FROM FINBACKS TO HUMPBACKS: INVESTIGATION OF THE
EVOLUTIONARY HISTORY OF BALAENOPTERIDAE

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Jessica Ann Martin
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The Undersigned Faculty Committee Approves the
Thesis of Jessica Ann Martin:

From Finbacks to Humpbacks: Investigation of the Evolutionary History of
Balaenopteridae

Annalisa Berta, Chair
Department of Biology

Todd Reeder
Department of Biology

Arion Mayes
Department of Anthropology

Tom Deméré
Department of Geological Sciences

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ABSTRACT OF THE THESIS

From Finbacks to Humpbacks: Investigation of the Evolutionary History of Balaenopteridae

by

Jessica Ann Martin

Master of Science in Biology with a Concentration in Evolutionary Biology
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Mysticeti (baleen whales) is one of two major clades of Cetacea (whales and dolphins). Balaenopteridae (rorqual whales) is the most speciose and morphologically diverse group of crown mysticetes. Despite having the largest number of extant species of any mysticete lineage, as well as many fossil taxa, the phylogenetics of Balaenopteridae remain unresolved. This study investigates the evolutionary relationships of extant and extinct balaenopterids and places a new fossil species of *Balaenoptera* into a phylogenetic context.

A new species of balaenopterid, *Balaenoptera colcloughi* sp. nov. is described from the upper Pliocene San Diego Formation (2-4 million years ago). Cranial and postcranial material from four specimens in the collections of the San Diego Natural History Museum is assigned to this species. The specimens of this new taxon represent an ontogenetic series (one adult and three sub-adults).

The phylogenetic relationships recovered in this study are consistent with previous analyses. Monophyletic Balaenidae, Eschrichtiidae, and Balaenopteroidea were all recovered in the analyses. Balaenopteridae was found to be paraphyletic in most analyses conducted. The analyses also recovered previously recognized relationships among extant balaenopterids. A novel finding of these analyses was a close relationship between the extant *Megaptera novaeangliae* and *Balaenoptera physalus*, and extinct *Balaenoptera colcloughi*, *Balaenoptera siberi* and ‘*Megaptera*’ *hubachi*. The nesting of *M. novaeangliae* with *B. physalus* and other species of *Balaenoptera* is evidence that questions the recognition of a separate genus for the humpback whale, *M. novaeangliae*, from the rest of the balaenopterids (*Balaenoptera*).

Divergence dating was used to investigate the temporal context of mysticete evolution. This study identified and utilized a phylogenetic and geologically supported set of fossil calibrations for Mysticeti by examining the impact of calibration choice. This set was tested against the commonly used fossils for calibration and it was found that calibration choice affects the level of confidence of age estimates. The use of external calibrations on dating mysticete divergence events was also found to improve the precision of the age estimates. The age estimates from these analyses were consistent with previous analyses. Balaenopteridae appears to have diverged as a clade in the middle to late Miocene, and this datum corresponds to a subsequent increase in mysticete diversity in the latest Miocene and into the Pliocene. While divergence estimates suggest a long history for some of the extant species, there is little to no fossil record of taxa assignable to extant *Balaenoptera*. Future
work of improvement on divergence methods and descriptions of new fossil balaenopteroid taxa will be critical to improving the understanding of the evolutionary history of Balaenopteridae.
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CHAPTER 1

INTRODUCTION

Cetacea is a lineage of marine mammals that includes living whales, dolphins and porpoises, with 86 recognized extant species (Committee on Taxonomy, 2011). Cetaceans include some of the largest animals alive today (i.e. the blue whale, *Balaenoptera musculus*) and the evolution of this clade has fascinated scientists for years. Crown Cetacea (known as Neoceti) contains two monophyletic lineages, Odontoceti (toothed whales) and Mysticeti (baleen whales). While all cetaceans possess anatomical adaptations for life in water, extant mysticetes are united by having baleen, which is a filter feeding apparatus comprised of keratin. Extant Mysticeti includes 14 species (Committee on Taxonomy, 2011) in four major lineages: Balaenidae (right and bowhead whales), Eschrichtiidae (gray whale), Balaenopteridae (rorqual whales), and Neobalaenidae (pygmy right whale). Balaenopteridae is the largest and most diverse mysticete family. There are currently eight recognized extant species and possibly 20 fossil species in this clade (Deméré et al., 2005; Bisconti, 2010a; Committee on Taxonomy, 2011).

The extant species within Balaenopteridae are represented by two genera, *Balaenoptera* and *Megaptera*. Extant balaenopterids include *Balaenoptera acutorostrata* (North Atlantic minke whale), *Balaenoptera bonaerensis* (Antarctic minke whale), *Balaenoptera borealis* (Sei whale), *Balaenoptera edeni/brydei* (Bryde’s whale), *Balaenoptera musculus* (Blue whale), *Balaenoptera physalus* (Fin whale), *Balaenoptera omurai* (Omura’s whale), and *Megaptera novaeangliae* (Humpback whale).

The taxonomy of balaenopterids is an issue of concern and the included extant taxa are often cited in the literature as “six to nine” species (Deméré et al., 2005). The unclear number of species is related to the conflict surrounding the taxonomy of the *Balaenoptera edeni* and *Balaenoptera brydei* species-complex. *Balaenoptera edeni* was first described by Anderson (1878) from Burma (Kato and Perrin, 2009). *Balaenoptera brydei* was originally described by Olsen in 1913, with a more detailed description provided later (Lönneberg, 1931). However, Olsen (1913) never designated a type specimen for *B. brydei*. These two
species were initially included in a complex with *B. borealis*, however Junge (1950) examined the three species and documented morphologic differentiation between *B. edeni/brydei* and *B. borealis*. Molecular studies have since shown clear distinction of *B. borealis* from the other species, though all three species are closely related (Sasaki et al., 2006).

At present, *B. brydei* is recognized as a subspecies of *B. edeni*, *B. e. brydei* (Committee on Taxonomy, 2011). However, debate continues about the legitimacy of this taxon and there is no universally accepted treatment of the complex. Some authors continue to use *B. brydei* as a species, particularly in molecular analyses with sequences previously labeled as *B. brydei* but have not been confirmed (i.e. McGowen et al., 2009; Steeman et al., 2009). Some authors lump sequences of the two taxa in a consensus taxon (Deméré et al., 2008), which relies on the authors’ knowledge of (and confidence in) the source of the molecular data. Other workers exclude *B. brydei* entirely (Marx, 2010), and still other authors avoid the issue altogether, such as Pyenson and Sponberg (2011), who did not sample either taxon, simply noting that they are “taxonomically unstable”.

Wada et al. (2003) described a new species, *B. omurai* (Omura’s whale), from Japan. This species has been shown to be distinct on the basis of both molecular and morphological data (Wada et al., 2003; Deméré et al., 2005; Sasaki et al., 2006).

Five of the eight extant balaenopterid species have subspecies (including the previously mentioned *B. edeni/B. brydei*). For example, the minke whale, *B. acutorostrata*, has three subspecies, including an unnamed dwarf form (Committee on Taxonomy, 2011). As more molecular data becomes available, the extent of differentiation of these subspecies will be more completely investigated; however, this is beyond the scope of this study.

The most comprehensive review of balaenopteroids (Eschrichtiidae + Balaenopteridae, called Balaenopteroidea), Deméré et al. (2005), listed 16 nominal fossil species (of 24 investigated). Since then, four new extinct balaenopterid species have been described, mostly from the Pliocene/Miocene of Europe (Bisconti, 2007a, 2007b, 2010a; Bosselaers and Post, 2010). Thus, there are currently 20 fossil balaenopterids recognized, and more taxa known that need further description and study.

Our understanding of the phylogenetic positions and character evolution of extinct balaenopterids has been hindered by incomplete fossil descriptions. This is especially true for
fossil taxa described in the late 19th century; many of these descriptions focus on relatively few characters. For example, numerous fossil cetaceans were identified by P. Van Beneden in the late 1800s, though many have been recognized as *nomina dubia* based on lack of diagnostic characteristics, stemming from a general incompleteness of the fossil material (Deméré et al., 2005; Bosselaers and Post, 2010).

Fossil balaenopterids are found in Miocene and Pliocene deposits globally, specifically from the western Pacific coasts and southern Europe. The balaenopterid fossil record indicates that this clade appeared in the late Miocene to early Pliocene (~7-12 million years ago [Ma]), though reliably aged fossil balaenopterid taxa are closer to 5 Ma (McGowen et al., 2009). For example, if the fossil mysticete *Mauicetus sp.* is identified as a stem balaenopterid, as has been recently proposed (Steeman, 2007; Geisler et al., 2011), this would suggest a late Oligocene to early Miocene divergence of the clade. Molecular estimates range even wider, from approximately 11 to 28 Ma (Jackson et al., 2009; McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010). Divergence dating of mysticetes is explored further in a later section.

**PHYLLOGENETICS OF BALAENOPTERIDAE**

Despite intense interest in cetacean systematics, the phylogenetic relationships of mysticetes are not well resolved (Sasaki et al., 2005; Marx, 2010; Zhou et al., 2011). Major controversies concern the positions of Neobalaenidae and Eschrichtiidae, as well as the relationships within Balaenopteridae (Deméré et al., 2005; Sasaki et al., 2005; Bisconti, 2007a; Jackson et al., 2009; Marx, 2010). The sources of these conflicts are the relationships produced by molecular and morphologic data.

Within Balaenopteridae, relationships among species are contentious. For example, while *B. acutorostrata* and *B. bonaerensis* (the minke whales) are unquestionably sister taxa, the relationship of this species pair to the other balaenopterids differs among phylogenetic hypotheses (Figures 1 and 2). The sister relationship of the fin whale (*B. physalus*) and the humpback (*M. novaeangliae*) is consistently supported by molecular but not morphological data. Thus, this sister relationship nests *Megaptera* within Balaenopteridae, rendering *Balaenoptera* paraphyletic. The evolutionary history of balaenopterids is also ambiguous because there are few fossil taxa assigned to extant lineages. One example is the

One of the main issues in the phylogenetic inference of mysticetes is the relationship between Eschrichtiidae and Balaenopteridae (Figure 1-3). Morphological phylogenies consistently place the gray whale sister to the rorqual clade, rendering both monophyletic. This clade, comprised of Eschrichtiidae + Balaenopteridae and their most recent common ancestor, is called Balaenopteroidea. However, molecular hypotheses often place *E. robustus* within Balaenopteridae, rendering the clade paraphyletic (Rychel et al., 2004). Historical mitochondrial control region and cytochrome *b* studies recovered a paraphyletic Balaenopteridae (Sasaki et al., 2005), but this hypothesis is not strongly supported by the mitochondrial data. Morphological and some molecular studies did not obtain this result, and instead strongly supported a monophyletic Balaenopteridae (Deméré et al., 2005; Sasaki et al., 2005; Yang, 2009; Figure 3).
Another source of confusion surrounding the position of taxa outside of Balaenopteridae is due to the relationship of balaenopterids to extinct ‘cetotheres’ (Figure 4-6). ‘Cetotheres’ are an early-diverging stem baleen-bearing group of mysticetes. This large and diverse clade (at least 16 included genera) has been recently investigated (Bouetel and de Muizon, 2006; Steeman, 2007; Kimura and Hasegawa, 2010; Marx, 2010) and some phylogenetic resolution has been proposed. The clade has been split into two monophyletic groups, Cetotheriidae sensu stricto (including Cetotherium rathkii, Piscobalaena nana, and Mixocetus elysius) and the Isanocetus-group (including Aglaocetus patulus and Diorocetus hiatus) (Kimura and Hasegawa, 2010). The monophyly of the Isanocetus-group has been questioned previously (e.g. Bouetel and de Muizon, 2006; Steeman, 2007; Deméré et al., 2008) and continues to be investigated (Kimura and Hasegawa, 2010).

Beyond the above split of the group, the position of individual ‘cetotheres’ within the phylogeny of Mysticeti remains largely unresolved, thus leaving a gap in our understanding of the mysticete evolution. This is important relative to Balaenopteridae because one of the
hypothesized phylogenetic positions of ‘cetotheres’ places them sister to Balaenopteroidea, while another hypothesis positions ‘cetotheres’ sister to Balaenopteridae (Kimura and Hasegawa, 2010). The lack of understanding of the position of ‘cetotheres’ obscures investigation of the evolution of morphological adaptations shared by these clades. While ‘cetotheres’ are selected as comparison taxa, the phylogenetics of ‘cetotheres’ is beyond the scope of this study.

Though many of the conflicts among balaenopterids are taxonomic (i.e. improper classification; Deméré et al., 2005), there are other potential underlying causes. It has been postulated that issues may stem from a rapid radiation of species at the origin of the clade (Jackson et al., 2009) or are a reflection of ghost lineages (gaps in fossil record) (Sasaki et al., 2005). A solid phylogenetic understanding of relationships is crucial to investigations into the physical drivers and timing of the evolution of clades. There is also a lack of well-supported divergence age estimates for many mysticete lineages (McGowen et al., 2009). By
Figure 4. Phylogenetic relationships of extinct and extant Mysticeti with a focus on relationships of Balaenopteridae. This topology was based on combined data from Deméré et al., 2005, was pruned to include species sampled in the current study and includes bootstrap support values at the nodes. The original study did not include Balaenoptera bonaerensis.

utilizing the divergence dating of Mysticeti, a better understanding of the timing of the evolution of the clade can be investigated.

**DIVERGENCE DATING OF MYSTICETI**

Molecular divergence dating is a method that estimates the time since the split of two lineages using a molecular clock. Divergence dating is important because a reliably dated tree topology provides the opportunity to explore a larger range of questions about macroevolution and evolutionary processes within a clade (Donoghue and Benton, 2007). A molecular clock is the rate at which DNA sequences between two lineages diverge (via nucleotide substitution) across a time span (Pulquério and Nichols, 2007). A calibration is the use of specific lineage information (e.g. first appearance, molecular rate) that must be applied to the molecular clock to give it a basis to provide absolute temporal estimates from the analyses. The sources of temporal information for calibration purposes are either molecular
rate information (such as a mutation rate) or information from the fossil record. Calibrations are crucial because an absolute age cannot be derived from molecular data alone (Ho and Phillips, 2009). Absolute dating can be derived from radiometric dating from a geologic horizon or from a known (molecular) mutation rate (Donoghue and Benton, 2007; Ho and Phillips, 2009), however for most lineages this type of information is not known or not consistent across studies. Thus, another form of age information is needed for use in divergence dating analyses.
Figure 6. Phylogenetic relationships of extinct and extant Mysticeti with a focus on relationships of Balaenopteridae. This tree is a combined topology from Marx, 2010, was pruned to include species sampled in the current study and includes bootstrap support values at the nodes.

The fossil record has long provided scientists with a time scale (Donoghue and Benton, 2007) and it has an important application in the molecular divergence dating of clades. The age associated with a fossil species is applied to a branch on the phylogeny to ‘anchor’ the nearest node, thus providing a temporal basis to the tree. The associated age of a node on that phylogeny is interpreted as corresponding to the age of the divergence of thelineages stemming from that node. Using a fossil in this manner stems from the ideal situation that lineages split one at one time (cladogenesis), and the oldest fossil records of both lineages should be the same age (Donoghue and Benton, 2007).

Use of misinterpreted fossil information (in terms of phylogenetic position or taxonomic affiliations) as calibration to a molecular clock has been demonstrated to bias and
skew divergence age estimation. Thus fossil choice plays a crucial role in conducting these analyses (van Tuinen and Hadly, 2004; Donoghue and Benton, 2007; Ho et al., 2008; Pyron, 2011; Lukoschek et al., 2012; Parham et al., 2012). Previous use of fossils for calibrations has been unsatisfactory and increasing awareness of this problem has inspired new methods for utilizing and evaluating fossil calibrations (Lukoschek et al., 2012).

This study evaluates the use of fossils in the context of their placement relative to the ingroup (i.e. mysticetes) and the selection of various fossil calibrations including both internal and external calibrations. In the simplest terms, an internal fossil calibration is a minimum age calibration that is set within the ingroup. An external calibration is minimum age calibration that is placed outside of the group of study. Intuitively, inclusion of both types of calibrations should improve resolution of the timing of divergences. Some studies have found supporting evidence for this idea (van Tuinen and Hadly, 2004; Pyron, 2010), while others have disagreed, suggesting uncertainty in external calibrations may bias the estimates because of nucleotide rate shifts (Jackson et al., 2009; Dornburg et al., 2012).

Recent studies have also added to the growing consensus that the use of multiple independent fossil calibrations provides a better estimate than use of a single calibration (Ho and Phillips, 2009; Lukoschek et al., 2012). Multiple calibrations can reduce the effects of error in fossil choice, though the error must be in one direction (i.e. too old, too young) (Lukoschek et al., 2012). However, fossils are often utilized without consideration of the phylogeny of the clade.

Divergence dating analyses of cetaceans have been previously conducted (Jackson et al., 2009; McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010; Geisler et al., 2011). Only Jackson et al. (2009) specifically focused on mysticete divergence dating. However, this study had poor taxonomic sampling (i.e. only four balaenopterids and one balaenid, no neobalaenid and no eschrichtiid). Unique to the Jackson et al. (2009) study is the use of multiple individuals for each species to investigate intraspecific variation among the nuclear alleles. The focus of this study was the loci themselves and their influence on the dates produced, and though fossil calibrations were used, these calibrations were not evaluated for their effect on the resulting ages.

The largest and most comprehensive study to date is McGowen et al. (2009), which had nearly complete taxon sampling of extant cetaceans and a wide array of nuclear and
mitochondrial loci were utilized to determine a large-scale phylogeny of Cetacea. However, McGowen et al. (2009) only assigned age estimates to divergences using mitochondrial data. Though Slater et al. (2010) and Steeman et al. (2009) used divergence ages to produce diversification rate estimates, the derivation of the dates from fossil calibrations was not a focus of their studies. Steeman et al. (2009) used fewer genes, but utilized both mitochondrial and nuclear genes.

Many investigations into divergence dating of Cetacea have focused their calibrations (Geisler et al., 2011) on the divergence of crown Cetacea (Steeman et al., 2009; Slater et al., 2010) or divergences within Odontoceti (McGowen et al., 2009). However, molecular rates of evolution in mysticetes differ from the rates in odontocetes and this rate variation could be a factor in the inconsistency of divergence estimates between the two lineages of Neoceti (Jackson et al., 2009; Dornburg et al., 2012). Thus, use of calibrations specific to Odontoceti and odontocete outgroups when analyzing mysticete divergences may bias age estimates (Jackson et al., 2009; Dornburg et al., 2012).

Little evaluation of cetacean fossil information utilized as calibrations for molecular clock analyses has been done. Most previous analyses of Cetacea (excluding Geisler et al., 2011, which focused on odontocete radiations), used the same fossil calibrations with little explanation of the choice made. While these calibrations have produced age estimates that are reasonable relative to the fossil record (though not completely satisfactory) and utilized multiple methods of analysis platforms (i.e. r8s, MULTIDIVTIME, BEAST), the lack of phylogenetic stability of extinct mysticetes specifically should suggest caution in use of this fossil data. An evaluation of the commonly used mysticete fossil calibrations is needed and should be compared to other potential fossils that could provide a better choice for producing divergence estimates.

**OBJECTIVES**

The main objective of this study is to investigate the evolutionary history of the Balaenopteridae clade, using appropriate phylogenetic methods and inclusion of well preserved extinct taxa. A morphological character matrix comprised of both new and previously published characters was combined with published molecular data to infer a phylogeny of extant and extinct balaenopterid whales. This total-evidence approach was used
to investigate the species-level relationships within Balaenopteroidea. A second objective is
the description of a new fossil species of *Balaenoptera* and inclusion of this taxon in the
phylogenetic analyses. A final objective is to investigate newer concepts in the evaluation of
fossil data in divergence dating analyses. These were applied to the mysticete phylogeny to
explore their effects on the resulting age estimates of mysticete clades, with specific focus on
the evolution of balaenopteroids.
CHAPTER 2

MATERIALS AND METHODS

Measurements of the crania, bullae, periotics, and postcranial material of the new species of extinct *Balaenoptera* were taken using a mechanical caliper and were measured to the nearest tenth of a centimeter. These measures are figured in Appendix A (Figures 42-50), and summarized in tables in the fossil description section of this study.

Specimens and photographs of specimens examined in this study are housed at the following institutions: LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; NSMT, National Science Museum of Tokyo, Tokyo, Japan; SDNHM, San Diego Natural History Museum, San Diego, California, USA; SDSU, San Diego State University, San Diego, CA, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Anatomical abbreviations are as follows: ALB, anterior lobe of tympanic bulla; ALR, anterolateral ridge of tympanic bulla; ANM, anterior process of malleus; APE, anterior process of periotic; APM, ascending process of the maxilla; APP, ascending process of the premaxilla; ASI, articular surface of the incus; AWP, anterior wing of the parietal; BO, basioccipital; BI, body of incus; BPP, bony projections on periotic; CB, crus breve (incus); CNVII, cranial nerve seven (internal auditory meatus); CNVIII, cranial nerve eight (internal auditory meatus); ELF, endolymphatic foramen; EO, exoccipital; FC, fenestra cochleae; FI, facet for incus (on malleus); FR, frontal; FM, foramen magnum; FP, foramen pseudovale; HM, humerus; IRB, involcral ridge of tympanic bulla; LA, lacrimal; LSI, lenticular surface of incus; MC, metacarpal; MX, maxilla; MXP, maxillary pocket; MRB, main ridge of tympanic bulla; NA, nasals; OC, occipital condyle; OT, optic tube; PA, palatine; PC, periotic; PH, phalanges; PLB, posterior lobe of tympanic bulla; POP, paraoccipital process (of exoccipital); PGS, post-glenoid process of the squamosal; PL, palatine; PLF, perilymphatic foramen; PM, premaxilla; PP, posterior process of periotic; PR, parietal; PRM, promontorium; PT, pterygoid; RD, radius; SC, sulcus for the chordate tympani; SF,
Phylogenetic analyses were conducted to resolve the relationships of the extant and extinct members of Balaenopteridae. Specimens examined for the morphological study represent all extant genera of mysticetes (Appendix B). Although three species of the right whale, *Eubalaena*, are known, for this study a single species (*Eubalaena glacialis*, the North Atlantic right whale) was employed since balaenids are not the focus of this study and were utilized here as an outgroup. The two other *Eubalaena* species (*E. australis* and *E. japonica*) are not included in the phylogenetic analyses because they are nearly morphologically indistinguishable as separate taxa and there has been some taxonomic debate over the relationships of these three species (Marx, 2010; Churchill et al., 2011). *Balaenoptera edeni* and *B. brydei* were lumped into a single taxon (*B. edeni*) in the morphological matrix, based on recommendations of Perrin (2009) and the Committee on Taxonomy (2011). As stated previously, a full scale morphological and molecular study needs to be conducted on this species complex, however, that is beyond the scope of the present study. All other extant mysticetes are included in the analyses (Appendix B).

Selection of fossil taxa for inclusion in the ingroup was based on taxonomic validity (Deméré et al., 2005; Bosselaers and Post, 2010) and relative completeness of specimens. The new fossil species described in this study, *Balaenoptera colcloughi*, was included in these phylogenetic analyses in order to determine its phylogenetic position. *Balaenoptera siberi* is included because it is known from two nearly complete specimens (Pilleri and Pilleri, 1989; Pilleri, 1990) and is currently the only recognized extinct member of *Balaenoptera*. *Eobalaenoptera harrisoni* (Dooley et al., 2004) was reported as the oldest member of the balaenopteroid lineage, and although only a small portion of the rostrum was recovered with the holotype, characters of the petrotympanic region and postcrania were preserved. ‘*Megaptera’ hubachi* and ‘*M.’ miocaena’ are included because of their taxonomic affinities to *M. novaeangliae*, however both have been recently questioned (Deméré et al., 2005; Bisconti, 2010b). Three fossil taxa (*Diunatans luctoretemergo*, *Archaebalaenoptera castriarquati*, *Plesiobalaenoptera quarantellii*) have been assigned to the balaenopterid
lineage since the last review of balaenopteroids (Deméré et al., 2005) and the specimens preserve enough diagnostic features for phylogenetic analysis. Finally, *Protororqualus cuvieri* was included in this analysis. The holotype specimen is now lost but an in-depth description was recently published by Bisconti (2007b), reviewing all the notes and figures of this taxon, in order to include it into a phylogenetic analysis. These taxa, including all extant Balaenopteridae taxa, represent the ingroup taxa of this project.

As there is a lack of consensus of the identity of a stem balaenopterid or which extinct taxon is sister to balaenopterids, fossil taxa that are currently recognized (e.g. Deméré et al., 2005; Bosselaers and Post, 2010) as ‘cetotheres’ (or found positioned outside of Balaenopteroidea), are also included for outgroup purposes of this study. These include *Mixocetus elysius*, *Cetotherium rathkii* (*Cetotheriidae sensu stricto*), *Diorocetus hiatus*, and *Aglaocetus patulus* (*Isanocetus*-group). Another taxon, the Pliocene ‘cetothere’ *Piscobalaena nana* (*Isanocetus*-group) is also included due to the large number of specimens (six) and the fact that it is known from the same formation as *B. siberi*, the Pliocene Pisco Formation of Peru (Bouetel and de Muizon, 2006).

Also included in the present study are fossil representatives from the other mysticete lineages (Balaenidae and Eschrichtiidae) as outgroups. A fossil representative of Neobalaenidae is not included due to the lack of formally described taxa and the inaccessibility of a recently discovered fossil reported by Graf (2011). However, age information from this specimen is utilized in the divergence dating analyses (see Divergence Dating section). Future analyses will need to include this specimen, however it first needs to be described.

*Mauicetus parkii* and *Eomysticetus whitmorei* are early edentulous mysticetes (Deméré et al., 2008) and represent an outgroup to balaenopterids. *Mauicetus parkii* is included despite being outside crown Balaenopteridae due to the purported importance of this fossil to the mysticete crown lineages (Steeman, 2007; Geisler et al., 2011). *Aetiocetus weltoni*, a toothed mysticete, was also included as an outgroup.

The divergence dating matrix also includes four artiodactyl species as outgroup taxa to Cetacea (*Bos taurus*, *Hippopotamus amphibius*, *Choeropsis liberiensis*, *Sus scrofa*).

Based on the recommendations of Deméré et al. (2005) and Bosselaers and Post (2010), several fossil taxa were excluded from this analysis. *Balaenoptera sibbaldina* was
excluded due to the lack of a holotype and the inability to resolve its phylogenetic position. Bosselaers and Post (2010) reviewed North Sea taxa originally described by Van Beneden in the late 19th century and listed specific reasons why these taxa were likely invalid, such as phylogenetic placement or lack of diagnostic material (see Bosselaers and Post, 2010:355). They recommended exclusion of Balaenoptera borealina, B. sibbaldina, Balaenoptera rostratella, Megapteropsis robusta/Megaptera affinis. For these reasons, these taxa were not included in the present analysis. Plesiocetus was excluded due to the loss of the holotype specimen. Cetotheriophanes capellini (Brandt, 1873) was not found to be positioned within Balaenopteridae in previous phylogenies of the group, thus it was excluded from this analysis. Another taxon Praemegaptera (Hampe and Baszio, 2010) is not included here because it needs to be formally described (Deméré, pers. comm., January 2011). Balaenoptera floridana was not included in this study because of taxonomic conflict between this taxon and Balaenoptera cortesi var. portisi. Balaenoptera cortesi was originally designated to a specific European specimen and later specimens attributed to this taxon are determined to belong to a separate genus by Deméré et al. (2005), and B. floridana, which is recognized as a synonym of B. cortesi, was suggested to be referred to the same new genus (Deméré et al., 2005).

Balaenoptera davidsonii (Deméré, 1986) was not included in the phylogenetic analyses though specimens were examined in the collections of the SDNHM. The dentary of mysticetes include a number of diagnostic features and B. davidsonii is described based on a mandible. Due to the lack of cranial specimens confirmed for this species, it was excluded from the analyses. Deméré et al. (2005) originally included SDNHM 80102 as a member of this taxon, but this specimen is now associated with a new distinct species of the same age.

Finally, a neonate specimen of Balaenoptera physalus (SDSU S970) was used for comparison purposes in discussing the ontogeny of the new fossil species described in this study. SDSU S970 was not included in the morphological dataset for the phylogenetic analyses.

In total, thirty-three extant and extinct mysticete taxa were included in the phylogenetic analyses. A complete list of these taxa is found in Appendix B. While this is not the largest taxonomic sample of mysticetes (Marx, 2010), this matrix includes the largest,
updated number of extinct balaenopteroids currently recognized as members of the balaenopterid clade (since the review of the group in Deméré et al., 2005).

**Character Choice**

One hundred and twenty-nine morphologic characters were examined in this study. The characters include features from the skull (n=44), dentary (n=12), petrotympanic (n=37), axial skeleton (n=8), forelimb (n=7) and soft anatomy (n=21). The soft anatomical characters for extinct taxa were coded as missing. The axial skeleton includes the hyoid and soft anatomy includes the baleen apparatus. The characters used in this study include new as well as previously published characters (Ølsen, 1913; Miller, 1923; Omura, 1964; Barnes and McLeod, 1984; Cooper, 2004; Deméré et al., 2005; Bisconti, 2007a; Deméré et al., 2008; Churchill et al., 2011; Ekdale et al., 2011). The baleen characters were derived from Young (2012) and Deméré et al. (2008). Soft anatomical characters were coded from Deméré et al. (2008), with a few changes. Alternative character states were evaluated from personal examination of specimens and published descriptions. Character states are coded by numbers (0-5). A ‘?’ refers to characters that are not possible to score due to incompleteness or poor/lack of preservation. The symbol, ‘-‘, refers to characters that are absent from a taxon but present in others. This designation is mostly utilized for soft anatomical features, which cannot be scored for fossils.

A complete list of the characters examined in this study is found in Appendix C. The character matrix will be available on the Morphobank website (O'Leary and Kaufman, 2007).

The molecular matrix used in this study is from McGowen et al., 2009 and includes all extant mysticetes. The matrix is comprised of a total of 41,540 aligned nucleotide positions (complete mitochondrial genomes and 45 nuclear loci). Sequences representing *B. brydei, E. japonica,* and *E. australis* are removed from the matrix due to taxonomic controversy. This molecular matrix is currently the largest in number of base pairs (and genes) available and has complete taxon coverage of all mysticete species for the mitochondrial genome.

The molecular matrix was downloaded from TreeBase (Study ID 10190). The sequences were inspected visually to ensure proper formatting and alignment, using Mesquite.
The optimal models for the data partitions were determined by McGowen et al. (2009; p. 893) as GTR+I+G for all partitions, and this model was used in the analyses in this study as well.

**Phylogenetic Analysis**

Maximum parsimony and Bayesian analyses were conducted on the morphological matrix. All characters were treated as unordered. The parsimony analysis was conducted using the program PAUP* v.4b10 (Swofford, 2002). A heuristic search was conducted with random stepwise addition and tree bisection-reconnection (TBR) branch swapping. The search was performed for 1000 replicates (i.e. the process was conducted 1000 independent times). One hundred bootstrap replicates with one thousand heuristic random stepwise searches were also conducted. A strict consensus and 50% majority rule tree were additionally derived from the resulting trees of each analysis, using the consensus functions in PAUP. Bayesian inference was utilized using MrBayes v. 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The Markov chain Monte Carlo (MCMC) analysis was conducted under default parameters and four simultaneous chains. The analysis was sampled at every 1000 generations and run for a total of 15 million generations, with the first 10% discarded as burn-in. The Mk + Gamma (Lewis, 2001) model was applied to the morphological matrix. Congruence was assessed using the Tracer program, after examination of the likelihood values of the runs reaching the same (or nearly the same value), as well as the lack of fluctuation in the cold chain values.

