The Taxonomic and Evolutionary History of Fossil and Modern Balaenopteroid Mysticetes

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Balaenopteroids (Balaenopteridae + Eschrichtiidae) are a diverse lineage of living mysticetes, with seven to ten species divided between three genera (*Megaptera*, *Balaenoptera* and *Eschrichtius*). Extant members of the Balaenopteridae (*Balaenoptera* and *Megaptera*) are characterized by their engulfment feeding behavior, which is associated with a number of unique cranial, mandibular, and soft anatomical characters. The Eschrichtiidae employ suction feeding, which is associated with arched rostra and short, coarse baleen. The recognition of these and other characters in fossil balaenopteroids, when viewed in a phylogenetic framework, provides a means for assessing the evolutionary history of this clade, including its origin and diversification. The earliest fossil balaenopterids include incomplete crania from the early late Miocene (7–10 Ma) of the North Pacific Ocean Basin. Our preliminary phylogenetic results indicate that the basal taxon, "*Megaptera*" *miocaena* should be reassigned to a new genus based on its possession of primitive and derived characters. The late late Miocene (5–7 Ma) balaenopterid record, except for *Parabalaenoptera baulinensis* and *Balaenoptera siberi*, is largely undescribed and consists of fossil specimens from the North and South Pacific and North Atlantic Ocean basins. The Pliocene record (2–5 Ma) is very diverse and consists of numerous named, but problematic, taxa from Italy and Belgium, as well as unnamed taxa from the North and South Pacific and eastern North Atlantic Ocean basins. For the most part Pliocene balaenopteroids represent extinct species and genera and reveal a greater degree of morphological diversity than at present. The Pleistocene record is very limited and, unfortunately, fails to document the evolutionary details leading to modern balaenopteroid species diversity. It is evident, however, that most extant species evolved during the Pleistocene. Morphological and molecular based phylogenies support two competing hypotheses concerning relationships within the Balaenopteroidea: (1) balaenopterids and eschrichtiids as sister taxa, and (2) eschrichtiids nested within a paraphyletic Balaenopteridae. The addition of fossil taxa (including a new Pliocene species preserving a mosaic of balaenopterid and eschrichtiid characters) in morphological and "total evidence" analyses, offers the potential to resolve the current controversy concerning the possible paraphyly of Balaenopteridae.

KEY WORDS: Taxonomy, Evolution, Mysticeti, Balaenopteridae, Eschrichtiidae, "Total evidence" phylogeny.

INTRODUCTION

Extant mysticetes include four lineages: Balaenidae (right whale and bowhead), Eschrichtiidae (gray whale), Neobalaenidae (pygmy right whale) and Balaenopteridae

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(rorquals and humpbacks). Eschrichtiids and balaenopterids are included within the crown clade Balaenopteroidea (*sensu* Geisler and Sanders, 2003). Balaenopterids are the most taxonomically and morphologically diverse group of living mysticetes and include the blue whale (*Balaenoptera musculus*), the largest living animal with individuals typically 25 m in length, as well as the more diminutive minke whale (*Balaenoptera acutorostrata*) with individuals averaging only 10 m in length. Balaenopterids are widely distributed occupying most of the world's oceans from tropical to polar waters. Balaenopterids are commonly known as rorquals from the Norwegian word "rørhval," which refers to the many longitudinal folds of skin (furrows) that extend from approximately the chin almost to the umbilicus in members of this group. Other conspicuous specializations (i.e., flat, streamlined rostrum; expansive ventral throat pouch; flacid tongue; relatively short baleen plates; and frontomandibular stay; Lambertsen *et al.*, 1995; Werth, 2000) of extant members of the family are related to their engulfment feeding strategy. This strategy involves active pursuit of prey, passive opening of the mouth, expansion and engorgement of the ventral throat pouch with prey-laden water, adduction of the lower jaw, and muscular contraction of the ventral throat pouch resulting in expulsion of water through the baleen apparatus to concentrate prey in the oral cavity (Pivorunas, 1979; Lambertsen, 1983).

The Balaenopteridae was first proposed as a family of mysticetes by Gray (1864). Later Gray (1868) proposed inclusion of the Eschrichtiidae with the Balaenopteridae at a higher rank, the Balaenopteroidea. Although some workers have argued for a different arrangement (i.e., inclusion of the extinct "Cetotheriidae" in the Balaenopteroidea and elevation of the Eschrichtioidea to a new rank; Mitchell, 1989), monophyly of the Balaenopteroidea has been supported by recent morphological (Geisler and Luo, 1996; Geisler and Sanders, 2003) and molecular studies (Arnason *et al.*, 1993; Arnason and Gullberg, 1994, 1996; Rychel *et al.*, 2004).

Extant balaenopterids include six to nine species in two genera, *Balaenoptera* and *Megaptera* (Table I). Two subfamilies of the Balaenopteridae have been recognized by some workers, the Megapterinae and the Balaenopterinae, based on the distinct flipper morphology of the humpback whale (*Megaptera novaeangliae*) relative to the "short flippered" rorquals of the genus *Balaenoptera* (Rice, 1998). Subspecies have been described for four balaenopterids (see below). Although recognizing two subfamilies of Balaenopteridae, McKenna and Bell (1997) proposed a different membership, the Balaenopterinae including both *Megaptera* and *Balaenoptera* and the Eschrichtiinae, elevated to a new rank in their classification and comprised of the monotypic genus

Table I. Taxonomic List of Extant Balaenopteroids

Balaenopteridae
    Balaenoptera acutorostrata Lacépède, 1804—Minke whale
    Balaenoptera bonaerensis Burmeister, 1867—Antarctic minke whale
    Balaenoptera borealis Lesson, 1828—Sei whale
    Balaenoptera brydei Olsen, 1913—Bryde's whale
    Balaenoptera edeni Anderson, 1879—Eden's whale
    Balaenoptera musculus (Linnaeus, 1758)—Blue whale
    Balaenoptera omurai, Wada *et al.*, 2003—Omura's whale
    Balaenoptera physalus (Linnaeus, 1758)—Fin whale
    Megaptera novaeangliae (Borowski, 1781)—Humpback whale

Eschrichtiidae
    Eschrichtius robustus (Lillijeborg, 1861)—Gray whale
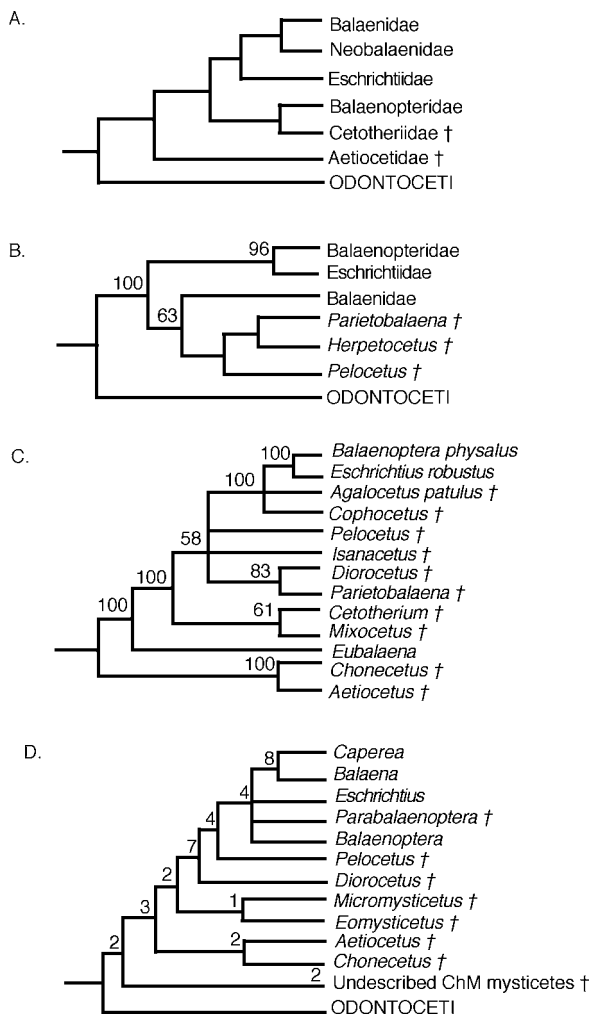
Fig. 1. Previous morphological hypotheses. (A) Noncladistic analysis of skull characters (McLeod *et al.*, 1993). (B) Maximum parsimony phylogeny of basicranial characters (Geisler and Luo, 1996) with bootstrap (>50) values indicated. (C) 50% majority rule consensus tree (Kimura and Ozawa, 2002). (D) Strict consensus of 21 most parsimonious trees using morphological characters (Geisler and Sanders, 2003), numbers are Bremer support values.

