2011)
D	Artiodactyla matrix 18: involucrum (thickening of medial wall of auditory bullae) Artiodactyla matrix 91: incisors form two parallel rows
D to O	Artiodactyla matrix 222: tail flukes (if do not accept osteological correlate) Artiodactyla matrix 223: sweat glands absent (if "blood sweat" glands of hippos are homologous to sweat glands of other mammals) No matrix: nasal plugs (Heyning and Mead, 1990) No matrix: outer ears (pinnae) absent (Nowak, 1991)
D to M	No matrix: transition from herbivory to piscivory/carnivory (based on fossilized stomach contents of basilosaurids; O'Leary and Uhen, 1999 and references therein)
E	Artiodactyla matrix 133: compressed talonid basins (convergent with Mesonychia at branch 2) Artiodactyla matrix 134: molar entoconid lost (convergent with Mesonychia at branch 2) Artiodactyla matrix 140: molar trigonid ∼twice, or more, the height of talonid (convergent with Mesonychia + *Canis* at branch 1) Artiodactyla matrix 141: molar shearing facets No matrix: transition from herbivory to piscivory/carnivory (based on osteological correlate: shape of teeth – e.g., Spaulding et al., 2009) No matrix: robust tail (Madar, 2007; Thewissen et al., 2007; Cooper et al., 2011)
E to F	Artiodactyla matrix 137: molar metaconids absent/vestigial (convergent with a subclade of Mesonychidae at branch 3)
F	Artiodactyla matrix 83: large mandibular foramen No matrix: transition from freshwater to saltwater (depositional environment, isotopes, crown cetaceans in saltwater; Roe et al., 1998; Clementz et al., 2006. This perspective is dependent on the environmental interpretation for *Ambulocetus* (Thewissen et al., 1996)
F to G	Artiodactyla matrix 77: loss of incisive foramina (and vomeronasal organ, if trust osteological correlate)
H	Artiodactyla matrix 148: short cervical vertebrae
I to M	No matrix: tail flukes (if shape of caudal vertebrae represents valid osteological correlate; Buchholtz, 1998, 2007; Gingerich et al., 2009)
K	Artiodactyla matrix 19: small pterygoid sinus Artiodactyla matrix 81: posterior positioning of nasals (anterior nasal edge between canine and P1) Artiodactyla matrix 151: narrow sacral contact (only one sacral vertebrae)
K to M	No matrix: 1st major reduction of hindlimbs (Geisler, pers. obs.)
L	Artiodactyla matrix 81: posterior positioning of nasals (between P1 and P2) Artiodactyla matrix 151: no sacral contact
M to N	Artiodactyla matrix 19: anteriorly expanded pterygoid sinus
O	No matrix: no replacement of teeth (monophyodonty; Thewissen and Hussain, 1998; Uhen, 2000, 2004; Geisler, pers. obs.) No matrix: 2nd major reduction of hindlimbs: feet lost and hindlimbs completely internal (Geisler, pers. obs.) Crown Cetacea matrix 296: joints between humerus and radius and between humerus and ulna are both flat and meet at an obtuse angle
P	Crown Cetacea matrix 76: telescoping of skull 1 (nasal process of maxilla partially covers supraorbital process of the frontal)
Q	Crown Cetacea matrix 76: telescoping of skull 2 (nasal process of maxilla completely covers supraorbital process of the frontal)
P to T	Crown Cetacea matrix 80: anterior edge of nasals – change from state 2 (in line with P2) to state 6 (in line with gap between postorbital process and anterior tip of zygomatic process or in line with anterior tip of zygomatic process) Crown Cetacea matrix 95: single blowhole but nasal passages separate Crown Cetacea matrix 98: melon hypertrophied Crown Cetacea matrix 104: inferior vestibule No matrix: phonic lips (Cranford et al., 1996, 2011) No matrix: olfactory bulb absent (Slijper, 1962; Oelschläger, 1992; Thewissen et al., 2010) No matrix: cribriform plate absent (Burrows and Smith, 2005; Geisler, pers. obs.) No matrix: turbinals absent (Geisler, pers. obs.)
P to V	No matrix: major brain expansion (Marino et al., 2004; Boddy et al., 2012)
S to T	Crown Cetacea matrix 23: no double-rooted teeth (homodonty 1) Crown Cetacea matrix 33: accessory cusps absent from posterior dentition (homodonty 2)
T	Crown Cetacea matrix 114: vertex sutures shifted to the left
U	Crown Cetacea matrix 95: one blowhole and nasal passages merged
W	Crown Cetacea matrix 87: right nasal passage small relative to left
W to X	Crown Cetacea matrix 113: only one nasal bone
Y	Crown Cetacea matrix 113: both nasal bones absent No matrix: tooth enamel absent (Meredith et al., 2009 and references therein)

Table 1 (*continued*)

Branch	Character state
Z	No matrix: largest extant odontocete – *Physeter macrocephalus* (Nowak, 1991)
a	Mysticeti matrix 2: broad rostrum
b	Mysticeti matrix 4: thin lateral margins of maxilla Mysticeti matrix 57: straight mandibular ramus (not concave)
b to c	Mysticeti matrix 53: unsutured mandibular symphysis
c	Mysticeti matrix 38: palatal nutrient foramina present (also baleen if trust as osteological correlate; Deméré et al., 2008)
d	Mysticeti matrix 27: apex of occipital shield, change from state 0 (extension posterior to temporal fossa) to state 1 (extension to posterior half of temporal fossa) Mysticeti matrix 61: mineralized teeth in adults lost No matrix: tooth enamel absent (Meredith et al., 2009 and references therein)
e	Mysticeti matrix 7: reduction in length of nasals (long 0 to medium 1 or short 2) Mysticeti matrix 27: apex of occipital shield extends to anterior half of temporal fossa Mysticeti matrix 57: bowed mandibles
f	Mysticeti matrix 58: reduction in size of mandibular foramen
a to f	Mysticeti matrix 71: presence of baleen (if do not accept osteological correlate) No matrix: bulk filter feeding (Nowak, 1991)
a to g	No matrix: decreased relative brain size (Boddy et al., 2012)
g	Mysticeti matrix 69: numerous ventral throat grooves Mysticeti matrix 70: ventral throat pouch Mysticeti matrix 75: tongue reduced and predominantly connective tissue No matrix: synovial temporomandibular joint absent, instead fibrous (Lambertsen et al., 1995; Johnston et al., 2010; Berta, pers. obs.)
h	No matrix: largest extant mysticete – *Balaenoptera musculus* (Nowak, 1991)

Mammalodon; new observations by Fitzgerald (2010, 2012) justified recoding of character 53 (mandibular symphysis: sutured or not sutured) that previously was based on character states from Fitzgerald (2006). For the molecular partition, four changes were made: the DNA sequence alignment for *SRY* was updated by incorporating longer sequences (Nishida et al., 2007), and alignments of *AMEL* (Spaulding et al., 2009; Meredith et al., 2011b), *TBX4* (Onbe et al., 2007), and *ACTA2* (e.g., Caballero et al., 2008) were concatenated to the overall supermatrix. The resulting dataset is composed of 115 phenotypic characters, 32 transposon insertions, mitochondrial genomes (15,627 characters), and nuclear DNA data from 20 loci (14,363 characters). Outgroups include two extant odontocete taxa (Ziphiidae and *Physeter*), two extinct odontocetes (*Agorophius* and *Squalodon calvertensis*), and the basilosaurid *Zygorhiza*. Parsimony searches of the Mysticeti supermatrix were as in Deméré et al. (2008). For extant taxa in the matrix, bootstrap percentages, branch support, and PBS were calculated as described above. PBS scores were estimated for 23 data partitions: morphology, transposon insertions, mitochondrial genome, cetacean satellite sequences, *DMP1*, *ENAM*, *AMBN*, *ATP7A*, *BDNF*, *CSN2*, *KITLG*, *PRM1*, *RAG1*, *STAT5A*, *PKDREJ*, *LALBA*, *OPN1SW*, Y10 anonymous locus, Y13 anonymous locus, *SRY*, *AMEL*, *TBX4*, and *ACTA2*. Selected removals of individual data partitions (Gatesy et al., 1999) also were employed to examine the influence of different character sets in combined systematic analysis.

A primary goal of the present study is to reconstruct the array of anatomical changes that resulted in the unique, highly derived phenotypes of extant crown cetaceans (Fig. 2). Characters from the three supermatrices (Artiodactyla, crown Cetacea, Mysticeti) were optimized onto minimum length trees by parsimony to infer the simplest interpretation of character evolution for each trait of interest (Table 1; Artiodactyla supermatrix: 25 characters, crown Cetacea supermatrix: 14 characters, Mysticeti supermatrix: 14 characters). Additional observations from the literature, that were not explicitly encoded in the three supermatrices, also were mapped parsimoniously onto our overall composite phylogenetic hypothesis (Table 1; 15 characteristics; Slijper, 1962; Heyning and Mead, 1990; Nowak, 1991; Oelschläger, 1992; Cranford et al., 1996, 2011; Gatesy, 1997; Buchholtz, 1998, 2007; Roe

et al., 1998; Thewissen and Hussain, 1998; O'Leary and Uhen, 1999; Uhen, 2000, 2004; Marino et al., 2004; Burrows and Smith, 2005; Clementz et al., 2006; Madar, 2007; Thewissen et al., 2007, 2010; Gingerich et al., 2009; Meredith et al., 2009; Spaulding et al., 2009; Johnston et al., 2010; Cooper et al., 2011; Boddy et al., 2012; Geisler, pers. obs.).

3. Results and discussion

3.1. Phylogenetic position of Cetacea among extant mammals

Cladistic analysis of a large molecular supermatrix (Meredith et al., 2011a) was used to place Cetacea relative to extant mammalian diversity (Fig. 4) and to assess the distribution of support for relationships among cetacean families and their closest terrestrial relatives (Fig. 5). With Goloboff weighting, a single optimal cladogram was supported by the concatenated analysis of 26 nuclear gene fragments from species that represent most extant mammalian families (fit = −9120.60253). Among modern mammals, obligatorily aquatic sirenians (dugong and manatees) show the most similarity, in terms of overall body form, to cetaceans. Parsimony analysis of the molecular supermatrix, however, supports the parallel evolution of aquatic specializations in Cetacea and in Sirenia as in most previous large-scale molecular analyses (e.g., Murphy et al., 2001a,b). Relationships among the major clades of Mammalia generally agreed with results from explicitly model-based methods (Meredith et al., 2011a), with high bootstrap support for the placement of Cetacea within Artiodactyla and Sirenia within Afrotheria (Fig. 4). The phylogenetic position of Artiodactyla relative to several other laurasiatherian orders (bats, carnivorans + pangolins, perissodactyls) was not robustly resolved (Fig. 4), and parallels the difficulties encountered in recent attempts at delineating relationships among these taxa (Nishihara et al., 2006; Hou et al., 2009; McCormack et al., 2012; Nery et al., 2012; Zhou et al., 2012). With equal weighting of character state changes, relationships among artiodactyl families were as in the parsimony analysis with implied weights, but the sister group to Artiodactyla was Perissodactyla instead of Chiroptera.
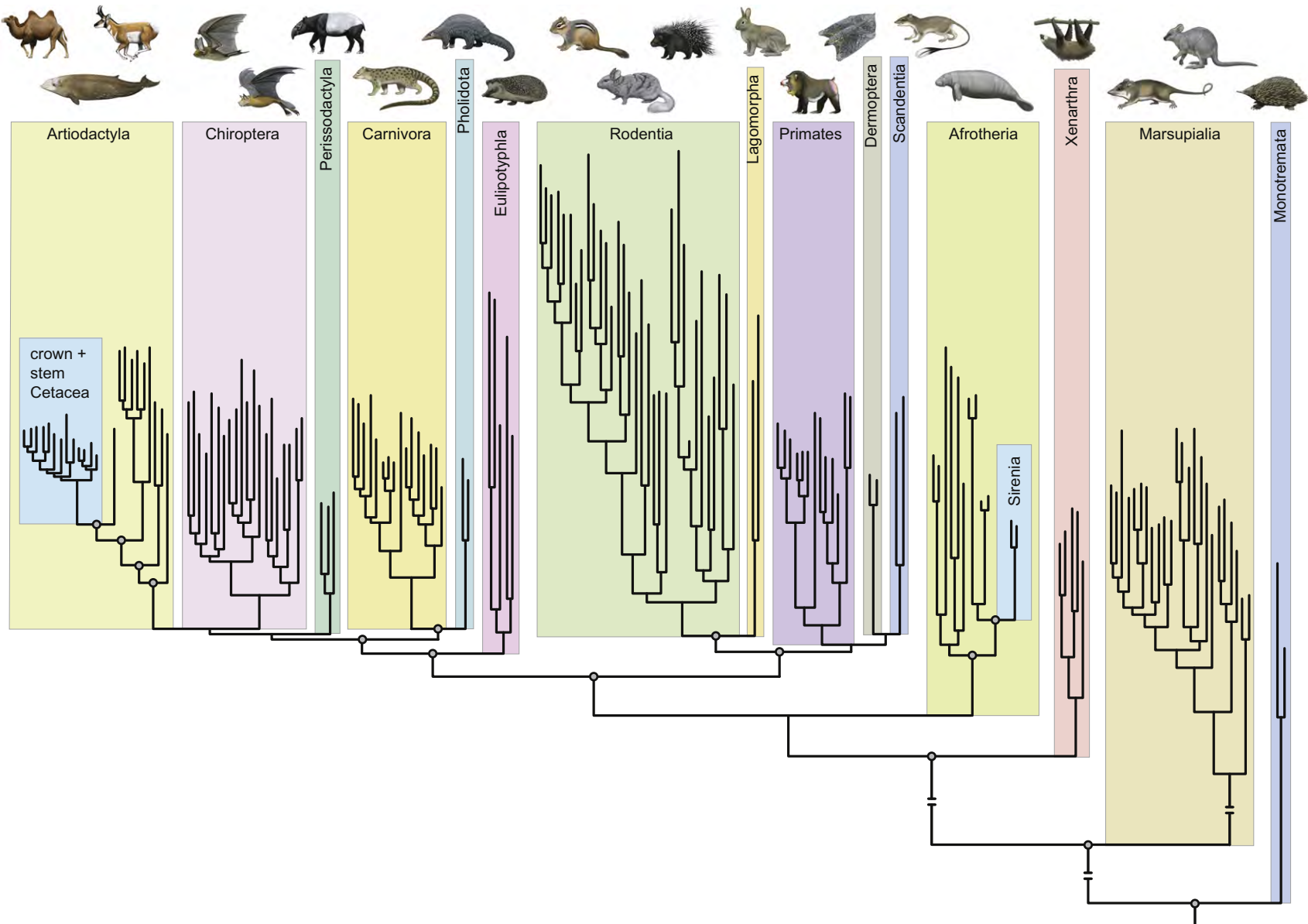
Fig. 4. The phylogenetic position of Cetacea relative to other extant mammals. Parsimony analysis of 26 nuclear loci (Goloboff weighting with $k = 2$) position Cetacea deep within Artiodactyla and distantly related to other obligately aquatic mammals (Sirenia). For the placements of aquatic mammals and for relationships among higher-level placental groups, circles at nodes indicate >90% bootstrap support. Branches are proportional to the number of substitutions optimized to branches; long basal branches with cross bars were truncated for aesthetics. The cladogram is rooted by vertebrate outgroups to Mammalia (*Gallus, Taeniopygia, Anolis, Xenopus, Danio*). Artwork is by Carl Buell.