An ordered analysis was also conducted for the morphological matrix using parsimony. Twenty-one characters were ordered (starred in Appendix C) and the analyses rerun, to observe the effect of ordering on this matrix. The characters were chosen based on ordering in their initial publication, if it was a previously published character. Not all of the multistate characters were ordered because ordering is used when the evolution of a characteristic is understood in terms of the morphologies appearing in a sequence. In this matrix, the evolution of some of the multistate characters evolutionary progression was either not known or was not in an ordered fashion, thus ordering those characters was unwarranted. An ordered analysis was not performed under the Bayesian scheme due to the lack of impact ordering had on the morphological analyses performed in parsimony.
The molecular matrix of McGowen et al. (2009) was also analyzed using parsimony and Bayesian inference. A GTR+I+G model was applied to the data and the differing genes were treated as separate partitions. The molecular data was also partitioned by codon position. The nuclear data and mitochondrial data were run separately and combined in a single analysis.

Finally, a parsimony and Bayesian analysis was conducted on the combined morphological and molecular matrix. A combined molecular and morphological phylogenetic analysis has been shown in simulations and empirical datasets to improve the phylogenetic resolution of both extant and fossil relationships (Wiens, 2009; Wiens et al., 2010). These analyses used the same parameter settings as the morphological analysis. The combined dataset was analyzed using separate partitions for the morphological, nuclear and mitochondrial data. The MK + gamma model of evolution (Lewis, 2001) was chosen for the morphological data and the GTR+I+G utilized for the molecular, which was also partitioned by gene and codon position. In total, there are 138 partitions. The combined dataset was analyzed using the CIPRES Webportal (Miller et al., n.d.).

**DIVERGENCE DATING**

The objective of the divergence dating analyses is to assess two sets of fossil taxa for calibration purposes in divergence dating of Mysticeti. Also, the use of external fossil information was assessed on the dating of the mysticete divergences.

Two sets of fossil taxa were tested on four internal nodes that also utilized one external calibration (Table 1).

<table>
<thead>
<tr>
<th>Node</th>
<th>Fossil Set 1</th>
<th>Age (Ma) and SD</th>
<th>Fossil Set 2</th>
<th>Age (Ma) and SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cetancodonta</td>
<td><em>Himalayacetus subathuensis</em></td>
<td>53.5, 1.0</td>
<td><em>Pakicetus sp.</em></td>
<td>48.6, 1.2</td>
</tr>
<tr>
<td>Neoceti</td>
<td><em>Llanocetus denticrenatus</em></td>
<td>34.2, 1.0</td>
<td><em>Simocetus rayi</em></td>
<td>30.0, 1.0</td>
</tr>
<tr>
<td>Mysticeti</td>
<td><em>Unnamed balaenid</em></td>
<td>28.0, 1.0</td>
<td><em>Eomyticetus whitmorei</em></td>
<td>28.0, 1.0</td>
</tr>
<tr>
<td>Balaenopteridae</td>
<td>‘<em>Megaptera</em>’ miocaena</td>
<td>7.3, 1.0</td>
<td><em>Balaenoptera siberi</em></td>
<td>6.0, 1.0</td>
</tr>
</tbody>
</table>
The first set (FS1) includes commonly used cetacean calibrations whose use in this context is questionable. Fossil set 2 (FS2) includes fossils that are more supported for use in dating analyses by current understanding of their phylogenetic position within their respective lineages and knowledge of the stratigraphic information for the localities in which these fossils were found. It is important to note that there remains no rigorous procedure for choosing the distribution for a node age (i.e. how to properly apply fossil information into a molecular clock analysis; (Lee and Skinner, 2011). The four nodes examined represent important divergence events in the history of Cetacea in general and of mysticetes in particular (Figure 7).

Figure 7. Topology showing the positions of the calibrations at nodes examined in this study.

The first node (Cetancodontia) represents the divergence of Cetacea from the Hippopotamidae lineage, which is the extant sister lineage of cetaceans (Spaulding et al., 2009). In FS1, this node is calibrated by *Himalayacetus subathuensis* (Bajpai and Gingerich, 1998), arguably the oldest described species of Cetacea. This fossil taxon was found in Eocene sediments of India, originally dated at 53.5 million years old (Ma)(Bajpai and Gingerich, 1998). However, the age of the rock unit from which this fossil was found has
been questioned and *Himalayacetus* may be younger than originally thought (Thewissen et al., 2001a). This species is known from only a partial left dentary, which limits the inclusion of this taxon in a phylogenetic analysis. *Himalayacetus* has not been included in previous phylogenetic analyses and its exact position relative to other cetaceans is unclear. In FS2, an alternative taxon for this node was used. *Pakicetus* is a well-represented genus of stem archaeocete (an extinct lineage of early cetaceans), with four recognized species (Gingerich and Russell, 1981). These taxa are middle Eocene in age, dated roughly 48.6-55.8 Ma (Xiong et al., 2009). The use of a pakicetid at this node in divergence dating has also been previously recommended (van Tuinen and Hadly, 2004; Geisler et al., 2011; Zhou et al., 2011), however, *Himalayacetus* continues to be used for mysticete dating (McGowen et al., 2009; Jackson et al., 2009; Steeman et al., 2009; Slater et al., 2010). The values for the temporal range applied to this fossil calibration represent the assigned age distribution recommended in Zhou et al. (2011).

The second node that was calibrated is the divergence of Neoceti (crown Cetacea). This node is typically calibrated by *Llanocetus denticrenatus* (as in FS1), the earliest known mysticete from the Eocene of Antarctica (Mitchell, 1989). This toothed mysticete is known from a partial dentary and skull and is approximately 34.2 Ma (Mitchell, 1989). There is another brief description of more complete cranial material recovered of the holotype of *L. denticrenatus*, however this has not been published (Fordyce, 2003a). Though this calibration has performed well in previous analyses, the relationship of *Llanocetus* within Mysticeti remains unclear (Fitzgerald, 2010) and until a formal description is of the type skull is published, use of this taxon should be cautioned against. Thus, in FS2, the calibration is based on the stem odontocete *Simocetus rayi* (Fordyce, 2002a). This is a well-described taxon that is consistently positioned as the oldest odontocete (Geisler et al., 2011). This taxon is dated to 28.0 Ma.

The third node calibrated in this study was of Mysticeti. This is typically calibrated by an unnamed archaic balaenid (Fordyce, 2002b), as in FS1. Though often cited and referred to in the literature, there has been no formal description of this taxon and its phylogenetic position has not been confirmed. This node is represented in FS2 by one of the earliest edentulous mysticetes (Deméré et al., 2008), *Eomysticetus whitmorei* (Sanders and Barnes, 2002). This taxon has been included in a number of phylogenetic analyses (e.g.
Deméré et al., 2008; Marx, 2010) and is believed to be one of the earliest edentulous mysticetes. It is dated between 23.0-28.4 Ma (Sanders and Barnes, 2002).

The final node of interest was the ingroup of this study (crown Balaenopteridae). Due to the phylogenetic instability of the group, this is a more subjective choice of fossils for calibration. The fossil taxon used to calibrate this divergence in FS1 is ‘Megaptera’ miocaena. This taxon was recognized as the oldest representative (11.2-6.5 Ma) of Balaenopteridae, but recently its taxonomy and phylogenetic position in the clade has been questioned and it has been recommended that it be moved to a separate genus (Bisconti, 2010b). In FS2, Balaenoptera siberi (Pilleri and Pilleri, 1989), a late Miocene (6.5-5.3 Ma) crown balaenopterid, was used. Its taxonomic affiliation to Balaenoptera has been supported in recent studies (Deméré et al., 2005; Marx, 2010).

Each of the calibrations was given a standard deviation value required by the lognormal distribution. A lognormal distribution for the prior is the most appropriate for modeling fossil information because it assumes the divergence event likely happened before the earliest appearance of the fossil taxa (Ho, 2007). This distribution has become the most common calibration type for fossil information (e.g. McGowen et al., 2009; Dornburg et al. 2012; Lukoschek et al., 2012) and acts as a broad minima (Pyron, 2011). This value was selected as objectively as possible, ensuring that it covered the entirety of the stratigraphic age range for each taxon. There is currently no rigorous method for selection of this value. It was computed here by selecting a standard deviation that encompassed the entire ages stratigraphic range (i.e. the confidence intervals for the ages of the stratigraphic unit in which the fossil was found), around the mean age.

Divergence times were estimated using both the nuclear and mitochondrial genes from the McGowen et al. (2009) supermatrix. The nuclear and mitochondrial data were run separately, in an attempt to minimize the effects of nucleotide saturation and differing gene histories between the two types of data. Although the issue of different gene histories is a factor in phylogenetic analysis, as well as divergence dating, it is a consideration that has been little applied to divergence dating specifically. Recent research on divergence dating has stressed the crucial impact of differing gene histories on ages produced in these analyses (Jackson et al., 2009; Duchène et al., 2011; Lukoschek et al., 2012) and that consideration has been little investigated in divergence dating.
An analysis was performed on the concatenated matrix (both mitochondrial and nuclear), however the analysis failed to reach stationarity. Thus this matrix is not presented in the results here. The nuclear and mitochondrial (separately) phylogenies produced from this dataset are one and the same, thus the resulting phylogeny does not impact the separate genetic analyses.

A relaxed uncorrelated molecular clock was implemented in BEAST v1.6 (Drummond and Rambaut, 2007). A GTR+I+G model was applied to the first, second and third codon positions. Base frequencies, substitution models and rate heterogeneity were unlinked across the partitions. A Yule process of speciation was implemented, which assumes a constant speciation rate per lineage (Drummond et al., 2006). Each analysis was run for 30 million generations and parameters were sampled every 3000 generations. The results of these analyses were examined for stationarity and convergence in the program Tracer v1.5 (Rambaut and Drummond, 2007) and the first three million generations were discarded as burn-in. An effective sample size (ESS) value greater than 200 is used here to indicate appropriate sampling of the posterior distribution (Fulton and Strobeck, 2010; Dornburg et al., 2012).

To test the effect of an external calibration on the dating of Mysticeti, a nuclear dataset of the RAG1 gene was created from sequences on the GenBank database. The dataset contained 59 extant taxa (Appendix D), including all mysticetes and representatives from the major outgroup clades of Odontoceti and Placentalia. Two marsupial taxa (Didelphis virginiana and Lagostrophus fasciatus) were also included for the external calibration. RAG1 was chosen because of its availability and recognition in previous divergence studies as a good locus for dating (Hugall et al., 2007).

The external calibration used was Juramaia sinensis, a eutherian mammal from the Jurassic (~160 Ma) (Luo et al., 2011). This taxon is used to calibrate the divergence of placental mammals from marsupials and monotremes. It was also utilized as a lognormal calibration (set as 160, 1.4) The divergence between these groups of mammals is critical for calibrating rates of evolution within eutherians and the age of J. sinensis sets a fossil calibration datum that coincides with the range of molecular estimates (Zhou et al., 2011). Both fossil sets were analyzed using the RAG1 matrix including separate analyses with and without the external calibration.
CHAPTER 3

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
MYSTICETI Flower, 1864/Gray, 1864
BALAENOPTEROIDEA Gray, 1868, sensu Mitchell, 1989
BALAENOPTERIDAE Gray, 1864
BALAENOPTERA Lacépède, 1804

Type Species: Balaenoptera acutorostrata Lacépède, 1804

Included species: Balaenoptera acutorostrata Lacépède, 1804, Balaenoptera bonaerensis Burmeister, 1867, Balaenoptera borealis Lesson, 1828, Balaenoptera davidsonii Cope, 1872 (Deméré, 1986 †, Balaenoptera edeni Anderson, 1879, Balaenoptera musculus Linnaeus, 1758, Balaenoptera omurai Wada et al., 2003, Balaenoptera physalus Linnaeus, 1758, Balaenoptera siberi Pilleri, 1989 †, Balaenoptera colcoughi, sp. nov. †

Definition: The monophyletic group containing the most recent common ancestor of Balaenoptera siberi and all its descendants, including Megaptera novaeangliae (which should be assessed as a member of the genus Balaenoptera).

Embedded diagnosis: The Balaenopteridae can be diagnosed from other mysticetes by possession of the following characteristics: a bluntly triangular supraoccipital shield; an abruptly depressed supraorbital process of the frontal; a long overlap between the ascending process of the maxilla and the anterior wing of the parietal; a narrowly elongate and rectangular ascending process of the maxilla; a slender and anterolaterally directed, triangular shaped zygomatic process of the squamosal; maxilla that overrides anterior portion of supraorbital process, creating a pocket; distal end of the humerus that forms a slight V-shape (convex); hourglass shaped digits (expanded distal and proximal ends, narrow shaft); reduced squamosal fossa; absence of a squamosal crease; a wing-like basioccipital process; high and dorsally rounded mandibular condyle; subcondylar furrow present on the mandibular condyle; dorsal elongate pars cochlearis; reduced mandibular foramen that is located ventral to the coronoid process. These characteristics are found in all currently recognized Balaenopteridae but in differing combination of traits.

In this description, B. colcloughi is compared to extant and extinct members of Balaenopteroidea. Additional comparisons are made to balaenids, C. marginata, and stem extinct mysticetes where appropriate.
**Balaenoptera Colcloughi n. sp.**

*Etymology:* The new species is named *Balaenoptera colcloughi* in honor of Jim Colclough, who is a preparator of fossil mysticetes at the San Diego Natural History Museum. Jim is a longtime preparator at the museum and is responsible for most of the preparation of the specimens of this new species.

*Diagnosis:* The new species possesses the following unique combination of characters relative to other extant and fossil *Balaenoptera:* dorsal sagittal crest on the nasals, medial flare of anterior margin of palatine, presence of squamosal crease and zygomatic crest, absence of squamosal cleft, and the exposure of the alisphenoid between the pterygoid and squamosal in the temporal region.

*Holotype:* SDNHM 80101, a complete skull with both petrosals and tympanic bullae, 35 vertebrae (atlas, dorsal/lumbar, caudal), 10 chevrons, 15 ribs belonging to the right side of the body, 3 phalanges and one carpal. The skull is on display at SDNHM and only the dorsal side is available for study. This specimen is the largest skull of the four recognized specimens and represents an adult individual based on size and suture closure. The combination of the ontogenetic age and preservation is the reason that it was chosen as the holotype of the new species.

*Paratypes:* SDNHM 83695, a nearly complete skull, with both petrosals preserving the malleus, incus and stapes, a partial bulla, both jugals, one chevron, rib fragments, both scapulae, humeri and radii, one carpal, five metacarpals, nine phalanges, all seven cervical vertebrae, five thoracic vertebrae and two lumbar vertebrae; SDNHM 90150, a partial skull missing the anterior portion of the left rostrum, with both petrosals and tympanic bullae; SDNHM 80102, a mostly complete skull with both petrosals and partial tympanic bullae, atlas, seven thoracic vertebrae, four lumbar vertebrae, an isolated neural arch, vertebral processes, vertebral epiphyseal plates and five ribs.

SDNHM 80102, the smallest of the four specimens, represents a subadult individual based on unfused occipital sutures on the skull (Walsh and Berta, 2011) and possession of unfused vertebral epiphyseal plates. SDNHM 83695 and SDNHM 90510 are also both identified as sub-adults. SDNHM 90150 possesses unfused ventral sutures of the basioccipital and SDNHM 83695 has unfused vertebral epiphyseal plates.

Mysticete occipital joints (i.e. supraoccipital, basioccipital, exoccipitals) complete their development during the adolescence (post-birth) and studies have focused on the posterior portion of the braincase (Walsh and Berta, 2011). This includes the fusion of occiput bones on each side of the braincase (dorsal and ventral). Walsh and Berta (2011) found that the sutures of these joints close before the end of the first year of life, thus they can be used to age mysticete osteological specimens.
A neonate *Balaenoptera physalus* specimen used in Walsh and Berta’s (2011) study, SDSU S970, was examined for comparison with SDNHM 80102 (Figure 8). The fossil specimen is slightly larger (zygomatic width of SDNHM 80102 is 77 cm while SDSU S970 is roughly 51 cm).

Figure 8. Comparison of the posterior occipital bones of the smallest specimen (SDNHM 80102; top) of *Balaenoptera colcloughi* and a neonate fin whale, *Balaenoptera physalus* (SDSU S970; bottom). Scale bar =15 cm.

SDNHM 80102 was included in Walsh and Berta (2011) as a fossil example in their study. This study determined that SDNHM 80102 is a “calf” [subadult], using the osteological pattern of suture closure for *B. physalus* and *M. novaeangliae*. This specimen
was ruled to be older than a neonate, however, based on the degree of closure of the basioccipital/basisphenoid suture is closed and barely noticeable. The exoccipital/supraoccipital and basioccipital/exoccipital joints are also closed but noticeable. These joints close rapidly as the animal progresses past birth and approaches calf stage, based on *B. physalus* (Walsh and Berta, 2011). While neonate status cannot be completely ruled out for this specimen, the evidence from their study suggests it is unlikely to be that young.

Final evidence to support identification of SDNHM 80102 and 83695 as subadults is the lack of fusion of the epiphyseal plates of the vertebrae. These plates fuse with maturity. Most of the vertebrae associated with these two specimens were unfused, with well-defined growth plates. Even still, many either had a partially broken and displaced plate or were missing a plate altogether. Isolated vertebral epiphyseal plates were found with SDNHM 80102.

Based on this evidence, it can be reasonably assessed that, though younger animals, SDNHM 80102, 83695, and 90150 were older than neonates. Judging by size, SDNHM 83695 and SDNHM 90150 were likely closer in age to each other, and both were older than SDNHM 80102, which was nearly a third smaller.

**Locality:** All four specimens of the new *Balaenoptera* species were found in strata of the San Diego Formation. The San Diego Formation is an Upper Pliocene marine deposit and is exposed in southwestern San Diego County, California, USA. It was deposited during a marine transgression and contains both marine and nonmarine sediments (Deméré, 1983). The formation is composed of yellow-brown, medium- to fine-grained sandstone, with smaller conglomeratic layers and other lithologic variability. It has produced a diversity of Pliocene vertebrates, including whales, pinnipeds, sharks and birds (Deméré, 1983, 1994).

The San Diego Formation is dated to approximately 2 to 4 million years old. The formation is correlated to the Blancan North American Land Mammal Age (Deméré, 1986). SDNHM 80101 and SDNHM 83695 were discovered in the Sunbow neighborhood (SDNHM Locality 4519). SDNHM 80102 was found in the Otay Ranch Village area (Locality 4500). SDNHM 90150 was also recovered from Otay Ranch Village but from a different locality (SDNHM Locality 4678).
DESCRIPTION

General Features: The dorsal skull description is based on the holotype (Figure 9). Description of the ventral portion of the skull is based on the paratypes (SDNHM 90150 and 83695), since the ventral side of the holotype was not available for study (on exhibit).

Figure 9. The four specimens of *Balaenoptera colcloughi* in oblique anterodorsal view. The holotype (SDNHM 80101) at far left, paratypes (SDNHM 80102, 90150, 83695; left to right respectively). Scale bar = 15 cm.

All four specimens are nearly complete skulls, especially the dorsal side. Ventrally, the most complete specimen is SDNHM 90150, which is the only specimen to preserve the pterygoid fossa. The rostrum of is 76% of the condylobasal length in SDNHM 80101 and SDNHM 83695 (the other two specimens did not have complete rostra). The temporal fossa is 36% of the zygomatic width of SDNHM 90150 and 28% in SDNHM 83695. SDNHM 80101 and SDNHM 80102 range in between those values. The skull of the new species is roughly straight in lateral view, with a ventral curve in the rostrum. Arching of the rostrum is variable in crown balaenopterids, and this new species displays arching most similar to *Balaenoptera physalus*.

Maxilla: The lateral margins of the maxilla are thin. The maxilla slopes gradually, at roughly a 15 degree angle from the posterior point of the ascending process of the maxilla, in the ventral direction from the midline to lateral margins. There are 14 foramina preserved on the posterior portion of the dorsal side of the bone. In dorsal view, the anterior end of the maxilla is located posterior to the anterior-most extension of the premaxilla. The lateral border of the maxilla converges on
the longitudinal axis of the skull anteriorly, giving the rostrum a triangular shape. The lateral margins of the maxilla are 3 mm thick in SDNHM 80101 and SDNHM 83695. The lateral edges of SDNHM 80102 display evidence of a shark bite. The lateral process of the maxilla is perpendicular to the longitudinal axis medially, and curves slightly posteriorly towards the lateral most edge.

An important characteristic of Balaenopteridae is the overriding of the (posterior) maxilla dorsally over the anterior portion of the supraorbital process of the frontal. This creates what is termed the “balaenopterid pocket”, which is a diagnostic feature of crown Balaenopteridae. *Balaenoptera colcloughi* shares this character with all extant Balaenopteridae, as well as *B. siberi, A. castriarquatii, M. hubachi* and *P. cuvieri*. The APM is exposed dorsally and developed as a broad bar (Figure 10). The posterior edge of APM is elevated above the level of the supraorbital process of the frontal and overlaps with the anterior wing of the parietal. The APM is generally shaped like a bar (or rectangle), with a consistent width until reached the posterior most portion, which expands in lateral width. The APM of this species is nearly identical to *Diunatans luctoretemergo* (Bosselaers and Post, 2010) in general shape. This feature is very similar to *B. physalus*, though the anterior portion of this process is thicker in the fin whale. Other *Balaenoptera* do not expand laterally at the posterior portion of the process, mostly consistent in thickness throughout, or tapering off to a point at the posterior end.

The antorbital notch of the maxilla is in line with the antorbital process of the supraorbital process of the frontal.

On the ventral side of the skull, the maxilla also preserves multiple lateral nutrient foramina. Bony vascularizations on the palate of edentulous mysticetes are believed to be osteological correlates of baleen and the laterally arranged lateral nutrient foramina are interpreted as unique to baleen bearing mysticetes (Deméré et al., 2008). The new species preserves anterior foramina with elongate sulci that are parasagittally arranged. The posterior foramina possess radially arranged sulci and there is no open maxillary groove.

The parasagittal arrangement of the anterior nutrient sulci on the ventral side of the maxilla is a condition shared among all extant members of *Balaenoptera*, all extinct balaenopterids, some ‘cetotheres’ and balaenoids. While *M. novaeangliae* also possesses parasagittally arranged anterior foramina and elongated sulci, it differs from all the others by
Figure 10. The nasal region (cranial apex) of *Balaenoptera colcloughi* (SDNHM 80101). Abbreviations in Methods. Scale bar = 15 cm.
possessing multiple rows of posterior foramina without well-developed sulci. It shares this pattern with the gray whale lineage (Eschrichtiidae; Deméré et al., 2008).

These structures have been observed in fossil edentulous mysticetes previously, mostly ‘cetothere’ species, including *D. hiatus* and *A. patulus*. Their condition differs little from the extant balaenopterid condition, with the exception of distinctly longer posterior sulci (Deméré et al., 2008). *B. colcloughi* resembles the condition seen in extant balaenopterids.

On the palate, the maxillae are divided into a right and left concave surfaces by a medial keel (exposing the vomer). In the posterior portion of the ventral side, the maxilla expands laterally at the antorbital notch and forms an infraorbital plate. The infraorbital plate ventrally overlaps the supraorbital process of the frontal anterior to the optic canal. There is a distinct groove located at the medial edge of this plate, which is overlapped by the lateral border of the palatine. The posterior border of the maxilla is M-shaped, with two convex (apex in anterior direction) points relative to the posterolateral most point of the bone.

*Premaxilla*: The premaxillary-maxillary suture is unfused. The premaxilla broadens laterally as it reaches the anterior end of the narial opening and then narrows medially posterior to the opening. Anterior to the narial opening, the premaxilla is uniformly sized and rectangular. It narrows to a medial point at the anterior most end of rostrum. This narrowing begins relatively level with the anterior most extension of the maxilla, thus the premaxilla has a longer anterior extension and makes up the anterior most point of the rostrum.

Posterior to the narial opening, near the anterior border of the nasals, the premaxilla ‘twists’ as the medial border rotates ventrally (Figure 10). The premaxilla narrows at the level of the anterior margin of the nasal bones. The ascending process of the premaxilla is rectangular in shape. The posterior margin of the ascending process of the premaxilla contacts the supraoccipital. The posteromedial extension of this process is rounded and level with the posterior border of the nasals, while the posterolateral point of the premaxilla is slightly pointed and level with the posteromedial corner of the ascending process of the maxilla.

*Nasals*: The lateral border of the nasals share contact with the ascending process of the premaxilla. The position of the narial fossa is roughly parallel to the antorbital notch (Figure 9). The nasals are short in length, compared to the condylobasal length (Table 2).
Table 2. Cranial Measurements (cm) for *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurement</th>
<th>SDNHM 80101</th>
<th>SDNHM 80102</th>
<th>SDNHM 83695</th>
<th>SDNHM 90150</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Length of skull</td>
<td>242.57</td>
<td>133.35</td>
<td>181.90</td>
<td>186.50</td>
</tr>
<tr>
<td>2. Condylobasal length</td>
<td>244.48</td>
<td>134.35</td>
<td>185.10</td>
<td>188.50</td>
</tr>
<tr>
<td>3. Rostrum length</td>
<td>185.42</td>
<td>91.80</td>
<td>141.10</td>
<td>-----</td>
</tr>
<tr>
<td>4. Zygomatic width</td>
<td>130.50</td>
<td>77.00</td>
<td>107.65</td>
<td>108.25</td>
</tr>
<tr>
<td>5. Width at antorbital notch</td>
<td>81.35</td>
<td>47.40</td>
<td>----</td>
<td>62.40</td>
</tr>
<tr>
<td>6. Nasal width</td>
<td>7.55</td>
<td>----</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>7. Nasal length</td>
<td>9.10</td>
<td>~11.00</td>
<td>~14.55</td>
<td>----</td>
</tr>
<tr>
<td>8. Temporal fossa width</td>
<td>41.75</td>
<td>30.60</td>
<td>30.40</td>
<td>39.55</td>
</tr>
<tr>
<td>9. Length of occipital shield</td>
<td>51.70</td>
<td>32.70</td>
<td>37.90</td>
<td>----</td>
</tr>
<tr>
<td>10. Basicranium width</td>
<td>75.50</td>
<td>48.75</td>
<td>60.25</td>
<td>65.00</td>
</tr>
<tr>
<td>11. Occipital condyle width</td>
<td>21.40</td>
<td>16.50</td>
<td>20.05</td>
<td>19.80</td>
</tr>
</tbody>
</table>

*Note.* ~ Indicates an Approximate Value.
See Also: Figure 42, in Appendix A.

Anteriorly, the medial corner is bluntly pointed and extends farther anteriorly than the lateral corner. The lateral edges of the nasals are dorsal to the medial portion, making them slightly dorsally concave. The posterior margin of the nasals is nearly straight. The anterior half of the dorsal surface possess a sagittal keel. The anterior edge of the nasal is oriented dorsoventrally. The posterior most edge of the nasal bone is relatively positioned in line with the anterior half of the supraorbital process of the frontal.

The nasals are highly variable among balaenopterids. The anterior portion of nasals is similar to *B. physalus, M. novaeangliae, D. luctoretemergo* and ‘M.’ *hubachi* in that the margin is nearly u or v-shaped. The anterior half of the dorsal surface of nasals possess a sagittal keel, as in *B. physalus, E. robustus, M. novaeangliae* and ‘M.’ *hubachi*. The general shape of the nasals in this new species is more similar to *Megaptera* than to species of *Balaenoptera*. The most noticeable feature that unites the two is the medial keel extending the length of the dorsal surface of the nasals.

The posterior most edge of the nasal bone is relatively positioned at the same level with the anterior half of the supraorbital process of the frontal, a feature shared with most balaenopterids, except *B. musculus, B. omurai* and *Parabalaenoptera baulinensis*.

*Jugals:* Both left and right jugals are preserved in SDNHM 83695 and 80101. The jugals are long (15.5 and 19.5 cm, respectively) and thin (mediolateral width). The ventral margin is nearly straight from lateral view. The anterior and posterior portions of the jugal curve medially, the anterior end to a larger degree. At the anterior margin, the bone curves dorsally. The anterior projection narrows slightly
from this corner and terminates as a rounded knob. From the posterior side of this knob two thin bony projections emerge. The dorsal projection is wider than its ventral counterpart and slightly bends ventrally. The ventral projection is thin and straight. The posterior end of the jugal is flattened. There is a distinct ridge that begins at the ventroposterior most corner, which has somewhat rounded edge, and travels dorsally up the middle of the flattened dorsal posterior projection.

**Lacrimal:** The lacrimal is exposed at the lateral most termination of the maxillary pocket, above the anterior edge of the orbit. It is located between the supraorbital process of the frontal (posterodorsal) and infraorbital plate of the maxilla (anteroventral). It is loosely connected to the supraorbital process of the frontal and has a tighter connection to the maxilla. The lacrimal is a thin rectangular bar that narrows and tapers as it extends medially. These are characteristics that *B. colcloughi* shares with other edentulous mysticetes. The medial portion of the lacrimal is located more antero-dorsally than the lateral portion. The lacrimals of SDNHM 80101 are 16 cm long.

**Frontal:** The slope of the laterally extended supraorbital process of the frontal is abruptly deflected below the vertex of the skull, a diagnostic feature of balaenopteroids. The supraorbital process of the frontal is moderately broad antero-posteriorly and moderately elongate transversely, relative to the overall dimensions of the skull (Figure 11). It is also dorsoventrally flat with a slight depression in the medial portion of the process. The posterior-medial corner of the frontal is covered by the large extension of the anterior wing of the parietal. The anterior edge of the SOPF is overlapped dorsally by the posterior extension of the maxilla, creating the maxillary pocket characteristic of balaenopterids.

The ventral side of the SOPF envelopes the optic ‘tube’ (also called orbital canal [Steeman, 2009]), which houses the optic nerve. The lateral edge is U-shaped, opening ventrally; this makes up the dorsal roof of the orbit. Medially, the edge is flat but the anterior and posterior corners are located ventrally. The connection with the jugal is located ventral to this lateral edge. The orbit is located above the level of the ventral surface of the exoccipital.

The optic canal is found on the ventral side of the supraorbital bone of the frontal, and the optic nerve traveled through it in life. In the juvenile (SDNHM 80102), the optic canal is ventrally open, however in one of the subadults (SDNHM 90150) it is ventrally closed by a lamina from the anteroventral surface of the supraorbital. Unfortunately, this feature was not preserved in SDNHM 83695 and unavailable for study in SDNHM 80101. This character deserves further investigation because it is highly variable among the extant balaenopterid species, even adult specimens.