Eschrichtius. As will be further discussed we found no support for recognition of separate subfamilies within the Balaenopteridae.

Prior phylogenetic studies of mysticetes based on morphology either failed to employ rigorous systematic methods or included limited taxon/character sampling. McLeod *et al.* (1993) presented the first morphological analysis of mysticetes, which recognized the Balaenopteroidea as including the Balaenopteridae and "Cetotheriidae" but not the Eschrichtiidae (Fig. 1(A)). Geisler and Luo (1996) focused on basicranial characters among

12 extinct and extant taxa and found support for a Balaenopteridae + Eschrichtiidae grouping (Fig. 1(B)). Kimura and Ozawa (2002) included several toothed mysticetes (*Chonecetus* and *Aetiocetus*), numerous "cetotheres" (*Isanacetus*, *Pelocetus*, *Diorocetus*, *Parietobalaena*, *Cetotherium*, *Mixocetus*, *Cophocetus*, and *Aglaocetus*), and representatives of modern lineages (except for *Caperea*) in their phylogenetic analysis of mysticetes. Their results recognized a paraphyletic "Cetotheriidae" and a sister group relationship between Eschrichtiidae and Balaenopteridae (Fig. 1(C)). Dooley *et al*. (2004) used a subsample of characters (primarily from the petrotympanic complex) and a limited number of fossil and extant mysticetes to find support for a paraphyletic Balaenopteridae with the Eschrichtiidae nested within this clade. In the most comprehensive morphological study of cetacean phylogeny to date Geisler and Sanders (2003) presented a detailed phylogenetic analysis of 51 extant and extinct taxa scored for 304 characters. A strict consensus of the most parsimonious trees (Fig. 1(D)) supported: (1) inclusion of Miocene "cetotheres" *Diorocetus* and *Pelocetus* and extant mysticetes in a clade distinct from the earliest baleen bearing taxa, the eomysticetids; and (2) a monophyletic Balaenopteroidea composed of Balaenopteridae and Eschrichtiidae but not "Cetotheriidae," contra McLeod *et al*. (1993). We follow the use of Balaenopteroidea as defined by Geisler and Sanders (2003).

Relationships among balaenopteroid species based on molecular data have never been fully resolved and have either suggested that balaenopterids and eschrichtiids are sister taxa or that eschrichtiids are nested within balaenopterids. Arnason *et al*. (2004) presented an analysis of the complete mitochondrial genome for mysticetes although not all species were included. In their analysis the Balaenopteridae was found to be monophyletic with *Eschrichtius* as its sister taxon (Fig. 2(A)). The molecular datasets of Gatesy *et al*. (1999) and Cassens *et al*. (2000) supported this same result. The recent molecular study of Rychel *et al*. (2004) incorporated mitochondrial and nuclear sequence data and confirmed support for a paraphyletic Balaenopteridae (Fig. 2(B)). Further relationships within balaenopteroids supported by this latter study include the two minke whale species (*B. acutorostrata* and *B. bonaerensis*) separated by *Eschrichtius* from the remaining species of *Balaenoptera*. The latter clade includes *B. physalus* and *Megaptera* as sister taxa and *B. musculus* as sister to *B. borealis* and *B. brydei*.

Our report has three primary objectives: (1) to review the taxonomic status of extant and extinct balaenopteroids, (2) to add new fossil taxa and investigate species level phylogenetic relationships of balaenopteroids including re-evaluation of many described morphological characters and new character states, and (3) to test hypotheses of balaenopteroid phylogeny by comparing morphological, molecular, and combined total evidence datasets.

MATERIALS AND METHODS

Specimens (including holotypes) of fossil and modern balaenopteroid mysticetes were examined at a number of museums and universities (see later). This survey provided a comprehensive view of the taxonomic distribution of osteological features and morphological diversity within this group. Qualitative, as well as quantitative, observations were made and formed the basis for development of a large morphological database critical to phylogenetic analysis of Mysticeti. For the current study only a portion of this database was used.
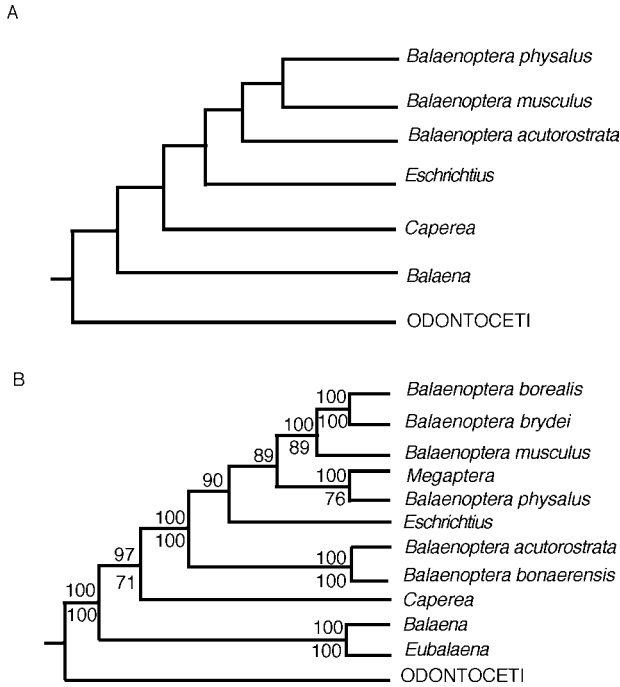
Fig. 2. Previous molecular hypotheses. (A) Maximum likelihood phylogeny of concatenated amino acid sequences of 12 mitochondrial protein coding genes (Arnason *et al.*, 2004). (B) Maximum likelihood phylogeny inferred from the combined analysis of mtDNA and nuDNA (Rychel *et al.*, 2004). Numbers below branches correspond to bootstrap proportions from uniformly weighted parsimony analysis (<0.50 not shown).

Institutional Abbreviations: ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA; CASG, California Academy of Sciences, Department of Geology, San Francisco, California, USA; ChM, The Charleston Museum, Charleston, South Carolina, USA; GRM, Indian Museum, Calcutta, India; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MB, Museum für Naturkunde, Humboldt–Universitat zu Berlin; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MGB, Museo Geopaleontolgico "Giovanni Capellini," Bologna, Italy; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MPP, Museo Paleontolgico Parmense, Parma, Italy; MGPT, Museo di Geologia e Paleontologia, Universita di Torino, Torino, Italy; MSNT, Museo di Storia Naturale e del Territorio dell'universita di Pisa, Pisa, Italy; NSMT, National Science Museum, Tokyo, Japan; NRIFSF, National Research Institute of Far Seas Fisheries, Fisheries Research Agency, Shizuoka, Japan; RMNH, National Museum of Natural History, Leiden, Netherlands; SDSNH, San Diego Natural History Museum, San Diego, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, US National Museum of Natural History, Washington, D.C., USA; VMNH, Virginia Museum of Natural History, Martinsville, Virginia, USA.