Fig. 5. The phylogenetic position of Cetacea relative to other extant artiodactyls. In parsimony analysis of all extant artiodactyl families, 26 nuclear loci and transposon insertions group Cetacea closest to hippos. Branch support is shown to the right of nodes; bootstrap percentages are in parentheses to the right of nodes and below branch support scores. Boxes at internodes show partitioned branch support scores (dark green: >+5, light green: 0 to +5, yellow: 0, orange: <0 to −5, red: <−5) for the following datasets (left to right from top): *TTN, CNR1, BCHE, EDG1, RAG1, RAG2, ATP7A, TYR1, ADORA3, BDNF, ADRB2, PNOC, A2AB, BRCA1, BRCA2, DMP1, GHR, VWF, ENAM, APOB, IRBP, APP, BMI1, CREM, FBN1, PLCB4*, transposon insertions. The cladogram is rooted using representatives of Perissodactyla (odd-toed ungulates; not shown). Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Combination of the nuclear DNA data from Meredith et al. (2011a; 35,603 aligned basepairs) with transposon insertions (Nikaido et al., 1999, 2001, 2006, 2007; 101 characters) was used to assess the distribution of character support among datasets for subclades of Artiodactyla, and in particular all nodes that connect the last common ancestor of crown Artiodactyla to extant cetaceans (Fig. 5). In the single minimum length tree for the combined molecular supermatrix (20,667 steps), inter-relationships of different families generally were consistent with several other recent supermatrix analyses of Cetacea and Artiodactyla (e.g., McGowen et al., 2009; Spaulding et al., 2009; Steeman et al., 2009; Chen et al., 2011; Geisler et al., 2011; Zhou et al., 2011) and with transposon insertion data (Nikaido et al., 1999, 2001, 2006, 2007; Chen et al., 2011). Parsimony analysis yielded 100% bootstrap support for 18 of 21 nodes within Artiodactyla.

Branch support and partitioned branch support (PBS) compare the fit of a dataset to the shortest trees that contain a particular clade to the fit of that dataset to the shortest trees that lack that clade (Bremer, 1994; Baker and DeSalle, 1997). Thus, these measures can be seen as comparisons between the optimal tree(s) and the next best option(s), given the parsimony criterion. Each supported clade represents the primary signal of the dataset, and the shortest trees that lack particular supported clades represent the secondary signal in the dataset. For example, in our phylogenetic analysis of Artiodactyla, monophyly of Cetacea is favored (Fig. 5). In the best suboptimal tree that lacks a monophyletic Cetacea, Odontoceti groups with Hippopotamidae to the exclusion of Mysticeti (21,085 steps), but this is a poor alternative. The bootstrap percentage for Cetacea is the maximum (100%), branch support for this clade is +418, and PBS is positive for all 27 data partitions. None of the 27 data partitions in the supermatrix are more consistent with the secondary signal than the primary one. To overturn Cetacea one would have to add at least 419 hypothetical characters that contradict Cetacea to the Artiodactyla supermatrix.

Fifteen artiodactyl subclades in the tree (Fig. 5) include Cetacea or occur within Cetacea. Fourteen of these show bootstrap support
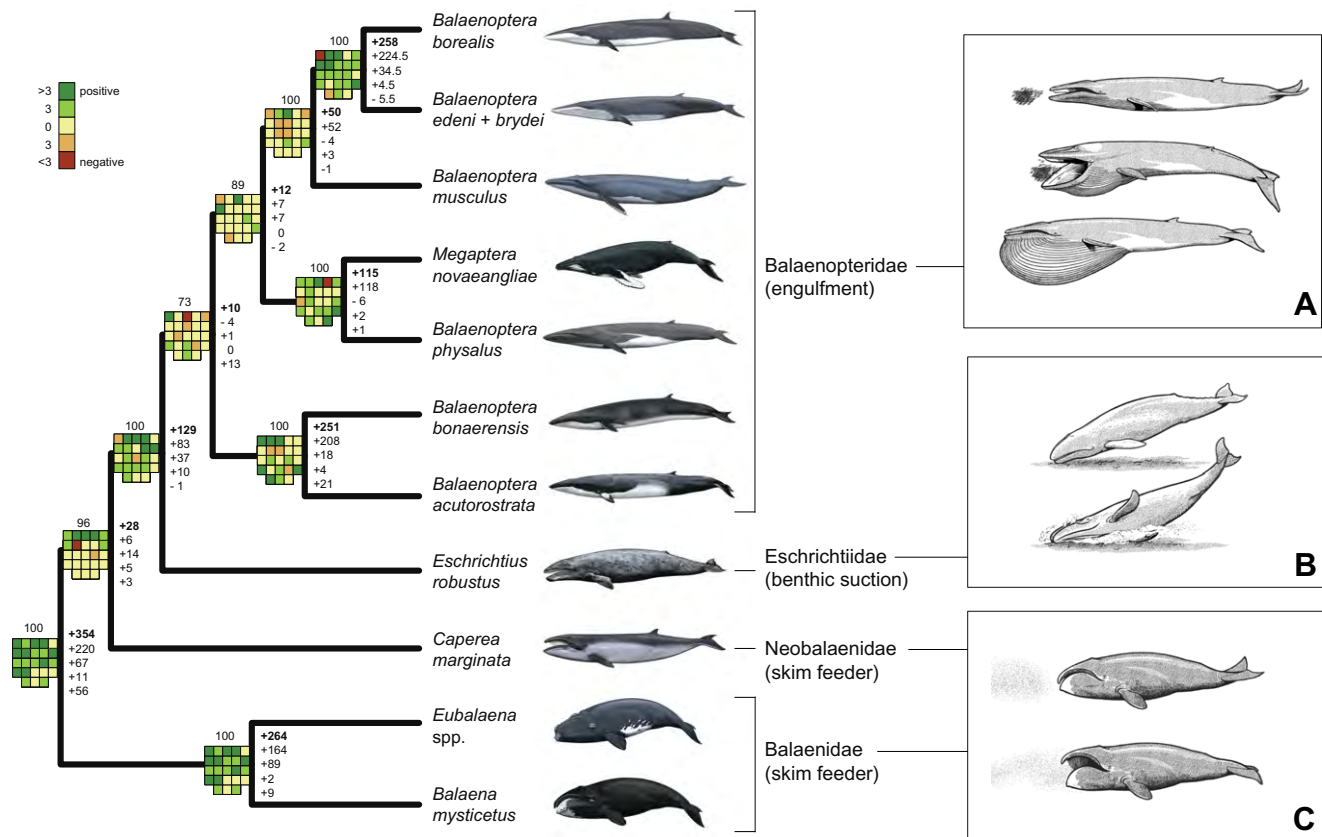
Fig. 6. Phylogenetic relationships of extant Mysticeti (baleen whales) based on combined parsimony analysis of 23 datasets. Filter-feeding mode of each mysticete family is shown (A–C). To the right of nodes, the following are listed from top to bottom: Branch support (bold), partitioned branch support (PBS) for mitochondrial genome, PBS for all nuclear DNA, PBS for transposon insertions, PBS for morphology. Boxes at internodes also show PBS scores (dark green: >+3, light green: 0 to +3, yellow: 0, orange: <0 to −3, red: <−3) for the following datasets (left to right from top): morphology, transposon insertions, mitochondrial genome, cetacean satellite sequences, *DMP1*, *ENAM*, *AMBN*, *ATP7A*, *BDNF*, *CSN2*, *KITLG*, *PRM1*, *RAG1*, *STAT5A*, *PKDREJ*, *LALBA*, *OPN1SW*, Y10 anonymous locus, Y13 anonymous locus, *SRY*, *AMEL*, *TBX4*, *ACTA2*. Bootstrap percentages are above internodes. The cladogram is rooted using representatives of Odontoceti (not shown). Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of 100%, but branch support and PBS vary widely, indicating that character evidence for these clades is not equivalent despite identical bootstrap percentages. Branch support scores range from +418 (Cetacea) to only +20 (Synrhina = all extant odontocetes but Kogiidae + Physeteridae), and PBS ranges from positive for all 27 data partitions (Cetacea) to positive for 11 and negative for four data partitions (Plicogulae = Balaenopteridae + Eschrichtiidae + Neobalaenidae). Delphinida + Ziphiidae, the node with weakest branch support within Cetacea (+9; bootstrap 92%), had nine positive PBS scores and only three negative scores, which indicates that three partitions prefer a secondary phylogenetic hypothesis (Fig. 5). Overall, relationships of cetacean families to each other and to more distantly related terrestrial artiodactyls were supported robustly with a preponderance of data partitions favoring the primary, rather than the secondary, phylogenetic signal. This contrasts with subclades of Pecora (cattle, antelopes, deer, musk deer, pronghorn, and giraffes), a side-branch in the artiodactyl ancestry of Cetacea. Despite high bootstrap support for some inter-relationships within Pecora, many data partitions support the secondary signal better than the primary phylogenetic signal in the supermatrix (Fig. 5). The extreme is the controversial grouping of Antilocapridae (pronghorn) with Giraffidae (giraffes; five positive and seven negative PBS scores). Removal of only one gene (*BRCA1*) from the supermatrix shifts preference from Antilocapridae + Giraffidae to the secondary signal, a positioning of Antilocapridae as the sister group to remaining pecorans (e.g., Spaulding et al., 2009; Hassanin et al., 2012). Conflict among genes within

Ruminantia is consistent with the view that pecoran ruminant families are the product of a rapid phylogenetic radiation (Hassanin et al., 2012 and references therein).

3.2. Three supermatrix topologies: Artiodactyla, Odontoceti, and Mysticeti

To construct a composite phylogenetic hypothesis for Artiodactyla that includes extinct diversity but also acknowledges the critical influence of molecular data, we merged results from analyses of three large combined matrices (Artiodactyla, crown Cetacea, and Mysticeti) into a supertree of supermatrix topologies as suggested by de Queiroz and Gatesy (2007). The Artiodactyla supermatrix provides a phylogenetic hypothesis for stem cetaceans, the placement of Cetacea among artiodactyls, and outgroup relationships. Parsimony analysis yielded ten minimum length trees (36,352.92 steps) and a well-resolved strict consensus (Supplementary Online Fig. 1). Branch support is low at most nodes due to missing data, a dense sampling of extinct taxa that subdivide internal branches, and high levels of homoplasy for some characters. The strict consensus of minimum length trees is perfectly congruent with our supermatrix analysis of extant mammalian families (Fig. 4). Within Artiodactyla, Hippopotamidae is the extant sister group to Cetacea, and Ruminantia (mouse deer and pecorans), Suina (pigs and peccaries), and Camelidae (camels and llamas) branch as sequentially more distant relatives to the hippo + whale clade. Eleven extinct lineages are positioned in a
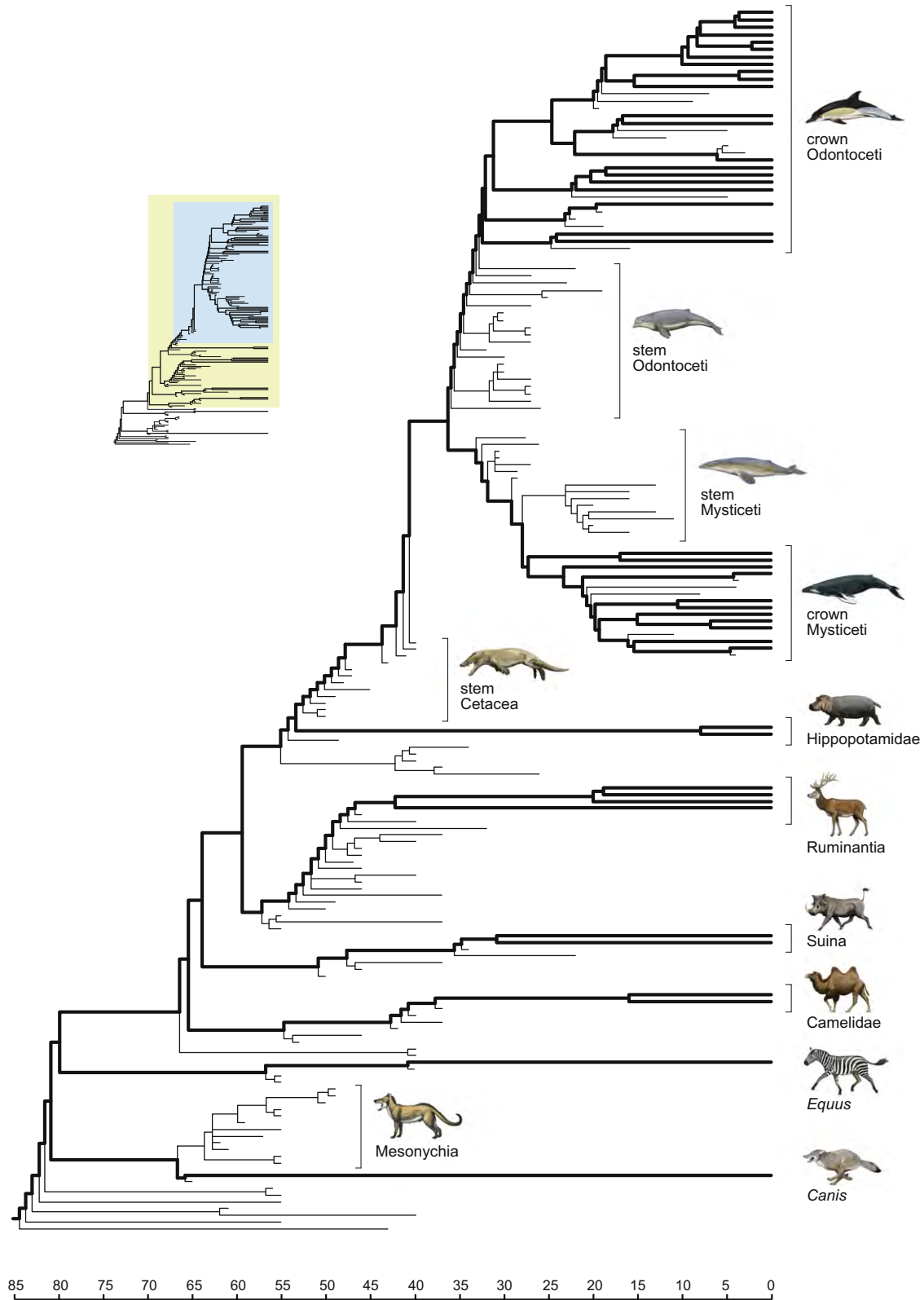
Fig. 7. A composite phylogenetic hypothesis for Artiodactyla, including Cetacea. The overall tree is the result of merging topologies derived from supermatrix analyses of three concatenated datasets that include molecular, phenotypic, and fossil information: Mysticeti (Deméré et al., 2008; this study), crown Cetacea (Geisler et al., 2011), and Artiodactyla (Geisler et al., 2007; Spaulding et al., 2009; this study). Thick branches connect extant taxa in the tree, and thin branches represent extinct lineages. Brackets to the right delimit clades and stem groups to crown clades; the small, inset tree delimits Cetacea (blue) and Artiodactyla (yellow). Approximate evolutionary time-scale, in millions of years, is at the base of the figure (see Section 2 for basis). For the mysticete section of the composite tree, one of the six minimum length trees derived from the Mysticeti supermatrix is shown here. Relationships derived from the Artiodactyla supermatrix (stem Cetacea, basal artiodactyl relationships, outgroups) and from the crown Cetacea supermatrix (Odontoceti) are based on strict consensus trees. Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

pectinate array on the stem lineage to crown Cetacea. Mesonychia (Mesonychidae + Hapalodectidae), a group of carnivorous hoofed mammals that show distinctive similarities to early stem cetaceans (Van Valen, 1966; O'Leary, 1998; Geisler and Luo, 1998; Luo and Gingerich, 1999), were positioned in a clade that is sister to Artiodactyla + Perissodactyla (Supplementary Online Fig. 1). These phylogenetic results are broadly consistent with the recent supermatrix analyses of Geisler et al. (2007), Geisler and Theodor (2009), and Spaulding et al. (2009), which each contributed data to the Artiodactyla supermatrix analyzed here. However, the phylogenetic placements of anthracotheriids, extinct selenodont artiodactyls, and other fossils vary among these trees. In each analysis, the evolutionary relationships of many extinct terrestrial artiodactyl taxa are unstable, despite the robust support for subgroupings of extant taxa (also see O'Leary and Gatesy, 2008).