The posterior curve of the SOPF is gently rounded but the posterior facing edge is nearly (dorsoventrally) straight (Figure 11). The posterior ventral edge is located anterior to
Figure 11. Lateral view of the basicranium of *B. colcloughi* (SDNHM 80101). Abbreviations in Methods. Scale bar = 15 cm (Anterior to left).

the posterior dorsal edge of the curve. The postorbital process of the SOPF reaches, and slightly overlaps dorsally, the anterior point of the zygomatic process of the squamosal. This corner is rounded with a small posteriorly protruding boss on the posterior side of the corner.

The exposure of the frontal is reduced in the interorbital region, equivalent to the exposure of the parietal in this region (see below). The anterior wing of the parietal-frontal suture is lobate and elongated, another balaenopterid feature.

*Parietal*: The anterior wing of the parietal begins anterior to the cranial vertex and extends into posterior of the vertex, creating a long overlap with the ascending process of the maxilla and the supraorbital process of the squamosal. The AWP is vertical in anteroposterior section but curves medially at its posterior portion. The parietal-squamosal suture is long, relatively straight, and dorso-ventrally and slightly posteriorly oriented.

The exposure of the parietal in the interorbital region is reduced, similar to most balaenopterids, with the exception of *B. omurai* and the extinct *Protororqualus*. 
Supraoccipital: The supraoccipital is triangular in shape in dorsal view (Figure 9). The lambdoidal crest of the supraoccipital is raised (more dorsal) in relation to the medial portion of the bone, creating a depression in the middle portion of the shield (Figure 12). In SDNHM 80101, there is a raised section of bone near the lateral margin, located posteriorly to the anterior tip of the supraoccipital. These are not interpreted to be occipital tuberosites, as found in eschrichtiids. The anterior apex of the supraoccipital is broadly rounded (Figure 10). The apex of the occipital shield extends to the level of the orbit. The lateral margins of the shield are slightly concave, more so towards the posterior portion of the shield. The shield broadens posterolaterally. The supraoccipital is anteriorly depressed (lateral to the midline of the skull) at the level of the occipital condyles and the paraoccipital processes flare posterolaterally from this depression.

Figure 12. Posterior view of *B. colcloughi* (SDNHM 80101). Abbrevations in Methods. Scale bar = 15 cm.

The anterior apex of the supraoccipital of *B. colcloughi* is wide and round. The only extant balaenopterid with this shape is *B. physalus*, but this characteristic is also seen in extinct species ‘*M.* hubachi’, ‘*M.* miocaena’, *B. siberi* and *D. luctoretemergo*. The apex of the occipital shield extends to the level of the orbit, a feature seen only in balaenopterids and a ‘cetothere’, *A. patulus*. The lateral margins of the shield are laterally concave, a feature of extant *Balaenoptera* and some fossil balaenopterids, as well as Eschrichtiidae.
**Exoccipital:** The exoccipital projects laterally and posteriorly in dorsal view. The posterolateral corner extends posterior to the occipital condyles (Figure 12, Table 2). This corner also extends posterior to the postglenoid process of the squamosal. The paraoccipital processes are large and extend laterally to the postglenoid process of the squamosal. The paraoccipital processes dorsally overlap the post glenoid process and create tube-like spaces, in which the posterior process of the petrosals reside. The posterior edge of the paraoccipital process of the exoccipital is located in a transverse line with the posterior edge of the occipital condyles. The new species shares this trait with extant *B. acutorostrata, B. bonaerensis, B. borealis, B. musculus, E. robustus* and *C. marginata*. This characteristic is also shared with *P. baulinensis, U. gramensis*, as well as members of Cetotheriidae *sensu stricto, C. rathkii* and *M. elysius*.

The occipital condyles are longer than wide (Figure 12) and concave. The ventromedial borders of the condyles do not contact one another, but are closer to one another than the dorsomedial borders. The foramen magnum is heart-shaped with rounded borders in posterior view. A slender, flat shelf is created on the ventral floor of the foramen magnum due to its slope.

**Squamosal:** The squamosal shares a suture with the lateral border of the supraoccipital shield (Figure 11) (forming the posterior portion of the lambdoidal crest), a trait shared with all edentulous mysticetes. The squamosal is uniform in width and extends laterally. The zygomatic process of the squamosal is anteriorly and laterally directed (Figure 12). The zygomatic process is long and slender, relative to other balaenopterids. The lateral portion of the zygomatic process is rounded and slightly crescent shaped in lateral view. The anterior tip of this process is positioned below the postorbital corner of the supraoccipital process of the frontal and the tip is rounded.

The squamosal fossa is poorly defined in *B. colcloughi*. The squamosal fossa is present but reduced in all *Balaenoptera* but is absent in *M. novaeangliae*. The fossa is also reduced in balaenids. The only fossil balaenopterids with this feature are *D. luctoretemergo* and ‘M.’ *hubachi*.

The squamosal crease, a flexure of the bone within the squamosal fossa region (Kellogg, 1924) is present in the new species, as it is in extant balaenopterids. As the squamosal extends laterally from parietal-squamosal suture in the temporal region, it ‘bulges’ slightly anteriorly, roughly at the location of the zygomatic crest. *Balaenoptera colcloughi* possesses a bulge on the posterolateral edge of the squamosal, although it is more accentuated in SDNHM 80101 compared to other specimens. The squamosal cleft is absent in *Balaenoptera colcloughi*, a feature shared with all crown balaenopterids with the exception of *Megaptera novaeangliae*. 
A small portion of the pterygoid can be seen in lateral view in the temporal fossa, representing the dorsal extension of the pterygoid and its suture with the squamosal. The foramen pseudovale is located within the squamosal, with one border shared with the pterygoid. The suture between the two bones is oriented roughly anterior posteriorly, with a small section running laterally to meet the foramen pseudovale.

The falciform process of the squamosal is expanded anteroventrally. The glenoid fossa and zygomatic arch of the squamosal are elevated above the level of the palate. The ventral surface of the squamosal is smooth and dorsally concave. The posteroverentral extension flares laterally and has a curved posterior margin (Figure 12).

The posterior width of the squamosal is smaller relative to that of stem mysticetes (e.g. A. patulus, D. hiatus). The zygomatic process is long and slender, another feature that it shares with M. novaeangliae, as well as P. quarantellii. The zygomatic crest is also present in M. novaeangliae, B. borealis, and B. edeni. Bosselaers and Post (2010) identified a bulge on the posterolateral edge of the squamosal, which they identified as a diagnostic character for D. luctoretemergo. This bulge also appears to be present in B. colcloughi. The posterior portion of the squamosal between D. luctoretemergo and B. colcloughi is very similar. The zygomatic crest is exaggerated in the juvenile specimen (SDNHM 80102) compared to the adult (SDNHM 80101), where the crest is present but barely noticeable.

**Palatine:** The palatines of Balaenoptera colcloughi are large and roughly winged-shaped (posterior portion shown in Figure 13). The anterior margin of the palatine flares medially, a feature only seen in B. borealis, M. novaeangliae and the extinct Eschrichtiodes gastaldii. The bone widens posteriorly but narrows just anterior to the optic canal, at the level of the ventral overlap of the maxilla by the frontal. The posterior palatine extends posterolaterally and slightly underlaps the pterygoids. The medial margins of the right and left palatine do not meet, and the vomer is exposed ventral to the palatines.

**Pterygoid:** The lateral projections of the vomer form the medial wall of the pterygoid fossa. Due to expansion of the falciform process, the anterolateral diameter of the pterygoid is narrowed dorsal to the hamular process. The posterior extension of the hamular process of the pterygoid is poorly preserved in the new species (Figure 13). A small exposure of the pterygoid can be seen in the ventromedial wall of the temporal opening. The foramen pseudovale (Figure 14) is bordered on one side by the pterygoid bone, near the suture with the squamosal. This characteristic is variable in balaenopterids, as discussed later. The pterygoid contacts the squamosal posterior to this foramen.
A character commonly used in mysticete studies is the position of the foramen pseudovale (or oval window). However, this character has been questioned in the past (Bisconti, 2007a). There is much variability in the position of the foramen pseudovale across species in *Balaenoptera* species. The foramen pseudovale in *B. colcloughi* is roughly 3 cm wide and positioned within the squamosal of the specimens. However, it is polymorphic in its contact with the pterygoid suture (SDNHM 80102 vs. SDNHM 90150). In SDNHM 90150, the foramen directly contacts the pterygoid suture whereas in the smaller (and presumably younger) SDNHM 80102 the foramen is further from the suture, not positioned along the contact (though still relatively close). Due to the variation in this foramen between the
specimens of *B. colcloughi*, and observations from other specimens over the course of this study, it can be inferred that this variation may be due to ontogeny.

The pterygoid fossa is a covered antero-ventrally by the hamular process of the pterygoid. The hamular process of the pterygoid slightly overlaps the palatine on its medial border. The pterygoid fossa is bounded dorso-medially by the palatine and laterally by the squamosal bone. This fossa is confluent at the postero-ventral end to the space that houses the petrotympanic complex. The posterior extension of the palatine dorsally covers the anterior portion of the fossa, however the lack of preserved pterygoid hamuli may be why it doesn’t extend further.

*Alisphenoid:* There is a small portion of the alisphenoid exposed on the temporal wall between the pterygoid and squamosal in *B. colcloughi*, a feature seen in no other taxon in this study. Some balaenopterids (i.e. *B. acutorostrata*, *B. edeni*, *B. borealis*, *B. musculus*) have an exposure of the alisphenoid between the pterygoid,
squamosal and parietal. The bone is also exposed in the cranial cavity of SDNHM 90150 (see Braincase section).

**Vomer:** In ventral view, the vomer is exposed along the entire median line of the skull, between the medial borders of the maxilla. The vomer is nearly hidden at a point on the rostrum roughly a third of the distance from anterior tip, where the two maxilla meet medially. Posteriorly, the vomer is underlapped by the palatines (Figure 13); however the palatines never contact one another medially, thus the vomer can be seen along the midline. Dorsal to the palatines, the keel narrows to form a ventral crest, called the vomer keel (or vomerine crest). The bone emerges from the palatines as a ‘nasal plate’ with the keel located along the midline of the skull. The vomer lateral to this keel is slightly concave ventrally. The shape of the nasal plate of the vomer is roughly triangular. The postero-lateral margins of the plate are more posteriorly located than most of the bone, with the exception of the keel, which extends to the suture with the basioccipital. This gives the vomer-basioccipital suture a slightly ‘m’-shape. The postero-lateral edges of this vomer plate are nearly straight with corners that overhang the pterygoid fossa. The vomer has a distinct posterior expansion adjacent to the pterygoids. The median keel of the vomer extends to the vomer-basioccipital suture.

The vomer displays a mosaic of primitive and derived characteristics observed in this new species. The vomer is rounded and broad in ventral view, similar to many extant balaenopterids. The posterior extension of the nasal (dorsal) plate of the vomer is most similar to the condition in *B. physalus* and *B. omurai*. The vomer in other extant species of balaenopteroids lack this posterior extension, although many fossil mysticetes, like some ‘cetothers’ (e.g. *A. patulus* and *D. hiatus*), possess this trait. The vomer keel extends posteriorly to the vomer-basioccipital suture, a feature also observed in ‘*M.* miocaena’ and *B. omurai*. It is possible these characters are also found in the stem balaenopterid, *U. gramensis*, however it was difficult to determine from published figures (Steeman, 2009). Overall, the characteristics of the vomer for this new species most closely resembles those found in *B. omurai*. The vomer has a distinct posterior expansion adjacent to the pterygoids, a trait characteristic of *Balaenoptera physalus* and *B. omurai*. This posterior extension of the vomer keel is also observed in ‘*M.* miocaena’ and *B. omurai*, as well as some ‘cetothers’.

**Basioccipital:** This bone is exposed on the ventral side of the skull and is generally symmetrical from the midline. The suture between the basioccipital and the posterior extension of the vomer is still slightly open (Figure 13), another indication of the young age of the specimens (SDNHM 83695, SDNHM 90150). The basioccipital processes are large and rounded anteriorly and they are ventrally positioned compared to the occipital condyles. The lateral borders of these processes overlap the medial portion of the cavity that houses the periotoic. The lateral borders of the basioccipital process are thin and slightly convex. The lateral
edge is adjacent but separated from the medial edge of the tympanic bulla, and it forms the postero-lateral wall of the peribullary fossa (Bouetel and de Muizon, 2006). The bone is ventrally concave near the occipital condyles.

**Braincase:** The supraoccipital, which makes up the roof of the endocranial cavity, is missing in SDNHM 90150. The skull was transversly sheared just dorsal to the level of the squamosal and occipital condyles. This preservation provides a unique opportunity to study the internal structure of the brain case of the new fossil species. However, due to preservation, foramen for entry of arteries and nerves (such as the carotid or the optic nerve) were not preserved or could not be identified in this specimen. The sutures are also difficult to see between most of the bones, but their rough location can be determined.

The posterior floor of the braincase is composed of the basioccipital. Sutures are difficult to identify but the posterolateral basioccipital meets the squamosal at a broad, rounded margin. The braincase widens laterally at the squamosal. The basisphenoid and orbitosphenoid suture is not completely fused, an indication of a subadult individual. The anterior margin of the basioccipital meets the basisphenoid, which continues anteriorly as the anteroventral floor of the braincase. This suture is slightly open, an indication of the young age of this individual.

Ventrally, the basioccipital makes up the cerebral surface of the endocranial cavity (Bouetel and Muzion, 2006). A distinct ridge extends anterodorsally from the posteromedial ventral segment of the basioccipital on the nasopharangeal surface. Lateral to this ridge, the squamosal forms the lateral wall of the braincase and along the lateral edges is a dorsally oriented eminence. This eminence is the alisphenoid (which is fused to others in adults) appears on both sides of the braincase, against walls that form the medial border of the temporal fossa (thus the alisphenoid is exposed on the lateral walls of the braincase). This feature coincides with the location of the carotid foramen (which is not preserved).

**Petrosal:** The lateral projection of the anterior process is robust (Figure 15, Table 3). The apex of the anterior process is narrowly triangular. There are also tiny, bony projections protruding from the ventroposterior portion of the anterior process. An embayment is formed at the junction of the anterior process and the promontorium. The hiatus Fallopii is located on the ventral surface of the promontorium, within the seam between the anterior process and the promontorium.

The promontorium is ventrally flattened. The suprameatal region of the petrosal is elevated dorsal (above) to the anterior process. The crista transversa is high and reaches the cerebral surface (Figure 15D). The fenestra cochlae is small relative to the fenestra vestibuli.
Figure 15. Petrosal of *B. colcloughi* (SDNHM 83695). (A) Ventral, (B) Dorsal, (C) Posterior, (D) Dorso-medial views. Abbreviations in Methods. Scale bar = 5 cm.
Table 3. Petrosal Measurements (cm) for *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurements</th>
<th>SDNHM 80102</th>
<th>SDNHM 83695</th>
<th>SDNHM 90150</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Posterior process length</td>
<td>8.6</td>
<td>10.0</td>
<td>~10.0</td>
</tr>
<tr>
<td>2. Promontorium length</td>
<td>4.3</td>
<td>6.2</td>
<td>4.5</td>
</tr>
<tr>
<td>3. Anterior process length</td>
<td>6.0</td>
<td>6.0</td>
<td>-----</td>
</tr>
<tr>
<td>4. Width of anterior process</td>
<td>3.3</td>
<td>3.2</td>
<td>-----</td>
</tr>
</tbody>
</table>

*Note.* ~ Indicates an Approximate Value.

See Also: Figure 43, in Appendix A.

The endolymphatic and perilymphatic foramina are arranged *en echelon* and divided by a small, dorsoventrally oriented bony septum. Within the internal auditory meatus, the openings for the vestibulocochlear nerve canals are larger in size than the openings for the facial nerves. In the epitympanic region, the stapedial fossa and the facial nerve sulcus are confluent. The stapedial fossa is small and compressed. The endocranial opening for the facial nerve canal is circular in shape.

The petrotympanic region of balaenopterids is highly variable and the new species exhibits a suite of shared characteristics in this region. Bony projections were found in each periotic of *B. colcloughi* (Figure 15). These projections protrude from the ventroposterior portion of the anterior process, in the space between the process and the promontorium. A similar feature has been noted in *B. omurai*, *E. robustus* and *U. gramensis* (Steeman, pers. comm., October 2011). Ekdale et al. (2011) also noted “variably developed” bony projections from this region in specimens of *B. physalus* and postulated these features may be age related, occurring in older individuals. However, the specimens in this study belong to younger individuals. The morphology of these projections is also potentially different. The projections of *B. colcloughi* are tube-like (columnar), and appear to have a ‘spongy’ interior texture in the middle of the tube. Further investigation into the ear complex of mysticetes may help clarify this character.

The character of the narrowly separated perilymphatic foramen from the fenestra cochlae in dorsolateral aspect is a feature uniting *Balaenoptera* species. Another feature that this new species shares with other *Balaenoptera* species is a well-developed short keel at the contact between the stylomastoid fossa and ventral surface of promontorium. This is another feature that suggests the crown position of this new species among balaenopterids. A small fenestra cochlae relative to the fenestra vestilubi is a feature found in species of *Balaenoptera*.
and in the gray whale. The position of the hiatus Fallopii is a character shared with *M. novaeangliae* and *E. robustus*.

The stapedial fossa and the facial nerve sulcus are confluent, as also seen in *B. borealis, M. novaeangliae* and *E. robustus*. The relative size of the stapedial fossa is small and compressed, as in the minke whales and *B. physalus*. The endocranial opening for the facial nerve canal is circular in shape, a feature that is variable among balaenopterids. The malleus in this new species most closely resembles the malleus of *M. novaeangliae* (Bosselaers and Post, 2010; Figure 16). The incus is long and slightly curved as in *M. novaeangliae*.

*B. colcloughi* also possesses a robust lateral projection of the anterior process, seen also in all extant balaenopterids, except the minke whales (*B. acutorostrata* and *B. bonaerensis*). This is also seen in ‘*Megaptera* ‘hubachi’. A narrowly triangular apex of the anterior process is also shared with extant Balaenopteridae, as well as *D. natans, E. harrisoni, P. quarantellii*, and *P. nana*. It shares fewest periotic characters with *B. acutorostrata* compared to the other extant balaenopterids.

The stylomastoid fossa extends from the pars cochlearis onto the posterior process. The contact between the stylomastoid fossa and the ventral surface of the promontorium is well developed as a short keel. The posterior cochlear crest is a medially extended shelf adjacent to the fenestra cochleae. The posterior process is posterolaterally oriented relative to the long axis of the pars cochlearis. The attachment for the tensor tympani muscle is indistinct. The promontorial groove on the medial side of the pars cochlearis is absent. The perilymphatic foramen is narrowly separated from the fenestra cochleae in dorsolateral aspect (Figure 15c).

**Tympanic Bulla**: The tympanic bulla is ovoid in ventral view (Figure 16a). The medial margin is dorsoventrally flattened. The main ridge of the bulla is long and extends to the anterior end. The dorsoventral edge of the main ridge is rounded. The posterior portion of the medial margin of the main ridge is elevated and flattened. The involucral ridge is laterally retracted from the main ridge (Figure 16b). The anterolateral ridge (or shelf) is weakly developed. The conical process (~1.5 cm tall) is broad and about half the size of the sigmoid process. The conical process has a thick anterior lip, consistent in thickness across the whole lip (Figure 16b). The sigmoid process is 3 cm tall. This process is robust with a thick tympanic lip, relative to the minke whales (*B. acutorostrata* and *B. bonaerensis*). The sigmoid process is straight and located anterior to the midline. The sigmoid fissure and lateral furrow are strongly present. The median furrow of the bulla is
Figure 16. Left tympanic bulla of *B. colcloughi* (SDNHM 90150). (A) Ventral, (B) Dorsal, (C) Medial, (D) Lateral views. Abbreviations in Methods. Scale bar = 3 cm.
absent. The involucrum possesses a weakly developed dorsal posterior prominence (Figure 16b). In medial view, the dorsal involcral surface is relatively straight and is convex adjacent to the Eustachian notch. The length of the anterior lobe is slightly smaller than the posterior lobe, and roughly half the total length of the bulla (Table 4).

### Table 4. Tympanic Bulla Measurements (cm) for Balaenoptera colcloughi

<table>
<thead>
<tr>
<th>Measurements</th>
<th>SDNHM 80101</th>
<th>SDNHM 80102</th>
<th>SDNHM 83695</th>
<th>SDNHM 90150</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Length of bulla</td>
<td>9.0</td>
<td>9.0</td>
<td>9.1</td>
<td>8.5</td>
</tr>
<tr>
<td>2. Height of sigmoid process</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>3.0</td>
</tr>
</tbody>
</table>

*Note. ~ Indicates an Approximate Value.*

See Also: Figure 44, in Appendix A.

The bulla exhibits the general morphology of a balaenopterid. This includes an ovoid shape, involucral ridge that is laterally retracted, thin anterior lip of the conical process, and an absent or weak dorsal posterior prominence (Figure 16).

However, there is a high degree of inter-specific variability in the bulla of these whales. The posterior portion of the medial margin of the main ridge in the new species is elevated and flattened, as in Balaenoptera musculus and Balaenoptera physalus. However, the new species does not possess other features of B. musculus, such as a posterior extension of the bulla, an autapomorphy of B. musculus (Ekdale et al., 2011). The new species has a shorter conical process (~1.5 cm), compared to B. physalus and the minke whales, which have a taller process amongst extant balaenopterids.

**Malleus:** Both the left and right mallei are preserved in SDNHM 83695 (Figure 17). The right malleus is also present in SDNHM 80102. In situ, the malleus is attached to the sigmoid process of the tympanic bulla via the gonial process. The attachment pedicle is anteriorly robust and is separated by a deep groove. There is a distinct furrow between the two (ventral and dorsal) facet tubercles. The width across these facet tubercles is 1.3 cm. While both are rounded, the dorsal facet is larger. In posterior view, a process protrudes medially, and overlaps the dorsal facet. In lateral and dorsal view, this process forms a nearly 90° shelf. The greatest length of the malleus is 1.7 cm. The sulcus for the chorda tympani (Mead and Fordyce, 2009) is present on the anterior process.

**Incus:** The right incus of SDNHM 80102, and both incudes from SDNHM 83695 are preserved (Figure 18). The incus is long (1 cm), slightly curved and generally triangular. The articular surface is a broad U-shaped depression and is wider than the anterior crus breve. The crus breve is short and broad. The body of the incus is slender and the lenticular process has a rounded end.
Figure 17. Malleus of *Balaenoptera colcloughi* (SDNHM 83695). A) Dorsal view, B) Medial, C) Anterior view. Abbreviations in Methods. Scale bar = 5 mm. (Anterior is directed out of the page).
Figure 18. Incus of *Balaenoptera colcloughi* (SDNHM 83695). (A) Lateral, (B) Ventral, (C) Medial views. Abbreviations in Methods. Scale bar = 5 mm.
**Stapes:** The stapes is preserved in SDNHM 80102, 83695, and 90150. The stapes is slender and does not appear to be curved. The base and head of stapes are flat and disc shaped. The neck of the stapes widens posteriorly into the anterior and posterior crus, with an open stapedial foramen, giving the bone an overall stirrup-like appearance.

**Postcranial Skeleton**

*Vertebrae:* Three skulls of *B. colcloughi* (SDNHM 80101, 80102, 83965) have associated axial skeletal elements. The neural arches and transverse process of most vertebrae are broken or fragmentary. The vertebral epiphyses of SDNHM 80101 are fused, indicating an adult specimen, while the epiphyses of SDNHM 80102 and 83695 are unfused, indicating these are subadult individuals. The general morphology of the vertebrae are typical of crown mysticetes (with the exception of the highly specialized *Caperea marginata*).

*Atlas:* The atlas is preserved in SDNHM 80102, 80101 and 83695 (Figure 19; Table 5). The neural arch has a short, wide neural spine that projects somewhat posteriorly. A large foramen is present on each side of the anterior portion of the neural arch. The cerebrospinal artery and an intervertebral vein would have passed through this foramen (Bougetel and de Muizon, 2006). Two smaller foramen are preserved ventral to this opening. The neural canal narrows ventrally, giving it a V-shape. At the midpoint of the neural opening, there are two small, pointed processes protruding medially from the level of the articular surfaces.

The transverse processes are thick and long, extending slightly anteriorly. The dorsal portion of the neural canal overhangs the canal opening (protrudes out over centrum). A thick tubercle is present on the posterior-ventral portion of the neural arch where the transverse processes begins. A subtle ridge is present from this point to the anterior-lateral tip of the transverse process, giving the process the appearance of an anterior ‘twist’. The anterolateral most corner of the process is rounded and positioned anterior and dorsal to the posterolateral most corner of the process (which is also rounded).

The articular surfaces for the occipital condyles are smooth, obliquely oriented, and strongly concave. The surfaces are widely separated dorsally and not in contact ventrally. The articular surfaces for the axis are slightly convex and oriented roughly dorsoventrally. The surfaces are connected at the ventral arch and the midpoint of that arch is anteriorly depressed (for connection with the odontoid process of axis). This transition is smooth, with no visible sutures or points of disconnection between the surfaces. The ventral arch is thick and a posterior tubercle is present.
Figure 19. Posterior view of the atlas of *Balaenoptera colcloughi* (SDNHM 80101 bottom left; 83695 top right; 80102 bottom right) and a minke whale, *Balaenoptera acutorostrata* (SDNHM 23642; top left). Scale bar = 10 cm.

Table 5. Atlas Measurements (cm) for *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurements</th>
<th>SDNHM 80101</th>
<th>SDNHM 80102</th>
<th>SDNHM 83695</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Atlas length</td>
<td>19.5</td>
<td>14.8</td>
<td>18.7</td>
</tr>
<tr>
<td>2. Atlas width</td>
<td>40.8</td>
<td>20.9</td>
<td>32.6</td>
</tr>
<tr>
<td>3. Articular width</td>
<td>21.0</td>
<td>18.3</td>
<td>20.5</td>
</tr>
</tbody>
</table>

See Also: Figure 45, in Appendix A.

*Axis:* The axis is preserved in SDNHM 83695 and SDNHM 80102 (Figure 20; Table 6). The neural canal is ovoid, slightly wider than tall. The neural arch possesses a small neural spine.

The odontoid process is rounded but wider dorsally than ventrally, giving it an upside-down teardrop shape. The odontoid process is well defined. The articular surfaces around the odontoid process are broad and kidney-bean shaped, as well as posteriorly concave. The articular surface with cervical vertebra 3 is roughly rounded (almost heart shaped in SDNHM 83695). It is anteriorly concave.
Figure 20. The anterior side of the axis of *Balaenoptera colcloughi* (SDNHM 83695 top right; 80102 bottom). Scale bar = 10 cm.

Table 6. Axis Measurements (cm) for *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurements</th>
<th>SDNHM 80102</th>
<th>SDNHM 83695</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Axis length</td>
<td>15.1</td>
<td>18.5</td>
</tr>
<tr>
<td>2. Axis width</td>
<td>17.3</td>
<td>20.3</td>
</tr>
</tbody>
</table>

See Also: Figure 46, in Appendix A.

The lateral portions of the parapophyses and diapophyses were broken in both specimens. The transverse processes are posteriorly directed. The dorsal transverse processes (parapophyses) are slightly thinner than the ventral processes (diapophyses).
Cervical vertebrae: All seven cervical vertebrae were recovered for SDNHM 83695 and CV4-7 were recovered with SDNHM 80102 (Figure 21 and 22).

Figure 21. Cervical vertebrae of Balaenoptera colcloughi (SDNHM 80102), including the atlas (A), atlas (B), CV3 (C) and CV7 (D). Scale bar = 10 cm.

The cervical vertebrae are unfused. The neural canal of these vertebrae are roughly triangular in shape in SDNHM 80102. The shape is more ovoid in SDNHM 83695 but this is most likely due to preservational compression. The neural spine is straight (anterodorsally) and protrudes dorsally on the posterior portion of the neural arch. Each vertebra has a wide, rounded postzygapophyses that overlaps with posterior cervical vertebra (Figure 22). Cervical vertebra 3 also possesses a prezygapophysis that overlap with the axis.

The transverse processes are anterolaterally oriented. In cervical vertebra 3, the processes are thin. In cervical vertebra 6 and 7, the transverse processes become ventro-dorsally wider, particularly near the centrum. The centrum becomes more rounded in the posterior cervical vertebrae, in all are slightly wider than tall. The cervical specimens for SDNHM 80102 either had unfused epiphysyal plates or where missing plates altogether. The (anterior-posterior) width of the centrum is larger in cervical vertebra 7 than vertebra 3.

Thoracic vertebrae: Seven thoracic vertebrae and five ribs are preserved in SDNHM 80102, the majority articulated with corresponding ribs (Figure 23). Thoracic vertebrae were identified based on attachment (or proximity to) ribs recovered for the species (Buchholtz, 2007).

These ribs remain in situ in a plaster jacket with corresponding dorsal vertebra and, due to crushing of the elements, are unable to be separated. However, based on the association of the ribs and the general structure of the vertebra, it is likely that these represent thoracic vertebra for this specimen. The neural spines are tall and the neural arch is
Figure 22. Complete cervical vertebral series of *B. colcloughi* (SDNHM 80102) in lateral view. Scale bar = 5 cm (Anterior is to the left.)
Figure 23. Thoracic vertebrae and associated ribs of *B. colcloughi* (SDNHM 80102). Scale bar = 10 cm.

triangular. There appears to be a posterior inclination of the neural spines. The transverse processes are long and uniform in width. These processes also appear to have a posterior inclination. The centra of the vertebrae are also nearly heart-shaped. Many are missing their epiphyseal plates and numerous isolated plates were recovered with this specimen.

Thoracic vertebrae were also recovered for SDNHM 80101 (Table 7). There are five vertebrae that can be identified as thoracic vertebrae in SDNHM 80101, but it is possible that there are more. Similar vertebrae make determining series boundaries difficult in cetaceans.

Table 7. Vertebræ Measurements (cm) for *Balaenoptera colcloughi* (SDNHM 80101)

<table>
<thead>
<tr>
<th>Measurement</th>
<th>TV29</th>
<th>TV27</th>
<th>TV?24</th>
<th>LV20</th>
<th>LV17</th>
<th>LV14</th>
<th>CV8</th>
<th>CV5</th>
<th>CV1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertebra length</td>
<td>&gt;12.5</td>
<td>&gt;13.2</td>
<td>&gt;14.1</td>
<td>21.8</td>
<td>22.6</td>
<td>20.3</td>
<td>20.6</td>
<td>12.4</td>
<td>5.8</td>
</tr>
<tr>
<td>Vertebra width</td>
<td>&gt;36.8</td>
<td>60.1</td>
<td>&gt;47.7</td>
<td>54.9</td>
<td>46.1</td>
<td>41.7</td>
<td>15.3</td>
<td>12.1</td>
<td>5.1</td>
</tr>
</tbody>
</table>

*Note.* > indicates process is broken and would have made the measurement larger. The identity of the position of the vertebra are tentative.

See Also: Figure 47, in Appendix A.
(Buchholtz, 2011). The poor preservation of the neural arch and transverse process of the vertebra in these regions in *B. colcloughi* further obscures the exact transition. A high thoracic count is seen in extant balaenopterids (*B. musculus, B. physalus*; True, 1904), however it is likely that either some of this section is missing or just unable to conclusively identify as thoracic vertebra.