Anatomical Abbreviations: APM, ascending process of maxilla; APPMX, ascending process of premaxilla; AWP, anterior wing of parietal; CBL, condylobasal length; SOPF, supraorbital process of frontal, SOS, supraoccipital shield; ZW, zygomatic width.

Stratigraphic and Biochronologic Assignments: Ka–10^3 years (kilo annum); Ma–10^6 years (mega annum). For temporal units the standard marine stages of the Neogene and Quaternary are used sensu Harland *et al.* (1990). For several of the fossil mysticetes from the Italian and Belgian Neogene the original informal stratigraphic names are retained.

SYSTEMATICS

The following is an abridged taxonomic review of nominal species of extant and extinct balaenopteroids. For most extant species the taxonomic and nomenclatural decisions of Rice (1998) are followed. More complete nomenclatural synonymies for extant taxa can be found in Hershkovitz (1966).

Many fossil balaenopteroids have been discovered and described during the last 150 years. Sorting out the nomenclatural history and taxonomic validity of these fossil taxa is a daunting task and has been attempted by several workers including True (1912), Kellogg (1922, 1931), Deméré (1986), and Zeigler *et al.* (1997). In this paper we discuss 24 nominal fossil species (Table II) and recognize 16 as valid (or potentially valid) balaenopterids, two as valid eschrichtiids, four as *nomina dubia*, and two as junior synonyms. Included in the list of taxa are fossil balaenopteroids named and described by Van Beneden (1880, 1882) from the Pliocene (Scaldisian) deposits of Antwerp, Belgium. Unfortunately, these taxa present an especially difficult case of nomenclatural uncertainty. Bernard Du Bus was apparently responsible for accumulating the fossils for scientific study, however, he evidently kept few notes and did not actually collect the fossils. Instead soldiers were paid to recover the fossils from excavations for new fortifications in the city of Antwerp. Reportedly, their pay was based on gross weight of specimens and not on quality of specimens (O. Lambert, 2003, personal communication). Thus, isolated vertebrae and broken skulls were recovered more often than intact skulls and skeletons. The soldiers also had no training and either just took specimens from spoil piles or maybe excavated them, but without any care for keeping discrete specimens together. To make matters worse, Du Bus died before Van Beneden began to seriously work on the collection leaving Van Beneden with no direct information about the provenience of individual specimens. In spite of this, Van Beneden and his colleagues went ahead and sorted through the enormous collection of fossils and brought some order to it. Van Beneden and his associates may have used circular reasoning in assigning isolated fossil remains to different species. It seems that they started with a preconception of what the skeleton of a species should look like (based on size or ecomorphology or hypothesized similarity to extant taxa) and then assigned isolated bones to that taxon based on resemblance to this typological ideal. The fact that Van Beneden did not designate type specimens for his species further compounds the nomenclatural problems. We are thus left with a series of named fossil species, most based on an extensive series of cranial, mandibular, and postcranial fossil elements, none of which is designated as a holotype and none of which can unambiguously be directly associated with any other fossil element (i.e., from the same individual).

The dilemma we now face is what to do with these nominal taxa that are well established in the literature and for which we have such exquisite illustrations in the atlas

Table II. Taxonomic Status of Nominal Fossil Balaenopteroids

Original nomenclature	Family	Proposed nomenclature	Age
Balaena cortesii Fischer (1829)	Balaenopteridae	possibly *Balaenoptera*	Piacenzian
Balaena cuvieri Fischer (1829)	Balaenopteridae	new genus	Piacenzian
Balaena definata Owen (1844)	Balaenopteridae	*nomen dubium*	Pleistocene
Balaena emarginata Owen (1844)	Balaenopteridae	*nomen dubium*	Pleistocene
Balaena gibbosa Owen (1844)	Balaenopteridae	*nomen dubium*	Pleistocene
Balaenoptera borealina Van Beneden (1880)	Balaenopteridae	*Balaenoptera borealina*	Zanclian
Balaenoptera cortesi, var. *portisi* Sacco (1890)	Balaenopteridae	new genus	Piacenzian
Balaenoptera floridana Kellogg (1944)	Balaenopteridae	same new genus as *B. c.* var. *portisi*	Zanclian
Balaenoptera musculoides Van Beneden (1880)	Balaenopteridae	junior synonym of *Balaenoptera garopii*	Zanclian
Balaenoptera rostratella Van Beneden (1880)	Balaenopteridae	*Balaenoptera rostratella*	Zanclian
Balaenoptera ryani Hanna and McLellan (1924)	Balaenopteridae	new genus	Tortonian
Balaenoptera sibbaldina Van Beneden (1880)	Balaenopteridae	*Balaenoptera sibbaldina*	Zanclian
Balaenoptera siberi Pilleri and Pilleri (1989)	Balaenopteridae	*Balaenoptera siberi*	Messinian
Burtinopsis minutis Van Beneden (1880)	Balaenopteridae	*Balaenoptera minutis*	Zanclian
Burtinopsis similis Van Beneden (1872)	Balaenopteridae	*Balaenoptera similis*	Zanclian
Cetotherium gastaldii Strobel (1875)	Eschrichtiidae	new genus	Piacenzian
Cetotherium (*Cetotheriophanes*) *capellinii* Brandt (1873)	Balaenopteridae	*Cetotheriophanes capellinii*	Piacenzian
Eobalaenoptera harrisoni Dooley *et al.* (2004)	family indet.	*Eobalaenoptera harrisoni*	Serravalian
Eschrichtius [sic] *davidsonii* Cope (1872)	cf. Eschrichtiidae	*Balaenoptera davidsonii*	Piacenzian
Megaptera affinis Van Beneden (1880)	Balaenopteridae	junior synonym of *Megapteropsis robusta*	Piacenzian
Megaptera hubachi Dathe (1983)	Balaenopteridae	possibly *Balaenoptera*	Piacenzian
Megaptera miocaena Kellogg (1922)	Balaenopteridae	new genus	Tortonian
Megapteropsis robusta Van Beneden (1872)	cf. Eschrichtiidae	*Megapteropsis robusta*	Zanclian
Parabalaenoptera baulinensis Zeigler *et al.* (1997)	Balaenopteridae	*Parabalaenoptera baulinensis*	Messinian
Plesiocetus garopii Van Beneden (1859)	Balaenopteridae	*Plesiocetus garopii*	Zanclian

that accompanied the taxonomic text of Van Beneden (1882). Possible solutions include (1) a comprehensive reexamination of all of the syntypes figured and discussed by Van Beneden (1880, 1882), selection of a lectotype for each nominal taxon, and publication of new species' descriptions and diagnoses based on those lectotypes; or (2) recognition of all of Van Beneden's taxa as *nomina dubia* and suppression of their names. In the first case the main problem is deciding on which of the many syntypes (isolated skull fragments, petrosals, tympanic bullae, mandibles, vertebrae, ribs, or pectoral elements) to choose as diagnostic of a particular taxon. Certainly most workers would prefer that crania with associated petrosals and tympanic bullae should be used at a minimum over isolated mandibles,

vertebrae, and ribs. And in fact, the majority of fossil mysticete taxa named in the twentieth century are based on holotype specimens that include at least partial skulls with associated petrosals, bullae, and mandibles. Without this level of completeness it is extremely difficult to make valid comparisons between nominal fossil mysticete taxa.