The topology for Mysticeti was based on an extension of the combined dataset from Deméré et al. (2008), and relationships within Odontoceti were derived directly from our recent supermatrix study of crown Cetacea (Geisler et al., 2011). Cladistic analysis of the Mysticeti supermatrix yielded six trees (12,248 steps) that were the same as those recovered by Deméré et al. (2008); branch

support scores were nearly identical to that study (Deméré et al., 2008; their Fig. 3). Relationships among extant mysticete taxa were well supported according to bootstrap and branch support scores, but the distribution of support among datasets implied some weaknesses/conflicts (Fig. 6). In particular, two nodes within Mysticeti have more negative than positive PBS scores, indicating that multiple data partitions favor the secondary phylogenetic signal in the supermatrix over the primary one. Balaenopteridae, engulfment-feeding rorquals, is particularly unstable. Five data partitions favor the secondary phylogenetic signal in the supermatrix (*Eschrichtius* [gray whale] nested within Balaenopteridae) over the primary supermatrix signal (balaenopterid monophyly: four positive and five negative PBS scores; Fig. 6); removal of the morphological data partition from the supermatrix yields a paraphyletic Balaenopteridae, a result that has been supported several times in previous analyses of molecular data (Sasaki et al., 2005; McGowen et al., 2009; Slater et al., 2010; Hassanin et al., 2012). In addition to conflict in the placement of *Eschrichtius*, relationships within Balaenopteridae are dependent on a single linkage group. The placement of the blue whale, *Balaenoptera musculus*, as the sister group to *B. borealis* + *B. edeni/brydei* (four positive
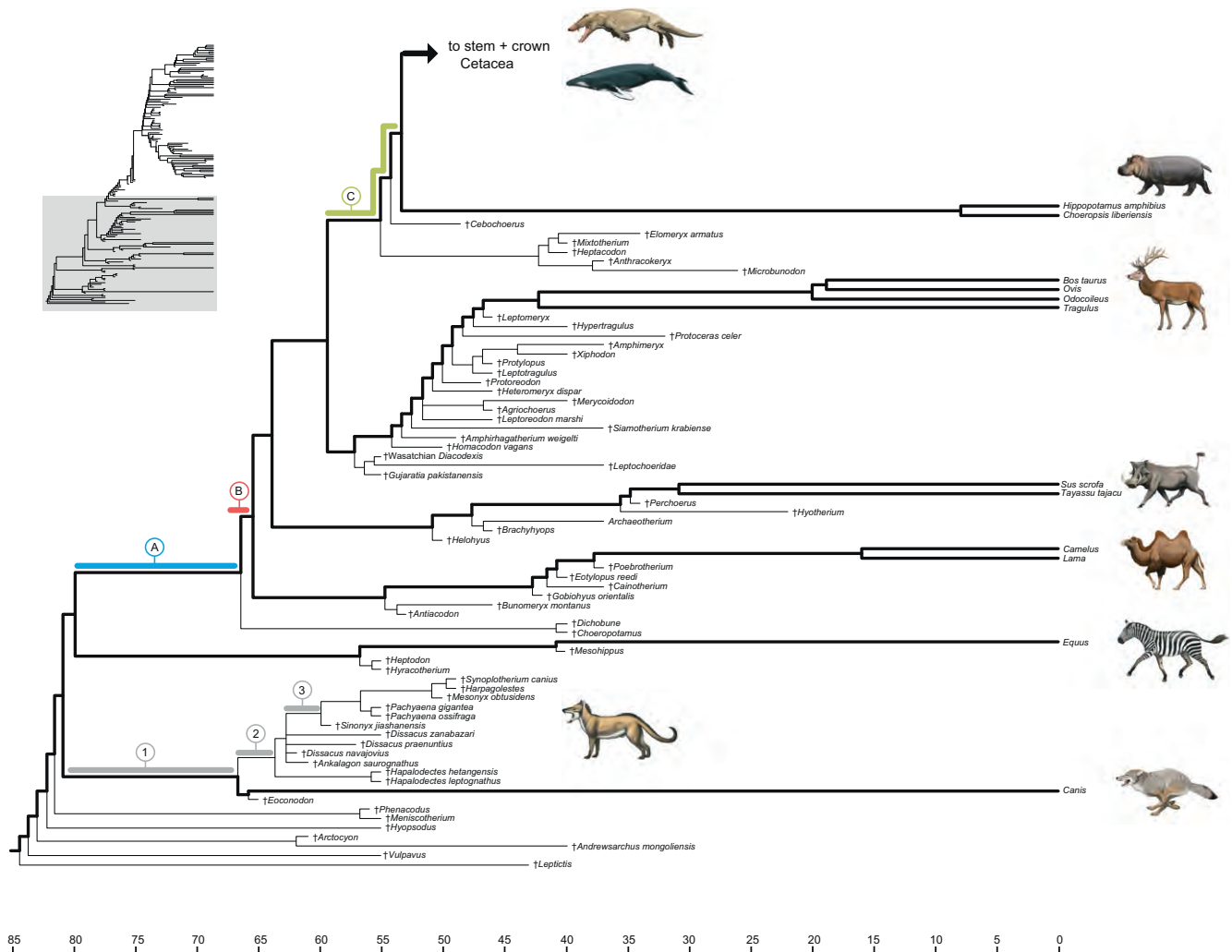

Fig. 8. The non-cetacean section of the composite phylogenetic hypothesis for Artiodactyla. Thickened colored bars above branches (A–C) mark optimizations of various evolutionary changes on the lineage that leads to Cetacea (see Table 1). Gray bars above branches (1–3) indicate character state changes that are interpreted as convergences between early stem whales (see Fig. 9) and mesonychians. Thick branches connect extant taxa in the tree, and thin branches represent extinct lineages. The small, inset tree delimits (in gray) the section of the overall composite topology (Fig. 7) that is shown here at a larger scale. Approximate evolutionary time-scale, in millions of years, is at the base of the figure. Relationships derived from the Artiodactyla supermatrix are based on a strict consensus of trees. Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
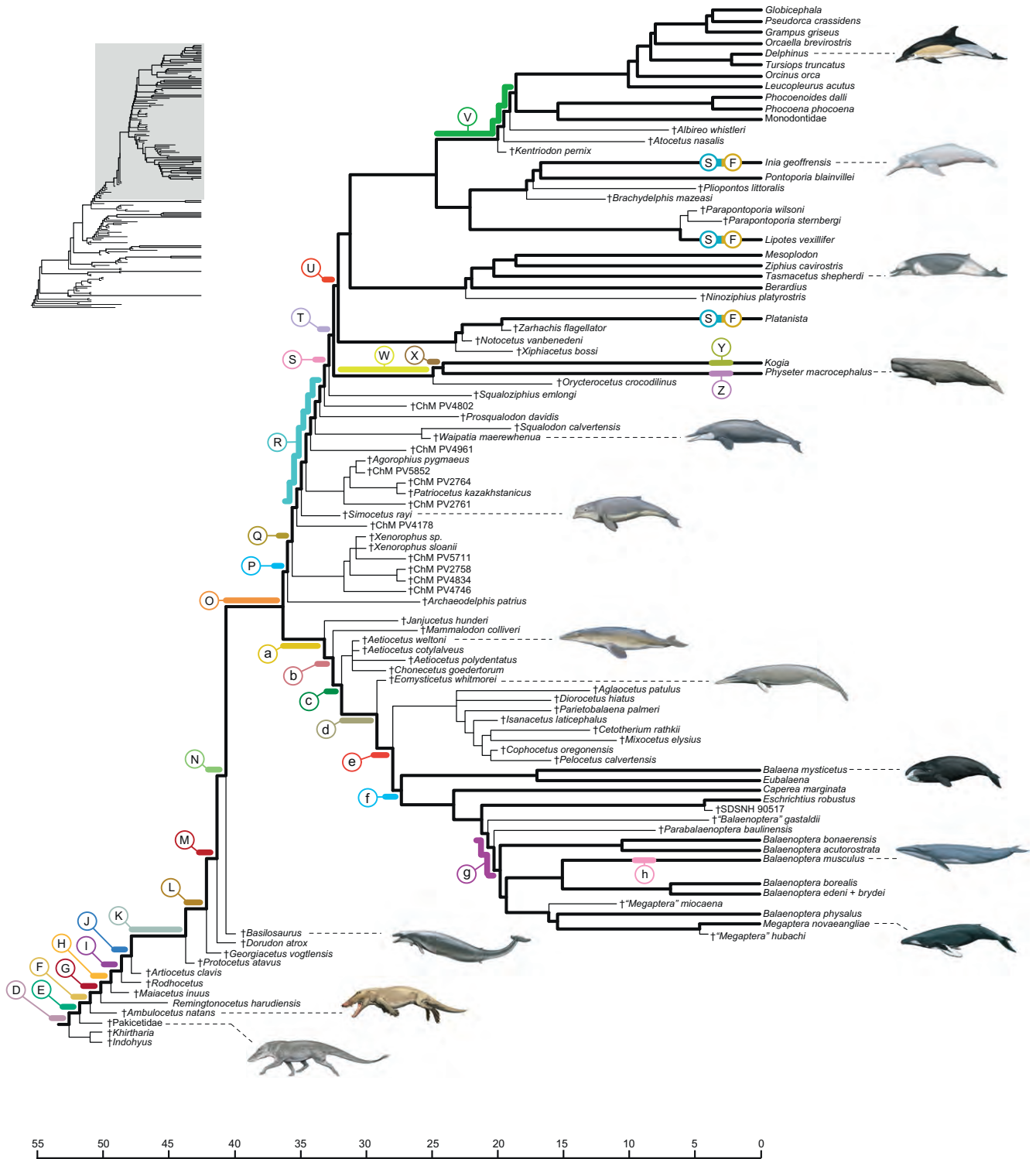
Fig. 9. The cetacean section of the composite phylogenetic hypothesis for Artiodactyla. Thickened colored bars above branches (D–Z and a–j) mark optimizations of various evolutionary changes within Cetacea (see Table 1). The three S = F symbols (blue and brown) are positioned on branches where parallel moves from saltwater to freshwater environments are inferred in the river dolphins – *Inia*, *Lipotes*, and *Platanista*. Thick branches connect extant taxa in the tree, and thin branches represent extinct lineages. The small, inset tree delimits (in gray) the section of the overall composite topology (Fig. 7) that is shown here at a larger scale. Approximate evolutionary time-scale, in millions of years, is at the base of the figure. For the mysticete section of the tree, one of the six minimum length trees derived from the Mysticeti supermatrix is shown. Relationships derived from the Artiodactyla supermatrix (stem Cetacea) and from the crown Cetacea supermatrix (Odontoceti) are based on strict consensus trees. Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and six negative PBS scores) collapses upon deletion of mitochondrial data from the supermatrix. Thus, despite an abundance of genetic, morphologic, and fossil data as well as high bootstrap percentages and branch support, the phylogenetic relations of crown mysticetes remain controversial.

Given the instability of the hypothesis presented here, we contend that the recent reordering of mysticete taxonomy endorsed by Hassanin et al. (2012) is premature. Based on mitochondrial genome data, a single linkage group, these authors argued for a completely revised nomenclature for Mysticeti. Because *Eschrichtius*

robustus (Eschrichtiidae) is nested inside of Balaenopteridae according to mitochondrial data, they resurrected two genera (*Rorqualus* and *Pterobalaena*) and altered the content of Balaenopteridae. Some purely molecular analyses have weakly supported balaenopterid monophyly to the exclusion of *Eschrichtius*, but these results were only upheld for a subset of the stochastic models employed (Sasaki et al., 2005; mitochondrial genes) or were based on a supermatrix that excluded most of the published DNA data for Mysticeti (Steeman et al., 2009). In the present analysis, we combined mitochondrial genomes, multiple nuclear loci, transposon insertions, and morphology (including fossils) into a much more comprehensive mysticete matrix. The combined molecular data in our supermatrix do support a paraphyletic Balaenopteridae as in Hassanin et al. (2012), but the support is weak; the addition of only 115 morphological characters to the 30,022 molecular characters in the Mysticeti supermatrix overturns the controversial molecular result. Much of the phenotypic evidence for balaenopterid monophyly in the Mysticeti supermatrix comes from characters related to the complex engulfment feeding apparatus of balaenopterids (Figs. 1, 2 and 6; see "*3.3.4 Feeding Apparatus and Diet*" below). The family Balaenopteridae was erected, in part, based on these characters (Demére et al., 2005 and references therein). This distinctive phenotypic evidence should not be completely ignored, especially given the strength of its signal relative to the weak molecular signal from >30,000 characters.

3.3. A composite supertree of supermatrix topologies: phylogenetic blueprint for a modern whale

Among extant taxa, relationships inferred from the crown Odontoceti supermatrix (Geisler et al., 2011) and from the Mysticeti supermatrix (Fig. 6) are completely congruent with each other and with relationships derived from the Artiodactyla supermatrix (Supplementary Online Fig. 1). This permitted straightforward integration of the three phylogenetic hypotheses into a supertree of supermatrix results (Fig. 7). The composite tree is based on the assumption that Mysticeti, Odontoceti, and crown Cetacea are each monophyletic groups; these clades are supported by all of the phylogenetic analyses presented here and by a variety of previous studies. The clade of three extant odontocetes in the Artiodactyla supermatrix tree was replaced by the Odontoceti clade of 53 taxa (21 extant and 32 extinct) derived from the crown Cetacea supermatrix. Likewise, the mysticete clade of 11 extant and 20 extinct taxa from the Mysticeti supermatrix tree was substituted for the single extant mysticete in the Artiodactyla supermatrix tree. The resulting supertree (Figs. 7–9) was used as a framework to map the evolutionary histories of traits that characterize extant cetacean species (Fig. 2).