Unfortunately, the thoracic vertebrae of SDNHM 80101 are missing the neural arch. Most are also missing the lateral ends of the transverse processes. The few vertebrae that do possess transverse processes are convex. These vertebrae are at the anterior end of the column. The anterolateral corner of the transverse process is located dorsally in relation to the posterolateral corner. The process itself is relatively straight, with the lateral ends just slightly ventral to the connection of the process to the centrum. The centra are heart-shaped.

Five thoracic vertebrae were also associated to SDNHM 83695. Though these are still in preparation, the general features noted above are observed in these specimens. The transverse processes of these vertebra are slightly dorsally oriented (as well as straight laterally directed).

*Lumbar vertebrae:* Lumbar vertebrae were preserved in SDNHM 80102 and SDNHM 80101. Two (provisional) lumbar vertebrae were also recovered with SDNHM 83695. The spinous processes of the lumbar vertebrae are posteriorly inclined. The transverse processes are oriented laterally and horizontally.

Four isolated vertebrae of SDNHM 80102 are tentatively placed in this series based on the general shape of the centrum and lack of ribs (Buchholtz, 2007). These four are missing all processes, and are simply represented by centra. The centra are ovoid shape and wider than tall.

There are twelve lumbar vertebrae associated with SDNHM 80101 (Table 7). These have rounded centra with laterally long and relatively straight lateral projecting transverse processes. The lateral ends of the process are slightly rounded and the neural arch is relatively tall. There is a slight posterior inclination in the neural arch of this new species.

*Caudal vertebra:* Ten caudal vertebrae are preserved in SDNHM 80101 (Table 7). Chevrons are associated with nine of these vertebrae. The anterior caudal vertebra has a short neural arch and long transverse processes. Posteriorly, the caudal vertebrae become more compact, with all processes becoming smaller, until completely absent in the last five vertebrae. Large foramen are preserved on the dorsal and ventral margins of the vertebrae. The caudal vertebrae are generally round while last two caudal vertebrae are more squarer than rounded (Figure 24). The centrum of the last vertebra is slightly medially concave.
Chevrons: There are nine chevrons associated with the caudal vertebrae of SDNHM 80101 (Figure 25). The largest in size is the second from anterior, followed by the third from anterior. The first (anterior) Chevron is triangular shaped, which makes a V-shape with a strong posterior inclination ventrally. The dorsal portion is wider (anteroposteriorly) than the ventral portion. The second and third Chevron are broad dorsally and ventrally, and is thinnest at the medial portion of the bone. The dorsal margins are rounded and smooth. These represent the connection with the corresponding caudal vertebra. In all chevrons, the two dorsal projections are generally v-shaped and about the same width apart. These dorsal margins remain roughly the same size throughout the chevrons as well, and are flared slightly in the middle.

Ribs: Thirteen ribs were recovered for SDNHM 80101, nearly all appearing to belong to the right side of the animal, with the exception of the first rib, for which
two (one from each side) are associated with the specimen. Many of these ribs were nearly complete, or missing just the head of the rib.

The first rib from both sides of the animal are preserved. This rib is easily diagnosable, as it is much wider and flattened (in lateral view) compared to the other ribs (Figure 26).

![Figure 26. First rib (top), middle rib (tentatively identified as 5th) and a posterior rib (bottom) from the right side of Balaenoptera colcloughi (SDNHM 80101). Scale bar = 15 cm.](image)

The remaining ribs are generally long and thin (Table 8). Thin sulci are preserved on these ribs. The anterior ribs are circular in cross section, while the posterior ribs are relatively flattened. The ribs are single-headed. The head of the ribs are small with a long neck. The neck of the posterior ribs is relatively uniform in width and the dorsal curve is nearly straight.
Table 8. Rib Measurements (cm) for *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Rib 1</th>
<th>Rib 3</th>
<th>Rib 6</th>
<th>Rib 9</th>
<th>Rib 13</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>71.9</td>
<td>82.2</td>
<td>94.3</td>
<td>102.0</td>
<td>100.6</td>
</tr>
<tr>
<td>Width</td>
<td>7.7</td>
<td>3.7</td>
<td>4.3</td>
<td>3.5</td>
<td>6.9</td>
</tr>
</tbody>
</table>

See Also: Figure 48, in Appendix A.

Ribs from the posterior portion of the cage lack a capitulum and would have articulated with the vertebra with only the tuberculum. The angle of curvature in the ribs is less pronounced in the posterior region.

It appears the rib count in *B. colcloughi* is higher than *Piscobalaena nana*. The new species appears to have 13 ribs on each side. A specimen of *P. nana* was found with 11 ribs on each side (Bouetel and de Muizon, 2006). However, it is possible that *P. nana* also possessed this many ribs, due to the lack of a diagnosible first rib. Extant balaenopterids also have a higher rib count than *P. nana, with* 14 ribs in *B. physalus* and *M. novaeangliae* (True, 1904).

Scapula: Both scapula were recovered with SDNHM 83695. The right scapula is nearly complete (Figure 27) and only the ventral and dorsal portion of the left scapula is preserved. The scapula of mysticete whales is relatively simple (Benke, 1993) and lacks a distinct scapular spine. The glenoid fossa is rounded and convex. The rostral and caudal borders are relatively straight.

The scapular notch is present, located anterior to the acromion process. The acromoin and coracoid process are both present. The acromion process is long (Table 9) and extends ventrally, slightly curving dorsally. The coracoid process is short and thick. The glenoid fossa is oval shaped and curved dorsally.

The presence of a coracoid process of the scapula is one of the major distinctions between species of *Megaptera* and *Balaenoptera*. The presence of this feature in the new species is a plesiomorphy shared with *Balaenoptera* and Eschrichtiidae. The posterior edge of the scapula in *B. colcloughi* is uniformly straight, which differs from the medial curvature of *M. novaeangliae* (Cooper, 2004).

Humerus: The humerus (SDNHM 83695) is shorter than the radius (Table 10; Figure 28), massive and transversely flattened. It has a large and rounded articular head. The head is oriented vertically. The greater tubercle is directed antero-medially relative to the head and protrudes anteriorly as a rounded, large knob. It is located distal to the head and is much smaller in size. There do not appear to be any tuberosites on the proximal epiphysis, however this area is eroded. The medial side of the proximal end is relatively flat. The distal epiphysis flares.
Figure 27. Medial view of the right scapula of *B. colcloughi* (SDNHM 83695). Scale bar = 15 cm.

Table 9. Scapular Measurements (cm) for the Right Scapula of *Balaenoptera colcloughi*

<table>
<thead>
<tr>
<th>Measurement</th>
<th>SDNHM 83695</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Width of scapula</td>
<td>52.1</td>
</tr>
<tr>
<td>2. Length of scapula</td>
<td>&gt; 33.8</td>
</tr>
<tr>
<td>3. Length of acromion process</td>
<td>11.9</td>
</tr>
<tr>
<td>4. Width of acromion process</td>
<td>5.4</td>
</tr>
<tr>
<td>5. Length of coracoid process</td>
<td>4.2</td>
</tr>
<tr>
<td>6. Width of coracoid process</td>
<td>5.8</td>
</tr>
</tbody>
</table>

See Also: Figure 45, in Appendix A.
Table 10. Forelimb Measurements (cm) for *Balaenoptera colcloughi* (SDNHM 83695)

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Left</th>
<th>Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Humerus length</td>
<td>27.5</td>
<td>27.7</td>
</tr>
<tr>
<td>2. Humerus condylar width</td>
<td>14.8</td>
<td>15.3</td>
</tr>
<tr>
<td>3. Humerus distal width</td>
<td>14.5</td>
<td>14.5</td>
</tr>
<tr>
<td>4. Ulna length</td>
<td>34.6</td>
<td>36.8</td>
</tr>
<tr>
<td>5. Ulna width</td>
<td>5.6</td>
<td>5.4</td>
</tr>
<tr>
<td>6. Radius length</td>
<td>35.1</td>
<td>30.6</td>
</tr>
<tr>
<td>7. Radius width</td>
<td>6.7</td>
<td>7.5</td>
</tr>
</tbody>
</table>

See Also: Figure 46, in Appendix A.

anterior-posteriorly relative to the shaft. There is no deltopectoral crest present on the anterior portion of the shaft.

The distal facets are well preserved and are relatively smooth and flat. The distal end forms a slight V-shape (convex). A bony septum between the radial and ulnar facets is not present, however, this may be due to preservation.

The distal end of the humerus is somewhat V-shaped, a derived character of balaenopterids. This orientation and the flatness of the radial and ulnar facets indicate an immobile elbow joint (Cooper, 2004), a characteristic of all crown mysticetes. This restricts the movement of the flipper and is likely connected to feeding styles of these whales.

Interestingly, the only difference between *Megaptera* and *Balaenoptera* is the orientation of the articular head. In most balaenopterids, the capitulum is vertically oriented, while in the humpback it is angled, which is also seen in balaenids. Probably the most diagnostic feature of the humpback whale is the flippers and the greater range of motion at the elbow joint in *Megaptera* compared to other balaenopterids (Cooper, 2004).

Another humeral character is the lack of a deltopectoral crest on the anterior portion of the humeral shaft (diaphysis). ‘Cetotheres’ (e.g., *D. hiatus*, *Pelocetus calvertensis*, *Thinocetus arthiritis*) and *E. whitmorei* both possess this crest. Extant mysticetes lack a crest. The only recognized fossil mysticetes to lack the crest are *Balaena ricei* and ‘*M.’ hubachi’ (Cooper, 2004). This is another feature that unites ‘*M.’ hubachi’ and *B. colcloughi* and supports a crown placement of this new taxon.

*Ulna*: The olecranon process of the ulna of SDNHM 83695 is reduced. Despite breakage on the distal end, the vertical projection of this process descends from the level of the distal epiphysis. The shaft is ovoid in cross section, transversely flat and convexly bowed. The ulna is thinner and flatter than the radius.
Figure 28. Forelimb elements (humerus, radius, ulna, carpal, metacarpals and phalanges) of SDNHM 83695. Abbreviations in Methods. Scale bar = 15 cm (Anterior is towards the top of the page).
(Figure 28; Table 10). Despite the olecranon process of the ulna being broken in the new species, it appears reduced and potentially descending from the level of the distal epiphysis. These features are unique (among balaenopterids) to *M. novaeangliae*, while *Balaenoptera* (fossil and extant) possess a hatchet-like olecranon process.

**Radius:** The radial shaft is ovoid in cross section, longer anterior-posteriorly than wide (SDNHM 83695; Table 10). The anterior end of the bone is slightly bowed posteriorly, forming a gently sloping convex anterior edge. It is generally flat medio-laterally. The radius is wider transversely and generally larger than the ulna (Table 10, Figure 28). The proximal facet for articulation with the humerus is slightly convex but generally flat. The radial shaft is slightly larger than the ulnar shaft in medio-lateral diameter (Table 10), a characteristic of faster swimmers, like the rorquals (Cooper et al., 2007).

**Carpals, Metacarpals, Phalanges:** One carpal, six metacarpals and nine phalanges were recovered for SDNHM 83695. The rounded, ovoid carpal bone (Figure 28) is tentatively identified as the lunate. The medial and lateral sides are nearly flat and the articular surfaces are rugose in texture. Three metacarpals and five phalanges were identified as belonging to the right manus, and three metacarpals and four phalanges to the left manus. Based on the larger size and shape, it is likely that most of the metacarpals from both flippers are represented. The phalanges preserved likely represent the proximal phalanges due to their thickness and difficulty distinguishing between these and the metacarpals. The digits are hourglass-shaped (expanded distal and proximal ends, narrow shaft), a distinctive feature of balaenopterids and clearly suggest the new species is a member of this lineage. The structure of these bones indicates this new species possessed a narrow and elongate flipper with the middle digits tightly appressed (Cooper et al., 2007).

Three phalanges and one carpal were recovered with SDNHM 80101. The phalanges are small, flat and hourglass shaped. Two are more rectangular and flatter than the phalanges of SDNHM 83695, which suggests these were distal phalanges. The carpal SDNHM 80101 is small and rounded, though not nearly as rugose as the carpal of SDNHM 83695. This suggests the carpal of SDNHM 80101 is possibly the scaphoid, though due to its incompleteness, this cannot be confirmed.

**SIZE OF BALAENOPTERA COLCLoughI**

The total length of *Balaenoptera colcloughi* was estimated using equations from Pyenson and Sponberg (2011). These estimates were based on the holotype specimen only,
since it was the only adult specimen and utilized cranial measurements from Table 2 (measures 2, 4, 5, 10, 12). The total length was estimated to be 1114.31 cm. Using the other equation that the authors provided, and based solely on the condylobasal length (Table 2, measure 2), the estimated body length was 1281.01 cm (see Pyenson and Sponberg (2011) for details). Lambert et al. (2010) compiled total lengths for many extinct and extant mysticete taxa, and this data was used and supported by Pyenson and Sponberg (2011).

Compared to measurements of a sample of extinct and extant mysticetes presented in Lambert et al. (2010), *B. colcloughi* is most comparable in total length to the Bryde’s whale, *B. brydei*, which is one of the smaller species of extant Mysticeti. The forelimb measurements of *B. colcloughi* (Table 10) are also comparable in size and proportion to *B. acutorostrata* (Benke, 1993).

Pyenson and Sponberg (2011) used *Balaenoptera siberi* as a proxy fossil taxon for their study because much of the total skeleton is known (from the paratype, Pilleri (1990)). *B. siberi* is roughly equivalent in size (1000-1119 cm) to *B. colcloughi*. Pyenson and Sponberg (2011) suggested the evolution of extremely large body size in mysticetes (> 1500cm) is a recent phenomenon in cetacean history, based on estimated lengths from fossil balaenopterids. The relatively small total length estimate of the Pliocene *B. colcloughi* adds support to this statement.
CHAPTER 4

RESULTS

MORPHOLOGICAL ANALYSES

Parsimony: There were 126 parsimony informative characters in the morphological dataset. Parsimony analysis of the unordered morphological data resulted in sixteen most parsimonious trees, with a tree length (L) of 537 steps (consistency index [CI] = 0.432, retention index [RI] = 0.578, homoplasy index [HI] = 0.568). The strict consensus is shown in Figure 29.

The analysis with 21 ordered characters (see Appendix C) resulted in 486 most parsimonious trees (CI = 0.42, HI = 0.58, RI = 0.59), with L = 559. The topology was similar to that found in the unordered parsimony analysis. The only difference in relationships between the ordered and unordered results is the weakly supported (BS = 59) sister relationship between ‘cetotheres’ Aglaocetus patulus and Diorocetus hiatus, which was not recovered in the ordered analysis. Character weighting and ordering does not appear to have much of an effect on the relationships among balaenopterids, at least as found in this study. The relationships discussed below will refer to the unordered analysis.

The relationships between many of the taxa are consistent with previous phylogenetic hypotheses. Crown Mysticeti and Balaenidae (BS=100) were recovered as monophyletic and both were strongly supported. The clade containing Caperea marginata and the balaenids is strongly supported (BS = 98). A monophyletic Eschrichtiidae (BS=58) was weakly recovered sister to a weakly supported clade containing Archæbalaenoptera castriarquati and Protororqualus cuvieri. Balaenopteridae is weakly supported as monophyletic, to the exclusion of these two taxa.

A paraphyletic Balaenoptera was found. An alternative possibility of this result is that it could be interpreted to indicate that B. siberi and the members of the unresolved clade are not members of Balaenoptera, which is unlikely. This is a strong reflection of the diversity of morphologies exhibited by many balaenopterids, a reflection observed in the relationship of Megaptera novaeangliae in an unresolved clade with Diunatans luctoretemergo, Eobalaenoptera harrisoni, ‘Megaptera’ hubachi, and Balaenoptera.
Figure 29. Strict consensus of the unordered parsimony analysis for morphological characters only. Bootstrap support values are shown below the node, when present. Those without values have a bootstrap value below 50.
colcloughi. The extinct balaenopterid, *Balaenoptera siberi*, is weakly supported as sister to this unresolved clade. The unresolved taxa were clearly separated from crown *Balaenoptera*. The recently described extinct species from Europe, *Uranocetus gramensis*, was found nested within crown *Balaenoptera*, sister to *Balaenoptera acutorostrata* + *Balaenoptera bonaerensis*. This relationship is unique to this analysis and is weakly supported. The minke whale relationship was well supported (BS=93).

Thought to be an early representative of the balaenopterid lineage, ‘*Megaptera*’ *miocaena* was found removed from *Balaenoptera*, (and Balaenopteridae), sister to *Plesiobalaenoptera quarantellii*. The ‘cetotheres’ sampled in this matrix were found outside of Balaenopteroidea.

**Bayesian Inference:** The mean values of the two runs from the Bayesian analysis of the unordered morphological matrix were roughly the same. The average arithmetic mean was -1991.92 and the harmonic mean was -2839.69. The strict consensus tree of the two runs is shown in Figure 30.

The relationships found in the Bayesian analysis are similar to those of the parsimony analyses, with a few exceptions. Again, a close relationship of *C. marginata* + Balaenidae is well supported (Posterior Probability (PP) = 1.0), as is the clade containing the balaenids (PP = 0.98). *Cetotherium rathkii* and *Mixocetus elysius* are sister species (PP = 0.91) and found sister to an unresolved clade containing the balaenopteroids.

The unresolved node in the consensus tree contains many (22/33) of the taxa sampled in this study. There was some resolution within this weakly supported clade. Eschrichtiidae is recovered as monophyletic but not strongly supported (PP = 0.89), however is located in the unresolved clade with Balaenopteridae. *Piscobalaena nana* was also found within this unresolved group, which is a unique topology to this analysis. There was some resolution of relationships within Balaenopteridae. A sister relationship between *Eobalaenoptera harrisoni* and *P. cuvieri* is somewhat supported (PP = 0.60). Also, the minke whales were decently supported (PP = 0.88). A novel finding of this analysis was the weakly supported relationship (PP<0.50) of *Balaenoptera borealis* sister to the minke whale clade.

The largest difference between the Bayesian and parsimony analyses of the morphological data is the relationships of stem balaenopterids and the ‘cetotheres’. The sister clade of *A. patulus* and *D. hiatus* is in an unresolved clade with the balaenids + *C. marginata*
Figure 30. The 50 percent majority rule consensus phylogeny of the two simultaneous Bayesian runs of the morphology data. Support values are represented by posterior probability values below the nodes.
clade, outside of crown Balaenopteroidea, a unique placement in this analysis (versus parsimony).

**Combined Analyses: Morphology and DNA**

*Parsimony:* The unordered combined analysis resulted in 648 most parsimonious trees (TL = 7940, CI = 0.62, RI = 0.45, HI = 0.38). A strict consensus is shown in Figure 31.

Interestingly, in this topology, all ‘cetotheres’ (both clades) are found in crown Mysticeti. Most of the other relationships from this analysis are congruent with the morphology only analysis. *Caperea marginata* is found sister to the balaenids (BS=99). *Eschrichtius robustus*, the extant gray whale, is within an unresolved clade with Balaenopteridae. This is not completely unexpected, not only due to the lack of resolution overall, but also because a paraphyletic Balaenopteridae is a common finding with molecular studies of mysticetes (e.g. McGowen et al., 2009; Dornburg et al., 2012). Eschrichtiidae is monophyletic although weakly supported (BS=60). The minke whale relationship, as well as the clade containing *Balaenoptera musculus* + *Balaenoptera edeni* + *Balaenoptera omurai* + *Balaenoptera borealis* were again recovered. The relationship of *M. novaeangliae* + *B. siberi* + ‘M.’ hubachi + *B. colcloughi* was also recovered. Novel to the total evidence analysis is the strongly supported inclusion of *Balaenoptera physalus* in this clade. This is a direct result of the inclusion of molecular data, because this is a very strongly supported relationship in published molecular analyses (e.g. Rychel et al., 2004; Sasaki et al., 2005), though not always recovered in morphological analyses (e.g. Bouetel and de Muizon, 2006; Marx, 2010).

*Bayesian:* The Bayesian total evidence analysis topology was mostly consistent between the two consecutive runs. The average arithmetic mean was -129610.96 and the harmonic mean was -159701.72. Based on the output from MrBayes, it should be noted that this analysis might not have fully converged at fifteen million generations. The reason for this is the large difference between the likelihood values of this run, as well as the lack of stationarity displayed by the runs in the program Tracer (see Methods). The analysis was stopped at this point due to time constraints of this project and the limitations of computational energies (i.e. usage limitations on time in CIPRES Portal). The consensus topology of the runs is shown in Figure 32.

The topology is identical to the consensus of the morphology-only Bayesian analysis, and consistent with the total evidence parsimony analysis. The major difference between
Figure 31. Strict consensus of the concatenated morphology + DNA parsimony analysis. Bootstrap support values are shown below the node, when present.
Figure 32. The majority rule consensus tree from the total evidence Bayesian analyses. Posterior probability values (supported by >50%) are shown below the node.
these topologies is seen in the resolution surrounding the unresolved clade containing the balaenopterids.

The ‘cetotheres’ *A. patulus* and *D. hiatus* were not recovered as sister species, but *C. rathkii* and *M. elysius* were (PP=85)). These taxa were found outside the well-supported (PP=81) unresolved clade that contains crown Mysticeti.

There was little resolution within crown Mysticeti, with the exception of a few relationships. The close relationship between *C. marginata* and the balaenids was well supported (PP=99) and the balaenid clade, though an unresolved clade, was also well supported (PP=99). The sister relationship of the eschrichtiids was also well supported (PP=93). The minke whales were recovered as sister (PP=99) and a sister relationship between *B. edeni* and *B. borealis* was also recovered (PP=75).

**DIVERGENCE DATING**

The data sets (mitochondrial and nuclear) of McGowen et al. (2009) were analyzed independently to ensure that they produced the same topology prior to the divergence dating analyses (Figure 33). The relationship of *Eubalaena* and *Balaena* were enforced as a sister taxa, to ensure testing of one topology. In these topologies, clade relationships follow the standard extant relationships, i.e. Balaenopteridae include all members of *Balaenoptera* and *Megaptera*, Eschrichtiidae includes *Eschrichtius*, Balaenidae includes *Balaena* and *Eubalaena*, and Neobalaenidae is represented by *Caperea*. In the results presented here, the typical molecular phylogenetic relationship of a paraphyletic Balaenopteridae due to the nesting of *Eschrichtius* within the clade.

The results of the divergence dating analyses are presented below by the dataset analyzed and the fossil information used to calibrate each analysis (FS1 and FS2, see Methods). The ages reported are the mean age estimates, followed by the 95% highest probability density (HPD) range, which represents a confidence interval in these analyses. All age estimates are in Ma (millions of years).

Full results for each analysis can be found in Appendix E, Tables 13-22.

**McGowen et al. (2009) Mitochondrial Dataset:**

The mitochondrial dataset of McGowen et al. (2009) was utilized in multiple analyses in the current study to test the effects of outgroups and external calibrations on mysticete divergence dating. The topology recovered was
consistent across runs and includes a paraphyletic Balaenopteridae with respect to Eschrichtiidae and C. marginata sister to the balaenopteroids.

**Fossil Set 1 Mysticeti Only:** The divergence age of Mysticeti was estimated at 29.062 Ma (28.04-30.96 HPD) with a divergence of balaenopterids around 16.08 Ma (10.72-21.31 HPD). The divergence of the minke whales (*B. acutorostrata* and *B. bonaerensis*) was recovered at 5.94 Ma (3.09-8.54 HPD).

This analysis had relatively strong ESS values for the calibrated nodes, however both the posterior and prior distributions had low values (Table 13 and 14, in Appendix E).

**Fossil Set 2 Mysticeti Only:** The divergence ages obtained from this analysis (Figure 34; Table 13 and 14, in Appendix E) were slightly older than those found in the equivalent analysis using the first fossil calibration set. Mysticeti was found to have diverged 29.06 Ma (28.75-31.08 HPD) and Balaenopteridae originated 16.46 Ma (11.17-21.72 HPD). The minke whales diverged around 6.07 Ma (3.37-8.87 HPD).

The ESS values for this run were greater than the previous run, except for the posterior and prior values, which are still poor.

**Fossil Set 1 with full taxa set:** This analysis (Figure 35; Table 15 and 16, in Appendix E) recovered a divergence age for Neoceti of around 36.31 MA (34.25-39.87 HPD). Mysticeti originated 28.64 Ma (28.04-29.58 HPD) and
Figure 34. Topology and resulting divergence age estimates for Mysticeti from McGowen et al. (2009) mitochondrial FS2 analyses. Blue bars represent the 95% HPD for each node estimate for the full taxon sample and orange bars are the 95% HPD of the Mysticeti only analysis. Not all nodes are shown for clarity.

Figure 35. Topology and estimated divergence ages of McGowen et al. (2009) mitochondrial FS1 analysis. The blue bars represent the 95% highest probability density for each node estimate. The numbered circles indicate a fossil calibration at that node.
Balaenopteridae 11.77 Ma (8.84-14.87 HPD). Minke whale species diverged from one another 4.53 Ma (2.41-6.74 HPD).

The ESS values for this run were good, with the exception of Balaenopteridae. The prior distribution and Neoceti values were < 200, but both were greater than 100.

Fossil Set 2 with full taxa set: The divergence ages obtained from this analysis (Figure 35; Table 15 and 16, in Appendix E) were nearly identical to the first fossil set, with the former resulting in slightly younger age estimates.

In this analysis, Neoceti is hypothesized to have originated 34.92 Ma (30.62-39.52 HPD). Mysticeti diverged 28.58 Ma (28.03-29.45 HPD) and Balaenopteridae diverged at 11.46 Ma (8.82-14.3 HPD). The minke whale lineage (*B. acutorostrata* and *B. bonaerensis*) diverged from one another 4.53 Ma (2.41-6.74 HPD).

The ESS values were generally worse than in the first fossil set, with the exception of Balaenopteridae and Mysticeti.

McGowen et al. (2009) combined nDNA dataset:

This dataset included the nuclear data from the McGowen et al. (2009) supermatrix analysis. Due to time constraints and the large size of the matrix, the ESS values for these analyses are poor and external calibrations could not be tested. The topology produced in this analysis is identical with that of the mitochondrial only analysis.

Fossil Set 1: The divergence ages obtained from this analysis (Figure 36) were generally older than those produced in the mitochondrial analyses. The divergence of Mysticeti is dated at 30.03 Ma (28.02-34.33 HPD) and Balaenopteridae at 9.58 Ma (7.344-13.447 HPD). The minke whales diverged approximately 5.14 Ma (1.88-9.06 HPD).

The ESS values of this analysis were very low. The lone exception is the value of the Cetacea-Artiodactyl calibration.

Fossil Set 2: The divergence ages obtained here (Figure 36) were noticeably younger in this analysis than that of the first fossil set. The divergence of Mysticeti was estimated at 30.93 Ma (28.05-43.61 HPD) and Balaenopteridae originated 7.71 Ma (6.073-10.554 HPD).

The divergence of the minke whales occurred at 3.31 Ma (1.14-6.08 HPD). The ages in this analysis of the split of *Balaenoptera* (and *Megaptera*) are significantly younger than in the first fossil calibration set (Appendix E).

The ESS values of this analysis are poor and in general produced lower values than the FS1 run. The exception is the ESS of Neoceti and the prior distribution, although the values are still low.
Figure 36. Topology and resulting age estimates for Mysticeti from McGowen et al. (2009) combined analyses. Blue bars represent the 95% HPD for each node estimate for the FS1 analysis and orange bars are the 95% HPD of the FS2 analysis. Not all nodes are shown for clarity.

**RAG1 Dataset**

The RAG1 dataset was used to test the effect of external calibrations on a nuclear gene dataset of mysticetes, thus this dataset was run under both fossil calibrations schemes, with and without the external calibration. Differences in ages were observed as a factor of the external calibration, not due to use of a single locus. The topology of this analysis was consistent with the McGowen et al. (2009) combined nuclear analyses, but slightly different than those produced from the molecular only runs (Figure 33). The primary difference is in the position of *C. marginata*, which was forced in this analysis as sister to the balaenids given the topology produced in the phylogenetic section of this study. Eschrichtiidae was recovered sister to Balaenopteridae, and *Balaenoptera* was found to be paraphyletic due to *M. novaeangliae*, which is nested within the clade and sister to *B. physalus*. This topology was recovered for all RAG1 dataset analyses.

*Fossil Set 1:* Neoceti diverged at 35.25 Ma (34.24-37.15 HPD), with the origination of Mysticeti approximately 29.41 Ma (28.04-32.27 HPD). Balaenopteridae diverged from other mysticetes at 9.13 Ma (8.46-12.98 HPD). The minke whale lineage diverged from other balaenopterids at 2.17 Ma (0.2-6.8 HPD).

The posterior distribution and likelihood values of this run were supported by high ESS, though the prior density had a weak ESS.
**Fossil Set 2:** The analysis of the RAG1 dataset using FS2 (Figure 37) produced similar results to the first fossil set, with younger mean dates and slightly smaller confidence intervals. Neoceti diverged 31.92 Ma (30.02-36.26 HPD), with Mysticeti diverging 29.07 Ma (28.03-30.642 HPD). Balaenopteridae diverged from other mysticetes at 7.9 Ma (6.02-11.92 HPD). Minke whales diverged from other balaenopterids 1.76 Ma (0.01-5.67 HPD).

![Figure 37. Large-scale view of the RAG1 FS2 analysis without the external calibration. Blue bars represent the 95% HPD for each node estimate. The numbered circles indicate a fossil calibration at that node.](image)

The posterior and likelihood values of this run were supported by high ESS, albeit slightly lower values than the FS1 run. The prior density was much higher in this run, however (180.09 versus 19.47 in FS1).

**Fossil Set 1 + External Calibration:** Compared to FS1 without the external calibration (*Juramaia sinensis*), the age estimates produced with the external calibration were slightly older within Cetacea. The origin of Neoceti was dated to 35.32 Ma (34.24-37.37 HPD), with Mysticeti diverging 29.44 Ma (28.03-32.326 HPD). Balaenopteridae was recovered as originating 9.39 Ma (7.34-13.85 HPD) and minke whales appeared 2.53 Ma (0-7.39 MA).
Though the mysticete divergence ages were little affected, the stationarity of this run was better than the run without the external calibration. The ESS values for this analysis were higher, and the ESS of the prior was much closer to a desirable value (138.35).

*Fossil Set 2 + External Calibration:* The divergence ages obtained in this analysis (Figure 38) were older than the run of this fossil set with no external calibration. However, the divergence ages here (FS2) were younger than the divergence ages produced with the external calibration of the first fossil set (Figure 39).

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**Figure 38.** Large-scale view of the RAG1 FS2 analysis including the external calibration (green circle). Blue bars represent the 95% HPD for each node estimate. The numbered circles indicate a fossil calibration at that node, the ‘E’ represents the calibration of *J. sinensis.*

The divergence of Neoceti is recovered as 32.14 Ma (30.02-37.12 HPD) and the origin of Mysticeti was dated to 29.09 Ma (28.04-30.75 HPD). Balaenopteridae is found to have originated 8.11 Ma (6.05-12.56 HPD) and the divergence of the minke whales is estimated at 1.88 Ma (0.4-5.81 HPD).