Returning to the problem of Van Beneden's Belgian fossils, if we are to select a lectotype, which of the many isolated skeletal elements should be selected and what should be done with all of the remaining syntypes of that taxon? This dilemma arises because Van Beneden based his descriptions on isolated and/or fragmentary skeletal parts that cannot unambiguously be shown to represent parts of single individuals. As an example, when Van Beneden (1872, 1882) named the enigmatic "cetothere" *Herpetocetus scaldiensis* he assigned to it a disparate assortment of isolated cranial, petrotympanic, mandibular, axial, and pectoral elements. Among this referred material the mandible is by far the most morphologically distinct element with its unique "retroarticular" angular process (Van Beneden, 1882, plate 103; Deméré and Cerutti, 1981). However, Van Beneden did not select the mandible, or any other particular element, as the holotype. In the 1970s and 1980s more complete specimens of small fossil mysticetes with *Herpetocetus*-type mandibles were found in Pliocene deposits in Japan and the United States (California and Virginia) including nearly complete skulls with associated petrotympanic, mandibular, axial, and pectoral elements (Barnes, 1977; Oishi and Hasegawa, 1995). We have examined some of the more complete specimens (NSMT, UCMP, and SDSNH) and in making direct comparisons with the syntypes of Van Beneden's *Herpetocetus scaldiensis* it is clear that the isolated tympanic bullae, and skull parts referred by Van Beneden to *H. scaldiensis* do not belong to the same taxon that has the distinctive *Herpetocetus*-type mandible. So, what then is *Herpetocetus*? Is it a taxon based on the mandible, or do we assume that the syntype tympanic bullae are actually diagnostic of this taxon and select one as the lectotype and then erect a new taxon for the mandible? These difficult questions underscore the nomenclatural nightmare surrounding the Belgian fossil mysticetes. It may be that we have to wait until partial or complete skeletons of each taxon are discovered in the future. But, in the meantime we face taxonomic paralysis.

For now both solutions are beyond the scope of this report and instead we choose to merely list each taxon, summarize its nomenclatural history, provide a listing of assigned elements, and briefly discuss relevant morphological aspects of the more diagnostic elements (e.g., crania, petrosals, tympanic bullae, and mandibles). In spite of providing these limited discussions of diagnostic elements, the problem remains. We cannot accurately compare other previously described or newly discovered fossil material to the various nominal Belgian fossil taxa because the current hypodigm for each taxon consists of a mixture of skeletal remains from different parts of the skeleton none of which can be unambiguously known to truly represent the named species.

Fossil balaenopterids described during the 19th century from the Italian Pliocene pose different and more easily solved nomenclatural problems. In most cases these species were established on a single specimen, often a complete or nearly complete skeleton. Thus, the recognition of holotypes can be based on monotypy. Nomenclatural issues primarily concern a plethora of names that have been used for individual species, including sometimes the use of the same binomen by different workers for different specimens. Clearing up these problems is generally a matter of priority and, in some cases, the establishment of new genera to contain divergent species. In this report we provide nomenclatural synonymies,

provenance data, and brief discussions of characteristic morphologies for these Italian balaenopterids, but stop short of naming new genera pending the completion of more comprehensive studies in progress by us and our colleagues.

Living Balaenopteroids

Balaenoptera acutorostrata Lacépède, 1804

Type: None formally designated. Species based on general accounts and description of a young individual stranded in 1791 near Cherbourg, France.

Type Locality: Cherbourg, France.

Age: Recent; a fossil record from the Pliocene of Japan (Oishi and Hasegawa, 1995) needs to be confirmed.

Discussion: Two subspecies have been distinguished in the Northern hemisphere (Omura, 1975): *B. acutorostrata* in the North Atlantic and *B scammoni* in the North Pacific (Rice, 1998). A third unnamed subspecies the "dwarf' minke whale is mainly distributed in lower latitudes of the Southern hemisphere. This "dwarf" minke population has been more closely allied with the northern minke population than with the Antarctic species (*B. bonaerensis*) on the basis of morphology (osteology and external anatomy; Best, 1985; Arnold *et al*., 1987) and mtDNA (Wada *et al*., 1991). The dwarf minke whale is much smaller than the Antarctic minke whale and possesses the distinct white flipper mark that is characteristic of the species in the Northern hemisphere and absent in the Antarctic species (Perrin and Brownell, 2001). Another alleged subspecies *B. a. thalamaha* (Deranyagala, 1963) described from a stranded animal in Sri Lanka is of dubious validity as noted by Rice (1998) and the unique color pattern of the baleen plates indicates that it may not be a minke whale.

Caretto (1970) proposed a fossil subspecies, *Balaenoptera acutorostrata cuvieri*, from the Pliocene of Italy. As discussed by Deméré (1986) Caretto combined almost all nominal Italian Pliocene balaenopterids under this single subspecies concept. This extreme case of taxonomic lumping is unjustified and places in synonymy several clearly valid fossil species (e.g., "*Balaenoptera*" *cortesi*, "*Balaenoptera*" *cuvieri*, and "*Balaenoptera*" *cuvieri* var. *portisi*; see below).

Balaenoptera bonaerensis Burmeister, 1867

Type: Complete skeleton in Buenos Aires Museum.

Type Locality: Near Belgrano, Buenos Aires, Argentina.

Age: Recent; no fossil record.

Discussion: Osteological and external features have been used to distinguish the Antarctic minke whale from the North Pacific and North Atlantic minke whales as well as from a third morphotype, the "dwarf" minke whale (e. g., Williamson, 1959; Best, 1985; Arnold *et al*., 1987). Omura (1975), in a detailed comparison of populations of *B. acutorostrata* with Antarctic populations of *B. bonaerensis*, concluded that although some differences exist (i.e. narrower skull and rostrum, asymmetrically pigmented baleen plates, absence of distinct white band on flippers in B. *bonaerensis*) the taxonomic validity of *B. bonaerensis* is uncertain given the limited number of specimens studied and amount of individual (i.e., age and gender) variation observed. These similarities have led others

(Utrecht and Spoel, 1962; Oshumi *et al*, 1970; Omura, 1975; Reynolds *et al*., 1999) to conclude that recognition of *B. bonaerensis* as a distinct species is not warranted. However, molecular features (RFLP and mtDNA; Pastene *et al*., 1994; Arnason and Gullberg, 1994) have been used to distinguish this species from the "dwarf" minke whale as well as from the subspecies of Northern hemisphere minke. Arnason *et al*. (1993) determined the nucleotide sequence in the control region of mtDNA was likewise greater than that between any two species of *Balaenoptera*. Preliminary osteological studies by us have found several morphological features (e.g., larger size and shorter AWP/APM overlap) that in the future may prove useful in diagnosing this taxon.

Balaenoptera borealis Lesson, 1828

Type: Skeleton in Museum für Naturkunde, Humboldt—Universitat zu Berlin. Unfortunately this specimen is now missing and was apparently lost during Allied bombing of the museum during World War II (O. Hampe, personal communication).

Type Locality: Schleswig-Holstein, Lubeck Bay, near Gromitz, Germany.

Age: Recent; a fossil record reported from the Pleistocene of Japan (Oishi and Hasegawa, 1995) needs to be confirmed.

Discussion: Two subspecies are recognized (Tomilin, 1946; Rice, 1998), one in the Northern hemisphere (*B. borealis*) and a somewhat larger one in the Southern hemisphere (*B. b. schlegellii*). The Sei whale is a distinct species of *Balaenoptera* distinguished largely on its moderate body size, slender and elongate nasals, narrow and dorsally arched rostrum with nearly straight lateral margin, posteriorly elongate "spur" on infraorbital plate of maxilla, steeply sloping palatines, and deep and transversely compressed posterior portion of vomer.

Balaenoptera brydei Olsen, 1913

Type: None designated.

Type Locality: Saldanha Bay, western Cape Province, South Africa.

Age: Recent; no fossil record.