Characters that have transformed on the lineages leading to extant cetaceans (in **bold** below) can be grouped into ten categories: (1) habitat preference and environmental transitions, (2) reproduction, (3) integument, (4) feeding apparatus and diet, (5) blowhole and respiration, (6) organization of the skull, (7) echolocation, vocalization, and auditory structures, (8) locomotion, (9) chemosensory perception, and (10) brain and body size. Character state changes were mapped to internodes in the composite supermatrix tree (Figs. 7–9) and are summarized in Table 1. Following discussion of different character systems and the generality of various evolutionary novelties on the lineages that terminate at extant cetaceans, we review the overall phylogenetic pattern, outline avenues for future research, and reiterate the critical importance of joining genomic and paleontological data in macroevolutionary studies.

3.3.1. Habitat preference and environmental transitions

Characterization of a modern cetacean feature as an aquatic adaptation requires, at the minimum, an understanding of its pre-cursor condition in terrestrial relatives as well as an estimate of when the ancestors of Cetacea committed to an aquatic lifestyle. It is also critical to pinpoint the particular types of aquatic environments that early cetaceans inhabited because some habitats, such as the open ocean, are far removed from land whereas others, like rivers and lakes, are in close proximity to terrestrial food sources. When habitat preferences of extant taxa are mapped onto the composite phylogenetic hypothesis (Figs. 7–9), it is equally parsimonious to infer that the ancestor of hippos + cetaceans was marine with later entry into freshwater habitats by the ancestor of all hippos (two steps), as it is to infer that the ancestor of hippos + cetaceans lived in freshwater habitats, followed by the ancestor of all cetaceans entering marine habitats (two steps). A third scenario, in which the common ancestor of hippos + cetaceans was purely terrestrial, followed by a move to freshwater by hippos and a transition to saltwater by cetaceans, also requires two steps and denies any recognition of similarity between the aquatic preferences of these taxa.

Stable isotopes from the bones of fossil cetaceans and their extinct relatives as well as the depositional environments of fossils provide critical, additional evidence for differentiating among the above scenarios. As observed in extant species, the ratios of oxygen and carbon isotopes in mammalian bone can be used to distinguish species that inhabit marine environments from those that inhabit freshwater environments (Clementz and Koch, 2001). For example, the differences in oxygen isotope ratios between freshwater and marine taxa largely reflect differences in the water ingested; freshwater is isotopically lighter (i.e. more ^{16}O) than seawater because the former is the evaporate of the latter. Water molecules with ^{16}O evaporate more readily than those with ^{18}O (Roe et al., 1998). Oxygen isotope ratios indicate that pakicetid cetaceans ingested freshwater (Roe et al., 1998; Clementz et al., 2006), a finding that is corroborated by the fact that pakicetid fossils have been recovered with the bones of terrestrial mammals in what appear to be fluvial (i.e., freshwater) conglomerates (Williams, 1998). Extinct, stem cetaceans that branch off from more crownward positions in our tree (e.g. *Georgiacetus*; Fig. 9) have isotopic values typical of marine environments and have been found in unambiguous marine deposits (Roe et al., 1998).

Although terrestrial mammals and freshwater mammals often drink from the same sources of water, the latter can be differentiated from the former by having more ^{16}O. This occurs because terrestrial species lose ^{16}O during sweating whereas aquatic species gain ^{16}O from the isotopically light waters they inhabit via ingestion or passive exchange through the skin (Clementz and Koch, 2001). Based on such comparisons, pakicetids and raoellids, basal branches that are sequential sister groups to all other cetaceans, were primarily aquatic (Thewissen et al., 2007). This reconstruction is further supported by the depositional environment of fossils as well as the occurrence of dense, osteosclerotic bones in both taxonomic groups; this trait has evolved in several aquatic/semi-aquatic taxa, presumably to obtain negative buoyancy (Wall, 1983; Gray et al., 2007; Thewissen et al., 2001, 2007, 2009; Cooper et al., 2011). If these inferences for extinct taxa are accepted, then three successive outgroups to marine cetaceans (i.e. hippopotamids, raoellids, and pakicetids; Figs. 7–9) occurred in, or still inhabit, freshwater environments. Thus it is simpler to reconstruct the transition from land to sea within Artiodactyla in the following way: an **initial move to freshwater** in the common ancestor of hippos + cetaceans (branch C), followed by **entrance into a marine environment** after the split from Pakicetidae on branches F–G (i.e. two steps). If the common ancestor of hippos + cetaceans was marine or purely terrestrial, unparsimonious scenarios of three or more environmental transitions are necessary to explain the data.

Following the move from land to freshwater and then to marine environments, several cetacean lineages subsequently **returned to**

freshwater habitats (Cassens et al., 2000; Hamilton et al., 2001). Most notably, the three families of river dolphins – Lipotidae (Chinese), Platanistidae (Indian), and Iniidae (Amazonian) – live in freshwater habitats and share a variety of phenotypic similarities with each other (Geisler and Sanders, 2003). We mapped the evolution of habitat, freshwater versus marine, onto the crown Cetacea section of our composite tree (Fig. 9). Each family of river dolphins (Lipotidae, Iniidae, Platanistidae) was reconstructed as having been independently derived from marine ancestors, as might be expected given the geographic distances that separate members of these three freshwater lineages (Geisler et al., 2011).

3.3.2. Reproduction

Extant cetaceans are not able to support themselves on land, in contrast to some of their more primitive, Eocene relatives (Thewissen et al., 1996, 2001; Gingerich et al., 2001). Therefore, modern cetaceans must mate in an aquatic setting, **give birth underwater**, and also **nurse their offspring underwater**. Semi-aquatic hippopotamids also commonly choose to give birth and nurse their offspring underwater, rare traits within Mammalia (Slijper, 1956, 1962; Gatesy, 1997). For our composite phylogenetic hypothesis, the evolution of these two "aquatic" characters maps to the common ancestral branch shared by hippos and cetaceans (branch C; Fig. 8), but this optimization is based wholly on the character distributions of extant taxa. Basilosaurids, *Dorudon* and *Basilosaurus* in our composite tree (Fig. 9), generally are interpreted as obligately aquatic due to their vestigial hindlimbs. Like extant whales, these extinct stem cetaceans presumably birthed and nursed underwater. Recently described fossils of the protocetid *Maiacetus*, an Eocene whale that retained large hindlimbs, could have some bearing on the primitive birthing behavior of cetaceans. In our phylogenetic hypothesis, this genus is placed on the stem lineage of Cetacea at a more basal branching point in the tree relative to basilosaurids (Figs. 9 and 10). Gingerich et al. (2009) described a diminutive fossil skeleton inside of a much larger *Maiacetus* individual, and the small individual was interpreted as a near term *Maiacetus* fetus, with its skull directed toward the posterior end of the mother whale. Gingerich et al. (2009) argued that this was sufficient evidence to conclude that cephalic parturition was likely the norm for this early stem whale. Furthermore, these authors suggested that *Maiacetus* gave birth on land because a head-first exit from the birth canal is the "universal" birthing mode in large-bodied land mammals, and contrasts with the tail-first births commonly observed in captive delphinid cetaceans and other aquatic tetrapods (Gingerich et al., 2009). There is, however, a major problem with this line of reasoning; hippopotamuses commonly give birth in the water and head-first (Slijper, 1956). Given that Hippopotamidae is the extant sister group to Cetacea and that hippopotamids give birth on land or in the water, either head or tail first, it is not possible to infer from the fossil evidence whether *Maiacetus* birthed on land or underwater. In a commentary on the cephalic birth of a porpoise, Gol'din (2011) noted that even within extant Cetacea, cephalic births are relatively common in some species. A further complication is that tail-first births are the norm in some large-bodied land mammals (e.g., Asian elephant [*Elephas*]; Mellen and Keele, 1994).

Like cetaceans, hippopotamuses also are known to mate in the water, and further, the male reproductive organs of cetaceans share similarities with the semi-aquatic hippos and more distantly related, terrestrial artiodactyl species. Among artiodactyls, scrotal testes are the norm. **Absence of the scrotum** is restricted to cetaceans and hippos (Gatesy et al., 1996 and references therein) and maps to branch C in our overall phylogenetic hypothesis (Fig. 8). A **fibro-elastic penis** with **sparse cavernous tissue** is a hallmark of Artiodactyla, including cetaceans (Slijper, 1962), and is to our knowledge not present in any other extant mammalian clade.

The fibro-elastic penis has a more general phylogenetic distribution than absence of the scrotum and maps to branches A–B, the stem lineage to crown group Artiodactyla (Fig. 8).

3.3.3. Integument

Modern cetaceans are highly streamlined, and their bodies are **nearly hairless**. Cetacean skin **lacks sweat glands**, and **sebaceous glands are absent** as well (Slijper, 1962; Ling, 1974; Nowak, 1991). Among artiodactyls, hippopotamids again are the only species that share any of these traits; hippos are nearly hairless and also lack sebaceous glands (Luck and Wright, 1964). These reductions had previously been considered convergent aquatic specializations but are most parsimoniously interpreted as further evidence for the monophyly of Cetacea + Hippopotamidae (branch C; Fig. 8; Gatesy et al., 1996). The loss of sweat glands likely represents a more recent evolutionary event, and with delayed transformation optimization, maps to the cetacean stem lineage (branches D–O; Fig. 9). For hippopotamids, the presence of sweat glands was conservatively coded as ambiguous (?). Hippos have subdermal glands that secrete a viscous "blood sweat" that acts as an antibiotic sunscreen (Saikawa et al., 2004). Some workers have suggested that these glands are modified sweat glands, but this interpretation is debatable (Crisp, 1867; Allbrook, 1962; Luck and Wright, 1964).

3.3.4. Feeding apparatus and diet

Mesonychia represents an extinct clade of presumably carnivorous ungulates that date back to the Paleocene, and it includes the families Hapalodectidae and Mesonychidae. The teeth of early stem cetaceans and mesonychians are very similar, and dental characters have long supported a close relationship between the two (Van Valen, 1966; O'Leary, 1998). Based on our composite tree (Figs. 7–9), these features are considered convergent with mesonychians (Fig. 8, branches 1–3), and we have mapped four that specifically relate to the lower molars on the tree for Cetacea: elevation of the trigonid (branch E), loss of the metaconid (branches E–F), compression of the talonid (branch E), and loss of the entoconid (branch E) (Fig. 9). As noted by Szalay (1969) in his paper on the dental evolution of mesonychians, these and other dental changes (not discussed here) resulted in a much simpler form of occlusion between the upper and lower molars. In many therian mammals, the lower molars consist of two sets of cusps or crests forming two triangles in occlusal view: a high trigonid mesially and a low talonid distally. During occlusion, the trigonid fits within a corresponding triangular gap between the upper teeth and in doing so shears along the cutting edges of the preceding and succeeding upper molars. The talonid typically forms a crushing basin that occludes with the protocone of the upper molars (Crompton, 1971; Luo et al., 2007). In both mesonychians and basal cetaceans, the common tribosphenic pattern of basal marsupials and placentals was significantly altered. The metaconid of the trigonid was reduced and eventually lost in mesonychians and whales, greatly reducing the shear between the trigonid and the upper molars (Szalay, 1969). The talonid was substantially lowered, lost its medial wall including the entoconid, and became highly compressed transversely. These features essentially transformed the talonid into a simple blade. Taken together, these changes in the lower molars of archaic cetaceans can be viewed as important initial steps in modifying the complex molar morphology of terrestrial artiodactyls into the **simple conical tooth morphology** of extant odontocetes, and it has been argued that these changes marked the initial transition from **herbivory to carnivory/piscivory** within Artiodactyla (Thewissen et al., 2007, 2011; Spaulding et al., 2009).

Despite the dental similarities described above, there are important differences between the lower molars of mesonychians and early cetaceans. Whereas later mesonychians evolved robust teeth with strong apical wear and complex enamel microstructure,

suggestive of bone-crushing (Szalay and Gould, 1966; Stefen, 1997), early cetaceans developed nearly vertical wear-facets that leave the apices of the cusps largely intact (O'Leary and Uhen, 1999). The vertical wear-facets are here optimized as a synapomorphy of Cetacea (branch E; Fig. 9) that reverses later in evolutionary history with the loss of tooth occlusion, in agreement with the conclusions of O'Leary and Uhen (1999). These authors suggested that the unusual wear facets of early stem cetaceans are osteological correlates of aquatic, piscivorous predation based on multiple occurrences of basilosaurids that contained fish bones among their fossilized stomach contents. Although a transition to carnivory/piscivory is suggested by the simplified dentition of even earlier stem whales (Pakicetidae), the stomach contents of basilosaurids represent the most compelling, direct evidence for the transition from the primarily herbivorous diet of terrestrial artiodactyls to the derived piscivorous/carnivorous diet of extant odontocete cetaceans, and constrain the origin of piscivory on the cetacean stem lineage to branches D–M (Fig. 9).

By contrast, raoellids (*Indohyus* + *Khirtharia*), the extinct sister group to Cetacea, have a molar morphology that is commonly seen in herbivorous mammals. Despite the differences in morphology between the teeth of cetaceans and raoellids, the lower molars of the raoellid *Indohyus*, like those of stem cetaceans, are dominated by wear facets that form during initial occlusion of upper and lower teeth. However, the size and orientation of these wear facets are quite different (Thewissen et al., 2011). *Indohyus* and stem cetaceans do share one derived dental feature: incisors aligned in an anteroposterior row on an elongate premaxilla that transformed on branch D (Fig. 9; Thewissen et al., 2007). In terrestrial artiodactyls that have upper incisors, the anterior incisors are distinctly medial to the posterior incisors, forming an arc. The aligned incisors in early cetaceans are quite large and caniniform. Together these features likely helped early cetaceans to capture and secure prey. Whether this interpretation is also valid for *Indohyus* will have to wait until the morphology of the incisors and premaxilla of *Indohyus* are fully described.

Unlike most other placental mammals, extant odontocetes **do not replace any of their teeth** (van Nievelt and Smith, 2005). By contrast, early stem cetaceans such as the pakicetid *Ichthyolestes pinfoldi* (Thewissen and Hussain, 1998) and the basilosaurids *Zygorhiza kochii* and *Dorudon atrox* (Uhen, 2000, 2004) replaced their teeth, as evidenced by specimens that preserve both deciduous and permanent teeth, or their corresponding alveoli. Given that Basilosauridae is either a paraphyletic assemblage that gave rise to crown Cetacea (e.g., Fig. 9, *Dorudon* + *Basilosaurus*; Uhen, 2004), or is the exclusive sister group to this clade (Fitzgerald, 2010; Martínez-Cáceres and de Muizon, 2011), then it is most parsimonious to infer that the lack of dental replacement (monophyodonty) evolved once on the branch leading to the most recent common ancestor of crown Cetacea (branch O; also see Uhen and Gingerich, 2001). The fossil record is consistent with this scenario given that dental replacement has not been observed in any stem odontocete or mysticete. However, it should be noted that the vast majority of extinct cetaceans are represented by holotypes only, thus it is possible that the fossil record is not capturing the convergent loss of dental replacement in odontocetes and mysticetes. The selective pressure(s) that might have driven the loss of dental replacement in crown cetaceans is unclear, as is the case for other mammals that do not replace their teeth (e.g. pinnipeds, several moles, aardvark; van Nievelt and Smith, 2005). Unlike most mammals, extant cetaceans **do not masticate their food** and instead filter feed, swallow entire prey items, or swallow chunks of prey. The loss of occlusion and wear between upper and lower teeth in cetaceans may have enabled a single generation of teeth to remain functional for the entire life of an individual. Another possibility is that precocious development in cetaceans (Webb, 1997) allows for adult-

sized teeth to fit inside the mouth of young cetaceans, a hypothesis suggested to explain various instances of monophyodonty in placental mammals (van Nievelt and Smith, 2005).