Interestingly, the ESS values of the FS2 external runs were lower in the cetacean divergences than in the FS1 external run, however the opposite is observed in the values of
Figure 39. Topology and resulting age estimates for Mysticeti from the RAG1 analyses. Blue bars represent the 95% HPD for each node estimate for the FS1 plus *J. sinensis* analysis and orange bars are the 95% HPD of the FS2 plus *J. sinensis* analysis. Not all nodes shown for clarity.

the more inclusive clades (i.e. Placentalia and Cetancodonta). Also, the value for Mysticeti is greater in the second fossil set.
CHAPTER 5

DISCUSSION

CLADE MEMBERSHIP OF BALAENOPTERIDAE

The relationships of the mysticete clade, Balaenopteridae, have been ambiguous to researchers and recent focus has involved the fossil taxa of this clade. The results presented above recovered some consistent relationships across the analyses while other novel relationships were also found.

Broad scale mysticete relationships recovered in this study are largely congruent with previous hypotheses. One such relationship is the finding of a monophyletic Balaenidae. *Balaenella brachyrrhynus* changed positioned within the balaenids (sister to *Eubalaena glacialis* or sister to *E. glacialis* + *Balaena mysticetus*) but was always consistently across analyses (and well supported) within Balaenidae.

The divergence of Balaenoidea (*Caperea marginata* + Balaenidae) and Balaenopteroidea (*Eschricthius robustus* + Balaenopteridae) within crown Mysticeti is documented but not well supported in most analyses in this study, except for the total evidence parsimony analysis (BS=97). This is in contrast to the hypothesis of a close relationship between *C. marginata*, Eschrichtiidae, and Balaenopteridae that is typically recovered in molecular and total evidence analyses (Deméré et al., 2008; McGowen et al., 2009: see Marx [2010] for discussion). However, the evidence supporting this relationship from the Bayesian analyses of the current study is weak, due to the lack of resolution at this node.

Balaenopteroidea, the clade that contains the most recent common ancestor of Eschrichtiidae and Balaenopteridae and all their descendants, is recovered in all analyses. From this study, Balaenopteroidea is supported by three unequivocal synapomorphies: 1 (0≥1) slightly dorsoventrally arched rostrum, 2 (0≥1) narial fossa at level of antorbital notch, 61 (0) ovoid tympanic bulla, 76 (0≥2) supraorbital process of frontal abruptly deflected ventrally from cranial vertex.
According to the parsimony morphology-only analysis (the preferred topology of this study), Balaenopteridae is defined as the lineage that included the most recent common ancestor of *P. baulinensis* and *B. acutorostrata*, and all of its descendants. Balaenopteroidea would then be defined as the lineage that included the most recent common ancestor of *E. robustus* and *B. acutorostrata*, and all its descendants.

Balaenopteridae was recovered as a weakly supported monophyletic group in the morphology-only parsimony analysis but not recovered in the other analyses (due to lack of resolution), though the paraphyletic group recovered was moderately supported in the Bayesian analyses (PP = 0.68, 0.81). This clade is supported by five unequivocal synapomorphies: 10 (0≥3) long overlap of APM and AWP, 43 (0≥3) numerous ventral throat grooves that extend past throat region [extant], 65 (0≥3) anterolateral shelf/ridge present on tympanic bulla, 66 (0≥1) thin anterior lip of conical process, 97 (0≥1) tongue reduced and predominantly composed of connective tissue [extant].

These findings, however, are not well supported by the combined DNA + morphology analyses (both parsimony and Bayesian), in which Balaenopteridae is found to be paraphyletic. This paraphyly of Balaenopteridae is due to the inclusion of Eschrichtiidae, a topology that often results from molecular analyses (e.g. Rychel et al., 2004; McGowen et al., 2009). When the molecular data is analyzed separately, *E. robustus* was found well supported within Balaenopteridae in both the mitochondrial and nuclear datasets (Figure 29), which is consistent with previous molecular studies. The gray whale was consistently found sister to *Eschrichtioides gastaldii*, an extinct member of Eschrichtiidae, and the pair was well supported in all analyses.

Monophyly of *Balaenoptera* is not necessarily supported in these analyses. This is largely due to the placement of *Megaptera novaeangliae*, and its close affinity to extinct *Balaenoptera* taxa (i.e. *Balaenoptera siberi* and *Balaenoptera colcloughi*) (see below).

The relationships of extant balaenopterids correspond roughly to the lineages identified in the mitochondrial study of Sasaki et al. (2005). The first lineage (‘Lineage I’) is the well-supported sister relationship of the minke whales (*Balaenoptera acutorostrata + Balaenoptera bonaerensis*). The minke whale sister group relationship was recovered in every analysis conducted in the present study and is well supported by previous
investigations (Deméré et al., 2005; Sasaki et al., 2005; Sasaki et al., 2006; Deméré et al., 2008; McGowen et al., 2009; Marx, 2010; Dornburg et al., 2012).

Another lineage (Sasaki et al., 2005; Sasaki et al., 2006: ‘Lineage III’) recovered here is the close relationship of *Balaenoptera musculus* + *Balaenoptera edeni* + *Balaenoptera borealis* + *Balaenoptera omurai*. These taxa are often recovered together in both molecular and morphological analyses, however the exact relationships among the four are not well supported. Most consistently recovered in this study is the sister group of *B. borealis* + *B. edeni*, with *B. omurai* sister to that clade. *Balaenoptera musculus* is recovered sister to the other three taxa, although the positions of *B. musculus* and *B. omurai* change slightly across the analyses.

The relationship between *Balaenoptera physalus* and *M. novaeangliae* is highly supported in most molecular and combined published analyses (i.e. Rychel et al., 2004; Sasaki et al., 2005; Sasaki et al., 2006; Deméré et al., 2008; McGowen et al., 2009; Dornburg et al., 2012). However, as in this study, this relationship is not always recovered in morphology-only analyses (Bisconti, 2008; Bosselaers and Post, 2010), but cannot be rejected by examining the morphological characteristics themselves. Thus, there is weak support for this lineage (‘Lineage II’; Sasaki et al., 2005; Sasaki et al., 2006), consistent with previous studies. It must be noted that not all previous studies recovered this relationship. In Rychel et al. (2004), for example, not all genes produced this relationship when analyzed individually, though it was strongly supported in the combined analyses.

The sister relationship of *Aglaocetus patulus* and *Diorocetus hiatus*, as well as *Cetotherium rathkii* + *Mixocetus elysius*, were recovered in almost all analyses, and relatively well supported in most (BS >60). In the morphology-only (parsimony and Bayesian) and total evidence parsimony analyses, the ‘cetotheres’ represented in this study were weakly nested within crown Mysticeti. This result agrees with several morphological studies (Steeman, 2007; Kimura and Hasegawa, 2010) that focused on ‘cetotheres’. However, in the total evidence Bayesian analysis, these four taxa are well supported (PP=0.75, 0.78) and found outside of crown mysticetes, a hypothesis supported by many other studies (Geisler and Sanders, 2003; Deméré et al., 2005; Bouetel and de Muizon, 2006; Deméré et al., 2008). Despite this group not being well sampled (and not the focus here) in the current study, it can
be interpreted here that the addition of molecular data (into total evidence analyses) recover a much closer affinity between the extant lineages, to the exclusion of the ‘cetotheres’.

Interestingly, the inclusion of fossil taxa did not have an effect on most of the extant taxa, with the exception of *Balaeoptera physalus*. In the molecular-only parsimony analyses, *B. physalus* is consistently found to be sister to *M. novaeangliae*, and in the combined morphology-only analysis, *B. physalus* is recovered in an unresolved clade with *M. novaeangliae* and a number of fossil taxa. However, in the morphology-only parsimony analysis, *B. physalus* was not found sister, nor phylogenetically close to *M. novaeangliae*. The Bayesian analyses cannot be interpreted to this extent because of the lack of resolution in resulting topologies from both morphology-only and combined.

*Parabalenoptera baulinensis* was strongly recovered as an early member of the balaenopteroid clade. The relative positioning of this taxon is consistent with some previous analyses (Ziegler et al., 1997; Bisconti, 2008, 2010a; Marx, 2010). An exception is Deméré et al. (2005), which weakly recovered *P. baulinensis* within crown Balaenopteridae, sister either to *B. musculus* or *B. physalus* in their total evidence analyses.

The positions of three extinct Italian balaenopterids, *Archaebalaenoptera castriarquati*, *Plesiobalaenoptera quarantellii*, and *Prototorqualus cuvieri* are less clear. All three are recovered among the large unresolved clade in the total evidence analyses. *Prototorqualus cuvieri* falls out as sister to *A. castriarquati* and *Eobalaenoptera harrisoni* when recovered as sister to another taxon. Unfortunately, the holotype specimen of *P. cuvieri* has been lost but the previously published information of the specimen was summarized in a recent review by Bisconti (2007b), with enough information to code this taxon for phylogenetic analysis.

A potential problem taxon is *E. harrisoni*. This taxon was originally described based on partial rostral, petrotympanic, and postcranial material (Dooley et al., 2004). However, more fossil material has since been recovered, though no formal publication has yet been released (Dooley, pers. comm., July 2011). The position of this taxon is highly variable in these analyses and more material will help in understanding its exact relationship among the balaenopterids.

The movement of *E. harrisoni* suggests that it is a “rogue taxa”, which is thought of as a taxon whose position is highly unstable in phylogenetic analyses, but with little effect on
the overall tree score (Thomson and Shaffer, 2010). *Eobalaenoptera harrisoni* is one of the most incomplete taxa in this study (~73%; Appendix F), which is likely to be the reason as to why it is found all over the tree across these analyses. However, more interesting is another potential rogue taxon in this analysis, ‘*M.* miocaena’, which is relatively complete (~35%) for the fossil specimens. This taxon has been previously recommended as in need of taxonomic revision (Deméré et al., 2005; Bisconti, 2010b) and the findings of the current study support this idea.

A few unique relationships were recovered among the balaenopterids. First, *Uranocetus gramensis* was found weakly supported as sister to the minke whales in the morphology-only parsimony analyses. In the Bayesian analyses, the position of *U. gramensis* is found well outside crown Balaenopteridae, which is consistent with the original study of this taxon (Steeman, 2009; Figure 19). Both relationships were weakly supported, so neither relationship can be rejected.

The new balaenopterid species, *B. colcloughi*, is consistently recovered nested with *M. novaeangliae*, albeit weakly supported. These taxa share a number of unique characters, such as a lack of squamosal crease, slender and elongated zygomatic process of the squamosal (both plesiomorphies) and features of the nasals. Though this sister relationship is not well supported in the consensus phylogenies, these taxa are included in the large unresolved clade (with other taxa, see below) in every analysis, found in this clade together more than any other taxon. However, *B. colcloughi* also shares features characteristic of the genus *Balaenoptera*, such as presence of a maxillary pocket, a blunt supraoccipital shield, depressed supraorbital process of the frontal, narrowly separated perilymphatic foramen and fenestrae cochlae of the petrosal. The placement of this new fossil taxon into the genus *Balaenoptera* is supported by the close phylogenetic relationship of *B. colcloughi* to *B. siberi* and *B. physalus*. For example, the presence of a sagittal keel on the anterior half of the nasals is shared with *B. physalus* and *M. novaeangliae*, the only extant balaenopterids possessing this character. This character also is shared with *‘Megaptera’ hubachi* and *B. siberi* in the unresolved clade (and *P. cuvieri, E. robustus, C. marginata* outside the unresolved clade).

An interesting result of this study is the unresolved clade containing *B. colcloughi + M. novaeangliae + B. physalus + Diunatans luctoretemergo + B. siberi + ‘M.’ hubachi*. While this unresolved clade is novel to this study, the general relationship of these taxa to
each other has been recovered in previous analyses. For example, the parsimony morphology analysis of Deméré et al. (2005; Figure 7) recovered a sister group relationship of *B. siberi* + *B. physalus*, sister to ‘*M.’ hubachi*. The strict consensus of their total evidence phylogeny also recovered a similar relationship, with *B. physalus* sister to the humpback (*M. novaeangliae*) and in a clade with *B. siberi* and ‘*M.’ hubachi*. A close affinity between *M. novaeangliae*, ‘*M.’ hubachi, and *B. physalus* has also been recovered by others (Deméré et al., 2008; Bisconti, 2010b). *Balaenoptera siberi* has also been recovered as far inside crown Balaenopteridae, sister to *B. musculus* + *B. omurai* by Marx (2010; Figure 8).

The morphological analysis in the original publication of *D. luctoretemerigo* (Bosselaers and Post, 2010) recovered the taxon as sister to Balaenopteridae (and a monophyletic *Balaenoptera*). They also recovered a monophyletic *Megaptera*, including the humpback and both tentative extinct members, ‘*Megaptera*’ *miocaena* and ‘*M.’ hubachi’. However, taxon sampling was limited and did not include *B. siberi*.

Bisconti (2010b) (Figure 4) recovered a sister relationship between *D. luctoretemerigo* and *B. siberi*, albeit weakly supported. The two taxa were also recovered in an unresolved clade with ‘*M.’ hubachi* (the focus of the study) and all extant balaenopterids, as well as extinct balaenopterid taxa (*A. castriarquati, Parabalaenoptera baulinensis* + *P. quarantellii* and *P. cuvieri*).  

**Character Support for Balaenoptera Colcloughi**

The new taxon, *Balaenoptera colcloughi*, was recovered within an unresolved clade within Balaenopteridae in all analyses of this study. This unresolved clade was united by numerous morphological characteristics and discussion of these is warranted to the understanding of their place within this diverse family of mysticetes. The following discussion of characteristics is based solely on the morphology-only parsimony analysis (Figure 33). It was found that the new species possessed a suite of shared characteristics intermediate between *Balaenoptera physalus* and *Megaptera novaeangliae*.

The characters that distinguish the members of the unresolved clade are found predominantly in the nasal (ch. 3, 4, 5, 7, 19), squamosal (13, 14, 15, 21, 81) and forelimb regions (47, 59). Petrotympanic characters (62, 63, 65, 69, 71, 106, 125) also had an influence on this group of taxa.
Multiple characters of the nasal region unite the taxa in the unresolved clade including *B. colcloughi*. These include the shape of both margins (anterior (4) and posterior (5)), breadth of nasals (3) and presence of a sagittal keel (7). Though not every one of the unresolved clade taxa possesses the same state for all of these traits, each taxon possesses a state that is shared with another taxon in the group.

The squamosal is another important morphologic region in the phylogenetic analyses. One character of interest is possession of a long and slender zygomatic process of the squamosal (21), which is unique to *M. novaeangliae*. The new species described in this study, *B. colcloughi*, also possesses this character. Typical members of *Balaenoptera* have a stockier zygomatic process, though a long, slender process is seen in early toothed and edentulous mysticetes (i.e. *Aetiocetus weltoni, Mauicetus parkii, Eomysticetus whitmorei*).

While characters of the squamosal are frequently used in morphological matrices of previous analyses, there is still much ambiguity on the actual characters utilized in each analysis. Different anatomical terms have been used for the same character, such as the use of the terms squamosal cleft and crease. More detailed description and consistency in use of these characters is necessary to ensure the repeatability of the observations by other researchers.

The zygomatic crest is a feature often noted in character matrices of balaenopterids. Bisconti (2007b) described this character as “dorsal border of the squamosal posterior to the zygomatic process crest-like (states are (0) no and (1) yes)”. Bosselaers and Post (2010) employed possession of a zygomatic crest as a character of *Balaenopteridae* but did not provide a character definition. However, they described the crest in the text of the squamosal description, stating “the mediodorsal edge of the zygomatic process possesses a sharp sigmoid crest that merges posteriorly with the lambdoid crest” (p. 340).

For clarity of discussion, this character is termed the zygomatic crest in this study. Taking the previous definitions into account for consistency, the character is here defined as a sharp crest that is located on the dorsal side of the squamosal along the zygomatic process. The plesiomorphic state is the absence of this character (state 0), with apomorphic characters crest present on dorsal side of squamosal (1) and strongly defined crest on dorsal side of squamosal (2). The minke whales do not possess a crest (state 0), while *B. physalus, B. musculus, and B. omurai, B. siberi, D. luctoretemergo* and *E. robustus* possess a pronounced
crest. Possession of a weaker crest is shared by *M. novaeangliae*, *B. borealis*, *B. edeni*, *B. colcloughi*, ‘*M.’ hubachi’, as well as *C. marginata*.

The squamosal cleft is another feature of interest. The squamosal cleft is previously defined as a posterior extension of the squamosal suture into the squamosal fossa (Deméré et al., 2005). Bosseleurs and Post (2010) described the cleft of *D. luctoretemergo* as running parallel to the parietal squamosal suture, and visible from dorsal view of the skull (p. 340). The presence or absence of the squamosal cleft is coded in Bisconti (2007b: ch. 69) but not discussed in their description.

This study utilizes character (14) from Deméré et al. (2005). The plesiomorphic state (0) is the absence of the cleft, while the apomorphic states describe the contact of the present cleft (contacts pterygoid (1); contacts alisphenoid (2); contacts parietal (3)). The squamosal cleft is present in *M. novaeangliae*, unique among crown balaenopterids. *B. colcloughi* lacks this character, as does ‘*M.’ miocaena*. The biological significance of the interdigitation of the bones in this cleft is not quite understood but in most recent studies of balaenopterids this region is described in detail.

The squamosal crease, a deep flexure in the region of the squamosal fossa (Kellogg, 1924; Deméré et al., 2005; Bisconti, 2006, 2007b; Bosseleurs and Post, 2010) is present in the extant species of *Balaenoptera*. It is not observed in *Megaptera novaeangliae*.

The ventral extension of the squamosal on the medial wall of the temporal fossa in crown mysticetes contacts and in some cases forms the foramen pseudovale (26). The foramen pseudovale is a cranial opening for the mandibular nerve (Mead and Fordyce, 2009) and has been coded as highly variable in previous studies of balaenopterids. The phylogenetic significance of this character is not yet understood, but (as mentioned in the fossil description) has been postulated as an ontogenetically related character. This study supports that finding, as the position of the foramen is polymorphic in *B. colcloughi*. All states are found (variably) among balaenopterids.

The exposure of the alisphenoid in the temporal region (25) is also highly variable among balaenopterids. The alisphenoid is exposed between the squamosal and pterygoid in *B. colcloughi*. This state is observed in most extant balaenopterids, with the exception of *M. novaeangliae*. The exposure of the alisphenoid on the temporal wall is also observed in some ‘cetotheres’ (e.g. *Titanocetus sammarinensis* [Bisconti, 2006]).
Another important morphological region in mysticetes that has been under recent investigation is the petrotympanic complex. This region has been historically important to cetacean evolution (Geisler and Luo, 1996; Luo and Gingerich, 1999; Steeman, 2010; Ekdale et al., 2011), as it provides an opportunity to study the evolution of a specific morphological complex relative to the adaptation of this group to an aquatic lifestyle. This study utilizes 35 of the petrotympanic characters described and used in Ekdale et al. (2011), a comprehensive examination of the morphology of the petrotympanic complex of mysticetes. That study found little resolution within Balaenopteroidea, when constructing a phylogeny exclusively based on petrotympanic characters. It did recover the divergence between balaenoids (Caperea + Balaenidae) and balaenopteroids. Their phylogeny supported the minke sister relationship but also a sister relationship between B. musculus and B. physalus. They conclude that the petrotympanic complex exhibits some phylogenetic signal, especially in the divergence of Balaenoidea and Balaenopteroidea.

The overall phylogenetic pattern in Ekdale et al. (2011) is supported in all analyses of the current study. Twenty-nine percent (38/129) of the characters used in the present study are from the petrotympanic region.

The morphologies displayed by the fossil taxa in the unresolved group including the humpback and fin whale represent a mosaic of primitive and derived traits of balaenopteroids, based on parsimony reconstructions. It is possible to think about these species as snap-shots in evolutionary time. It is known from present day organisms that when populations diverge (on their way to becoming different species), there is a span of time where the morphologies may potentially indicate divergence (Steiper and Young, 2008), while the molecular information indicates that it has not occurred (i.e. morphologically different to distinguish as a species but not reproductively isolated). In other words, there is a gap of unknown amount of time between the molecular divergence of a lineage and the origination of the synapomorphy (Magallón, 2004). Compounding the issue is that there are also differing ideas on the process of speciation, whether the changes between species are bifurcating (two species split from one ancestor that goes extinct) or if the changes are more gradual, with potentially multitudes of morphologies exhibited by a species as a characteristic spreads across a population (i.e. punctuated gradualism; Smith, 1994; de Queiroz, 1998). The speciation process is something that is not observable in the fossil record.
(Magallón, 2004) and paleontological species must be defined in terms of observed morphology while extant species possess other (genetic, ecological) data (Smith, 1994).

Due to this lack of data with fossil species compared to extant taxa, researchers often do not even think about their taxa as in this ‘grey’ area of species divergence. Is it possible that some of the morphologies exhibited in fossil mysticetes may represent this condition? Some Pliocene balaenids are known to display intermediate morphologies compared to the extant genera *Balaena* and *Eubalaena*, but found in close (but tenuous) relationship to the extant lineages (Bisconti, 2005; Churchill et al., 2011). A newly described fossil species of *Eubalaena* (*E. shinshuensis*) could possibly represent this situation, as its morphologies have found it strongly nested in an unresolved clade with the rest of *Eubalaena*. This is additionally relevant because the extant membership of this genus is also recently questioned, with a conflict between the molecular and morphological data in whether or not there are two or three extant *Eubalaena* species (Bisconti, 2005; Churchill et al., 2011).

In terms of *B. colcloughi*, which displays a morphology intermediate between *B. physalus* and *M. novaeangliae* based on the characters presented above, it could be interpreted that this taxon may be an extinct representative of the lineage leading to an extant species, prior to the emergence of the extant species but after the split between the two. Along the same lines, *B. colcloughi* could even be a representative of an ancestral taxon from which these two species diverged. The divergence between the fin and humpback was recovered as 5-12 Ma in the mitochondrial analyses but recovered as a younger range (0.8-8 Ma) in the nuclear data. The nuclear divergence age range spans the late Pliocene, from which *B. colcloughi* is known (2-4 Ma). This does not falsify the hypothesis of *B. colcloughi* as a possible representative of this splitting event. It is interesting to note that *D. luctoretemergo* and ‘*M.’ hubachi’ are also found within the *B. colcloughi* + *M. novaeangliae* + *B. physalus* unresolved clade and, like *B. colcloughi*, are Pliocene aged.

Unfortunately, it is very difficult to test speciation events using the fossil record. Population level studies of fossil taxa require larger sample sizes rarely available to begin to consider such a possibility.
**MEGAPTERA AND BALAENOPTERA**

The humpback whale, *Megaptera novaeangliae*, is the monotypic extant representative of the genus *Megaptera*. There is no question based on previous analyses of the close relationship between the genera *Megaptera* and *Balaenoptera* within the family Balaenopteridae, however the exact relationship of the genera hasn’t been clear in recent phylogenetic analyses. Morphologically, *M. novaeangliae* possesses unique characters that make it readily identifiable from other balaenopterids (see previous characters discussion). In previously published morphological phylogenetic analyses, the humpback is found sister to a monophyletic *Balaenoptera* (Figure 40). However, in previously published molecular analyses, *M. novaeangliae* is consistently found nested within Balaenopteridae and sister to *B. physalus*. The overall morphologic similarity of *Megaptera* to the other balaenopterids, as well as this consistent molecular result, calls into question the taxonomic legitimacy of *Megaptera* as a separate genus from *Balaenoptera*.

Classification of species and higher taxa levels has been a hotly debated field for years (de Queiroz, 1998) and recent researchers have begun to reinvestigate historical classification of groups (e.g. delphinids (Geisler et al., 2011)). Based on the phylogenetic species concept, lineages are defined by monophyly (Smith, 1994; de Queiroz, 1998), which includes an ancestor and all its living descendants. This clade is defined by a possession of shared derived characters, whether they are morphologic or molecular. Monophyly is crucial to defining a group under this species concept because it represents biological reality in grouping organisms together based on characteristics shared. The purpose of a classification scheme is to possess a biologically realistic basis to the grouping of organisms. A paraphyletic group (ancestor plus some but not all of the descendants) is not necessarily realistic because different researchers may not agree on the exact membership of this group, i.e. could be a group based on a skull characters but possess different descendant members depending on a postcranial character. A paraphyletic *Balaenoptera* (Figure 41) would make it difficult to classify and group the members because of the high morphological disparity among the members of this clade. More importantly, it would exclude members of the clade based on autapomorphies of the different species, which would cloud the overwhelming evidence of the close relationship of all members of this family.
Figure 40. Previous phylogenetic hypotheses of balaenopterid whales, showing the variability in the position of *Megaptera novaeangliae* among extant taxa of the group, utilizing different sources of data (A) Bisconti, 2010 [morphology]; (B) Marx, 2010 [morphology]; (C) McGowen et al., 2009 [combined molecular]; (D) Yang, 2009 [mitochondrial] and this study [combined]; (E) Rychel et al., 2004 [combined molecular].
Figure 41. Alternative hypotheses for the phylogenetic position of *Megaptera novaeangliae*. A paraphyletic *Balaenoptera* is represented by the topology on the left, while a monophyletic *Balaenoptera* on the right.

A closer examination shows that crucial to the diagnosis of *Megaptera* is the forelimb (flipper) morphology. In fact, many references to the differentiation of the two genera focus almost exclusively on the forelimb morphology (Rice, 1998). For example, *Megaptera* lacks both the acromion and coracoid process of the scapula, processes that are present in species of *Balaenoptera*. The high mobility of the forelimb of the humpback whale is attributable in part to the lack of these processes (Cooper et al., 2004).

Most forelimb characters of *Megaptera* are morphologically similar (e.g. hourglass shaped phalanges), but proportionally larger in size (longer) than *Balaenoptera* species, with the exception of *B. musculus* (blue whale; Benke, 1993). However, the adult blue whale is the largest of all balaenopterids, roughly twice as large in total body size as adult humpbacks. Thus, the proportionally long flipper is a diagnostic character of *M. novaeangliae*, with the flipper reaching nearly a third (~30%) of the total body length (Benke, 1993). Members of *Balaenoptera* possess a flipper that ranges from 11% (*B. physalus*) to 16% (*B. acutorostrata*) of the total body length. The flipper of *B. musculus* is roughly 14% of its total body length.

The possession of a more mobile and elongated flipper in *M. novaeangliae* is likely related to its feeding behavior, as all (extant) balaenopterids are lunge-feeders (Cooper et al., 2004). Lunge feeding requires a quick forward movement, and while these whales do not use their flippers to propel themselves, the flippers are also critical in steering and maneuverability (Arnold et al., 2005b).

Though it is readily distinguishable from other balaenopterids, the specific features of the flipper are clearly derived from its shared ancestry with the other members of the
balaenopterid lineage. In other words, the balaenopterid flipper morphology is a
synapomorphy of the clade and the humpback condition is an autapomorphy. It is obvious,
based on the general morphology of the bones in the flipper, that the humpback flipper is a
further derivation of the balaenopterid condition.

It must also be noted that there are also two fossil members questionably assigned to
the Megaptera lineage (‘M.’ miocaena and ‘M.’ hubachi), but both have come under
taxonomic scrutiny in the last few years (Deméré et al., 2005; Bisconti, 2010b). Bisconti
(2010b) recently published a reexamination of ‘M.’ hubachi and found it did not form a
monophyletic group with M. novaeangliae and that the taxon should be renamed (Bisconti,
2010b). The current study supports these suggestions. ‘M.’ miocaena was consistently
recovered outside the unresolved clade including M. novaeangliae and ‘M.’ hubachi, and
separated from this unresolved clade by numerous taxa. While having recovered a close
relationship between ‘M.’ hubachi and M. novaeangliae in some phylogenies, these taxa are
just as closely related to numerous extinct species, including B. siberi (whose identity as a
Balaenoptera has not been questioned), D. luctoretemergo and the newly named B.
colcloughi. Bisconti’s (2010b) investigation of ‘M.’ hubachi highlighted the fact that it did
not share apomorphic features of M. novaeangliae, such as those of the frontal, squamosal
and dentary. This could indicate a similar situation for ‘M.’ hubachi as for B. colcloughi, as
an extinct representative of the Megaptera lineage prior to the appearance of M.
novaeangliae.

The high degree of morphological variability has been difficult to describe for
balaenopterids and is seen across many of the extant and extinct species. Additional fossil
taxa have revealed morphologies that don’t necessarily fit into a clear view for the
evolutionary trajectory of these whales, at least given the current phylogeny. Evidence of
rapid radiation of ecomorphologies in early cetaceans and the crown clades, such as in body
size and diversification, is currently being investigated (Steeman, 2009; Slater et al., 2010;
Dornburg et al., 2012).

The classification of Balaenoptera based on most recent phylogenetic evidence is a
paraphyletic group due to inclusion of Megaptera. Both previous molecular and combined
data analyses, as well as the morphological analyses represented in this study and others,
consistently recover this paraphyly. Based on the reasons stated in this section, it is suggested here that *Megaptera novaeangliae* be reclassified as *Balaenoptera novaeangliae*.

**Divergence Dating**

To further explore the history of this clade, accurate timing of the radiation of Balaenopteridae (as well as of mysticetes in general) is necessary. Applying a temporal scale can enable further studies on diversification and the evolutionary drivers of a clade. The most appropriate way of applying a time scale to phylogenetics is the use of divergence dating. The divergence dating analyses conducted here (Table 11) were to test two ideas: the importance of fossil choice for calibration purposes and the placement of these calibrations relative to the ingroup of study. The resulting analyses from the RAG1 dataset used compiled tested both of these ideas most appropriately, and though the ages produced were in the younger range of dates, compared to previous analyses (Table 12), were relatively well supported in terms of stationarity and ESS values.