Discussion: Rice (1998) reviewed the nomenclatural confusion surrounding populations of small rorquals that have gone under the names *B. brydei* and *B. edeni* in subtropical and tropical oceans. Based on osteology Junge (1950) and Omura (1959) considered these species synonymous, although noting consistent differences between skeletons of *B. brydei* and *B. edeni*. Soot-Ryen (1961) examined three skeletons of *B. brydei* from Curacao, South Africa and Japan with data from specimens of *B. edeni* from the Bay of Bengal to Sumatra and reported several differences in measurement ratios. These differences, however, were considered less significant by Omura (1966) than those between *B. edeni*–*B. brydei* and *B. borealis*.

According to Wada *et al*. (2003), *B. brydei* is distinct from *B. edeni* based on both molecular and morphological characters. They described a number of characters to distinguish *B. brydei* from *B. edeni* including: a broad APM, a frontal with small exposure on the vertex and no protuberances covering the APM, and a small alisphenoid exposure on the temporal wall. In all extant balaenopterids the APM is expanded posteriorly, thus this character is a synapomorphy at a more general level. We observed that among balaenopterids the degree of parietal exposure on the vertex and development of protuberances are, in

part, age related features. However, based on examination of referred skulls at NSMT and USNM we found that the alisphenoid feature does appear to be diagnostic, as does the broader APM. In addition, we noted that the shape of the elongated pterygoid hamulus in both taxa exhibited consistent differences: long and cylindrical in *B. brydei* and long and trapezoidal in *B. edeni*. Given these morphological differences we feel that the conclusion of Wada *et al.* (2003) regarding the recognition of *B. brydei* and *B. edeni* as distinct species of *Balaenoptera* has merit. Unfortunately, the lack of a type specimen (and the resulting morphological and molecular data) is a major obstacle to resolving the taxonomic problems surrounding this species complex.

Balaenoptera edeni Anderson, 1879

Type: GRM223 mounted skeleton, Indian Museum, Calcutta, India, collected by Major A.G. Duff and M. Duke.

Referred Material: RMNH 4003 skeleton, from Pul(a)u Sugi near Singapore.

Type Locality: Thyabu Choung Creek, Gulf of Marataban, between Sittang and Beeling Rivers, Myanmar.

Age: Recent; no fossil record.

Discussion: Recognition of this species as distinct from *B. brydei* is supported by mtDNA analysis (Dizon *et al.*, 1996, 1998) and some morphological data (Andrews, 1916, 1918; Wada *et al.*, 2003). Wada *et al.* (2003) observed that the holotype skull of *B. edeni* (Indian Museum, Calcutta) and the skull from Pula Sugi (in the Kepulauan Archipelago between Singapore and Sumatra) shared unique characters not seen in other *Balaenoptera* species. These characters include: slender APM, broadly exposed frontal with a pedestal-like protuberance covering a portion of the APM, and large alisphenoid exposure on the temporal wall. As discussed above under *B. brydei* we feel that the conclusion of Wada *et al.* (2003) in recognizing *B. edeni* as a distinct species of *Balaenoptera* has merit. However, a thorough taxonomic resolution of the *B. edeni-brydei* complex must await genetic identity of the holotype of *Balaenoptera edeni* (Perrin *et al.*, 2004) and a more complete morphological study of specimens assigned to this species complex.

Balaenoptera musculus Linnaeus, 1758

Type: None formally designated. Species based mainly on "*Balaena fistula duplici*" of Artedi (1783).

Type Locality: "Mari Scotico," the Firth of Forth, Scotland.

Age: Recent; a report of *Sibbaldus* sp. from the Pliocene of Japan (Oishi, 1997) suggests a possible fossil blue whale record, however, this identification is based on an isolated partial mandible (with possible pathologies) belonging to an animal much smaller than the extant *B. musculus*.

Discussion: The blue whale is distinguished on the basis of its large size and proportionally smaller dorsal fin positioned far back on the body (Sears, 2001). Miller (1923) illustrated a skull of *B. musculus* and emphasized its morphological features including broadly convex lateral maxillary margins, posteriorly positioned "blowhole," and relatively short and broad nasals. Rice (1998) recognized three subspecies: *B. m. musculus* Blue whale in the Northern hemisphere, *B. m. intermedia* "True Blue" found in Antarctic waters, and *B. m. brevicauda* pygmy blue from the Subantarctic Zone of the southern Indian Ocean

and southwestern Pacific Ocean. A fourth taxon *B. m. indica* Great Indian rorqual from the northern Indian Ocean is poorly known. The pygmy blue whale was distinguished by external morphological characters (Ichihara, 1966) and osteological features (Omura *et al.*, 1970). Other than geographic differences the distinctiveness of the other subspecies of blue whale, however, are unclear.

Balaenoptera omurai Wada *et al.*, 2003

Type: NSMT-M32505 adult female, complete skeleton.

Paratypes: NRIFSF1-8 five females and three males including longest baleen plate, earplug, and piece of 6th thoracic vertebrae from each animal. NRIFSF6 includes 18 additional baleen plates.

Type Locality: Tsunoshima Island, Japan.

Age: Recent; no fossil record.

Discussion: Morphological (osteology and external morphology) and molecular (mtDNA) characters were used to distinguish this new species from related species (Wada *et al.*, 2003). According to these authors *B. omurai* differs from all related species by having the following unique morphological characters: medially expanded posterior portion of APM concealing the posterior end of the premaxilla along the adjacent nasal and approximately 200 baleen plates per side. The authors cite additional morphological features characteristic of this taxon including: broad lateral extension of the parietal covering the posteromedial corner of the SOPF, convex lateral margin of the maxilla in dorsal aspect, alisphenoid separate from squamosal, two small foramina positioned on the parietal/squamosal suture, and mandibular angle extending posterior to condyle. While this manuscript was in review we were able to examine the holotype skull and a referred specimen in the NSMT collections. During this examination we confirmed the unique and diagnostic morphological features of *Balaenoptera omurai* and agree with its recognition as a new species of *Balaenoptera*. A more detailed morphological description of *B. omurai* based on several additional specimens is currently being prepared (T. Yamada and M. Oishi,, pers. comm.). Unfortunately, during the review process time constraints and the lack of access to molecular data for this taxon did not permit us to add *B. omurai* to our phylogenetic analysis.

Balaenoptera physalus (Linnaeus, 1758)

Type: None formally designated.

Type Locality: "Oceano Europaeo" specifically the Spitsbergen Sea.

Age: Recent; no fossil record.

Discussion: Fin whales are distinguished in having asymmetric pigmentation of the head region where the left side, both dorsally and ventrally, is dark slate, the right dorsal cephalic side is light gray and the right ventral side is white. This asymmetry also affects baleen plates; those on the left side and the rear two-thirds of the right side are gray whereas those on the front third of the right maxilla are yellowish (Aguilar, 2001). Tomilin (1957) noted that the vomer in *Balaenoptera physalus* has a distinctly expressed posterior expansion adjacent to the pterygoids on the basicranium. *Balaenoptera physalus* appears very closely related to *Balaenoptera musculus* and several hybrids have been described (Berube and Aguilar, 1998). Morphological differences in the vertebrae led Lönnberg

(1931) to distinguish two subspecies: *B. p. physalus* (Linnaeus, 1758) in the Northern hemisphere and *B. p. quoyi* (Fischer, 1830) in the Southern hemisphere. As reported by Rice (1998) these differences have not been confirmed, but Tomilin (1946) found that the two populations were distinguished based on body size. A third subspecies of fin whales, the pygmy fin whale *B. p. patachonica* Burmeister, 1865 was recently proposed (Clarke, 2004). It was suggested that these fin whales are the "small, dark fin whales" mentioned by and Mackintosh (1942) in southern latitudes. DNA analysis of these fin whales is pending. At this time there is insufficient evidence to recognize this subspecies (Perrin *et al*., 2004).