Extant odontocetes do not have distinct incisors, canines, premolars, and molars as is typical of other mammals (a condition referred to as heterodonty). Instead their teeth are typically similar in shape from front to back, a condition referred to as **homodonty** (Uhen, 2002). Other mammals have distinctive teeth for different tasks; incisors frequently help procure food whereas molars typically transform it into smaller pieces. Extant cetaceans do not chew their food, thus it is not surprising that the teeth in odontocetes are all caniniform (Uhen, 2002). The transition from heterodonty to homodonty among cetaceans is partially represented in the fossil record; however, it is complicated by difficulties in establishing homologies between teeth in different taxa. We took a simple approach to mapping this transition by focusing on two characters only: the number of double-rooted teeth (the teeth of all extant odontocetes have single roots) and the number of accessory cusps. In stem odontocetes, like *Waipatia* and *Squalodon* (Fig. 9), the anterior teeth are single rooted and single cusped whereas the posterior teeth are double-rooted and bear accessory cusps on the mesial and distal cutting edges (Kellogg, 1923; Fordyce, 1994). Optimization of these two characters on the crown Cetacea section of our tree indicates that the loss of all double-rooted teeth and accessory cusps occurred near the most recent common ancestor of crown odontocetes (branches S–T). Some stem mysticetes also retained functional teeth as adults, and a similar simplification in the number of cusps and loss and/or fusion of roots occurred in aetiocetids, a clade of toothed mysticetes (Deméré and Berta, 2008).

Stem cetaceans have enormous temporal fossae that are separated by a tall and prominent sagittal crest. The size of the temporal fossa suggests that the temporalis muscle, which closes the jaw, was very large in stem cetaceans and could exert considerable force at the apices of the upper and lower teeth (Uhen, 2004). We mapped a related character, the shape of the dorsal side of the intertemporal region on our tree for crown Cetacea (character 136; Geisler et al., 2011). The intertemporal region in cetaceans varies from a narrow strip of bone that forms a sagittal crest to a wide, nearly tabular surface. The wider the dorsal side of the intertemporal region, the smaller and more separate the right and left temporal fossae become. Basal toothed mysticetes, like *Janjucetus*, have a sagittal crest (Fitzgerald, 2006), whereas loss of the crest is optimized here as a synapomorphy of *Mammalodon* plus all other mysticetes. A further widening of the intertemporal region diagnoses crown Mysticeti. In odontocetes, the optimization of this character is a little less clear, but what can be inferred demonstrates convergent evolution with the mysticete condition. Some basal odontocetes lack a sagittal crest but retain a narrow intertemporal region (e.g. *Simocetus*) whereas all crown odontocetes, and a few stem taxa such as *Squalodon calvertensis*, have a much wider intertemporal region with sharp, laterally-directed crests that define the dorsal borders of much **reduced temporal fossae**. A smaller temporal fossa implies a weaker bite, and may have coevolved with the development of suction feeding; at least some reliance on suction feeding is interpreted to have evolved fairly early on the stem of Cetacea (Johnston and Berta, 2011). When suction feeding, cetaceans depress their tongue to enlarge the oral cavity and the resulting decrease in pressure allows them to suck in prey (Werth, 2006). This method of prey capture places little emphasis on the temporalis muscle; it need only close the jaw to prevent prey from escaping the mouth.

In terms of soft anatomy relevant to the transition from herbivory to piscivory/carnivory, many cetacean species are characterized by a **multi-chambered stomach**, as are representatives from most major clades of Artiodactyla (Slijper, 1962; Langer, 2001). Heyning and Mead (1986) suggested that the cetacean

forestomach could, in some taxa, function as a reservoir for water ingested during prey capture, followed by expulsion of the seawater after the prey item is secured. In our coding of stomach morphology, we recognized only two states: plurilocular (multi-chambered) and unilocular (single chambered). With this gross characterization and for the taxa sampled here, the simplest optimization implies that the ancestral artiodactyl possessed a multi-chambered stomach that evolved on branches A–B (Fig. 8), and this feature was inherited by extant camels, ruminants, peccaries, hippos, and cetaceans, but reversed within Suidae (pigs), a group that includes species with a mixed, omnivorous diet. Langer (2001) coded anatomical specializations of the stomach into multiple independent characters, and in this scheme, the multi-chambered stomachs of whales, hippos, ruminants, and tayassuids are not necessarily interpreted as being derived in the common ancestor of Artiodactyla.

The evolution of **batch filter-feeding** using **baleen** signified a major ecomorphological transition in cetacean evolution, and as such is an exemplar of evolutionary novelty (Deméré et al., 2008). This specialization enabled mysticetes to feed at lower trophic levels, perhaps facilitating a shift to enormous body size relatively early in the history of the clade (Werth, 2000; Fitzgerald, 2006; Slater et al., 2010). Based on the somewhat limited comparative data provided by extant taxa, both baleen and batch filter-feeding are reconstructed as evolving on the stem lineage to crown Mysticeti (branches a–f; Fig. 9). Recent phylogenetic analyses that incorporated fossils have attempted to detail the stepwise evolutionary transition from teeth to baleen in early fossil mysticetes, as well as morphological modifications that increased the size of the oral cavity, changes that facilitated the batch filter-feeding mode (Fitzgerald, 2006, 2010, 2012; Deméré et al., 2008; Deméré and Berta, 2008; Marx, 2010).

Early stem mysticete genera – such as *Janjucetus*, *Mammalodon*, *Chonecetus*, and *Aetiocetus* – possessed well-developed teeth as adults. Both *Janjucetus* and *Mammalodon* generally are reconstructed as raptorial pursuit predators or as suction feeders (Fitzgerald, 2006, 2010, 2012). By contrast, modern mysticetes possess only rudimentary tooth buds during fetal development, and these tooth remnants are resorbed before birth and therefore never used in prey capture (Flower, 1883; Slijper, 1962; Deméré et al., 2008 and references therein). All extant mysticetes completely lack a mineralized dentition in adults and instead rely on baleen to procure small food items in bulk. On our composite tree, the **complete loss of adult dentition** is optimized to have evolved in the common ancestor of *Eomysticetus* and all other edentulous (toothless) mysticetes (branch d; Fig. 9). Parallel decreases in numbers of teeth occur throughout crown Odontoceti, particularly in suction feeders (e.g., physeteroids, ziphiids), multiple increases in tooth counts map to taxa that seize individual prey items with their teeth (e.g., delphinids, river dolphins), and as in crown mysticetes, **tooth enamel has been lost** in the suction-feeding kogiids (pygmy and dwarf sperm whales; branch Y; Fig. 9) (Geisler and Sanders, 2003; Meredith et al., 2009 and references therein).

Baleen is a keratinous, sieve-like series of plates that is suspended from the palate of extant mysticetes and enables the bulk filtering of prey (Pivorunas, 1979). Baleen is rarely found associated with skeletal elements in the fossil record; however, a series of **nutrient foramina and grooves** on the lateral portion of the palate are interpreted most parsimoniously as osteological correlates of baleen (Deméré et al., 2008). In modern mysticetes, these features house the blood supply and innervation for the continuously growing baleen plates; lateral nutrient foramina are lacking in odontocetes and stem cetaceans. Aetiocetids, stem mysticetes that retained an adult dentition, also expressed small nutrient foramina and associated sulci that are preserved on the lateral portion of the palate (Deméré et al., 2008; Deméré and Berta, 2008).

Based on this critical fossil evidence, **baleen** was optimized to the common ancestor of Aetiocetidae and edentulous mysticetes (branch c; Fig. 9), before the loss of a mineralized dentition on branch d (Fig. 9). In this interpretation, aetiocetids are seen as transitional taxa that may have captured large prey with their teeth and also batch-fed on minute organisms with their proto-baleen, thus easing the transition to obligate filter-feeding via a multi-functional, intermediate morphology (Fitzgerald, 2006; Deméré et al., 2008; Deméré and Berta, 2008; but see Marx, 2010).

In addition to the evolution of baleen and loss of adult dentition, several critical modifications occurred in early stem mysticetes that resulted in expansion of the oral cavity. A **wide rostrum** (branch a), **thin lateral margins of the maxillae** (branch b), and mandibles that transition from slightly concave to straight (branch b) to **laterally bowed** (branch e) all contribute to the expansive gape of modern balaenopterid mysticetes, and these features here optimize in a sequential fashion on the stem lineage to crown Mysticeti (Fig. 9). Modern mysticetes display mandibular kinesis and extreme flexibility in movement of the lower jaws to further extend the oral cavity when feeding. This is, in part, accomplished by an **unsutured mandibular symphysis** in which the jaws are separated anteriorly by a dense fibrocartilagenous disc that is reinforced by fibrous tissue – marked on the mandible by a longitudinal symphyseal groove (Lambertsen et al., 1995; Johnston et al., 2010). In contrast, most cetaceans have a fused mandibular symphysis or a sutured symphysis united by fibrocartilage; these conditions limit independent movement of each mandibular body. Fossil material recently examined by Fitzgerald (2010, 2012) has clarified the condition of the mandibular symphysis in the toothed mysticetes, *Janjucetus* and *Mammalodon*. We incorporated these revised observations, and as a result, an unsutured mandibular symphysis is optimized to branches b–c, the common ancestor of Aetiocetidae plus all edentulous mysticetes (+ possibly *Mammalodon*), and precedes the loss of the mineralized dentition on branch d (Fig. 9). Crown mysticetes have evolved associated suites of anatomical modifications to aid in prey capture. Many of these features are related to how whales take in and then direct water within the mouth while feeding. This has been achieved in three ways, corresponding to divergent filter-feeding modes: engulfment, benthic suction, and obligate skimming (Fig. 6; Werth, 2000; Bouetel, 2005).

Engulfment feeding characterizes the hydrodynamically streamlined Balaenopteridae (Fig. 6A). During prey capture, the lower jaw of balaenopterids is opened at rapid swimming speeds of up to 3 m s^{-1} (Lambertsen et al., 1995; Goldbogen et al., 2007), and the mandibles are rotated, dislocated, and depressed to a position that is nearly perpendicular to the whale's body (Orton and Brodie, 1987). At the same time, numerous **longitudinal grooves** on the **ventral throat pouch** permit expansion of the gular cavity, which surrounds prey-laden water (Fig. 6A). A **reduced, fibrous tongue** in balaenopterid whales contrasts with the muscular tongue of other extant mysticetes and permits ingested water and prey to extend the throat pouch to the umbilicus in some species (Fig. 6A). Additionally, the **absence of a synovial temporomandibular joint** is another important feature of Balaenopteridae that allows for more flexibility in the rotation of the mandibles in multiple directions (Lambertsen et al., 1995). In balaenopterids this joint is composed of fibrous connective tissue. Recently, Johnston et al. (2010) suggested that *Eschrichtius robustus* (gray whale) also lacks a synovial temporomandibular joint based on dissection of a stranded specimen, but subsequent examination of better-preserved material contradicts that interpretation (Berta, pers. obs.). Derivation of the unique engulfment feeding specializations of Balaenopteridae listed above map to branch g (Fig. 9).

Other subclades of crown Mysticeti have evolved equally remarkable behaviors for straining batches of prey from seawater

Pivorunas, 1979). *Eschrichtius robustus* is the only extant species that utilizes benthic suction to filter-feed (Fig. 6B). When foraging, the gray whale turns on its side, rams its mouth into the sea floor, and then rapidly depresses its tongue, which draws in water, sediment, and benthic invertebrates (Werth, 2000). Skimmers – the balaenids *Eubalaena* and *Balaena*, as well as the neobalaenid *Caperea marginata* – swim slowly with mouth agape, usually feeding on aggregations of small, relatively immobile zooplankton (Fig. 6C; Werth, 2000). Movement of water is unidirectional, entering the anterior portion of the mouth, passing through the baleen filter, and exiting laterally from the posterior portion of the oral cavity (Sanderson and Wassersug, 1993; Werth, 2004). A key osteological character associated with this feeding style and readily detectable in the fossil record is arching of the rostrum. The rostra of skimmers are characteristically narrow and arched, creating a dorsally-expanded oral cavity that is filled with racks of extremely long baleen plates (Werth, 2000). The rostrum of *Eschrichtius* is only moderately arched, while the engulfment-feeding balaenopterids have rostra that are relatively flat with little dorsal expansion of the oral cavity. Optimization of the highly arched rostrum found in balaenids and *Caperea* is ambiguous on our tree, with parallel derivation of this feature or gain and then loss being equally parsimonious reconstructions, depending on whether the character is treated as ordered or unordered, and on how morphological variation was coded by different researchers (Deméré et al., 2008; Geisler et al., 2011).

3.3.5. Blowhole and respiration

The blowholes of extant cetaceans are functional equivalents to the nostrils of other mammals. With the exception of the giant sperm whale, *Physeter macrocephalus* (Heyning, 1989), all extant cetaceans have the blowhole positioned near the top of the head, approximately at a level above the eyes. Not surprisingly the external bony nares on the skull are in a far posterior position in extant cetaceans, and the nasal bones, which are typically long in mammals and roof over the nasal passages, are greatly reduced in size. It is generally thought that the elevated and **posterior position of the nares** minimizes the energy required for respiration in an aquatic environment (Heyning and Mead, 1990; Reidenberg and Laitman, 2008). The fossil record of Cetacea includes numerous transitional forms that document the posterior evolutionary movement of the bony nares (Whitmore and Sanders, 1976; Geisler and Sanders, 2003), and thus presumably the blowholes as well. We mapped the anterior edge of the nasals/posterior margin of the bony nares on our trees for Artiodactyla and crown Cetacea (Figs. 8 and 9). Basal cetaceans have a morphology that is similar to that of most other mammals; the nasal opening is at the tip of the rostrum (Thewissen and Hussain, 1998). Some of the later diverging stem cetaceans, such as *Protocetus*, have the edge of the nasals over the first premolar or the diastema that precedes it. The ancestor of crown Cetacea is reconstructed as having the edge of the nasals positioned over the second premolar, as in the basilosaurid *Zygorhiza*. On the stem to Odontoceti, the edge of the nasals became aligned with the anterior edge of the orbit, then over the orbit itself, and finally moved to behind the orbit to reach the level of the zygomatic process in the most recent common ancestor of Synrhina (all extant odontocetes except the physeteroids). Many toothed mysticetes retained the condition seen in basilosaurids, and then at more recent, apical nodes evolved a derived condition where the anterior edge of the nares is aligned with the anterior edge of the supraorbital process of the frontal. The exact number of times this state evolved in Mysticeti is unclear, and any scenario requires homoplastic changes, but the overall pattern implies parallel retraction of the nasals in both Odontoceti and Mysticeti. For illustrative purposes, we show two transformations in this character on the stem lineage to Cetacea on branches K and L, as well as

further, independent retraction of the nasal aperture/reduction of the nasal bones on the stem lineage to crown Odontoceti (branches P–T) and on the stem lineage to crown Mysticeti (branch e) (Fig. 9). The first two changes represent movement of the anterior edge of the nasals from the primitive condition seen in *Artiocetus* (anterior to or over canine) to the more derived position expressed in *Georgiacetus* (between the first and second premolars). The third and fourth changes highlight the independent posterior movement of the blowhole in the two major extant clades of Cetacea.