**Table 11. Overall Comparison of Results of Divergence Dating Analyses with the External Calibration**

<table>
<thead>
<tr>
<th>Node</th>
<th>mtDNA FS1</th>
<th>mtDNA FS2</th>
<th>RAG1 FS1</th>
<th>RAG1 FS2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(</td>
<td>(</td>
<td>(</td>
<td>(</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>55.08</td>
<td>50.74</td>
<td>56.27</td>
<td>50.53</td>
</tr>
<tr>
<td></td>
<td>(53.53-58.33)</td>
<td>(48.61-55.68)</td>
<td>(53.53-63.69)</td>
<td>(48.61-55.34)</td>
</tr>
<tr>
<td>Neoceti</td>
<td>36.31</td>
<td>34.92</td>
<td>35.32</td>
<td>32.14</td>
</tr>
<tr>
<td></td>
<td>(34.25-39.87)</td>
<td>(30.62-39.52)</td>
<td>(34.24-37.37)</td>
<td>(30.02-37.12)</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>28.64</td>
<td>28.58</td>
<td>29.44</td>
<td>29.09</td>
</tr>
<tr>
<td></td>
<td>(28.04-29.57)</td>
<td>(28.03-29.45)</td>
<td>(28.03-32.37)</td>
<td>(28.04-30.75)</td>
</tr>
<tr>
<td>Balaenopteridae</td>
<td>11.77</td>
<td>11.46</td>
<td>9.39</td>
<td>8.11</td>
</tr>
<tr>
<td></td>
<td>(8.84-14.87)</td>
<td>(8.82-14.30)</td>
<td>(7.34-13.85)</td>
<td>(6.05-12.56)</td>
</tr>
<tr>
<td><em>B. physalus + M. novaeangliae</em></td>
<td>7.08</td>
<td>5.50</td>
<td>3.93</td>
<td>3.45</td>
</tr>
<tr>
<td></td>
<td>(3.51-8.33)</td>
<td>(3.22-8.49)</td>
<td>(0.09-7.93)</td>
<td>(0.21-6.83)</td>
</tr>
<tr>
<td><em>B. acutorostrata + B. bonaerensis</em></td>
<td>4.53</td>
<td>3.75</td>
<td>2.53</td>
<td>3.84</td>
</tr>
<tr>
<td></td>
<td>(2.45-6.74)</td>
<td>(2.04-5.59)</td>
<td>(0.00-7.39)</td>
<td>(1.88-5.81)</td>
</tr>
</tbody>
</table>

The resulting age estimates from the divergence dating analyses are broadly consistent with recent studies (Table 12). The divergence age estimates of Neoceti recovered
Table 12. Divergence Estimates from Previous Studies of Cetacea

<table>
<thead>
<tr>
<th>Node</th>
<th>McGowen et al., 2009</th>
<th>Steeman et al., 2009</th>
<th>Slater et al., 2010</th>
<th>Dornburg et al., 2012</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cetancodonta</td>
<td>n/a</td>
<td>n/a</td>
<td>54.5 (54.1-55.1)</td>
<td>~71 (53-85)</td>
</tr>
<tr>
<td>Neoceti</td>
<td>36.36 (34.24-40.14)</td>
<td>36-37 (from tree)</td>
<td>36.9 (34.4-39.9)</td>
<td>~37 (35-42)</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>28.79 (28.03-30.07)</td>
<td>28 (26-29)</td>
<td>28.8 (28.0-30.1)</td>
<td>~30 (28-31)</td>
</tr>
<tr>
<td>Balaenidae</td>
<td>5.38 (2.06-9.60)</td>
<td>(~7.5-10) (from tree)</td>
<td>~5-7 (from tree)</td>
<td>~10 (9-12)</td>
</tr>
<tr>
<td>Balaenopteroidea</td>
<td>13.80 (8.99-19.32)</td>
<td>n/a</td>
<td>~12-14 (from tree)</td>
<td>~14 (10-19)</td>
</tr>
<tr>
<td>Balaenopteridae *</td>
<td>n/a</td>
<td>(10-18)</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>B. physalus + M. novaeanglia</td>
<td>7.06 (3.49-10.90)</td>
<td>~10.8 (from tree)</td>
<td>~6-7 (from tree)</td>
<td>~5.5 (5-6)</td>
</tr>
<tr>
<td>B. acutorostrata + B. bonaerensis</td>
<td>4.92 (1.72-8.83)</td>
<td>~5.5 (from tree)</td>
<td>n/a</td>
<td>~5 (4-8)</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates values not provided. * indicates Balaenopteridae monophyly found. Estimates ‘from tree’ were not directly given and derived from the published topology. (Mean Followed by 95% HPD). All ages are in millions of years (Ma).

in this study were generally a few million years younger than previous analyses, which supported an approximately 36 Ma divergence (McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010). The first fossil set (FS1) calibrated this node using a stem mysticete *Llanocetus dentricrenatus* (34.2 Ma) and produced an average divergence age estimate of 35-36 Ma across the analyses. The second set (FS2) produced younger divergence estimates of approximately 30-32 Ma, calibrated using a stem odontocete *Simocetus rayi* (30.0 Ma). These divergence estimates support divergence of Neoceti near the Eocene-Oligocene boundary, which previously has been proposed by Fordyce (2003b).

In the present analyses, Mysticeti was found to have originated in the early Oligocene (Rupelian), consistent with previous studies. A range of ~28-31 Ma is also proposed in previous studies for this event (Sasaki et al., 2005; McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010; Dornburg et al., 2012). A well-referenced but undescribed fossil balaenid was recovered from roughly 28 Ma marine strata in New Zealand (Fordyce, 2002b; Sasaki et al., 2005). This is the same age (Chattian) utilized here for *Eomysticetus whitmorei*, a well-supported edentulous stem mysticete. The fact that multiple taxa can be attributed to Mysticeti for this time period indicates that several lineages existed contemporaneously.
Also, biogeographically, these fossil taxa were found in different regions (New Zealand and eastern coast of United States), indicating a global diversity of stem cetaceans.

Additionally, a recently published abstract reported a fossil neobalaenid from Angola (Graf et al., 2011). This specimen is the first record of a fossil representative of this monotypic (extant) mysticete lineage. This fossil was found in strata dated to the early (to middle) Miocene, roughly 15 Ma. Although the addition of this fossil as a calibration point was attempted in these analyses, the program BEAST does not allow for calibration of a monotypic lineage. Thus, this calibration point could not be directly tested. However, the resulting divergence age of this lineage from the analyses performed here supports the presence of Neobalaenidae in the earlier Miocene. Description of this fossil specimen is much anticipated, as this taxon not only provides the first evidence of this lineage in the fossil record, but also may provide a critical calibration point for dating Mysticeti.

The middle-late Miocene (Serravallian-Tortonian) is recognized as a period of increased diversity for both clades of neocetes (Steeman et al., 2009; Uhen, 2010; Dornburg et al., 2012). It is around this time that fossils identified as balaenopterids first appear in the geologic record.

The analyses conducted in this study support a late middle Miocene (Serravallian) to early late Miocene (Tortonian) divergence date for Balaenopteridae. Previous analyses have favored a Serravallian first appearance of the clade, however analyses here more generally support the younger age. This difference is due to the use of *B. siberi* and ‘*M.* miocaena’ as calibration points for these mysticetes. This study utilized younger fossil constraints than previous analyses because of the uncertainty of the taxonomic affinity of the older calibrations (e.g. ‘*M.* miocaena’ in relation to the crown clade Balaenopteridae (discussed in next section).

Many balaenopterids are known from the Miocene-Pliocene boundary (5.3 Ma). Pliocene balaenopterids include *B. colcloughi, D. luctoretemergo, A. castriarquati, ‘M.’ hubachi*. Additionally, the fossil eschrichtiid, *E. gastaldii*, is also present in the Pliocene (Zanclean/Piacenzian). Thus, both the fossil record and divergence dating analyses provided here support a late Miocene divergence for Balaenopteridae and Eschrichtiidae.

The lineages of extant balaenopterids defined in Sasaki et al. (2005) and Sasaki et al. (2006) were recovered in the present analyses. The divergence ages of these lineages have
wide HPD ranges likely due to the uncertainty of the Balaenopteridae divergence. Previous studies have also recovered wide age ranges for species divergences within Balaenopteridae, and most support a divergence near the Miocene-Pliocene boundary or older, into the late Miocene (Jackson et al., 2009; McGowen et al., 2009; Steeman et al., 2009). While the ages recovered from the mitochondrial analyses in this study support the previous studies referenced above, the ages are younger, dating well within the Pliocene (into the latest Pliocene for the minke whale divergence). This is likely due to the differences in genetic history between mitochondrial and nuclear data (Jackson et al., 2009; Duchêne et al., 2011).

Some previous analyses (Sasaki et al., 2005; McGowen et al., 2009) recovered an older divergence between *M. novaeangliae* and *B. physalus* than between the minke whales (*B. acutorostrata* and *B. bonaerensis*). Most analyses conducted in this study also support this result. However, the combined analysis of FS1 in this study supports an opposite result. Dornburg et al. (2012) recovered nearly simultaneous divergences for the two groups, but with the minke whales having a greater and older confidence range (Table 12). Again, genetic history may be a big factor in this, especially taking the Dornburg et al. (2012) study into account, since these authors investigated and recovered numerous shifts (changes) in evolutionary rates of mitochondrial (only) data. The authors identified six different shifts in the Mysticeti tree, four of which fall within Balaenopteridae. Interestingly, *E. robustus* is recovered sister to *M. novaeangliae + B. physalus* but there was not a shift recovered around the gray whale. All shifts within Balaenopteridae were between *Balaenoptera* species, including a rate shift between the humpback and fin whale (Dornburg et al., 2012).

Unfortunately, timing of the divergences of Balaenopteridae is not further clarified from the analyses presented here. The resulting divergence ages recovered here were not beyond the range of previous analyses, and exhibit a wide temporal range for some nodes. Further published descriptions of fossil specimens and attention to the use of the cetacean fossil record in divergence dating will be the main issues to resolve in order to narrow down the age estimates. Continued investigation into molecular evolutionary rates also has potential for improving divergence estimates (e.g. Duchêne et al., 2011; Dornburg et al., 2012).
Mysticete Calibration Choice

The results from analyses conducted here are consistent with previous suggestions of the importance of fossil calibration choice on divergence dating (van Tuinen and Hadly, 2004; Donoghue and Benton, 2007; Ho et al., 2008; Pyron, 2011; Lukoschek et al., 2012; Parham et al., 2012). Placement of the fossils in the preferred fossil set (FS2) and the decision of replacing the old fossils (FS1) are also supported by the findings in the phylogenetic portion of this project. Though the differences in age estimates produced by the two fossil calibration sets were slight, these were still significant differences, especially when taking the HPD ranges into account. FS2 produced younger divergence ages due to younger date settings, but often resulted in wider confidence intervals than FS1. However, an interesting pattern was noted when comparing the two fossil calibration sets. The exception to the FS1 producing older ages pattern in the analyses of mysticete taxa, in which the opposite is noted. Without any external influence on the extant taxa of Mysticeti, the younger fossil calibration set (FS1) (only Balaenopteridae calibration) actually produced older ages. This pattern was seen in both the mitochondrial dataset and in mysticete only runs of the RAG1 dataset (not shown). The ESS values for the nodes are very high but the values of the posterior and prior distributions are lower in FS2.

While acknowledging that it can be very difficult to assign a fossil taxon to crown or stem clades, placement of fossil taxon in these analyses has an important impact on age estimates due to the phylogenetic position of the taxon (i.e. relative position to the node). For Balaenopteridae, the boundary between crown and stem clades is not phylogenetically stable or well understood. For example, the Bayesian analyses in this study recover Megaptera miocaena as a stem mysticete in the individual runs. This has implications on the use of this taxon as a calibration in divergence dating. If the combined analyses, including both the morphological data for fossil taxa and the molecular information of the extant taxa from which the clock is based, recover this taxon as stem, it is thus less appropriate for use as calibration. ‘Megaptera’ miocaena has been used as a calibration in previous divergence analyses (i.e. Jackson et al. 2009) but with no justification of its phylogenetic position. Based on the phylogenetic analyses resulting from the analyses of the current project, this fossil should not be used as a calibration, as it was often recovered outside of Balaenopteridae. These results and the fact they differ from many previous analyses (e.g. Marx, 2010),
suggests that the phylogenetic relationships of ‘M.’ miocaena are still not well understood. The fossil used in FS2, *B. siberi*, has been recovered consistently within Balaenopteridae and is a better choice at this time for calibration of this node.

It is important to note that simultaneous phylogenetic analysis and divergence dating analyses (using Bayesian inference) would be beneficial and improve the accuracy of using fossils as calibrations (Pyron, 2011). Up until very recently, Bayesian programs have been incapable of directly running phylogenetic analyses in a divergence dating scheme, due to problems within this originally molecular scheme of handling fossil taxa. However, great progress on directly analyzing fossils and extant phylogenetically while calibrating divergence dating analyses has been made, with improvements to the software (e.g. Drummond and Rambaut, 2007) and improvements to methods, such as using fossils as terminal taxa (Pyron, 2011). These newer ideas could not be implemented in the current study due to timing of their release, however future work should apply these new ideas on divergence analyses of Cetacea.

It must be noted that the phylogenetic analyses of this study support the use of *Parabalaenoptera baulinensis* as a calibration for Balaenopteridae, because this fossil species is found as the oldest member of crown balaenopterids. This taxon has unfortunately been left out of many recent analyses of the group, though when included, the phylogenetic position found is well supported (e.g. Deméré et al., 2008; Geisler et al., 2011). Because the age information of this taxon is the same as *B. siberi*, it was not changed in the analyses here. However, due to the need to hold to a generalized standard across taxonomic groups, the results of this study support the use of *P. baulinensis* for calibration at this node instead of *B. siberi*.

Another calibration in need of discussion is the use of *Eomysticetus whitmorei* for Mysticeti. A separate taxon, *Mauicetus parkii* has been postulated for calibration of this node. Geisler et al. (2011) recently suggested the inclusion of this taxon in mysticete analyses due to its recent shift in phylogenetic position, closer to (but within) the crown Mysticeti. It had previously been relatively phylogenetically unstable, even positioned within crown Balaenopteridae (Steeman, 2007). This would significantly affect our understanding of the timing of Balaenopteridae, as *M. parkii* was found in strata of late Oligocene (or Chattian) age (~23.8-28.5 Ma). The age of this taxon is much older than any of the HPD ranges for the
divergence of Balaenopteridae produced in the analyses here (~6-18 Ma), and the within-Balaenopteridae hypothesis is not supported by phylogenetic analyses of the current study. *Eomysticetus whitmorei* is also not recovered in these analyses as a member of the crown Mysticeti clade, instead it represents the earliest edentulous mysticete and falls as a close stem member to the crown clade. Thus, it is still not the most ideal calibration choice (which would be a crown member of a clade) but as it has been published, well-studied, and often found within phylogenetic analyses of this clade (e.g. Deméré et al., 2008; Bisconti, 2007b; Marx, 2010), it is reasonable for use as a calibration given other options for this node.

Clearly, there is a discrepancy between the molecular age estimates and the ages of diagnosable fossils belonging to Balaenopteridae. This problem relates to the highly variable morphologies exhibited by not only fossil balaenopteroids, but also by the fossil sister group, the ‘cetothers’, which results in a lack of phylogenetic resolution for these mysticetes.

Important to this discussion is the lack of fossil specimens of extant species of Balaenopteridae, i.e. there are few to no representatives of modern taxa in the fossil record. A purported *M. novaeangliae* specimen was recovered Japan is from upper middle Pleistocene strata (~125,000 years old; Nagasawa and Mitani, 2004). The authors report this specimen as the oldest representative of *M. novaeangliae*, but there have been no other studies to support or falsify the claim.

These issues reflect a disconnect between the crown and stem species of Balaenopteridae. Obviously, molecular data cannot be collected from fossil species to help resolve this problem. However, the continued publication and phylogenetic analyses of fossil species of this clade has great potential to help resolve this issue.

Steiper and Young (2008:184) made the following observation in the context of discussing primate evolution:

…[this disconnect] raises the general question of whether characters typically used to diagnose crown groups can be assumed to be diagnostic of their earliest members. In other words, taxa will be difficult to recognize as crown members of a group if derived features used to characterize these groups were not present around the time of population splitting.

This point may be applicable to balaenopterids. However, the derived features of Balaenopteridae actually appear seemingly randomly within its fossil record or are found as autapomorphies of extant taxa. Coupled with the lack of a historical record (in terms of millions of years) for the extant species, this suggests that the lineage splitting events may
have not been necessarily driven by derivation of specialized features. Further investigation into the drivers behind the evolutionary history of cetaceans (e.g. Steeman et al., 2009) is key to resolution of some of these issues surrounding this clade.

Geisler et al. (2011) utilized measures of stratigraphic fit (MSM and GER) to determine that all trees with extinct taxa were statistically significant with the fossil record, suggesting that the fossil record of Neoceti is actually quite ‘good’ (well-sampled/well-supporting of general evolutionary history). The stability of some of the divergence estimates across the different divergence studies of cetaceans (i.e. split of Cetacea-Artiodactyl, divergence of Neoceti, divergence of Odontoceti and Mysticeti) provides support for this claim (McGowen et al., 2009; Steeman et al., 2009; Slater et al., 2010; Geisler et al., 2011).

The results of Geisler et al. (2011) offer an interesting context for Mysticeti. There is an abundance of mysticete fossils, especially from certain time periods (e.g. Oligocene and Pliocene) with more being described each year (e.g. Steeman, 2009; Bisconti, 2010a; Bosselaers and Post, 2010; Kimura and Hasegawa, 2010). Additionally, some fossil taxa are being redescribed from potentially important fossils discovered in the past century (e.g. Bisconti, 2010b; Fitzgerald, 2010). These efforts will only improve our understanding of not only the morphological and taxonomic diversity of this clade but also will provide information about the patterns and tempo of mysticete evolution.

A recent collaborative effort to improve the use of fossils as calibration points in divergence dating, Parham et al. (2012), laid out a set of ‘best practices’ for justifying fossils used in these analyses. Because of common knowledge of the error introduced by poor fossil choice and the need for discussion of fossil taxa used in cetacean estimates, this study agrees with the need for an \textit{a priori} assessment of fossils employed for calibration. The fossils used for calibration in the current study have been assessed in accordance with the protocol outlined by Parham et al. (2012) and the justifications for each can be found in Appendix G.

An example of the need for such a protocol can be seen in the divergence dating analysis of Dornburg et al. (2012). This is a molecular focused study that utilized multiple fossil calibrations. Interestingly, the authors calibrated the node representing the sister relationship between \textit{M. novaeangliae} and \textit{B. physalus} with the fossil taxon, ‘\textit{M.’} hubachi. Through citations, it is clear these authors attempted a background search on these fossils, however, they did not cite any studies that question this relationship (e.g. Deméré et al.,
Dornburg et al. (2012) acknowledged that the phylogenetic relationships within Mysticeti are contentious but made no effort to further justify their decision to use this taxon. ‘Megaptera’ hubachi is recovered in the unresolved clade with M. novaeangliae and B. physalus, thus use of this calibration is cautioned until the phylogenetic position of this taxon can be fully resolved. These authors also use Llanocetus to calibrate crown Cetacea, as well as the unnamed balaenid from New Zealand to calibrate Mysticeti, issues discussed previously in the current study.

**USE OF EXTERNAL CALIBRATIONS**

This study is the first to examine the use of external fossil calibrations (outside of Cetancodonta) and their performance relative to Cetacea and specifically Mysticeti. The external calibration, the eutherian Juramaia sinensis, had little effect on the age estimates within Cetacea, specifically within Mysticeti. However, by strict definition, the calibrations for Cetancodonta and Neoceti are technically external calibrations to the analyses here because the focus of the study is on Mysticeti, not Cetacea as a whole. Thus, to further examine the influence of these calibrations on Mysticeti, analyses of these taxa only were run. The analyses relied only on the fossil calibrations for Mysticeti and Balaenopteridae. This was done with both the mitochondrial and RAG1 matrix. The age estimates for both types of data, when run with only mysticete taxa were older than those produced with the full calibration set. The HPD intervals were also wider than in analyses including odontocetes. The ESS values for the prior and posterior distributions were the lowest in the analyses with only mysticetes among all other analyses. The Mysticeti calibration was relatively stable throughout all analyses and well supported by higher ESS values. These results suggest that the Balaenopteridae calibration is specifically causing an effect on the resultant ages produced.

These results indicate the importance of external calibrations of Cetancodonta and Neoceti. Support of calibration of the Cetacea-Artiodactyl split for divergence dating was noted in van Tuinen and Hadly (2004), “Relative stasis in the timing of the cetacean origin has been essential to its utility as a calibration in placental molecular clock studies” (pp. 201). They also referred to the Cetacea-Artiodactyl calibration as the most frequently used internal calibration point for studies of placentals. The current study also found general stasis
in the Cetacea-Artiodactyl split. This calibration is often utilized in divergence studies of Artiodactyls (e.g. Zhou et al., 2011), but not in studies of cetaceans. The issue of the closest extant relative to Cetacea was under debate in the early part of the 21st century (Gatesy and O’Leary, 2001) but the relationship between Hippopotamidae and Cetacea has been highly supported by both molecular and morphological data in recent years (Spaulding et al., 2009). Thus, use of fossil calibration at the node of the divergence of Hippopotamidae and Cetacea is phylogenetically supported and recommended for use in future divergence dating of cetaceans.

An interesting thought for this calibration involves the proposed closest extinct relative to Cetacea, the raeollids. This relationship became clear after the discovery of *Indohyus*, a raoellid from the Eocene of India (Thewissen et al., 2007). Recent studies have supported a clade of raoellids + Hippopotamidae + Cetacea, based mainly on morphology of the tympanic bulla (Geisler and Theodore, 2009; Uhen, 2010). Interestingly, *Indohyus* was found closer to Cetacea than Hippopotamidae (Thewissen et al., 2007; Geisler and Theodor, 2009), suggesting its potential for calibration of the divergence between the extant clades. The age of *Indohyus* is middle Eocene (Lutetian), roughly 48.6-37.2 Ma (PBDB), which would indicate that this taxon was contemporary with the pakicetids (earliest whales). This supports the divergence between Hippopotamidae and Cetacea to be around or before 48 Ma, such as found in the analyses here (~48-56 Ma; Appendix E). Unfortunately, *Indohyus* is currently unable to be directly applied as a calibration to most divergence dating methods due to the low capability of these methods to date matrices with both extant and extinct taxa. This issue, however, is a topic of recent investigation for divergence dating and has good potential for the future (Pyron, 2011).

Another reason for the discrepancy of age estimates between mysticete only analyses and those with external taxa is the difference between molecular rates of evolution between clades. It has been recognized that Odontoceti and Mysticeti possess different rates of molecular evolution, with mysticetes having the slower of the two (Kimura and Ozawa, 2002; Jackson et al., 2009; Dornburg et al., 2012). The differences in rates between these clades directly impacts dating analyses because a majority are run under a single relaxed molecular clock (i.e. in BEAST). A potential solution to this issue is the implementation of random local clocks (RLC) for divergence dating, which allows for multiple clocks in a
single analysis (Drummond and Suchard, 2010). This option is available in the latest version of BEAST (v.1.7) and use of the RLC is still in early phases, but its potential for improvement of divergence estimates has already been noted (Dornburg et al., 2012).

The use of external calibrations has been noted in recent studies of divergence dating. For example, Dornburg et al. (2012) suggested that caution be used in external calibrations because of evolutionary rate shifts between clades (noting this is especially important in depauperate clades). Pyron (2010), in his description and application of a methodology for assessing fossil calibrations in Gnathostomata (jawed vertebrates), found that the use of credible constraints toward the base of the tree [outgroup taxa] provide more robust estimates than the use of calibrations placed only near the terminal nodes. Meredith et al. (2011) tested external calibration use in a large-scale phylogenetic study of Mammalia and found support for use of multiple calibrations spread across the phylogeny in divergence dating for this large and diverse clade.

The current study supports the use of this calibration as an external calibration for a cetacean divergence analysis. This calibration provides a solid (soft bound) calibration for use in a full (taxonomic) cetacean study.

This study showed the impact of external calibrations on divergence dating of Cetacea, albeit a slight one for the ages of many of the mysticete nodes. Using the RAG1 data, there was not much of a difference in the ages derived with and without the external calibration. However, the impact was more noticeable in the mitochondrial analysis, where the divergence ages recovered from the analyses with the external calibrations were actually younger, and more consistent with the fossil record and previous molecular studies.

OTHER FACTORS IN DIVERGENCE DATING

As noted previously, nuclear and mitochondrial data do not necessarily produce the same results because of the differences in gene history and substitution rates (Sasaki et al., 2005; Dornburg et al., 2011; Lukoschek et al., 2012). This obviously can impact the divergence dates recovered from separate analyses and can have a contradictory influence in a combined analysis. In the analyses of this study, the nuclear dataset appears to produce generally younger ages.
One of the largest issues facing divergence dating with fossil calibrations, and an issue relevant to the cetacean record, is that these schemes are heavily reliant on the taxonomic accuracy of the described fossils (Morlon et al., 2011). This is directly related to the importance of the resolution of the cetacean phylogeny for further understanding of the tempo of evolution for the clade. It is well noted that the phylogenetic hypothesis is key to divergence dating (Pyron, 2011). These analyses produce dates as node estimates using branch length information and the more confident in the underlying topology we are, the more confident one can be in the temporal information produced from the relationships. For example, in the combined divergence analyses of this study, the young age of the \textit{B. physalus} + \textit{M. novaeangliae} split is directly related to the problem of paraphyly of Balaenopteridae. When not found monophyletic, \textit{E. robustus} is found sister to the pair and their divergence is pushed forward (younger) in time. The divergence estimate for the split of the pair from the gray whale is consistent with estimates of the split of the pair in analyses with a monophyletic Balaenopteridae. In fact, the HPD intervals are similar. The fossil record of Eschrichtiidae is small but of the same age (roughly) as more modern balaenopterid fossil taxa (Pliocene), suggesting potentially a Pliocene or younger divergence of these lineages. As mentioned previously, a paraphyletic Balaenopteridae, due to the inclusion of \textit{Eschrichtius}, is consistently found in molecular studies. It is possible that the divergence age of the paraphyletic Balaenopteridae is very young when including \textit{Eschrichtius} because the genes have not had enough time to fully diverge from one another (i.e. incomplete gene sorting) (Amaral et al., 2012).

This naturally extends to extinct taxa as well. A better understanding of the usefulness of fossil taxa used in these analyses will only improve the confidence in the estimates produced. As mentioned previously, this is definitely needed for the fossil record of balaenopteroids.

Another issue that was noted in the estimates employed by previous studies is that few reported the highest probability density for their estimates. Often these studies did not report estimates found for mysticetes, but this is not surprising since these studies did not focus their efforts on that specific clade. For example, Jackson et al. (2009) was excluded from Table 1 because the poor taxon sampling did not allow for appropriate comparison of
estimates (i.e. they did not include a sample of *E. robustus*, so estimates of Balaenopteridae/Balaenopteroidea would be inaccurate).

Beyond further resolution of the phylogeny, studies investigating the evolutionary rate of clades (e.g. Dornburg et al., 2012) and diversity (e.g. Marx, 2008; Uhen, 2010) are the next step in understanding the tempo of the evolutionary history of a group.
CHAPTER 6

CONCLUSIONS

*Balaenoptera colcloughi* is a new species of balaenopterid from the Pliocene San Diego Formation that possesses a unique combination of primitive and derived characters that indicate a crown-ward placement of the clade. The new taxon is identified as a member of *Balaenoptera* because it possesses derived balaenopterid characters such as a slightly dorsoventrally arched rostrum in lateral view, maxillary pocket, triangular supraoccipital shield, abruptly depressed supraorbital process of the frontal, ovoid tympanic bulla, and hourglass shaped digits. This taxon is identified by a unique set of characters, such as a lack of a squamosal crease (primitive), exposure of the alisphenoid between the pterygoid and squamosal in the temporal region (primitive), dorsal sagittal crest of the nasals (derived) and a flat medial margin of the main ridge of the bulla (derived). The referral of four specimens to this taxon provides the opportunity to examine ontogenetic differences between individuals of a single extinct taxon. Characters of the foramen pseudovale, optic canal and bony protrusions from the anterior process of the periotic were identified to be variable due to ontogeny.

*Balaenoptera colcloughi* is recovered from the phylogenetic analyses in an unresolved clade with extant *Balaenoptera physalus* and *Megaptera novaeangliae*, and extinct *Balaenoptera siberi*, *Diunatans luctoretemergo* and ‘*Megaptera’ hubachi’. The fossil species also adds to the growing diversity of Pliocene balaenopterids known from the global fossil record (e.g. *D. luctoretemergo*, ‘*M.’ hubachi, *Archaebalaenoptera castriarquati*).

The resulting relationships of the phylogenetic analyses conducted here are consistent with the previous study of balaenopterid mysticetes, Deméré et al. (2005) (Figure 4). For extant balaenopterids, the lineages identified in Sasaki et al. (2005) and Sasaki et al. (2006) are supported in the analyses here, which include a sister relationship of *Balaenoptera acutorostrata + Balaenoptera bonaerensis*, *Balaenoptera edeni* + *Balaenoptera omurai* + *Balaenoptera borealis* + *Balaenoptera musculus* and *M. novaeangliae* + *B. physalus*. These relationships do not change with the addition of fossil taxa, except for the inclusion of three
fossil taxa in an unresolved group with the humpback and fin whale. The consistent sister relationship between *M. novaeangliae* and *B. physalus* found in this study (as well as others) supports a reevaluation of the genus *Megaptera*. This includes evidence from both morphology, which has previously separated *Megaptera* from species of *Balaenoptera*, and molecular information, which has consistently nested *M. novaeangliae* as sister to *B. physalus*. The potential intermediate *B. colcloughi* positioned between the two also lends support to this idea, displaying morphological characteristics displayed in both species.

In the parsimony morphology analyses, *Parabalaenoptera baulinensis* is recovered sister to the rest of the balaenopterids and the gray whale clade (*Eschrichtius robustus* + *Eschrichtioides gastaldii*) is found outside of a monophyletic Balaenopteridae. In the other analyses, these taxa are found in a large unresolved clade with crown balaenopterids and other fossil taxa (e.g. *P. quarantellii*, *'Megaptera' miocaena*, *A. castriarquati*, *Eobalaenoptera harrisoni*, and *Uranocetus gramensis*). Further investigation into the possible stem balaenopterid taxa (e.g. *'M.' miocaena* and *E. harrisoni*) and descriptions of new fossil discoveries will help improve the understanding of the evolution of Balaenopteridae.

Divergence dating supports an early to middle Eocene (50-56 Ma) divergence of Cetancodonta and an early Oligocene divergence of Neoceti, corresponding roughly with the Eocene-Oligocene boundary (32-36 Ma). These ages are consistent with previous divergence analyses. These nodes are also found to produce consistent estimates across calibration schemes or study focus when they are calibrated with an appropriate fossil taxon. A wide range for age estimates of the divergence of Balaenopteridae has been previously proposed, however this study supports a mid to late Miocene (8-12 Ma) divergence of the clade. Numerous fossil balaenopteroids are known from the Pliocene and the divergence estimates support a late Miocene to early Pliocene (3-7 Ma) divergence for sister species in the crown Balaenopteridae.

Fossil calibrations tested here differed minimally in their age estimates. The second calibration set included fossil taxa from younger sediments, thus the age estimates produced by this set were slightly younger, as expected. However, the highest probability density range for the second fossil calibration set was generally smaller, providing a more precise estimate of time. The one exception for the second fossil set is the Balaenopteridae calibration. The
taxon used at this node was *B. siberi*. However *P. baulinensis* was found to be more appropriate for that node in the phylogenetic analyses of this study. Coincidentally, these taxa are contemporaneous in age and again support a divergence of Balaenopteridae at the Miocene-Pliocene boundary (~5 Ma).

Finally, the use of external calibrations were found to have a positive impact on the divergence dating of Mysticeti, narrowing the HPD ranges of some divergences and influencing ages toward one end of the interval, if the range was wide. The age estimates produced using calibrations of Mysticeti alone were older than those produced with addition of external calibrations. Despite recognized concerns about the nature of the molecular clock in current methods of divergence dating (i.e. Dornburg et al., 2012), this study finds that these effects more accurately reflect the fossil record of Mysticeti.

Future work should focus on the taxonomy and phylogenetic relationships of stem mysticetes, such as the ‘cetotheres’ and stem balaenopteroids. More taxonomic description of material must continue to be published and the inclusion of more taxa will likely help the understanding of the evolution of the balaenopterids as a clade. Divergence dating has received much attention by researchers recently and further investigation into potential impacting factors in these analyses, specifically the differences in molecular rates of evolution between species and genes, will continue to clarify the age estimates of mysticete evolutionary events. Direct inclusion of fossil taxa into divergence dating methods is currently being tested and this will be crucial in applying fossil data to the phylogeny and resulting estimates of divergences.
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APPENDIX A

DIAGRAMS FOR MEASUREMENTS
This appendix includes schematic diagrams and descriptions of the measurements for *Balaenoptera colcloughi*.