Megaptera novaeangliae (Borowski, 1781)

Type: None formally designated.
Type Locality: New England coast, USA.
Age: Recent; fossil records reported from the late Pleistocene of Florida (Morgan, 1994), the Pleistocene Champlain Sea, Canada (Harington, 1977), and the Holocene of Japan (Oishi and Hasegawa, 1995) need to be confirmed.
Discussion: Although two populations of humpbacks have been recognized as subspecies (e.g., see Tomilin, 1946; Ivashin, 1958), a phylogeographic analysis of restriction fragment length polymorphisms is not congruent with a subspecies designation (Baker *et al*, 1994). The diagnostic morphological characters of *M. novaeangliae* are well known and include: greatly elongated pectoral fin, scapula essentially lacking acromion and coracoid processes, laterally directed zygomatic process of the squamosal and absence of a squamosal crease, mandible with reduced coronoid process, and tympanic bulla with prominent dorsolateral prominence (Kellogg, 1922; Tomilin, 1946; Oishi and Hasegawa, 1995).

Eschrichtius robustus (Lilleborg, 1861)

Type: Partial skeleton (subfossil) in University Museum of Upsala, Sweden.
Type Locality: Graso, Roslagen, Upland, Sweden.
Age: Recent; fossil reported from the late Pleistocene of California, USA (Barnes and McLeod, 1984).
Discussion: Three populations of gray whales are known: the extinct North Atlantic population, the western North Pacific or "Korean" population, and the eastern North Pacific or "Californian" population. Previous workers (Cederlund, 1939; Deinse and Junge, 1937; Mead and Mitchell, 1984) found no morphological differences between the extinct Atlantic and extant Pacific gray whales. Earlier, Andrews (1914) reported that the skulls of Korean and Californian populations were virtually indistinguishable. A partial skeleton (LACM 122322) of *Eschrichtius robustus* was described by Barnes and McLeod (1984) from the upper Pleistocene San Pedro Formation (200–300 Ka not 120 Ka as reported by Barnes and McLeod) of southern California. As noted by these authors, the essentially complete skull of LACM 122322 preserves all of the diagnostic features of modern specimens of *Eschrichtius robustus* including: narrow and moderately arched rostrum, relatively small and steeply sloping occipital shield with paired tuberosities, large paroccipital processes, elevated external nares, and large nasals.

Fossil Balaenopteroids

Balaenoptera borealina Van Beneden, 1880

Balaenoptera borealina; Van Beneden, 1880, pp. 15–16.
Balaenoptera borealina; Van Beneden, 1882. pp. 71–73; plates 66–75.
Type: None designated.
Type Locality: Antwerp, Belgium.
Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).
Age: early Pliocene (Zanclian Stage).
Referred material: cranial, mandibular, axial, and pectoral elements (Van Beneden, 1880, 1882).

Nomenclatural summary: Because of problems concerning the lack of a type specimen (or a syntype consisting of at least a cranial vertex with associated petrotympanic) for this taxon, its recognition as a valid taxon is suspect.

Discussion: In his original description of this species Van Beneden (1880) did not discuss any diagnostic features and instead merely provided a general listing of the kinds of fossil elements in the collections of the IRSNB that he assigned to this taxon. As is typical of the Antwerp fossil material no holotype was designated and no discussion was provided as to whether any of the syntype fossil elements were associated and from the same individual. Later, Van Beneden (1882; plates 66–75) illustrated numerous isolated skeletal elements assigned to this taxon, but again did not designate a holotype. A lectotype could be selected from among the numerous syntypes assigned to this taxon, but none of the syntypes is complete enough to allow useful comparisons with other nominal fossil mysticetes. As shown by the careful taxonomic work of Kellogg (1924, 1934, 1969), erecting a new species of fossil mysticete on a single element is not defensible. Instead, fossil mysticete taxa should be established on partial skeletons preserving rostral, cranial, petrotympanic, mandibular, and if possible, postcranial elements.

Balaenoptera davidsonii (Cope, 1872)

Eschrichitus [sic] davidsonii Cope, 1872.
Balaenoptera davidsonii; Cope, 1890.
Cetotherium davidsonii; Cope, 1896.
Eschrichtius davidsonii; Gillette, 1975.
Balaenoptera davidsonii; Deméré, 1986.
Type: ANSP 12922, partial L dentary.
Locality: Balboa Park, San Diego, San Diego Co., California, USA.
Stratigraphy: San Diego Formation.
Age: late Pliocene (Piacenzian Stage).
Referred material: SDSNH 25190, nearly complete right dentary; SDSNH 80102, nearly complete skull lacking nasals.

Nomenclatural summary: Deméré (1986) provided a revised discussion of this taxon and concluded that it should be referred to the genus *Balaenoptera*.

Discussion: The holotype mandibular fragment was redescribed by Deméré (1986) who also referred a nearly complete mandible to this fossil balaenopterid. Characteristic balaenopterid features of these mandibles include: planoconvex cross sections of horizontal

ramus, thickest part of ramus above the midline, sinuous longitudinal outline of ramus and mandibular neck, small and dorsally placed mandibular foramen, and bulbous and posteriorly oriented mandibular condyle. A nearly complete skull (SDSNH 80102) is here referred to this taxon based primarily on size and proportions of the rostrum. *Balaenoptera davidsonii* is thus characterized as a small species of *Balaenoptera* (CBL = 139 cm, ZW = 85 cm) with a bluntly triangular SOS, abruptly depressed SOPF, long APM/AWP overlap, narrowly rectangular APM, slender and anterolaterally directed zygomatic processes, no squamosal crease, petrosal with transversely elongated promontorium and fenestra rotunda separate from perilymphatic foramen, tympanic bulla broadly inflated without median furrow, and mandible with transversely compressed ramus.

Balaenoptera definata (Owen, 1844)

Balaena definata Owen, 1844.
Balaenoptera definata; Lydekker (1887a,b).
Type: Partial right tympanic bulla.
Locality: Felixstow, Suffolk, England.
Stratigraphy: Red Crag.
Age: early Pleistocene (Calabrian Stage).
Nomenclatural summary: Because of its fragmentary nature, the holotype tympanic bulla is not diagnostic and the species is here considered a *nomen dubium*.
Discussion: Lydekker (1887a,b) assigned this species to *Balaenoptera* and suggested that it was a senior synonym of *Balaenoptera sibbaldina* Van Beneden, 1880. The holotype bulla of *Balaena definata*, although certainly a balaenopterid, is fragmentary and missing the posterior portion of the involucrum and the entire ventral wall of the epitympanic recess.

Balaenoptera emarginata (Owen, 1844)

Balaena emarginata Owen, 1844.
Balaenoptera emarginata (Owen, 1844); Lydekker, 1887a,b.
Balaena gibbosa Owen, 1844; Lydekker, 1887a,b.
Type: Partial right tympanic bulla.
Locality: Felixstow, Suffolk, England.
Stratigraphy: Red Crag.
Age: early Pleistocene (Calabrian Stage).
Nomenclatural summary: Because of its fragmentary nature, the holotype tympanic bulla is not diagnostic and the species is here considered a *nomen dubium*.
Discussion: Lydekker (1887a,b) assigned this species to *Balaenoptera* and considered it a senior synonym of *Balaena gibbosa* Owen, 1844 and *Balaenoptera rostratella* Van Beneden, 1880. The holotype bulla of *Balaena emarginata* is fragmentary and missing the entire ventral wall of the epitympanic recess.

Balaenoptera gibbosa (Owen, 1844)

Balaena gibbosa Owen, 1844.
Balaenoptera emarginata (Owen, 1844); Lydekker, 1887a,b.
Type: Partial right tympanic bulla.

Locality: Felixstow, Suffolk, England.

Stratigraphy: Red Crag.

Age: early Pleistocene (Calabrian Stage).

Nomenclatural summary: Because of its fragmentary nature, the holotype tympanic bulla is not diagnostic and the species name is here considered a *nomen dubium*.