Extant mysticetes have two soft tissue nasal openings (blowholes), similar to the pair of nostrils seen in terrestrial mammals. By contrast, a **single blowhole** is a synapomorphy of crown Odontoceti that transformed on the odontocete stem lineage (branches P–T; Fig. 9), in agreement with other studies (e.g. Heyning, 1997). A large mass of soft tissue is present on the forehead of odontocetes, thus fairly long soft tissue nasal passage(s) span between the external bony nares and the blowhole. In physeteroids (sperm whales), there are two soft tissue nasal passages that join and form one passage just proximal to the blowhole. By contrast, in all other crown odontocetes, the two nasal passages have merged (Heyning, 1989). Merged nasal passages represent a synapomorphy of, and the namesake for Synrhina (branch U), the clade that includes Platanistidae + Ziphiidae + Delphinida (Geisler et al., 2011). The functional significance of having one or two blowholes and the fusion of two nasal passages into one is unclear. The nasal passages of all extant cetaceans can be sealed by fleshy **nasal plugs** that slide into the external bony nares, and are pulled out by nasal plug muscles that originate on the premaxillae (Heyning and Mead, 1990). This character maps as a synapomorphy of the cetacean crown group (branches D–O; Fig. 9), although it is unclear where on the cetacean stem it evolved. Heyning and Mead (1990) noted that nasal plugs were possibly present in advanced archaeocetes because these taxa share, with extant cetaceans, a similar morphology of the premaxilla anterolateral to the external bony nares. Some authors had inferred that the nasal plugs are the origin of high frequency vocalizations in odontocetes (Evans and Prescott, 1962), but this idea has fallen out of favor as the weight of evidence suggests that the phonic lips are instead the source of odontocete vocalizations (see below).

Unlike most mammals, cetaceans have **three primary lung bronchi** instead of two (Slijper, 1962). The functional significance of the trait, in terms of specialization to an aquatic regime, is not known, and instead this character may be just a remnant of the ancient artiodactyl history of Cetacea. For extant taxa in our composite tree that could be coded from the literature, the three primary bronchi state was restricted to Artiodactyla, and was reconstructed as evolving in the common ancestor of this clade (branches A–B; Fig. 8). To our knowledge this character is not expressed by any other extant mammalian lineage.

3.3.6. Organization of the skull

The osteological anatomy of cetaceans is highly unusual as compared to other mammals, and many peculiarities are related to the process of **cranial telescoping**. As described by Miller (1923) in his monograph on the subject, telescoping is the evolutionary transformation where bones that previously contacted along vertical or near vertical sutures now contact along nearly horizontal sutures. To obtain this sutural reorientation, one bone "slid" over the other, similar to the way the nested cylinders of a mariner's telescope slide over each other when the scope is collapsed. We mapped two separate characters of cranial telescoping: (1) posterior expansion of the nasal process of the maxilla over the frontal on the crown Cetacea tree and (2) anterior expansion of the supraoccipital over the parietals and frontals on the mysticete section of our composite tree (Fig. 9). Like previous studies (e.g. Geisler and Sanders, 2003), we found the expansion of the nasal process

of the maxilla over most of the frontal to be a synapomorphy of Odontoceti (branch P), with further expansion expressed as a synapomorphy of the clade that includes all odontocetes except for the most basal taxon, *Archaeodelphis* (branch Q). The functional significance of the posterior expansion of the maxilla is uncertain, although Oelschläger (1990) suggested that it could help anchor the rostrum, which is long in most odontocetes. Anterior expansion of the supraoccipital that extends to the posterior half of the temporal fossa was found to be a synapomorphy of all edentulous mysticetes (branch d). A supraoccipital that extends to the anterior half of the temporal fossa is a synapomorphy of the clade including all toothless mysticetes but *Eomysticetus* (branch e). A similar anterior expansion of the supraoccipital occurs in burrowing rodents (Miller, 1923), and Courant and Marchand (2000) suggested that in both clades this morphology aids the alignment of the skull with the spinal column. In mysticetes, passive alignment of their large heads with the rest of the body would presumably reduce the metabolic demands of swimming (Courant and Marchand, 2000).

Odontocetes have **asymmetric skulls** where structures on one side are consistently larger than those on the other, a very rare condition within Mammalia (Mead, 1975). The function of such asymmetry is controversial but may be related to sound production, hearing, or accommodation for swallowing large prey (Heyning, 1989; MacLeod et al., 2007; Fahlke et al., 2011). While skulls of other mammals are not perfectly symmetrical, the degree of asymmetry is much less than in odontocetes, and the asymmetry fluctuates; i.e., in one individual a structure on the right side is larger, whereas in another individual from the same species, a structure on the left side is larger. Odontocete asymmetry is most pronounced in the soft tissue diverticula associated with the soft tissue nasal passages, but it also appears to a lesser degree in the bony external nares and surrounding osteological structures (Mead, 1975). We mapped three types of asymmetry on our tree (Fig. 9): (1) whether the bony nasal passages are the same or different sizes, (2) the number of nasal bones, and (3) whether the internasal and interfrontal sutures are on the median plane or shifted to one side. The first two characters evolved only in physeteroids (sperm whales); extant and extinct physeteroids have a left bony nasal passage that is nearly twice the size of the one on the right (branch W), and extant physeteroids lack either one or two nasals. The nasals of extant physeteroids (when present) are delicate, so it is therefore unclear if their absence in fossil physeteroids is real or a preservational artifact. Here we have mapped the loss of nasals based on character codings for extant physeteroids (branches W–X and branch Y; Fig. 9). A shift of the interfrontal and internasal sutures to the left side is optimized as a synapomorphy of the odontocete crown group (branch T). By contrast, in nearly all stem odontocetes, these sutures are centered on the sagittal plane, and a few crown odontocetes have reversed to this condition (e.g. *Pontoporia*, *Xiphiacetus*). It should be noted that Fahlke et al. (2011) recently described asymmetry in the skulls of several early, stem cetaceans. In these taxa, the internasal and interfrontal sutures are shifted subtly to the right side, not to the left as in odontocetes, and it is unlikely that the different conditions are strictly homologous.

3.3.7. Echolocation, vocalization, and auditory structures

Behavioral studies on bottlenose dolphins and other captive cetacean species have demonstrated that they use echolocation to find prey and navigate (e.g. Au, 1993). In echolocation, odontocetes produce high frequency clicks and whistles and then interpret the echoes of these vocalizations to develop an "audio picture" of their surroundings. Many odontocetes produce such high frequency vocalizations (May-Collado et al., 2007), and this suggests that all of these odontocetes echolocate. Among other mammals, echolocation has been demonstrated in microchiropteran bats, some shrews, and a few rodents (Thomas et al., 2004). Echolocation requires anatomical structures to produce sound, others to direct it, yet more to receive and transmit echoes, and finally others to perceive and interpret these echoes.

Although there have been several hypotheses for the source of odontocete vocalizations, recent experimental data have conclusively shown that the **phonic lips**, a constriction in the soft tissue nasal passage between the blowhole and skull, are the sources of odontocete vocalizations (Cranford et al., 1996, 2011). Those authors further report that when searched for, these phonic lips have been found in all odontocetes examined (32 species), and we tentatively conclude that the phonic lips evolved on the odontocete stem lineage (branches P–T; Fig. 9). The **melon** is a large, fatty organ situated immediately anterior to the phonic lips that forms the "forehead" bulge of delphinids and most other odontocetes. Although a much smaller and possibly homologous structure occurs in mysticetes (Heyning and Mead, 1990), as in previous studies (e.g. Heyning, 1997), we find a hypertrophied melon to be a synapomorphy of crown Odontoceti or to have evolved along the odontocete stem (branches P–T). The melon may function in focusing and directing sounds produced by the phonic lips (McKenna et al., 2011). The soft tissue nasal passages of odontocetes have a variety of diverticula, and the one mapped here on our composite tree, the **inferior vestibule**, is also reconstructed as a synapomorphy of the odontocete crown group or a more inclusive clade (see also Heyning, 1989). Possible functions of the inferior vestibule are the recycling of air during diving to produce vocalizations and the forward reflection of sound from the phonic lips (Reidenberg and Laitman, 2008).

In order for echolocation to be effective, odontocetes have to be able to hear and differentiate high frequency echoes. Like bats, that also echolocate, odontocetes have expanded basal turns of the cochlea (Ketten, 1992). The basal turn is where high frequency sounds are perceived, and those odontocetes that produce the highest frequency sounds also have the most expanded basal turns (i.e. type I cochlea of Ketten, 1992). By contrast, extant and extinct mysticetes have much narrower and higher cochleas. In addition, odontocetes have a much narrower laminar gap between the primary and secondary bony laminae that delimit the basilar membrane, which supports the hair cells. The basilar membrane and its related laminar gap in the basal cochlear turn are the critical determinants for the upper limit of high-frequency hearing. Thus it is not surprising that odontocetes generally have a narrower laminar gap in the basal cochlear turn relative to mysticetes (Fleischer, 1976; Ketten, 1992; Geisler and Luo, 1996; Luo and Marsh, 1996). The cochleas of several extinct odontocetes have been studied and these observations are consistent with specialization for high frequency sounds (Fleischer, 1976; Luo and Eastman, 1995). However, the exact phylogenetic positions of several key taxa/specimens in these two studies are not known.

The typical mammalian pathway by which sound reaches the middle ear, through the external auditory meatus and the tympanic membrane, is not effective underwater. In odontocetes, sound waves travel to the tympanic bulla enclosing the middle ear cavity through a large fat pad/body that extends from the mandible to the middle ear (Norris, 1968). One particular branch of this fat pad fits into a recess of the bulla and likely funnels the sound waves into this bone (Cranford et al., 2010). It was thought that sound waves entered the fat pad, anteriorly situated between thin lateral and medial walls of the mandible, via the "pan bone," a particularly thin portion of the lateral wall of the mandible. However, recent model-based studies suggest that a more efficient pathway to reach the fat bodies may be to enter the skull on the ventral side of the head between the mandibles (Cranford et al., 2008). We mapped the evolution of an **expanded mandibular foramen** on our composite phylogenetic hypothesis (Figs. 7–9) to trace the

evolution of the fat-body acoustic pathway. In most mammals, the mandibular foramen is small and only receives the inferior alveolar nerve and associated vessels; however, in odontocetes, the foramen is huge and receives the mandibular fat body as well. As noted by Nummela et al. (2007), pakicetids have a small mandibular foramen, whereas the foramen is large in *Ambulocetus*, suggesting that the fat pad evolved subsequent to the split of Pakicetidae from the remaining cetaceans in our analysis (branch F). Shape analysis of the mandibular foramen in odontocetes suggests that this feature may constrain acoustic function and thus influence sound reception characteristics (Barroso et al., 2012). In extant mysticetes, the mandibular foramen is much smaller than in odontocetes, and a fat body is situated lateral to the mandible (Yamato et al., 2012). We inferred the reduction of the mandibular foramen on branch f, crown Mysticeti (Fig. 9).

Although the mandibular fat pad provides an efficient means to transmit sounds to the middle ear, underwater sound also can take other routes through the skull because the density of bone is more similar to the density of water than air. Thus most mammals lose their ability to perceive the direction of sound if submerged (Nummela et al., 2007). It has been hypothesized that the **pterygoid air sinus** of cetaceans, a large diverticulum of the eustachian tube, acoustically isolates the tympanopetrosal (Fleischer, 1978) because sound would be reflected, not transmitted, at the air/bone interface. The pterygoid and peribullar air sinuses prevent intracranial sound waves that originated on the opposite side of the skull from reaching the middle ear. Instead, those sound waves initially would have to pass around the anterior portion of the head and would reach the ears at different times, allowing the direction of the sound to be differentiated (Fleischer, 1978; Nummela et al., 2007). The pterygoid air sinus, and its associated bony fossa, occurs in all extant cetaceans (Fraser and Purves, 1960). The earliest cetaceans lacked a pterygoid air sinus fossa, but a small sinus does occur in the middle Eocene stem cetaceans *Protocetus* and *Georgiacetus* (branch K) (Geisler et al., 2005). A very large sinus occurs in basilosaurids and was derived on branches M–N (Fig. 9); the condition in *Basilosaurus* is similar in size to those in extant mysticetes (Luo and Gingerich, 1999; Uhen, 2004). There is variation in the size and lobes of the pterygoid sinus among extant cetaceans, but the sinus and its fossa apparently occur in all crown cetaceans (Fraser and Purves, 1960).

In most mammals the petrosal bone is a component of the bony wall of the braincase. In extant cetaceans, the peribullar sinus wraps around the tympanopetrosal and provides **isolation of the earbones from the skull**, to varying degrees. The roof of the peribullar sinus cavity, when present, is formed by extensions of the parietal and bones of the basicranial stem (basioccipital, basisphenoid) (Fraser and Purves, 1960) and separates the peribullar sinus fossa and the cranial cavity (character 183; Geisler et al., 2011). We mapped the development of this bony partition on our tree and found that contact between the parietal and basicranial stem is an ambiguously optimized synapomorphy that emerges near the base of stem Odontoceti; there are several subsequent reversals to a partial partition or no partition at all, and this state evolved independently in the mysticete *Caperea*.

All extant and extinct cetaceans share pachyostosis (thickening) of the medial wall of the bulla, which is called the **involucrum** (Luo, 1998). Thewissen et al. (2007) showed that the raoellid *Indohyus* also had an involucrum, thus this feature is interpreted to have evolved on the branch leading to Raoellidae + Cetacea (branch D). The involucrum is widely assumed to be another specialization for underwater hearing. As discussed above, sound travels to the bulla in extant odontocetes via a fat pad, and the presence of a large mandibular foramen in nearly all cetaceans suggests that this auditory pathway evolved quite early. Under this hypothesis, the occurrence of a free-swinging mass of bone (i.e. involucrum) at-

tached to the margin of the bulla may enhance the bulla's response to these sound waves (Fleischer, 1978). However, the enlarged mandibular foramen (branch F) evolved subsequent to the derivation of the involucrum (branch D; Fig. 9; see above).