Figure 42. A schematic diagram of the cranial measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 2. Note: Measurement 2 is not included for clarity of the diagram.
Skull Measurements

1. Length of skull: measured from the anteriormost tip of the rostrum (premaxilla) to the posterior edge of the occipital condyles.
2. Condylar length: measured from the anteriormost tip of the rostrum (premaxilla) to the posterior point of the exoccipital.
3. Rostrum length: measured from the anteriormost tip of the rostrum (premaxilla) to the vertex of the skull (posterior most point of the ascending process of the maxilla).
4. Zygomatic width: greatest width of the skull measured from the anterior-lateral tip of the zygomatic process of the squamosal.
5. Width at antorbital notch: width across the skull from the antorbital notch of the maxilla.
6. Nasal width: greatest width measured from the lateral edge of the nasal across both nasal bones.
7. Nasal length: measured from the anteriormost point (along the midline) to the posterior edge of the nasals.
8. Temporal fossa width: width across the temporal fossa, measured from the medial edge of the zygomatic process of the squamosal (where it meets the posterior edge of the supraorbital process of the frontal) to posterior medial corner of the SOPF.
9. Length of occipital shield: greatest length of the supraoccipital, measured along the midline from the anterior most point to the posterior most point.
11. Occipital condyle width: greatest across the lateral edges of the occipital condyles.
Figure 43. A schematic diagram of the periotic measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 3.
**Periotic Measurements**
1. Anterior process width: greatest width of the anterior process at the midpoint of the length.
2. Anterior process length: greatest length of the anterior process.
3. Promontorium length: greatest length of the promontorium.
4. Posterior process length: greatest length of the posterior process.

**Figure 44.** A schematic diagram of the tympanic bulla measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 4.

**Tympanic Bulla Measurements**
1. Length of bulla: greatest length along the midline.
2. Height of sigmoid process: greatest length along midline of process.
Figure 45. A schematic diagram of the atlas measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 5.

**Atlas Measurements**
3. Atlas length: greatest length along the midline.
5. Articular width: greatest width across the articular surfaces that occlude to the occipital condyles.

Figure 46. A schematic diagram of the axis measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 6.
Axis Measurements
1. Axis length: greatest length along the midline.
2. Atlas width: greatest width at the midpoint of the length.

Vertebra Measurements
1. Vertebra length: greatest length along the midline.
2. Vertebra width: greatest width across the transverse processes.
Figure 48. A schematic diagram of rib measurements for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 8.

Rib Measurements

1. Length of rib: greatest length of the rib.
2. Rib width: greatest width across the rib at the midpoint of its length.
Scapula Measurements

1. Width of scapula: greatest width of medial portion of the scapula.
2. Length of scapula: greatest length at midline of scapula.
3. Length of acromion process: greatest length of coracoid process.
4. Width of acromion process: greatest width of coracoid process at mid-length of process.
5. Length of coracoid process: greatest length of acromoin process.
Figure 50. A schematic diagram of the forelimb measurements taken for *Balaenoptera colcloughi*. The numbers correspond to measurements in Table 10.
Forelimb Measurements

1. Humerus length: greatest length measured perpendicular to the midpoint of the condylar width.
2. Humerus condylar width: maximum width of humeral condyle.
4. Ulna length: greatest length measured along the midline.
5. Ulna width: greatest width measured at midpoint of length.
6. Radius length: greatest length measured along the midline.
7. Radius width: greatest width measured at midpoint of length.
APPENDIX B

LIST OF SPECIMENS
The following table includes osteological specimens examined over the course of this study. When taxa were unavailable for personal examination, observations were based on the literature.

<table>
<thead>
<tr>
<th>EXTANT TAXA</th>
<th>SPECIMEN</th>
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<tr>
<td>Balaena mysticetus</td>
<td>LACM 54479</td>
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<tr>
<td>Balaenoptera acutorostrata</td>
<td>SDNHM 23642, USNM 61715; True, 1904</td>
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<tr>
<td>Balaenoptera bonaerensis</td>
<td>USNM 504944</td>
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<tr>
<td>Balaenoptera borealis</td>
<td>USNM 504244, 571340</td>
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<tr>
<td>Balaenoptera edeni</td>
<td>LACM 84204, USNM 239307, 572922</td>
</tr>
<tr>
<td>Balaenoptera musculus</td>
<td>LACM 72562, USNM 124326; True, 1904</td>
</tr>
<tr>
<td>Balaenoptera omurai</td>
<td>NSMT 32992, 03536, 32505</td>
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<tr>
<td>Balaenoptera physalus</td>
<td>LACM 80620, USNM 301635, 504243, SDSU S970*; True, 1904</td>
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<tr>
<td>Caperea marginata</td>
<td>Morphobank Project, 2010</td>
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<td>Eschrichtius robustus</td>
<td>LACM 86047, 72551, USNM 364980; True, 1904</td>
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<td>Eubalana glacialis</td>
<td>USNM 301637, 20377; True, 1904</td>
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<th>FOSSIL TAXA</th>
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<tr>
<td>Aetiocetus weltoni</td>
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<td>Aglaocetus patulus</td>
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<td>Archaebalaenoptera castriarquati</td>
<td>Bisconti, 2007a</td>
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<td>Balaenella brachyrhynus</td>
<td>Bisconti, 2005</td>
</tr>
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<td>Balaenoptera colcloughi</td>
<td>SDNHM 80101, 80102*, 83695*, 90510*</td>
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<td>Balaenoptera siberi</td>
<td>Pilleri and Pilleri, 1989; Pilleri, 1990</td>
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<tr>
<td>Cetotherium rathkii</td>
<td>Morphobank Project, 2010</td>
</tr>
<tr>
<td>Diorocetus hiatus</td>
<td>Kellogg, 1968a</td>
</tr>
<tr>
<td>Dinatans luctoretemergo</td>
<td>Bosselaers and Post, 2010</td>
</tr>
<tr>
<td>Eobalaenoptera harrisoni</td>
<td>Dooley et al., 2004</td>
</tr>
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<td>Eomyistictus whitmorei</td>
<td>Sanders and Barnes, 2002</td>
</tr>
<tr>
<td>Eschrichtioides gastaldii</td>
<td>Bisconti, 2008</td>
</tr>
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<td>Mauicetus parkii</td>
<td>Marples, 1956</td>
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<td>‘Megaptera’ hubachi</td>
<td>Dathe, 1983; Bisconti, 2010b</td>
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<td>Mixocetus elysius</td>
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<td>Parabalaenoptera baulinensis</td>
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<td>Piscobalaena nana</td>
<td>Bouetel and Muizon, 2006</td>
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<td>Plesiobalaenoptera quarantellii</td>
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<td>Protororqualus cuvieri</td>
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<tr>
<td>Uranocetus gramensis</td>
<td>Steeman, 2009</td>
</tr>
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</table>

* Denotes a juvenile or subadult specimen.
Institutional Abbreviations: LACM, Natural History Museum of Los Angeles County, Los Angeles, California; NSMT, National Science Museum of Tokyo, Tokyo, Japan; SDNHM, San Diego Natural History Museum, San Diego, California; SDSU, San Diego State University, San Diego, CA; USNM, United States National Museum of Natural History, Washington, D.C.
APPENDIX C

MORPHOLOGICAL CHARACTER LIST
The following are the morphological characters utilized in this study. The original source of the character is given in parentheses, where appropriate. Characters labeled with an asterisk (*) were treated as ordered in the morphological ordered parsimony analysis.

1. Rostral curvature in lateral aspect (Barnes and McLeod 1984; Deméré et al., 2008:ch. 1)*
   0 = Straight
   1 = Slightly arched dorsoventrally
   2 = Moderately arched dorsoventrally
   3 = Strongly arched dorsoventrally

2. Position of the narial fossa (modified Deméré et al., 2005:ch. 7)*
   0 = Well anterior to antorbital notch
   1 = Parallel with or just anterior to antorbital notch

3. Nasal width relative to length (Deméré et al., 2008:ch. 8)*
   0 = Slender (15-25%)
   1 = Broad (26-45%)
   2 = Very broad (46-70%)
   3 = Extremely broad (>70%)

4. Shape of anterior margin of nasals (Deméré et al., 2005:ch. 10)
   0 = U or V shaped, posteriorly directed
   1 = Straight
   2 = U or V shaped, anteriorly directed

5. Shape of posterior margin of nasals (Deméré et al., 2005:ch. 11)
   0 = Frontals extend into the nasals in a W-shape
   1 = Frontals extend into nasals in a finger shape
   2 = Frontals extend into nasals in a U-shape
   3 = Straight or nearly straight margin
   4 = Nasals extend into frontals in a M-shape
   5 = Nasals extend into frontals in U or W shape

6. Nasals, dorsal surface (modified Deméré et al., 2005:ch. 12)
   0 = Flattened
   1 = Sagittal keel entire length
   2 = Sagittal keel anterior half

7. Posterior most edge of ascending process of maxilla (modified Deméré et al., 2008:ch. 14)*
   0 = Anterior to/anterior half of supraorbital process of frontal*
   1 = Posterior half of supraorbital process of frontal
   2 = At level of anterior tip of zygomatic process
   3 = At level of posterior region of temporal fossa

8. Maxillary-frontal suture (modified Deméré et al., 2005:ch. 18)
0 = Maxilla abuts frontal
1 = Maxilla overrides anteromedial portion of supraorbital process
2 = Maxilla overrides anterior portion of supraorbital process, creating a pocket

9. Ascending process of maxilla (Deméré et al 2005, modified Deméré et al., 2008:ch. 18)
   0 = Developed as bluntly-shaped triangular wedge
   1 = Developed as a broad bar, exposed dorsally
   2 = Developed as a narrow bar, exposed laterally
   3 = Absent

10. Ascending process of maxilla and anterior wing of parietal (modified Deméré et al 2005:ch. 20)*
    0 = Separate
    1 = Abutting or nearly abutting
    2 = Short overlap
    3 = Long overlap

11. Frontal, supraorbital process, size and shape (Miller, 1923; Deméré et al., 2008:ch. 22)*
    0 = Broad in anteroposterior dimension and short transversely
    1 = Moderately broad anteroposteriorly and moderately elongate transversely
    2 = Very narrow anteroposteriorly and very elongate transversely

12. Parietal, exposure on cranial vertex (Deméré et al., 2008:ch. 25)*
    0 = Long
    1 = Short
    2 = Parietal excluded from vertex

13. Squamosal fossa (modified Deméré et al, 2005:ch. 33)
    0 = Large and well developed
    1 = Reduced
    2 = Absent

14. Squamosal cleft (Deméré et al., 2005:ch. 34)
    0 = Absent
    1 = Present, contacts pterygoid
    2 = Present, contacts alisphenoid
    3 = Present, contacts parietal

15. Squamosal crest (this study)
    0 = No crest on the squamosal (absent)
    1 = Crest present on dorsal side of squamosal
    2 = Strong crest on dorsal side of squamosal

16. Palatines, anterior margin (modified Deméré et al., 2005:ch. 43)
    0 = Blunt, no flare
    1 = Flares medially
2 = flares laterally
3 = W-shaped

17. Palate, maxillary window on infraorbital plate (modified Deméré et al., 2008:ch. 40)
   0 = Absent
   1 = Present, embayment in posterior margin of infraorbital plate
   2 = Present, longitudinal opening anterior to and not reaching the posterior margin of infraorbital plate.

18. Paired occipital tuberosites on supraoccipital shield (Barnes and McLeod, 1984)
   0 = Absent
   1 = Present

19. Nasals, length compared to condylobasal length (McLeod et al., 1993; Deméré et al., 2005:ch. 8, Deméré et al., 2008:ch. 7)*
   0 = Long (15-25% of CBL)
   1 = Moderate (10-16% of CBL)
   2 = Short (5-10% of CBL)

20. Maxillae: Slope (modified Churchill et al., 2011:ch. 7)*
   0 = Slight or absent
   1 = Gradual
   2 = Steep

21. Zygomatic process of squamosal from lateral view (Bisconti, 2007a:ch. 37)
   0 = Long and slender
   1 = Short and stocky
   2 = Short and crescent-shaped

22. Anterior tip of supraoccipital (Bisconti, 2007a:ch. 63)
   0 = Round
   1 = Narrow and squared
   2 = Pointed
   3 = Narrow and round
   4 = Wide and round
   5 = Wide and squared

23. Posterior tip of ascending process of maxilla (Bisconti, 2007a:ch. 81)
   0 = Pointed
   1 = Rounded
   2 = Squared

24. Anterior tip of zygomatic process of squamosal (Bisconti, 2007a:ch. 93)
   0 = Posterior to postorbital corner of supraoccipital process of frontal
   1 = Very close
2 = Under the postorbital corner

25. Alisphenoid exposure in the temporal region (modified Bisconti, 2007a:ch. 113)
   0 = Alisphenoid in between squamosal, parietal, and palatine
   1 = No alisphenoid exposed in temporal fossa
   2 = Alisphenoid in between squamosal, parietal and pterygoid
   3 = Alisphenoid in between squamosal and pterygoid
   4 = Alisphenoid in between parietal and pterygoid

26. Position of the foramen ‘pseudo-ovale’ (modified Bisconti, 2007a:ch. 117)
   0 = Foramen within pterygoid
   1 = Foramen in between squamosal and pterygoid
   2 = Foramen within squamosal, contact with pterygoid by a suture.
   3 = Foramen within squamosal, no contact with pterygoid

27. Optic tube (Muller, 1954; Bisconti, 2007a:ch. 119)
   0 = Ventrally open
   1 = Ventrally closed by a lamina from the anteroventral surface of the supraorbital

28. Pterygoid hamulus (Bisconti, 2007a:ch. 150)
   0 = Undefined
   1 = Projecting posteriorly
   2 = Projecting medially

29. Mandible dentary, coronoid process (Deméré et al, 2008:ch. 60)
   0 = Large and spatulate
   1 = Finger-like and laterally deflected
   2 = Developed as coronoid crest
   3 = Developed as small knob and low crest
   4 = Developed as rounded process with low crest

30. Dentary, proportional size of mandibular angle relative to mandibular condyle in the
dorsoventral plane (Deméré et al., 2008:ch. 85)*
   0 = Angle larger than condyle
   1 = Angle and condyle similar in size
   2 = Angle half the size of condyle
   3 = Angle severely reduced

31. Dentary, subcondyle furrow (modified from Deméré et al., 2008:ch. 86)
   0 = Absent
   1 = Present, shallow
   2 = Present, deep

32. Rostral saddle (Arnold et al., 2005a:ch. 1)
   0 = Absent
   1 = Present
2 = Well developed

33. Nape field (Arnold et al., ch. 3)
   0 = Absent
   1 = Present
   2 = Light

34. Dorsal nape field (Arnold et al., 2005a: ch. 4)
   0 = Absent
   1 = Present
   2 = Linear and diffuse

35. Blowhole streaks (Arnold et al., 2005a: ch. 2)
   0 = Absent
   1 = Present
   2 = Well developed

36. Ventral nape streak (Arnold et al., 2005a: ch. 5)
   0 = Absent
   1 = Present

37. Ear stripe (Arnold et al., 2005a: ch. 6)
   0 = Absent
   1 = Present

38. Basal flipper coloration (Arnold et al., 2005a: ch. 7)
   0 = Uniform
   1 = Uniform with white leading edge
   2 = White base
   3 = Dark base

39. Distal flipper color (Arnold et al., 2005a: ch. 8)
   0 = Uniform coloration
   1 = Uniform with light leading edge
   2 = Dark grey coloration

40. Axillary patch (Arnold et al., 2005a: ch. 9)
   0 = Absent
   1 = Present
   2 = Well developed

41. Thorax field (Arnold et al., 2005a: ch. 10)
   0 = Uniform
   1 = Two-tone pigment, darker back and lighter underside, no intermediate light grey field
   2 = Light grey lateral field
3 = Dark thorax field and flank patch

42. Asymmetry, skin coloration (Arnold et al., 2005a:ch. 13)
   0 = Asymmetry absent
   1 = Asymmetry present
   2 = Asymmetry well developed

43. Ventral throat grooves (Deméré et al., 2008:ch. 69)
   0 = Absent
   1 = 2-10 confined to throat region
   2 = Numerous and terminate midbody
   3 = Numerous and extend at or posterior to the umbilicus

44. Dorsal fin (Deméré et al., 2005:ch. 72; modified Deméré et al., 2008:ch. 69)
   0 = Absent
   1 = Present and prominent
   2 = Present and small
   3 = Dorsal humps

45. Premaxillary-maxillary suture (Geisler and Sanders, 2003; Deméré et al., 2008 ch. 5)
   0 = Fused dorsally along the midline
   1 = Unfused

46. Fusion of cervical vertebrae (Deméré et al., 2005:ch. 67; Deméré et al., 2008:ch. 63)*
   0 = Unfused
   1 = Up to 6 vertebrae fused
   2 = All 7 vertebrae fused as compact unit

47. Acromoin process of scapula (Deméré et al., 2008:ch. 64)
   0 = Large
   1 = Reduced or absent

48. Coracoid process of scapula (Miller, 1923; Deméré et al., 2008:ch. 65)
   0 = Present
   1 = Absent (or reduced)

49. Curvature of fused basihyal-thyrohyal of the hyoid bone (Omura, 1964; Deméré et al., 2008:ch. 91)*
   0 = Strongly curved, straight length less than 75% of curved length
   1 = Straight length between 75-90% of curved length (slightly curved)
   2 = Straight length more than 90% of cuved length

50. Anterior process of hyoid (Omura, 1964; Deméré et al., 2008:ch. 91)
   0 = Absent
   1 = Short and robust
   2 = Long and slender
51. Fossa between the anterior processes of hyoid (Deméré et al., 2008:ch. 94)
   0 = Absent
   1 = Present

52. Narrow and elongate flippers (manus) with middle digits tightly appressed (Cooper et al., 2007)
   0 = Absent, paddleshaped flippers, not tightly appressed
   1 = Condition present

53. Rugosity of hyoid bone (Omura, 1964)
   0 = Smooth
   1 = Projections less corrugated
   2 = Rugose hyoid

54. Number of digits on the manus (Barnes and McLeod, 1984; Deméré et al., 2008:ch. 67).
   0 = 5 digits
   1 = 4 digits

55. Inclination of the spinous process of the dorsal/lumbar vertebrae (Olsen, 1913; Buchholtz, 2011)
   0 = No inclination
   1 = Slight posterior inclination
   2 = Strong posterior inclination

56. Scapular spine (Sanchez and Berta, 2010:ch. 2)
   0 = Prominent/Long
   1 = Reduced/Absent

57. Stylohyal shape of hyoid (Omura, 1964; Churchill et al., 2011:ch. 91)
   0 = Cylindrical
   1 = Flattened

58. Transverse process of lumbar vertebrae (Geisler and Sanders, 2003; Churchill et al., 2011:ch. 96)
   0 = Oriented ventrolaterally
   1 = Oriented laterally and horizontally

59. Olecranon process of the ulna (Churchill et al., 2011:ch. 105)
   0 = Slight vertical projection
   1 = Significant projection
   2 = Absent

60. Baleen (Deméré et al., 2008:ch. 71)
   0 = Absent
   1 = Present

61. Tympanic bulla, shape (Ekdale et al., 2011:ch. 1)
145

0 = Ovoid
1 = Rhomboidal

62. Tympanic bulla, medial margin (McLeod et al. 1993; Deméré et al., 2008:ch. 44)
   0 = Rounded/inflated dorsoventrally
   1 = Flattened dorsoventrally

63. Tympanic bulla, main ridge (modified from Ekdale et al., 2011:ch. 3)
   0 = Short, confined to posterior end
   1 = Long, extends to anterior end – dorsoventral edge rounded
   2 = Long, extends to anterior end – dorsoventral edge keeled
   3 = Keel indistinct

64. Tympanic bulla, involucral ridge and main ridge (Ekdale et al., 2011:ch. 6)
   0 = Coincident with medial ridge
   1 = Involucral ridge medially retracted

65. Tympanic bulla, anterolateral ridge or shelf (Ekdale et al., 2011:ch. 7)
   0 = Absent
   1 = Weakly present
   2 = Present as a ridge
   3 = Present as a shelf

66. Tympanic bulla, conical process thickness (Ekdale et al., 2011:ch. 9)
   0 = Thick
   1 = Thin anterior lip
   2 = Uniformly thin

67. Tympanic bulla, conical process height (modified Ekdale et al., 2011:ch. 8)
   0 = Short (low)
   1 = Tall

68. Periotic, lateral projection of anterior process (Deméré et al., 2008:ch. 47; Ekdale et al., 2011:ch. 18)
   0 = Absent
   1 = Present and small
   2 = Present and robust
   3 = Present and hypertrophied

69. Periotic, anterior process attached to promotorium (Ekdale et al., 2011:ch. 19)
   0 = Absent
   1 = Present with an embayment
   2 = Present, broadly attached (no embayment)

70. Petrosal, anterior process with sulcus for trigeminal nerve (Ekdale et al., 2011:ch. 21)
0 = Absent
1 = Present (located on anterolateral edge)

71. Petrosal, stylomastoid fossa (Ekdale et al., 2011:ch. 19)
   0 = Absent
   1 = Present, enlarged and extending to the pars cochlearis
   2 = Present, extending to the pars cochlearis and posterior process
   3 = Present, extending as a long groove on the posterior process

72. Petrosal, promontorium (Ekdale et al., 2011:ch. 46)
   0 = Rounded and convex ventrally
   1 = Flattened ventrally

73. Nasals, relative position of posteriormost edge (Deméré et al., 2008:ch. 12)*
   0 = Anterior to supraorbital process of the frontal
   1 = Anterior half of supraorbital process of frontal
   2 = Posterior half of supraorbital process of frontal
   3 = Zygomatic process
   4 = Posterior temporal fossa

74. Maxilla geometry/arrangement of lateral nutrient foramina and associated sulci (Deméré et al., 2008:ch. 54)
   0 = Posterior foramina with sulci radially arranged (no open maxillary groove) and anterior foramina with elongate sulci parasagittally arranged.
   1 = Posterior foramina coincident with open maxillary groove with numerous short transverse sulci and anterior foramina with elongate sulci parasagittally arranged.
   2 = Posterior foramina single, separate from open maxillary groove without well-developed sulci and anterior foramina with elongate sulci parasagittally arranged.
   3 = Posterior foramina multiple (roughly in two rows) without well-developed sulci (no open maxillary groove) and anterior foramina with elongate sulci parasagittally arranged.

75. Premaxilla, posterior process (Miller, 1923; Deméré et al., 2008:ch. 13)
   0 = No contact with frontals
   1 = Contacting frontals
   2 = Contacting frontals and forming robust ascending process

76. Frontal, supraorbital process, slope (Miller, 1923; Deméré et al., 2008:ch. 23)*
   0 = At level of vertex
   1 = Gradually sloping from vertex
   2 = Abruptly deflected from below vertex

77. Parietal/frontal, interorbital region (Deméré et al 2008:ch. 26)
   0 = Both large (=)
   1 = Parietal > Frontal
   2 = Frontal > Parietal (Esch.)
3 = Both reduced (B. musculus)
4 = Parietal excluded from interorbital region

78. Palatines, posterior extension (Deméré et al., 2005:ch. 42; Deméré et al., 2008:ch. 42)*
   0 = Extend to internal nares
   1 = Extend to slightly overlap the pterygoids
   2 = Long overlap of pterygoids nearly reaching pterygoid fossa

79. Palate, shape (Deméré et al., 2008:ch. 36)
   0 = Flat with no median keel
   1 = Median keel dividing palate into right and left concave surfaces

80. Paroccipital process, skull in ventral aspect (Deméré et al., 2008:ch. 43)*
   0 = Well anterior to occipital condyles
   1 = Parallel with occipital condyles
   2 = Posterior to occipital condyles

81. Squamosal, posterior width (exoccipital width relative to zygomatic width) (Deméré et al., 2005:ch. 36; Deméré et al., 2008:ch. 34)*
   0 = 50-70%
   1 = 70-80%
   2 = >80%

82. Apex of occipital shield (Deméré et al., 2005:ch. 29; Deméré et al., 2008:ch. 27)*
   0 = Extension posterior to temporal fossa
   1 = Extension to posterior one-half of temporal fossa
   2 = Extension to anterior one-half temporal fossa
   3 = Extension to orbit
   4 = Extension anterior to orbit

83. Occipital shield, lateral margins (Deméré et al., 2005:ch. 31)*
   0 = Convex
   1 = Straight
   2 = Concave

84. Parietal-Frontal suture, anterior wing (modified Deméré et al., 2008:ch. 95)
   0 = Anterior wing absent
   1 = Anterior wing present, lobate and short
   2 = Anterior wing present, lobate and elongate
   3 = Anterior wing present, angular and short

85. Position of posterior apex of the lambdoid crest (Bisconti, 2007a:ch. 83)
   0 = At level of the occipital condyles
   1 = Posterior to the condyles
   2 = Anterior to the condyles
86. Relationships of pterygoid and squamosal (Bisconti, 2007a:ch. 116)
   0 = Pterygoid does not appear in the temporal fossa
   1 = Anterolateral diameter of pterygoid not narrowed by the interposition of the falciform process of the squamosal
   2 = Anterolateral diameter of pterygoid narrowed dorsal to the hamular process owing to an anteroventral expansion of falciform process of squamosal
   3 = Pterygoid subdivided into two halves by the interposition of the falciform process of the squamosal

87. Squamosal, glenoid fossa and zygomatic process (Deméré et al., 2008:ch. 33)
   0 = Elevated
   1 = Depressed

88. Mandible, position of coronoid process (Deméré et al., 2008:ch. 81)
   0 = Located relatively close to mandibular condyle
   1 = Located relatively far anterior to mandibular condyle

89. Mandible, relative position of anterior border of mandibular foramen (Deméré et al., 2008:ch. 87)*
   0 = Anterior to coronoid process
   1 = In line with middle of coronoid process
   2 = In line with posterior edge of coronoid process
   3 = Posterior to coronoid process

90. Mandible dentary, curvature of ramus in dorsal aspect (McLeod et al, 1993; Deméré et al., 2008:ch. 57)*
   0 = Laterally concave
   1 = Straight
   2 = Laterally convex

91. Dentary, ventromedial groove (Deméré et al., 2008:ch. 56)
   0 = Absent
   1 = Present

92. Dentary, mandibular condyle orientation (Deméré et al., 2008:ch. 59)
   0 = Directed posteriorly
   1 = Directed dorsally
   2 = Directed posterolaterally

93. Dentary, medial torsion of the anterior portion (Deméré et al., 2008:ch. 89)
   0 = Absent
   1 = Present

94. Dentary, ventral surface of middle portion of mandible (Deméré et al., 2008:ch. 88)
   0 = Rounded
   1 = Blade-like keel
95. Dentary, shape of mandibular condyle (Deméré et al., 2008:ch. 83)
   0 = Transversly expanded and slightly cylindrical
   1 = Bulbous and spherical
   2 = Transversly compressed and ovoid

96. Dentary, postcoronoid elevation (Deméré et al., 2008:ch. 82)
   0 = Absent
   1 = Present

97. Tongue (Sanderson and Wassersug, 1993; Deméré et al., 2008:ch. 75)
   0 = Muscular
   1 = Reduced and predominately connective tissue

98. Longitudinal ridges on rostrum (Deméré et al., 2008:ch. 76)*
   0 = Absent or indistinct
   1 = Single, median ridge
   2 = Three longitudinal ridges

99. Caudal chevron (Arnold et al., 2005a:ch. 11)
   0 = Absent
   1 = Single chevron
   2 = Double chevron

100. Peduncle streak (Arnold et al., 2005a:ch. 12)
    0 = Absent
    1 = Peduncle patch restricted to ventral field
    2 = Light color continues as a light streak up the side of the peduncle

101. Tympanic bulla, median furrow (Ekdale et al., 2011:ch. 4)
     0 = Short, confined to posterior 40% of medial surface
     1 = Long, extending onto anterior 50% of medial surface
     2 = Absent

102. Tympanic bulla, dorsal posterior prominence (Ekdale et al., 2011:ch. 5)
     0 = Absent or weakly developed
     1 = Conspicuous

103. Tympanic bulla, posterior extension (Ekdale et al., 2011:ch. 10)
     0 = Absent
     1 = Present

104. Tympanic bulla, dorsal involcrum surface in medial view (Ekdale et al., 2011:ch. 11)
     0 = Relatively straight or slightly curved
     1 = Markedly sinuous and strongly concave
105. Tympanic bulla, dorsal surface of the involcrum adjacent to the Eustacian tube (Ekdale et al., 2011:ch. 12)
   0 = Convex
   1 = Planar

106. Tympanic bulla, elevated and flattened posterior portion of medial margin of the main ridge (Ekdale et al., 2011:ch. 13)
   0 = Absent
   1 = Present

107. Tympanic bulla, length of anterior lobe (Ekdale et al., 2011:ch. 14)
   0 = Long, 40% or greater than total length of bulla
   1 = Short, 30% or less than total length of bulla

108. Petrosal, shape of anterior process apex (Ekdale et al., 2011:ch. 20)
   0 = Rounded
   1 = Narrowly triangular
   2 = Bluntly triangular
   3 = Elongated and inflated

109. Petrosal, anterior process with prominent, tiny bony projections (Ekdale et al., 2011:ch. 22)
   0 = Absent
   1 = Present

110. Petrosal, orientation of posterior process (Ekdale et al., 2011:ch. 25)
   0 = Posterolaterally relative to long axis of pars cochlearis
   1 = At right angles to pars cochlearis

111. Petrosal, posterior cochlear crest (Ekdale et al., 2011:ch. 26)
   0 = Absent or reduced
   1 = Present, medially extending shelf adjacent to fenestra cochlae
   2 = Present, ventrally directed

112. Petrosal, attachment for tensor tympani muscle (Ekdale et al., 2011:ch. 28)
   0 = Present as enlarged fossa
   1 = Present as a groove
   2 = Absent or poorly developed

113. Petrosal, promontorial groove on medial side of pars cochlearis (Ekdale et al., 2011:ch. 29)
   0 = Absent
   1 = Present

114. Petrosal, ridge on anterolateral side of pars cochlearis, in ventral side (Ekdale et al., 2011:ch. 30)
0 = Absent  
1 = Present and low  
2 = Present and high, forms an anterior-posterior ridge  
3 = Present and well-developed

115. Petrosal, perilymphatic foramen in dorsolateral aspect (Ekdale et al., 2011:ch. 32)  
  0 = Widely separated from fenestra cochlae  
  1 = Narrowly separated from fenestra cochlae  
  2 = Confluent with fenestra cochlae

116. Petrosal, suprameatal region (Ekdale et al., 2011:ch. 34)  
  0 = At level of the anterior process  
  1 = Elevated above (dorsal) to the anterior process

117. Petrosal, crista transversa (Ekdale et al., 2011:ch. 35)  
  0 = Low, does not reach cerebral surface  
  1 = High, reaches cerebral surface

118. Petrosal, fenestra cochlae size relative to fenestra vestibuli (Ekdale et al., 2011:ch. 36)  
  0 = Small  
  1 = Large

119. Petrosal, arrangement of endolymphatic and perilymphatic foramina (Ekdale et al., 2011:ch. 38)  
  0 = Separate, with tiny bony septum that is anteroposteriorly oriented  
  1 = En echelon, divided by a tiny bony septum that is dorsoventrally oriented

120. Petrosal, relative size of internal openings for vestibulocochlear and facial nerve canals within the internal auditory meatus (Ekdale et al., 2011:ch. 40)  
  0 = Vestibulocochlear > facial nerve canal opening  
  1 = Vestibulocochlear = facial nerve canal opening

121. Petrosal, stapedial fossa and facial nerve sulcus (Ekdale et al., 2011:ch. 41)  
  0 = Separate  
  1 = Confluent

122. Petrosal, relative size of stapedial fossa (Ekdale et al., 2011:ch. 42)  
  0 = Small and compressed  
  1 = Large/hemispherical

123. Petrosal, contact edge between stylomastoid fossa and ventral surface of promontorium (Ekdale et al., 2011:ch. 44)  
  0 = Not well-developed  
  1 = Well-developed as a short keel  
  2 = Well-developed as elongate, broad flange
124. Petrosal, hiatus Fallopii (Ekdale et al., 2011:ch. 45)
   0 = Through ventral surface of promontorium
   1 = Within seam between promontorium and anterior process
   2 = Through ventral surface of anterior process

125. Petrosal, endocranial opening of facial nerve canal (Ekdale et al., 2011:ch. 47)
   0 = Circular
   1 = Oval-shaped
   2 = With anterior fissure

126. Humerus-radius length ratio (Deméré et al., 2008:ch. 66)
   0 = Humerus equal or longer than radius
   1 = Humerus shorter than radius

127. Baleen plate length versus width (modified Deméré et al., 2008:ch. 73; Young, 2012)
   0 = Long and compressed
   1 = Short and wide

128. Baleen bristle diameter (Deméré et al., 2008:ch. 74; Young, 2012)
   0 = Fine
   1 = Coarse

129. Baleen plate thickness (modified Deméré et al., 2008:ch. 72; Young, 2012)
   0 = Flexible
   1 = Rigid
APPENDIX D

DIVERGENCE DATING GENBANK INFORMATION
RAG1 Analyses

These taxa are those that were included in the external calibration mitochondrial divergence dating analyses. They were selected based on availability and overall taxonomic coverage of the major clades of placental mammals.