Discussion: As mentioned above, Lydekker (1887a,b) considered this taxon to be a junior synonym of *Balaena emarginata* and assigned both taxa to *Balaenoptera*. Like the other Red Crag nominal mysticetes of Owen (1844) *Balaena gibbosa* was established on a non-diagnostic element (i.e., a fragmentary tympanic bulla) and is here considered a *nomen dubium*.

Balaenoptera minutis (Van Beneden, 1880)

Burtinopsis minutus Van Beneden, 1880.

Burtinopsis minutus; Van Beneden, 1882, pp. 80–83, plates 97–102.

Balaenoptera minutis; Deméré (1986).

Type: None designated.

Type Locality: Antwerp, Belgium.

Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).

Age: early Pliocene (Zanclian Stage).

Nomenclatural summary: Because of problems concerning the lack of a type specimen (or a syntype consisting of at least a cranial vertex with associated petrotympanic) for this taxon, its recognition as a valid taxon is suspect. Deméré (1986, p. 291) considered *Burtinopsis* to be a junior synonym of *Balaenoptera* based on characters of the mandible (e.g., planoconvex cross sectional shape, bulbous and posteriorly directed condyle, and small and dorsally positioned mandibular foramen).

Discussion: Originally named *Burtinopsis minutus* by Van Beneden (1880) who indicated that bones of this taxon had been previously confused with those of *Balaenoptera rostratella*. He noted that this species was represented by an almost complete cranium (not illustrated in the 1882 monograph), fragments of jaws, an almost complete vertebral column, and some ribs. However, because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon. Further, the present location of the nearly complete cranium mentioned by Van Beneden is unknown and cannot be "mined" for diagnostic morphological features.

Balaenoptera rostratella Van Beneden, 1880

Balaenoptera rostratella; Van Beneden, 1880, p. 16.

Balaenoptera rostratella; Van Beneden, 1882, pp. 73–77, plates 76–86.

Junior synonym of *Balaenoptera emarginata* (Owen, 1844) fide Lydekker (1887a,b)

Type: None designated.

Type Locality: Antwerp, Belgium.

Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).

Age: early Pliocene (Zanclian Stage).

Nomenclatural summary: Because of problems concerning the lack of a type specimen (or a syntype consisting of at least a cranial vertex with associated petrotympanic) for this taxon, its recognition as a valid taxon is suspect. Van Beneden (1880, 1882) aligned

(presumably based on size) this fossil species with the extant minke whale (*Balaenoptera acutorostrata*), emphasizing that relationship with a similar specific name.

Discussion: Van Beneden (1880) indicated that this species was represented by an almost complete skeleton, however, in his monograph Van Beneden (1882) listed and illustrated only a series of isolated elements, each with different catalogue numbers. This listing included a partial mandible, cranial elements (parietal and squamosal), tympanic bullae, a petrosal, isolated cervical, thoracic, lumbar, and caudal vertebrae, and isolated pectoral elements. Because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon. It is noteworthy that the referred cranial fragment (MR 799), which consists of the apex of the SOS and the anterior portions of the right and left parietals, does not preserve typical balaenopterid features. Instead, the parietals are broadly exposed on the cranial vertex, are not vertically oriented in the anteromedial region of the temporal fossa, and lack an anterior wing that overlaps the AMP. In addition, the SOS has a rounded apex and is not bluntly triangular. This complex of primitive character states does not occur in any known species of fossil or modern *Balaenoptera*.

Balaenoptera sibbaldina Van Beneden, 1880

Balaenoptera sibbaldina; Van Beneden, 1880, pp. 14–15.
Balaenoptera sibbaldina Van Beneden, 1882, pp. 63–65, plates 49–51.
Junior synonym of *Balaenoptera definata* (Owen, 1844) fide Lydekker (1887a,b).
Type: None designated.
Locality: Antwerp, Belgium.
Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).
Age: early Pliocene (Zanclian Stage).
Nomenclatural summary: Because of problems concerning the lack of a type specimen (or a syntype consisting of at least a cranial vertex with associated petrotympanic) for this taxon, its recognition as a valid taxon is suspect.

Discussion: Van Beneden (1880, p. 15) established this species on an isolated petrosal and some vertebrae from different parts of the axial skeleton. Later, in his monograph Van Beneden (1882) listed and illustrated a partial occipital shield (of a juvenile individual), a right petrosal, an isolated posterior process of the petrotympanic, a partial rib, and isolated thoracic, lumbar, and caudal vertebrae. Because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon. Van Beneden (1880, 1882) aligned (presumably based on size) this fossil species with the extant blue whale (*Balaenoptera musculus*, known to Van Beneden as *Balaenoptera sibbaldus*), emphasizing that relationship with a similar specific name. Van Beneden emphasized that he was naming the fossil taxon *sibbaldina* presumably referring to the similar large size of the fossil and living blue whale.

Balaenoptera siberi Pilleri and Pilleri, 1989

Balaenoptera siberi Pilleri and Pilleri, 1989
Type: Complete skeleton including skull baleen, mandibles, flippers, and vertebral column. In private collection of Dr. Allejandro Pezzia Asserto (Pilleri and Pilleri, 1989).
Type Locality: Sacaco Basin, southern Peru.

Stratigraphy: Aguada de Lomas, Pisco Formation.

Age: late late Miocene (Messinian Stage).

Paratype: complete skeleton housed at the Staatliches Museum für Naturkunde, Stuttgart and described and illustrated by Pilleri (1990).

Nomenclatural summary: This taxon is a distinct fossil species of *Balaenoptera*.

Discussion: The skull is of moderate size (CBL = 228 cm, ZW = 111 cm) and intermediate between *Balaenoptera acutorostrata* and *B. borealis*. The APM are broad dorsally and extend posteriorly to the apex of SOS, which is bluntly truncated. The APPM also extend posteriorly to the apex of SOS. There is no exposure of frontal or parietal on the vertex. Instead, the posterior rostral elements (APM, APPM, and nasals lie adjacent to the SOS. The AWP broadly overlaps the APM and forms a vertical face in the intertemporal constriction medial to the abruptly depressed SOPF. The lambdoidal crests broadly overhang the anteroposteriorly narrow temporal fossae. The nasal bones are of moderate length and bluntly terminate anteriorly as a transverse surface (not anteriorly concave or medially tapered). The medial portion of the dorsal surface of the nasals appears to be slightly elevated longitudinally above the lateral margins of the nasals as in "*Megaptera*" *hubachii* and certain individuals of *Balaenoptera acutorostrata*. The SOPF/maxillary suture is marked by the characteristic balaenopterid "pocket." In dorsal aspect the maxillae are broadly convex laterally in a manner similar to that of *Balaenoptera musculus*. The anterior portions of the premaxillae are robust distal to the terminations of the maxillae. The ventral surface of the skull has not been prepared and the morphology of the petrotympanic elements has not been described.

<center>*Balaenoptera similis* (Van Beneden, 1872)</center>

Burtinopsis similis, Van Beneden, 1872, pp. 19–20.
Burtinopsis similis, Van Beneden, 1880, pp. 16–17.
Burtinopsis similis, Van Beneden, 1882, pp. 77–80, plates 87–96.
Balaenoptera similis; Deméré (1986).
Type: None designated.
Type Locality: Antwerp, Belgium.
Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).
Age: early Pliocene (Zanclian Stage).

Nomenclatural summary: Because of problems concerning the lack of a type specimen (or a syntype consisting of at least a cranial vertex with associated petrotympanic) for this taxon, its recognition as a valid taxon is suspect. As noted above Deméré (1986, p. 291) considered *Burtinopsis* to be a junior synonym of *Balaenoptera*.

Discussion: Originally named *Burtinopsis similis*. Van Beneden (1880) noted that bones of this small species had previously been confused with those of "*Plesiocetus*" *burtini* and mentioned that the taxon is based on tympanic bullae, petrosals, mastoids, skull fragments, a mandible, a partial vertebral column, and fragments of ribs. However, because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon.