3.3.8. Locomotion

Extant cetaceans propel themselves through the water by vertical movements of their extremely **robust tails** that terminate in **flukes**, which are horizontal, fibrous, fins at the tip of the tail (Fish, 1998). Although not quantified explicitly in the literature, robust caudal vertebrae characterize all extinct and extant cetaceans. A member of the sister group to Cetacea in our composite tree, *Indohyus*, has caudal vertebrae that are gracile, and the tail likely did not play a major role in generating thrust (Cooper et al., 2011). This contrasts with the condition in pakicetids (Madar, 2007). We tentatively position evolution of a robust tail to branch E, the common ancestor of Pakicetidae and all other cetaceans in our composite tree (Fig. 9). Parsimony optimization indicates that flukes are a synapomorphy of the cetacean crown group, although neontological data do not resolve where flukes evolved on the cetacean stem lineage (branches D–O). In extant cetaceans and sirenians, the position of the flukes, which are soft tissue structures, is correlated with a transition to wider vertebral bodies at the posterior of the tail. Vertebrae anterior to the flukes are much narrower, and the anterior edge of the flukes coincides with the change in vertebral dimensions (Buchholtz, 1998). Wide caudal vertebrae at the tip of the tail in basilosaurids support the hypothesis that these stem cetaceans had flukes although it seems unlikely that they served as the sole propulsive surface (Buchholtz, 1998, 2007). *Maiacetus*, which based on our analysis branches from a more basal position in the tree relative to basilosaurids, has narrow and elongate distal caudal vertebrae (Gingerich et al., 2009). This morphology implies that this taxon lacked tail flukes. If the osteological correlate of flukes is accepted as valid, the current fossil evidence partially constrains the evolution of flukes on the cetacean stem lineage (branches I–M), but exactly where on that lineage this feature evolved will remain unclear until more complete skeletal material of protocetids is described.

Whereas flukes enable cetaceans to generate thrust, **flippers** help them steer. The evolution of flippers involves several morphological changes including shortening of the long bones of the forelimb, hyperphalangy, interdigital webbing, and loss or extreme reduction of movement at all joints within the forelimb (Rommel and Reynolds, 2002; Cooper, 2007). The **loss of most movement at the elbow joint** is most easily inferred by observing this joint in lateral view; instead of being semicircular, the joint between the humerus and the radius and the joint between the humerus and the ulna are both flat and meet at an obtuse angle in nearly all cetaceans. We optimized this character on our composite topology, and it is a synapomorphy of crown Cetacea. Basilosaurids, the immediate outgroup(s) of crown Cetacea, have a curved and presumably functional, mobile elbow joint (Uhen, 2004). The shape of the joint has reversed in the extant ziphiid *Berardius*, but closer inspection of the joint surface in this taxon clearly indicates that mobility is severely limited (Geisler, pers. obs.).

Most extant cetaceans are characterized by the presence of a **dorsal fin**, a feature that is unique among living mammals, but that is also present in a variety of distantly related, aquatic vertebrate taxa (e.g., ichthyosaurs, cartilaginous fishes, bony fishes). Dorsal fins show a wide range of shapes and sizes in Cetacea, from extremely prominent (e.g., killer whale, *Orcinus orca*) to relatively superficial in relation to overall body size (e.g., blue whale, *Balaenoptera musculus*), to completely absent (e.g., bowhead whale, *Balaena mysticetus*). Fossil evidence bearing on the evolutionary history of dorsal fins is currently lacking, and unlike flippers and flukes, there are no known osteological correlates that signify the presence of a

dorsal fin in extinct species. Therefore, inferences bearing on the presence or absence of a dorsal fin in stem cetaceans and the pattern of evolution within crown Cetacea must rely on phylogenetic interpretations of variation among extant taxa (character 304; Geisler et al., 2011). A difficulty comes in coding this feature, because many cetaceans are characterized by a hump or low ridge where the dorsal fin is present in other species (e.g., giant sperm whale, gray whale, river dolphins). If these features are not considered to be true "fins," the simplest optimization on our composite tree implies that the common ancestor of crown Cetacea lacked a dorsal fin, and that the evolution of this fin is restricted to within the crown group. If a hump/ridge is interpreted as an intermediate state between absence and presence of a dorsal fin, the minimum length character mapping changes. With either coding, several independent derivations/losses of the dorsal fin are implied.

One of the most obvious ways that extant cetaceans differ from other mammals is the **absence of external hindlimbs**. However, elements of the hindlimb and the pelvic girdle are frequently found in extant cetaceans. A **vestigial pelvis** appears to be typical of mysticetes, and also occurs in many odontocetes. The reduced pelvis functions as an attachment point for muscles acting on the reproductive organs, such as the penis retractor muscle (Adam, 2002). Occasionally femora and in a few cases tibiae have been found in extant cetaceans (Thewissen et al., 2009), but these are sometimes interpreted as atavistic anomalies (Adam, 2002). The fossil record of cetacean hindlimb and pelvic bones is difficult to interpret, given the great reduction in size of these elements in crown cetaceans. We were only able to find a few examples of extinct crown cetaceans that preserve the pelvis (Benham, 1937; Bouetel and de Muizon, 2006). Most cetacean fossil skeletons lack elements of the pectoral girdle and limbs, but this generally is the result of taphonomic processes rather than evidence for true absence of these features. By contrast, the pelves of several stem cetaceans have been recovered, and some have been found with hindlimb elements (Fig. 3). For example, the hindlimbs of pakicetids are quite large and in gross morphology look much like those of their terrestrial relatives (Madar, 2007). Later stem cetaceans that are positioned higher up the tree, such as *Rodhocetus* (Gingerich et al., 2001), also have large hindlimbs, although the femur is relatively shorter than those of pakicetids. By contrast, basilosaurids, the immediate sister group(s) to crown Cetacea (*Dorudon* and *Basilosaurus*; Figs. 9 and 10), have diminutive hindlimbs that bear only three digits, and presumably would be unable to aid in locomotion on land. Although these vestiges are tiny relative to overall body size, given the occurrence of a functional knee joint and the presence of digits, it seems reasonable to assume that a portion of the hindlimb extended beyond the body wall. Thus there are at least two major steps in the reduction of hindlimbs, both of which occurred on the stem to the cetacean crown group: (1) great reduction in size of the limb, and (2) loss of distal elements of the limb and incorporation of any remaining hindlimb elements into the body wall. The first step is optimized conservatively to branches K–M; such hindlimb reduction to the degree observed in basilosaurids strongly suggests that cetaceans with this state were **obligately aquatic** (Thewissen and Bajpai, 2001). The second step is most parsimoniously inferred to have occurred on branch O (Fig. 9).

In extant cetaceans, the pelvis is highly reduced and far removed from the vertebral column (Fig. 2). By contrast, the pelvis is solidly anchored to one or more of the sacral vertebrae via a sacroiliac joint in terrestrial mammals. When the joint is surgically opened, the enlarged distal ends of the transverse processes of the sacral vertebrae and the adjacent surface of the ilium of the pelvis are rugose with interlocking bumps and depressions. This roughened surface is an osteological correlate of the sacroiliac joint, and it allows presence or **absence of the sacroiliac joint** to be in-

ferred in extinct taxa. It is widely assumed that this articulation is functionally important in terrestrial locomotion and in supporting an animal's body weight on land. The pelves of early stem cetaceans that branch from the base of the tree retain a broad sacroiliac joint, including pakicetids (Madar, 2007), *Ambulocetus* (Thewissen et al., 1996; Madar et al., 2002), and *Artiocetus* (Gingerich et al., 2001). *Protocetus* also has a sacroiliac joint, although the articular surface on the sole sacral vertebra is much narrower than that seen in earlier diverging cetaceans with hindlimbs; the reduction in articular surface maps to branch K (Fig. 9). *Georgiacetus* is the most basally positioned stem cetacean that lacks a sacroiliac joint (Hulbert, 1998), and the absence of an articulation is optimized as occurring on branch L, the last common ancestor of *Georgiacetus*, basilosaurids, and crown Cetacea.

Features in the hindlimbs of early stem cetaceans belie their artiodactyl ancestry. Until recently, the phylogenetic nesting of Cetacea within Artiodactyla was controversial among paleontologists (e.g., Luckett and Hong, 1998), and the idea that a carnivorous/piscivorous aquatic clade was derived from within the same group that includes common barnyard animals -pig, sheep, goat, cow, yak, camel, and llama – seemed farfetched. The recovery of postcranial data from ancient stem whales confirmed the specific prediction, based on analyses of molecular data (Gatesy et al., 1996), that the hindlimbs of very ancient whales would retain the distinctive features of a typical artiodactyl hindlimb, a paraxonic (even-toed) foot and a double-trochleated astragalus with a broad transverse contact between the astragalus and the cuboid (Gingerich et al., 2001; Thewissen et al., 2001). On the higher-level artiodactyl section of our composite tree (Fig. 8), this latter feature optimizes to the common ancestor of all artiodactyls including Cetacea (branch A). The paraxonic condition maps ambiguously to the same branch. These characteristic artiodactyl synapomorphies were then secondarily lost on the stem lineage to Cetacea; the double-trochleated astragalus and an even-toed hind foot have been transformed beyond recognition in Eocene basilosaurids such as *Basilosaurus* (Gingerich et al., 1990), and the entire foot has been lost in all crown cetaceans.

Presumably to improve streamlining, cetaceans have reduced or lost many unnecessary anatomical appendages. Body hair is lacking or very sparse, reproductive organs are internal, and unlike most extant mammals, the **outer ears (pinnae) are absent**; this loss is mapped on our composite phylogenetic hypothesis to branches D–O, the stem cetacean lineage. Extant cetaceans are often described as having a fusiform body shape, which is assumed to reduce drag as they move through the water. Another morphological change that allows them to adopt this sleek form is a **reduction in the length of the neck** and of the cervical vertebrae that compose it (Rommel and Reynolds, 2002). As compared to the length of the thoracic vertebrae, the cervical vertebrae of crown cetaceans and some stem cetaceans are very short. The change to a more compact neck is optimized to branch H, the common ancestor of *Maiacetus* and crown Cetacea. Additional shortening of the cervical vertebrae beyond the morphology of *Maiacetus* does occur in cetaceans; these more derived states were not recognized in our coding scheme in the Artiodactyla supermatrix. Extremely compressed cervicals often fuse in Cetacea (Rommel, 1990), and this feature was mapped using the crown Cetacea matrix and the Mysticeti supermatrix. These data imply homoplastic change with multiple fusions distributed across the overall phylogenetic hypothesis for the crown group.

3.3.9. Chemosensory perception

Extant cetaceans are characterized by reduced chemosensory reception. The olfactory bulb is present in mysticetes but is relatively small compared to terrestrial mammals (Thewissen et al., 2010). The **olfactory bulb is absent** in adult odontocetes for

species that have been examined thus far, and this structure only appears briefly in the embryonic stage (Flower, 1883; Slijper, 1962; Oelschläger, 1992; Thewissen et al., 2010). Two osteological correlates of olfaction are: (1) the cribriform plate (the portion of the ethmoid bone that forms part of the anterior wall of the braincase and contains numerous foramina that transmit olfactory nerves) and (2) the turbinals that are covered, in part, with olfactory epithelium (Rowe et al., 2005). Extant mysticetes retain a small cribriform plate and endoturbinals (Flower, 1883; Cave, 1988; Thewissen et al., 2010 and references therein), consistent with a larger proportion of functional olfactory receptor genes relative to odontocetes (McGowen et al., 2008; Hayden et al., 2010) and evidence of purifying selection on the mysticete olfactory marker protein gene (Kishida and Thewissen, 2012). By contrast, extant odontocetes **lack endoturbinals** and also **lack a cribriform plate**, although a few foramina pierce the anterior wall of the braincase in some species (Burrows and Smith, 2005). There have been several reports of endoturbinals in extinct odontocetes that are similar in size and complexity to the endoturbinals in extant mysticetes (Fordyce, 1994; Hoch, 2000), but the phylogenetic positions of these specimens are unclear. If these fossils represent stem odontocetes, then it is most parsimonious to infer that olfaction was lost once in odontocetes. However, if one or more of the fossils group within crown Odontoceti, then olfaction may have been lost multiple times in this clade. We tentatively place the loss of the cribriform plate and endoturbinals on the branch leading to crown Odontoceti (branches P–T; Fig. 9).

The vomeronasal organ is closely associated with olfaction and detects pheromones in mammals (Keverne, 1999). It appears that this structure is absent in extant cetaceans (Flower, 1883; Oelschläger et al., 1987), and at least one gene associated with vomeronasal chemoreception is a pseudogene in the group (Yu et al., 2010). In extant whales, the absence of the vomeronasal organ is correlated with **absence of the incisive foramina**, paired bilateral openings on the palate of most mammals through which the vomeronasal organ communicates with the oral cavity (Pihlström, 2008). If this correlation is an accurate means for inferring the presence or **absence of the vomeronasal organ**, then this feature was lost early in cetacean evolution, following the split between Pakicetidae and all remaining cetaceans in our phylogenetic hypothesis, but before the divergence of *Remingtonocetus* from the lineage that leads to crown Cetacea (branches F–G). At least one member of the Pakicetidae has reduced incisive foramina (Thewissen and Hussain, 1998) whereas remingtonocetids lack this feature entirely (Bajpai et al., 2011). The holotype and only known cranial specimen of *Ambulocetus natans*, which branched off the cetacean stem between the two aforementioned families, does not preserve the premaxilla.

3.3.10. Brain and body size

Many researchers have commented on the size of the cetacean brain in both absolute and relative terms (e.g., Worthy and Hickie, 1986; Marino, 1998; Marino et al., 2007; Boddy et al., 2012). Indeed, Cetacea includes the extant species with the largest brain in absolute size, *Physeter macrocephalus*, in addition to some delphinid species that have encephalization quotients greater than nonhuman primates (Marino, 1998; Marino et al., 2007). When mapped on a tree of extant cetaceans, absolute brain size is reconstructed as increasing from the common ancestor of crown Cetacea in both Odontoceti and Mysticeti; however, body size showed a different pattern, decreasing in Odontoceti and increasing greatly in Mysticeti (Slater et al., 2010; Boddy et al., 2012). Mapping of relative brain size (brain size adjusted for body size) on a tree of living cetaceans, Boddy et al. (2012) found that relative brain size increased from the common ancestor of crown Cetacea to Delphinoidea and decreased within Mysticeti. Marino et al. (2004) utilized

information on endocranial volume from the fossil record of Cetacea and noted two shifts in relative brain size: at the emergence of Odontoceti and of Delphinoidea (dolphins, porpoises, beluga, and kin). It is challenging to derive estimates of brain size and body size from extinct cetaceans that are incompletely preserved and to incorporate these taxa into phylogenetic hypotheses (Pyenson and Sponberg, 2011), but ignoring the fossil record eliminates potentially critical information on encephalization and body mass changes over time. For example, without fossils, the small relative brain sizes of stem cetaceans would be only hypothetical estimates.

Given that brain size and body size are continuously varying characters that have increased and decreased at various nodes across our overall composite tree (Fig. 7), we have simply noted lineages that lead to exceptionally **large body size** and **large relative brain size** (Fig. 9). Branch Z and branch h mark the largest extant species of Odontoceti (*Physeter macrocephalus*) and Mysticeti (*Balaenoptera musculus*), respectively. These gigantic mammals dwarf the earliest stem cetaceans in our analysis (Pakicetidae) that are approximately the size of dogs (Thewissen et al., 2001; Madar, 2007), and illustrate the upper limit of body size variation that has evolved within Cetacea over the past ~50 million years. Regarding brain size, we have marked the inferred episode of relative brain size increase in Odontoceti (branches P–V; Marino et al., 2004; Boddy et al., 2012) which ultimately led to Delphinidae (oceanic dolphins), the clade that includes the most highly encephalized species of Cetacea. Finally, the estimated decrease in relative brain size on the stem to balaenopterid mysticetes (branches a–g) is noted (Table 1; Boddy et al., 2012).