EU445021.1 Balaenoptera acutorostrata
EU445020.1 Balaenoptera bonaerensis
EU445018.1 Balaenoptera borealis
EU445019.1 Balaenoptera edeni
EU445017.1 Balaenoptera musculus
EU445016.1 Balaenoptera physalus
EU445015.1 Megaptera novaeangliae
EU445022.1 Eschrichtius robustus
EU445024.1 Balaena mysticetus
GQ368545.1 Eubalaena australis
GQ368546.1 Eubalaena glacialis
EU445025.1 Eubalaena japonica
EU445023.1 Caperea marginata
GQ368540.1 Delphinapterus leucas
GQ36857.1 Grampus griseus
EU697427.1 Steno bredanensis
EU189407.1 Pontoporia blainvillei
GQ368541.1| Mesoplodon peruvianus
EU697429.1 Stenella coeruleoalba
EU189405.1 Monodon monoceros
EU697424.1| Phocoena phocaena
EU189406.1 Inia geoffrensis
EU445014.1 Ziphius cavirostris
GQ368538.1 Phocoenoides dalli
EU697426.1 Pseudorca crassidens
EU445013.1 Physeter catadon
GQ368542.1 Tasmacetus shepherdi
GQ368535.1 Feresa attenuata
GQ368532.1 Tursiops truncatus
GQ368534.1 Lissodelphis borealis
GQ368544.1 Kogia sima
GQ368533.1 Stenella attenuata
GQ368536.1 Globicephala macrorhynchus
GQ368539.1 Neophocaena phocaenoides
AY011909.1 Hippopotamus amphibius
AF447520.1 Bos taurus
EU189401.1 Giraffa camelopardalis
EU189399.1 Odocoileus virginianus
JN633594.1 Cervus nippon
AY011880.1 Castor canadensis
AY011915.1 Felis catus
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<th>Species Name</th>
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<td><em>Nandinia binotata</em></td>
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<tr>
<td>AY011874.1</td>
<td><em>Trichecus manatus</em></td>
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<tr>
<td>AY011918.1</td>
<td><em>Ursus arctos</em></td>
</tr>
<tr>
<td>FJ603230.1</td>
<td><em>Lagostrophus fasciatus</em></td>
</tr>
<tr>
<td>AY011864.1</td>
<td><em>Didelphis virginiana</em></td>
</tr>
</tbody>
</table>
APPENDIX E

RESULTS OF DIVERGENCE DATING ANALYSES
Table 13. Divergence Estimates for the Mitochondrial Analysis of Mysticeti (Only): Fossil Set 1

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>16.079</td>
<td>21.307</td>
<td>10.715</td>
<td>626.159</td>
</tr>
<tr>
<td>Balaenidae</td>
<td>7.225</td>
<td>10.763</td>
<td>3.969</td>
<td>876.493</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.062</td>
<td>30.956</td>
<td>28.035</td>
<td>8541.32</td>
</tr>
<tr>
<td>Bal. acutorostrata +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bal. bonaerensis</td>
<td>5.936</td>
<td>8.542</td>
<td>3.090</td>
<td>n/a</td>
</tr>
<tr>
<td>Bal. physalus +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meg. novaeangliae</td>
<td>9.066</td>
<td>12.719</td>
<td>5.218</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>21.649</td>
</tr>
<tr>
<td>Prior</td>
<td>-43.299</td>
<td>-15.362</td>
<td>-59.126</td>
<td>17.353</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>1.4E3</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.

Table 14. Divergence Estimates for the Mitochondrial Analysis of Mysticeti (Only): Fossil Set 2

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenidae</td>
<td>7.416</td>
<td>10.883</td>
<td>4.456</td>
<td>911.797</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.061</td>
<td>31.080</td>
<td>28.751</td>
<td>8819.89</td>
</tr>
<tr>
<td>Bal. acutorostrata +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bal. bonaerensis</td>
<td>6.073</td>
<td>8.869</td>
<td>3.369</td>
<td>n/a</td>
</tr>
<tr>
<td>Bal. physalus +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meg. novaeangliae</td>
<td>9.338</td>
<td>12.973</td>
<td>5.649</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>5.139</td>
</tr>
<tr>
<td>Prior</td>
<td>-40.479</td>
<td>-5.840</td>
<td>-58.570</td>
<td>4.526</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>-4.8E4</td>
<td>4.7E2</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.
Table 15. Divergence Estimates for the Mitochondrial Analysis of McGowen et al., 2009 Full Dataset: Fossil Set 1

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cetacea</td>
<td>36.314</td>
<td>39.872</td>
<td>34.248</td>
<td>143.383</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>28.640</td>
<td>29.576</td>
<td>28.036</td>
<td>2217.37</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>35.225</td>
<td>39.872</td>
<td>34.248</td>
<td>n/a</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>55.075</td>
<td>58.332</td>
<td>53.527</td>
<td>767.980</td>
</tr>
<tr>
<td>Bal. acutorostrata + Bal. bonaerensis</td>
<td>4.530</td>
<td>6.744</td>
<td>2.405</td>
<td>n/a</td>
</tr>
<tr>
<td>Bal. physalus + Meg. novaeangliae</td>
<td>7.084</td>
<td>8.330</td>
<td>3.509</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>441.869</td>
</tr>
<tr>
<td>Prior</td>
<td>-322.179</td>
<td>-310.559</td>
<td>-334.545</td>
<td>101.517</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>2858.17</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.

Table 16. Divergence Estimates for the Mitochondrial Analysis of McGowen et al., 2009 Full Dataset: Fossil Set 2

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>11.455</td>
<td>14.297</td>
<td>8.819</td>
<td>69.876</td>
</tr>
<tr>
<td>Cetacea</td>
<td>34.918</td>
<td>39.520</td>
<td>30.622</td>
<td>39.479</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>28.578</td>
<td>29.445</td>
<td>28.028</td>
<td>3366.90</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>32.583</td>
<td>37.343</td>
<td>28.351</td>
<td>n/a</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>50.737</td>
<td>55.681</td>
<td>48.611</td>
<td>363.187</td>
</tr>
<tr>
<td>Bal. acutorostrata + Bal. bonaerensis</td>
<td>3.753</td>
<td>5.591</td>
<td>2.039</td>
<td>n/a</td>
</tr>
<tr>
<td>Bal. physalus + Meg. novaeangliae</td>
<td>5.496</td>
<td>8.490</td>
<td>3.218</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>118.273</td>
</tr>
<tr>
<td>Prior</td>
<td>-320.964</td>
<td>-305.116</td>
<td>-334.545</td>
<td>101.517</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>-1.3E5</td>
<td>2470.67</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.
Table 17. Divergence Estimates for the Analysis of McGowen et al., 2009
Combined Dataset: Fossil Set 1

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cetacea</td>
<td>54.255</td>
<td>55.623</td>
<td>53.423</td>
<td>1610.97</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>30.031</td>
<td>34.331</td>
<td>28.021</td>
<td>31.228</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>27.177</td>
<td>37.318</td>
<td>18.338</td>
<td>9.011</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>54.343</td>
<td>53.541</td>
<td>55.692</td>
<td>1618.55</td>
</tr>
<tr>
<td>Balaenidae</td>
<td>28.319</td>
<td>33.304</td>
<td>24.739</td>
<td>39.256</td>
</tr>
<tr>
<td><strong>Bal. acutorostrata +</strong>&lt;br&gt;<strong>Bal. bonaerensis</strong></td>
<td>5.142</td>
<td>9.057</td>
<td>1.882</td>
<td>n/a</td>
</tr>
<tr>
<td><strong>Bal. physalus +</strong>&lt;br&gt;<strong>Meg. novaeangliae</strong></td>
<td>3.915</td>
<td>6.072</td>
<td>0.810</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>6.860</td>
</tr>
<tr>
<td>Prior</td>
<td>-312.219</td>
<td>-299.113</td>
<td>-332.839</td>
<td>4.786</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>4.870</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.

Table 18. Divergence Estimates for the Analysis of McGowen et al., 2009
Combined Dataset: Fossil Set 2

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>7.717</td>
<td>10.554</td>
<td>6.073</td>
<td>11.509</td>
</tr>
<tr>
<td>Cetacea</td>
<td>33.888</td>
<td>45.412</td>
<td>30.067</td>
<td>5.541</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>30.932</td>
<td>43.606</td>
<td>28.051</td>
<td>7.498</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>25.313</td>
<td>32.560</td>
<td>17.142</td>
<td>40.259</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>49.511</td>
<td>51.294</td>
<td>48.613</td>
<td>596.728</td>
</tr>
<tr>
<td>Balaenidae</td>
<td>28.962</td>
<td>43.385</td>
<td>22.743</td>
<td>8.602</td>
</tr>
<tr>
<td><strong>Bal. acutorostrata +</strong>&lt;br&gt;<strong>Bal. bonaerensis</strong></td>
<td>3.308</td>
<td>6.084</td>
<td>1.142</td>
<td>n/a</td>
</tr>
<tr>
<td><strong>Bal. physalus +</strong>&lt;br&gt;<strong>Meg. novaeangliae</strong></td>
<td>0.564</td>
<td>1.854</td>
<td>0.102</td>
<td>n/a</td>
</tr>
<tr>
<td>Posterior</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>7.750</td>
</tr>
<tr>
<td>Prior</td>
<td>-297.937</td>
<td>-283.156</td>
<td>-314.628</td>
<td>11.583</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>-2.6E5</td>
<td>7.710</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.
Table 19. Divergence Estimates for the RAG1 Dataset Analysis without the External Calibration (*Juramaia sinensis*): Fossil Set 1

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>9.134</td>
<td>12.979</td>
<td>8.458</td>
<td>1624.51</td>
</tr>
<tr>
<td>Cetacea</td>
<td>35.247</td>
<td>37.145</td>
<td>34.238</td>
<td>2020.25</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.409</td>
<td>32.273</td>
<td>28.041</td>
<td>5350.58</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>31.326</td>
<td>36.776</td>
<td>22.858</td>
<td>534.539</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>55.229</td>
<td>58.895</td>
<td>53.526</td>
<td>1490.33</td>
</tr>
<tr>
<td>Placentalia/Eutheria</td>
<td>81.858</td>
<td>111.704</td>
<td>57.285</td>
<td>85.178</td>
</tr>
<tr>
<td><em>Bal. acutorostrata + Bal. bonaerensis</em></td>
<td>2.175</td>
<td>6.846</td>
<td>0.020</td>
<td>2512.93</td>
</tr>
<tr>
<td><em>Bal. physalus + Meg. novaeangliae</em></td>
<td>3.534</td>
<td>7.416</td>
<td>0.153</td>
<td>1386.89</td>
</tr>
<tr>
<td>Posterior</td>
<td>-1.0E4</td>
<td>-1.0E4</td>
<td>-1.0E4</td>
<td>370.00</td>
</tr>
<tr>
<td>Prior</td>
<td>-274.930</td>
<td>-257.391</td>
<td>-291.666</td>
<td>19.467</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-1.0E4</td>
<td>-9.9E3</td>
<td>-1.0E4</td>
<td>110.00</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.

Table 20. Divergence Estimates for the RAG1 Dataset Analysis without the External Calibration (*Juramaia sinensis*): Fossil Set 2

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>7.898</td>
<td>11.922</td>
<td>6.021</td>
<td>1526.70</td>
</tr>
<tr>
<td>Cetacea</td>
<td>31.916</td>
<td>36.262</td>
<td>30.023</td>
<td>1182.73</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.069</td>
<td>30.642</td>
<td>28.027</td>
<td>5947.96</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>28.353</td>
<td>34.587</td>
<td>20.398</td>
<td>565.312</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>49.861</td>
<td>52.620</td>
<td>48.608</td>
<td>3536.79</td>
</tr>
<tr>
<td>Placentalia/Eutheria</td>
<td>100.429</td>
<td>127.668</td>
<td>67.040</td>
<td>124.937</td>
</tr>
<tr>
<td><em>Bal. acutorostrata + Bal. bonaerensis</em></td>
<td>1.757</td>
<td>5.674</td>
<td>0.010</td>
<td>2583.39</td>
</tr>
<tr>
<td><em>Bal. physalus + Meg. novaeangliae</em></td>
<td>3.248</td>
<td>6.589</td>
<td>0.201</td>
<td>1078.38</td>
</tr>
<tr>
<td>Posterior</td>
<td>-1.0E4</td>
<td>-1.0E4</td>
<td>-1.0E4</td>
<td>382.000</td>
</tr>
<tr>
<td>Prior</td>
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<td>-258.128</td>
<td>-290.680</td>
<td>180.097</td>
</tr>
<tr>
<td>Likelihood</td>
<td>-9.9E3</td>
<td>-9.9E3</td>
<td>-9.9E3</td>
<td>3550.00</td>
</tr>
</tbody>
</table>

Note: ‘n/a’ indicates a node where an ESS value is not available.
Table 21. Divergence Dating Estimates for the RAG1 Dataset Utilizing the External Calibration (*Juramaia sinensis*) Fossil Set 1

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cetacea</td>
<td>35.322</td>
<td>37.372</td>
<td>34.240</td>
<td>1658.20</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.439</td>
<td>32.326</td>
<td>28.033</td>
<td>5281.52</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>32.172</td>
<td>36.937</td>
<td>25.229</td>
<td>565.079</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>56.267</td>
<td>63.685</td>
<td>53.532</td>
<td>731.395</td>
</tr>
<tr>
<td>Placentalia/Eutheria</td>
<td>161.510</td>
<td>165.377</td>
<td>160.006</td>
<td>5243.70</td>
</tr>
<tr>
<td><em>Bal. acutorostrata</em> + <em>Bal. bonaerensis</em></td>
<td>2.530</td>
<td>7.389</td>
<td>0.000</td>
<td>2487.03</td>
</tr>
<tr>
<td><em>Bal. physalus</em> + <em>Meg. novaeangliae</em></td>
<td>3.925</td>
<td>7.933</td>
<td>0.094</td>
<td>1277.60</td>
</tr>
</tbody>
</table>

*Note:* ‘n/a’ indicates a node where an ESS value is not available.

Table 22. Divergence Dating Estimates for the RAG1 Dataset Utilizing the External Calibration (*Juramaia sinensis*) Fossil Set 2

<table>
<thead>
<tr>
<th>Node/Value</th>
<th>Mean</th>
<th>95% Upper HPD</th>
<th>95% Lower HPD</th>
<th>ESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balaenopteridae</td>
<td>8.112</td>
<td>12.555</td>
<td>6.050</td>
<td>1387.20</td>
</tr>
<tr>
<td>Cetacea</td>
<td>32.143</td>
<td>37.117</td>
<td>30.023</td>
<td>668.199</td>
</tr>
<tr>
<td>Mysticeti</td>
<td>29.086</td>
<td>30.751</td>
<td>28.036</td>
<td>5689.31</td>
</tr>
<tr>
<td>Odontoceti</td>
<td>28.984</td>
<td>35.878</td>
<td>21.684</td>
<td>560.013</td>
</tr>
<tr>
<td>Cetancodonta</td>
<td>50.532</td>
<td>55.344</td>
<td>48.610</td>
<td>1917.27</td>
</tr>
<tr>
<td>Placentalia/Eutheria</td>
<td>161.633</td>
<td>165.877</td>
<td>160.003</td>
<td>5288.32</td>
</tr>
<tr>
<td><em>Bal. acutorostrata</em> + <em>Bal. bonaerensis</em></td>
<td>3.84</td>
<td>5.806</td>
<td>1.879</td>
<td>2911.51</td>
</tr>
<tr>
<td><em>Bal. physalus</em> + <em>Meg. novaeangliae</em></td>
<td>3.454</td>
<td>6.830</td>
<td>0.214</td>
<td>1456.91</td>
</tr>
</tbody>
</table>

*Note:* ‘n/a’ indicates a node where an ESS value is not available.
APPENDIX F

INCOMPLETENESS OF FOSSIL TAXA
This appendix contains the incompleteness values for each of the fossil taxa sampled in this study. Out of 129 morphological characters, 16 were soft characters that could not be coded for any of the fossils. The percentages listed below exclude the soft characters, thus are derived from a total 113 morphological characters.

<table>
<thead>
<tr>
<th>Fossil Species</th>
<th>Percent Incomplete</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Balaenoptera colcloughi</em></td>
<td>19%</td>
</tr>
<tr>
<td>‘<em>Megaptera’ miocaena</em></td>
<td>35%</td>
</tr>
<tr>
<td><em>Diunatans luctorememergo</em></td>
<td>50%</td>
</tr>
<tr>
<td><em>Eobalaenoptera harrisoni</em></td>
<td>73%</td>
</tr>
<tr>
<td><em>Plesiobalaenoptera quarantellii</em></td>
<td>54%</td>
</tr>
<tr>
<td><em>Archaebalaenoptera castriarquati</em></td>
<td>54%</td>
</tr>
<tr>
<td><em>Eschrichtioides gastaldeii</em></td>
<td>44%</td>
</tr>
<tr>
<td><em>Eomysticetus whitmorei</em></td>
<td>26%</td>
</tr>
<tr>
<td><em>Aetiocetus weltoni</em></td>
<td>36%</td>
</tr>
<tr>
<td>‘<em>Megaptera’ hubachi</em></td>
<td>36%</td>
</tr>
<tr>
<td><em>Balaenoptera siberi</em></td>
<td>59%</td>
</tr>
<tr>
<td><em>Parabalaenoptera bauninensis</em></td>
<td>43%</td>
</tr>
<tr>
<td><em>Uranocetus gramensis</em></td>
<td>40%</td>
</tr>
<tr>
<td><em>Mauicetus parkii</em></td>
<td>71%</td>
</tr>
<tr>
<td><em>Piscobaena nana</em></td>
<td>21%</td>
</tr>
<tr>
<td><em>Aglaocetus patulus</em></td>
<td>52%</td>
</tr>
<tr>
<td><em>Diorocetus hiatus</em></td>
<td>35%</td>
</tr>
<tr>
<td><em>Cetotherium rathkii</em></td>
<td>67%</td>
</tr>
<tr>
<td><em>Mixocetus elysius</em></td>
<td>58%</td>
</tr>
<tr>
<td><em>Balaenella brachyrrhynus</em></td>
<td>51%</td>
</tr>
<tr>
<td><em>Protororqualus cuvieri</em></td>
<td>54%</td>
</tr>
</tbody>
</table>
APPENDIX G

FOSSIL CALIBRATION JUSTIFICATION
Divergence of Cetacea and Hippopotamidae (Cetancodonta)

**Pakicetus inachus** [Gingerich and Russell, 1981]

1. The Geological Survey of Pakistan – University of Michigan (GSP-UM) 084, holotype of *P. inachus*. There are four species of *Pakicetus*, with a total of six specimens from Indo-Pakistan (PBDB), all Eocene aged (Thewissen et al., 2001a).

2. Thewissen et al. (2001b) demonstrated the stem position of *Pakicetus* relative to the rest of Cetacea. In their analysis, it is found sister to *Ambulocetus*. They found pakicetids more closely related to extant cetaceans than to artiodactyls using phylogenetics and highlighted cetacean synapomorphies of the ear. This study also includes many postcranial characteristics of artiodactyls, for example, in characters of the ankle (i.e. trochlea).

   Geisler and Sanders (2003) supported this relationship of *Pakicetus* as one of the most archaic within Cetacea and included specific characters of support, such as a low ridge on the basioccipital and possession of a sigmoid process. They also noted features shared with artiodactyls, such as the anterior edge of nasals above the incisors or canine. Uhen (2008) also found *Pakicetus* in the same phylogenetic position.

3. The phylogenetic hypothesis proposed in Thewissen et al. (2001b) is well accepted, at least in terms of the pakicetids. Also, the monophyly of Cetacea is recovered in all recent phylogenetic analyses, both morphological and molecular. Molecular studies have also corroborated the placement of *Pakicetus* (i.e. Spaulding et al. 2009). However, Spaulding et al. (2009) recovered *Ambulocetus natans* positioned as stem member of all of Cetacea, followed by *Pakicetus*. Interestingly, *A. natans* is from the same formation as *Pakicetus*, but was located in a younger bed (PBDB).

   *Pakicetus* was long considered the oldest whale before the discovery of *Himalayacetus* (Uhen, 2010). However, *Himalayacetus* is not supported phylogenetically as a confirmed member of Cetacea, the use of it over *Pakicetus* cannot be justified (see ‘Methods’).


5. The Kuldana Formation is represented by a thin tongue of continental (shallow sea) beds within a large sequence of foraminifera-bearing marine formation (Gingerich, 2003). This formation represents the Lutetian Stage of the middle Eocene, which is dated to 48.6-40.4 MYA (Thewissen et al., 2001; Gingerich, 2003; PBDB). Gingerich (2003) provided an in-depth geological examination of this formation in terms of the mammalian fauna (including *Pakicetus*) and confirmed (using multiple lines of evidence) that the Kuldana belongs to the early middle Eocene.

   Additional comments = This calibration is also utilized by Zhou et al. (2011) (though no justification given), Xiong et al. (2009) (which provided references for justification), and Dornburg et al. (2012). Also, this calibration is the focus of a paper by van Tuinen and Hadly (2004). While this paper did not specifically call for the use of this calibration, the rationale of using it as such is justified within the article. A review of calibrations at the split of Artiodactyls-Cetacea demonstrated some uncertainty of the dating of the Kuldana Formation.

Divergence of Crown Cetacea (Neoceti)

**Simocetus rayi** [Fordyce, 2002a]

1. Smithsonian Museum of Natural History (USNM) 256517, holotype specimen. This is the only recognized specimen of *S. rayi*. 
2. Fordyce (2002a) first described *Simocetus rayi* as in a “basal” position within Odontoceti. He described *S. rayi* as possessing some features unique to odontocetes (e.g. orbit, premaxilla and maxilla), but also some novel (e.g. bony nares structure, tooth complement, mandibular symphysis).

3. This taxon was included in the phylogenetic analysis of Fitzgerald (2010), who confirmed the position of *S. rayi* in Odontoceti. However, the author noted that it is not the most archaic morphologically (*Archaeodelphis patrius* and/or *Xenorophus* sp.). However, the stipulation is that *S. rayi* is the best-known stem odontocete, largely due to its detailed description. The presence of echolocation, a key feature of Odontoceti, is also inferred for this taxon (Steeman et al., 2009), which supports use of *S. rayi* in this phylogenetic position.

   Geisler et al. (2011) also confirmed the placement of this taxon and used their results as justification for calibrating their divergence analysis with *S. rayi*. Since the relationships of stem Mysticeti are more controversial and lack a justifiable calibration fossil (i.e. *Llanocetus denticrenatus*), *S. rayi* is a legitimate choice for use as representative of the split between the two major lineages of crown cetaceans.

4. Alsea Formation, Lincoln County, Oregon (Fordyce, 2002a; PBDB)

5. Fordyce (2002a) described the locality as the Upper Zemorrian stage of the late Oligocene. Noting a fault in the area of the locality, the exact stratigraphic position relative to the base of the formation was unknown. However, citing studies of foraminifera and vertebrate-bearing stratigraphy, the author states that the age is “presumably in the range of 30-23 MYA.”

   Prothero (2003) provided a detailed investigation of the Eocene/Oligocene chronostratigraphy of the US Pacific Northwest. The Upper Zemorrian stage was dated to a smaller time range, based on benthic foraminifera stages (using magnetostratigraphy and planktonic microfossils). The age deduced from this study ranges between 30-33 MYA, but again the author notes the unconformity. This correlates to the Rupelian Stage of the Oligocene, which is aged between 33.9 – 28.4 MYA (PBDB).

   Additional comments = *S. rayi* was used as a calibration previously by Geisler et al. (2011).

*Divergence of Crown Mysticeti*

**Eomysticetus whitmorei** [Sanders and Barnes, 2002]

1. Charleston Museum (ChM) PV4253, holotype specimen. There is only one recognized specimen of this taxon. A sister species, *E. carolinensis*, was reported in the same publication (Sanders and Barnes, 2002), for which there is also only one specimen (ChM PV4845). It was recovered from the same formation as *E. whitmorei*. However, *E. whitmorei* is a more complete specimen, thus often the genus is represented by that species.

2. This taxon possesses many characters of toothed mysticetes but is currently the earliest recognized toothless mysticete. Ear morphology, as in many cetacean studies, is very important to the position of *Eomysticetus* (Geisler and Sanders, 2003; Steeman, 2007). The degree of telescoping exhibited by this taxon is primitive and shares some characteristics with Archaeoceti (e.g. slender squamosals, narrow SOPF) (Sanders and Barnes, 2002).

3. The original publication did not include a phylogenetic analysis of the taxon. However, it has since been included in phylogenetic analyses, including Deméré et al. (2008), which recovered *Eomysticetus* as the base of edentulous mysticetes. Uhen (2010) also recovered this taxon as the earliest member of crown Mysticeti.
Steeman (2007) and Marx (2010) recovered *E. whitmorei* in a sister clade with *Mauicetus lophocephalus* in the base position, though this relationship is not overly well supported in either study. These taxa are both known from the late Oligocene, however the phylogenetic relationships of *Mauicetus* are contentious (Geisler et al., 2011).

It must be noted that the transition between toothed and toothless mysticetes is not well understood and currently under investigation by multiple authors (e.g. Deméré et al., 2008). Currently, *Eomysticetus* remains as the earliest representative of toothless mysticetes.

4. Chandler Bridge Formation, Dorchester County, South Carolina (Sanders and Barnes, 2002).

5. The Chandler Bridge Formation is late Oligocene in age and *Eomysticetus* was recovered from near the top of Bed 3, which was stated as ~28 MYA in Sanders and Barnes (2002). This formation, and the underlying Ashley Formation, are well known for producing cetacean fossils and have been extensively studied. The Ashley Formation is dated at approximately 30 MYA, with little time between the deposition of the two (~2 MYA). These dates were based on the biostratigraphic correlation of the Ashley Formation to a nanoplanktonic zone (Sanders and Barnes, 2002).

This formation is correlated with the lower Chattian age, which is dated to 28.4-23.3 MYA (PBDB). An investigation into the geologic super group in which the Chandler Bridge Formation is a part (the Trent Super group) confirmed the age estimate (Weems and Harris, 2008).

### Divergence of Crown Balaenopteridae

**Balaenoptera siberi** [Pilleri and Pilleri, 1989]

1. Unfortunately, the holotype specimen of *Balaenoptera siberi* is located in a private collection. However, not a year after the initial publication, a paratype was described (Pilleri, 1990), and this specimen is located in the Staatliches Museum für Naturkunde (47307 or PTM/5968/2008). Marx (2010) listed a specimen from this museum in his included taxon sample but did not provide a number.

2. The original publication of *B. siberi* did not include a phylogenetic analysis but the authors did make comparisons of their fossil to the extant *Balaenoptera acutorostrata*. They found enough evidence to support the placement of the taxon to *Balaenoptera*. Such evidence includes the possession of a “maxillary pocket”, nasal structure, and hourglass shaped phalanges (Deméré et al., 2005).

3. Deméré et al. (2005) classified *B. siberi* as a distinct species of *Balaenoptera* and phylogenetically recovered it in close relationship to *B. physalus* and *M. novaeangliae*. Marx (2010) recovered *B. siberi* in a close relationship to *B. musculus + B. omurai*. The current study recovered *B. siberi* in a polytomy at the base of crown Balaenopteridae.

4. Aguada de Lomas (Depo Arequipa), Pisco Formation, Peru (Pilleri and Pilleri, 1989).

5. In the original publication, the authors simply stated it was located in upper Miocene sediments (Pilleri and Pilleri, 1989). The Pisco Formation has produced many mammalian fossils, especially from the Messinian Age, of which the formation is dated (Deméré et al., 2005). This age is dated at 7.25 – 5.33 MYA (PBDB)

**Additional comments:** This taxon is listed as “invalid” by the Paleobiology Database, with a reasoning that it belongs to an improper subgroup. The current study disagrees with this statement. Geisler et al. (2011) used *Parabalaenoptera baulinensis* (Ziegler et al., 1997)
as calibration for this node instead of *B. siberi*. The specimens are both from the same aged sediments (~6.0 MYA), though the taxa clearly display different morphologies.

*External Calibration: Divergence of Eutherians*

**Juramaia sinensis** [Luo et al., 2011]
1. Beijing Museum of Natural History (BMNH) PM1143 (Luo et al., 2011)
2. Morphological analyses conducted in the original publication (Luo et al., 2011) found *Juramaia sinensis* among the “basal-most” eutherians. It was recovered in a polytomy with four other taxa; however, these taxa are 35 million years younger.
3. Because of the novelty of this find, this specimen has not been included in any other morphological analyses. However, Meredith et al. (2011) derived a molecular divergence estimate for this node of ~ 190 MYA, which supports the placement of *J. sinensis* (by age).
4. Daxigou Site, Jianchang County, Liaoning Provinence, China (Luo et al., 2011).
5. This formation is dated to be Middle-Late Triassic in age. Zircon dating of a neighboring area was dated to 164-165 MYA, while argon dating produced a date of 160.7 (+/- 0.4) (Luo et al., 2011; Supplementary Materials C). The original publication has an entire section investigating the geologic age of their specimen, citing multiple studies. The current study found no problem with their logic and accepts their geologic justification.