3.4. Summary and conclusions

The current analysis represents a first attempt at combining genomic and paleontological data to derive a wide-ranging phylogenetic hypothesis for Cetacea (Fig. 7) and a unified reconstruction of the many evolutionary novelties that characterize this group (Fig. 2). Crown cetaceans such as *Physeter macrocephalus* and *Balaenoptera musculus* (Fig. 1) are highly derived outliers relative to the majority of extant mammalian species, most of which are furry, four-limbed, terrestrial, and miniscule in comparison (Fig. 4). The phenotypic divide between extant cetaceans and even their closest living relatives (Figs. 1C and 5) indicates that extinction has erased much of the historical evidence of whale evolution. Luckily, recent fossil finds have contributed to a rapidly growing inventory of extinct taxa that fill in wide anatomical gaps (Fig. 3). To make sense of this diversity, however, the fossil record of whales must be organized phylogenetically to distinguish primitive from derived states and to reconstruct long sequences of anatomical transformation. Many paleontologists have attacked this problem through phylogenetic analysis of morphological characters, the only systematic evidence that can be garnered from whale fossils (e.g., Geisler and Sanders, 2003; Theodor and Foss, 2005; Thewissen et al., 2007; Fitzgerald, 2010; Marx, 2010), but the results often have been incongruent with trees based on large matrices of molecular data (e.g., Gatesy, 1998; McGowen et al., 2009; Steeman et al., 2009; Zhou et al., 2011).

The past two decades have seen the emergence and preeminence of genomic data in systematics (Delsuc et al., 2005), perhaps due to the sheer quantity of available data, the simplicity of nucleotide characters, as well as the tractability of molecular evolution models utilized in phylogenetic analysis, but a sole reliance on DNA sequences has limitations as a general approach to reconstructing the history of Life. Molecular systematic hypotheses that place cetaceans in the context of extant mammalian diversity (Figs. 4 and 5) represent 'phylogenetic skeletons' that are woefully incomplete in terms of documenting key anatomical transitions,
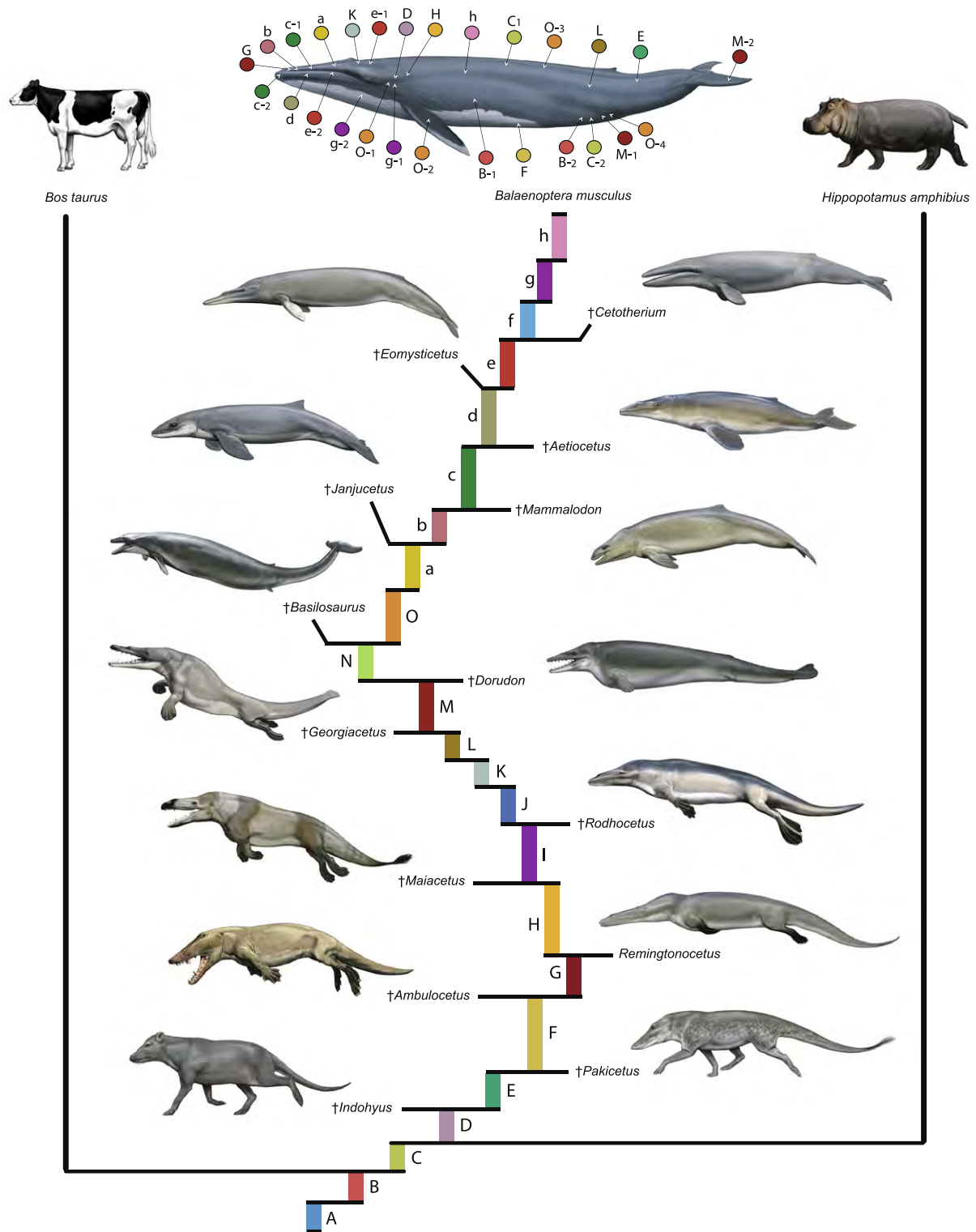
Fig. 10. A phylogenetic blueprint for a modern whale (*Balaenoptera musculus*). The topology traces the inferred evolutionary history of an extant cetacean based on results summarized in Figs. 7–9 and Table 1. Changes extend back to the base of Artiodactyla (A–D). The long sequence of character transformations on the stem lineage to crown Cetacea (branches E–O), on the stem lineage to crown Mysticeti (branches a–f), and within crown Mysticeti (branches g–h) has culminated in the extant blue whale. A subset of the changes on these internal branches (Table 1) are marked by colored circles that indicate the internode where each character evolved and, when applicable, the approximate anatomical position of each derived character state (delayed transformation optimization): B-1 = three primary lung bronchi and multi-chambered stomach, B-2 = fibro-elastic penis with sparse cavernous tissue, C-1 = sparse hair, sebaceous glands absent, and transition to freshwater, C-2 = scrotum absent, can give birth underwater, and can nurse underwater, D = involucrum (thickening of medial wall of auditory bulla), E = robust tail, F–G = transition to saltwater, G = incisive foramina absent and vomeronasal organ inferred absent, H = short cervical (neck) vertebrae, K = posterior positioning of nasal aperture, L = no articulation between vertebrae and pelvis (sacroiliac joint absent), M1 = very short hindlimbs, M2 = tail flukes inferred present, O-1 = external ears absent, O-2 = immobile elbow joint, O-3 = sweat glands absent, a = broad rostrum, b = thin lateral margins of maxillae, c-1 = lateral nutrient foramina on palate and baleen inferred present, c-2 = unsutured mandibular symphysis, d = no teeth in adults, e-1 = telescoping of skull (anterior extension of occipital shield), e-2 = bowed mandibles, g-1 = fibrous temporomandibular joint, g-2 = muscle of tongue reduced (predominantly connective tissue) and ventral throat pouch with numerous grooves, h = enormous body size. Branch lengths are not proportional to time. Artwork is by Carl Buell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and ironically must be fleshed out by the addition of fossilized bones. DNA sequences cannot be recovered from most extinct taxa, making genetic data relatively impotent with regard to the placement of fossils. Furthermore, despite the huge weight of character evidence provided by genomic information, morphological data can overturn phylogenetic hypotheses based on large compilations of molecular data. Although likely to be rare in the age of comparative genomics, this possibility was demonstrated here; the addition of only 115 phenotypic characters overturned a topology for Mysticeti supported by analysis of >30,000 molecular characters (Fig. 6).

Our research group and collaborators have therefore committed the past decade to merging morphology and molecules in combined supermatrix studies of Cetacea to reconcile paleontological and genomic evidence (Gatesy and O'Leary, 2001; O'Leary et al., 2004; Deméré et al., 2005, 2008; Geisler and Uhen, 2005; Geisler et al., 2007, 2011; O'Leary and Gatesy, 2008; Geisler and Theodor, 2009; Spaulding et al., 2009). In this more inclusive approach to systematics, phenotypic characters coded from extant taxa provide the critical link of homologies that connect phenotypic characters from fossils to molecular data from extant taxa. We have examined whale phylogeny at several hierarchical scales. Here, results from these supermatrix studies were merged to yield a single composite phylogenetic tree that encompasses the early derivation of whales as well as the subsequent diversification of crown group cetaceans (Fig. 7). The overall topology represents a phylogenetic blueprint for modern cetaceans, a hypothesis that summarizes the approximate age and relative sequence of changes that have occurred in the evolutionary construction of extant whales over the Cenozoic (Figs. 8 and 9; Table 1). Due to the inclusion of genomic data, our hypothesis disagrees with trees based on morphology alone in the deep nesting of Cetacea within Artiodactyla as well as contrasting relationships within both Odontoceti and Mysticeti. The rearrangement of extant lineages, in turn, forces a reinterpretation of anatomical homologs and alters the placement of extinct taxa in the tree.

The importance of morphological characters, particularly fossil data, is evident in a summary topology that tracks the evolutionary lineage that terminates at *Balaenoptera musculus* (Fig. 10). Based on molecular data alone, it is impossible to discern the relative order of the many important evolutionary modifications (Fig. 2) that have culminated in this remarkable species. The ancestral lineage that connects the basal node of Artiodactyla to the extant blue whale traverses 30 branch points in our composite tree, but only 9 of the 30 side branches include lineages that extend to the living biota (Fig. 7). Numerous extinct side branches permit reconstruction of a more fine-grained sequence of evolutionary change (Gauthier et al., 1988; Donoghue et al., 1989). Our summary of the available evidence (Figs. 7–10; Table 1) implies that a double-trochelated astragalus, the fibro-elastic penis, and a multi-chambered stomach evolved deep in the history of Cetacea over 60 million years ago (branches A–B), and that these changes were followed by the derivation of several "aquatic" specializations (sparse hair, loss of sebaceous glands, ability to nurse and birth underwater) in the common ancestor of Cetacea and Hippopotamidae (branch C) (Fig. 8). Over the next ~20 million years, the involucrum (branch D), simplification of the dentition (branch E), a robust tail (branch E), an enlarged mandibular foramen (branch F), the transition to saltwater (branches F–G), shortened neck vertebrae (branch H), separation of the pelvis from the vertebral column (branch L), posterior migration of the external nares (branch L), vestigial hindlimbs (branches K–M), reduction of elbow flexion (branch O), and many additional specializations evolved sequentially on the stem lineage to crown Cetacea (Table 1). From ~35–28 million years ago, the key anatomical traits that characterize filter-feeding whales were derived in succession on the stem to

crown Mysticeti (Fig. 9): a broad rostrum (branch a), an unsutured mandibular symphysis (branches b–c), palatal nutrient foramina and by inference baleen (branch c), loss of mineralized teeth (branch d), and bowed mandibles (branch e). Features that are unique to the engulfment feeding apparatus of balaenopterids (pleated throat pouch, reduced tongue, fibrous temporomandibular joint) and unprecedented body size evolved later, within crown group Mysticeti (branches g and h; Fig. 9). *Balaenoptera musculus* displays a mosaic of features acquired at various time depths over the past ~60 million years of artiodactyl evolution; our composite tree summarizes the age and phylogenetic generality of the various traits that characterize this highly derived species (Fig. 10).

Our hypothesis should be considered a starting point toward a more comprehensive phylogenetic analysis of whale origins and diversification. We see several obvious ways that improvements can be achieved. First, taxonomic sampling can be expanded. Several recent supermatrix studies have included nearly all extant species of Cetacea, but these efforts focused on molecular data (McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010). DNA sequences have been published for over 90 extant species, but effective integration of these data with the fossil record of Cetacea will require coding morphological characters from many more extant taxa to provide an overlap of systematic information. In terms of fossils, the sampling of extinct taxa in our composite tree focused on filling gaps on the stem lineages of Odontoceti, Mysticeti, Cetacea, Ruminantia, Suina, and Camelidae (Fig. 7). However, >700 wholly extinct artiodactyl genera have been described (McKenna and Bell, 1997; O'Leary et al., 2004). Many additional extinct taxa should be coded to yield a more detailed evolutionary reconstruction. Second, it would be preferable to compile a single supermatrix with a broadly applicable set of phenotypic characters that characterizes variation across both deep and shallow divergences within Artiodactyla. The present supertree of three supermatrix topologies (Fig. 7) is based on several assumptions of monophyly that would not be required if the same phenotypic characters were coded for all relevant taxa. This is a challenging task, but a recent effort to compile a morphological matrix across all mammalian orders demonstrates that several thousand phenotypic characters from diverse taxa can be scored with the aid of modern web-based tools (O'Leary and Kaufman, 2007) and cooperation among taxonomic specialists (Novacek et al., 2008). Third, genomic resources now permit a mapping of critical molecular changes that correlate with the unique specializations and degenerative features of whales. Recent studies of DNA sequences from Cetacea have documented convergent changes in the auditory genes of echolocating cetaceans and bats (Li et al., 2010; Liu et al., 2010; Davies et al., 2012), as well as adaptive evolution of brain development genes (McGowen et al., 2011, 2012; Xu et al., 2012) and *Hox* loci involved in forelimb development (Wang et al., 2009). Other work has characterized patterns of pseudogenization in Cetacea that parallel evolutionary losses at the phenotypic/behavioral level, including mutational decay of genes related to color vision (Levenson and Dizon, 2003), enamel formation (Deméré et al., 2008; Meredith et al., 2009, 2011b), olfaction (Kishida et al., 2007; McGowen et al., 2008; Hayden et al., 2010), taste (Jiang et al., 2012), and vomeronasal chemoreception (Yu et al., 2010). Further efforts that tie particular anatomical transformations to underlying molecular change will contribute to the emerging macroevolutionary synthesis.

As phylogenetics proceeds into the twenty-first century, a focus has been rightly placed on genome-scale datasets because of the nearly limitless supply of discrete systematic characters (Delsuc et al., 2005). Regardless, many neontologists recently have come to the realization that, moving forward, paleontological data will be essential for phylogenetic analysis, divergence dating, estimation of diversification and extinction rates, biogeography, and the

mapping of particular phenotypic traits (Wiens, 2009; Losos, 2011; Pyron, 2011; Slater et al., 2012). These revelations are not really new (Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992; Novacek and Wheeler, 1992; Smith and Littlewood, 1994; Smith, 1998), but instead indicate that even with the development of 'sophisticated' likelihood models, genomic data can advance the field only so far. We predict a blossoming relationship between paleontology and genomics in the coming years, with the hope that a more complete phylogenetic reconstruction of Life, including its many extinct lineages, will be achieved.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2012.10.012.

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