<center>"*Balaenoptera*" *cortesii* (Fischer, 1829)</center>

Balaena cortesii, Fischer, 1829, p. 527.
Plesiocetus cortesi in part of Van Beneden and Gervais 1868–1879.

Cetotherium cortesii; Strobel, 1881, pp. 10–11, plate 1, Fig. 3.

Balaenoptera cortesii; Kellogg, 1944, p. 446; Deméré, 1986, pp. 292–293.

Type: Partial juvenile skeleton collected in 1816 by G. Cortesi now housed at the Museo Paleontologico Parmense.

Locality: Montezago, Piedmonte, Italy.

Stratigraphy: marna azzurra.

Age: late Pliocene (Piacenzian Stage).

Referred Specimens: None.

Nomenclatural summary: Originally called "Baleine de Cortesi" by Desmoulins (1822), but later assigned to *Plesiocetus cortesii* by Van Beneden (1875). Van Beneden and Gervais (1868–1879) included several specimens under this binomen including the 1806 skeleton from Mount Pulgnasco (="*Balaenoptera*" *cuvieri*), the 1816 skeleton from Montezago (="*Balaenoptera*" *cortesi*), and the San Lorenzo skeleton of Capellini (=*Cetotheriophanes capellinii*). Kellogg (1944) and Deméré (1986) assigned the species to *Balaenoptera* pending further study, however, here we suggest that it represents a taxon outside *Balaenoptera*. We use quotation marks in this report to recognize this unstable nomenclatural situation.

Discussion: We were not able to examine this specimen and consequently have to rely on published descriptions and illustrations. *Balaenoptera cortesii* is a small species (mandible approximately 115 cm in length) based on a presumably adult individual (Desmoulins, 1822). Balaenopterid characters of this taxon include SOPF abruptly depressed below vertex; maxilla/frontal contact marked by frontal "pocket"; and mandible with broadly sinuous longitudinal outline.

"Balaenoptera" cortesi var. portisi Sacco, 1890

Balaenoptera (*Plesiocetus*) *cortesii* of Portis, 1885, p. 286, Figs. 42–47.

Balaenoptera cortesi var. *portisi*, Sacco, 1890.

Balaenoptera floridana; Kellogg, 1944.

Type: MGPT 13803: skeleton with disarticulated skull, partial left tympanic bulla, right and left mandibles, nearly complete vertebral column, ribs, and scapula.

Locality: Montafia, Piedmonte, Italy.

Stratigraphy: Sabbie d'Asti.

Age: late Pliocene (Piacenzian Stage).

Referred specimens: MCZ 17882, nearly complete right dentary; holotype of *Balaenoptera floridana* Kellogg, 1944; American Chemical Company phosphate pit, Pierce, Polk Co., Florida, USA; Bone Valley Formation, Pliocene. SDSNH 65769, nearly complete rostrum and partial cranium (basisphenoid and SOPF); SDSNH locality 3782, Chula Vista, San Diego County, California, USA; San Diego Formation, Pliocene. SDSNH 68698, partial cranium with left petrosal and tympanic bulla; SDSNH locality 4198, Chula Vista, San Diego County, California, USA; San Diego Formation, Pliocene. SDSNH 21507, complete left mandible; SDSNH locality 3068, San Diego, San Diego County, California, USA; San Diego Formation, Pliocene.

Nomenclatural summary: Portis assigned MGPT 13803 to the nominal taxon *Balenoptera* (*Plesiocetus*) *cortesii*. However, as noted above, the name *Balenoptera cortesii* is restricted to the smaller Montezago specimen. Sacco (1890) proposed the name *portisii* for MGPT 13803 and this usage is followed here. This taxon

is a basal balaenopterid as discussed below and should be placed in a new genus.

Discussion: The skull of the Montafia specimen described and illustrated by Portis (1885) is of moderate size (CBL = approximately 198 cm, ZW = 75 cm) and preserves a mosaic of primitive and derived character states. "Cetothere"-grade features include a relatively long intertemporal region with a long parietal exposure (lacking a sagittal crest) and short frontal exposure, no squamosal crease, and no AWP/APM overlap. Balaenopterid features include abruptly depressed SOPF, narrowly elongate APM, squamosal cleft not contacting parietal, promontorium height > length, triangular anterior process of petrosal, and small and dorsally placed mandibular foramen. Unique features include narrowly rounded SOS apex reaching to preorbital process of SOPF, elongate zygomatic process, delicate orbital rim of SOPF, large and nearly circular temporal fossa, elongate and narrow rostrum, relatively small tympanic bulla without medial furrow or dorsal lateral prominence, elongate horizontal ramus with shorter vertical diameter posteriorly, narrow mandibular condyle, and low laterally deflected coronoid process with long pre-coronoid crest. Several of these unique features are shared with the holotype of *Cetotheriophanes capellinii* (see discussion below).

Balaenoptera floridana is recognized here as a synonym of this taxon. The holotype right mandible (MCZ 17882) is nearly identical in size and shape to the mandible of the holotype of "*Balaenoptera*" *cortesi* var. *portisi*. This taxon is not a member of *Balaenoptera*, but instead appears to represent a new species of basal balaenopterid not directly ancestral to modern *Balaenoptera*. Recently collected fossils from the Pliocene of California (SDSNH) can also be referred to this taxon, which is currently being revised (Bisconti and Deméré, in preparation).

"*Balaenoptera*" *cuvierii* (Fischer, 1829)

Balaena cuvierii, Fischer, 1829, p. 527.
Cetotherium (*Cetotheriophanes*) *cuvierii*; Brandt, 1873, plate 20, figs., 1–12.
Plesiocetus cortesii; Van Beneden and Gervais, 1868–1879; Van Beneden, 1875, fig. 1; Zeigler *et al.*, 1997, fig. 8a.
Balaenoptera cuvierii; Kellogg, 1928, p. 191; Deméré, 1986, p. 293.
Type: Complete skeleton (21 feet in length) collected in 1806 by G. Cortesi; housed at the Museo di Storio Naturale di Milano until it was destroyed by Allied bombing during WWII.
Locality: Mount Pulgnasco, Italy; 1800 feet above sea level.
Stratigraphy: marna azzurra.
Age: late Pliocene (Piacenzian Stage).
Nomenclatural summary: Originally called "Baleine de Cuvier" by Desmoulins (1822) this important specimen has a complicated nomenclatural history (see Deméré, 1986). Although some workers were referring to this taxon by the species name *cortesi* as recently as 1997 (Zeigler *et al.*, 1997), it is clear that based on priority the Mount Pulgnasco specimen should be referred to the species *cuvierii*. This species is clearly a balaenopterid, but should be assigned a new generic name (M. Bisconti, personal communication). Unfortunately, the Mount Pulgnasco specimen has been destroyed.

Concerning the generic name *Plesiocetus*, this is a poorly diagnosed genus that has been used as a taxonomic wastebasket by numerous authors. In spite of the popularity of this

generic name as applied to several named "cetotheres" and balaenopterids, Kellogg (1931) convincingly showed that *Plesiocetus* is only valid for the species *Plesiocetus garopii* (see below).

Discussion: Balaenopterid characters of "*Balaenoptera*" *cuvierii* include: SOPF abruptly depressed below vertex; maxilla/frontal contact marked by frontal "pocket"; elongate APM; distinct AWP/APM overlap; anterior margin of SOPF expanded anteromedially, and mandible with broadly sinuous longitudinal outline. Primitive characters of this taxon include: distinctly triangular SOS; elongate squamosal fossa; broadly curved posterior margin of temporal fossa lacking a squamosal crease; and prominent postorbital processes of SOPF.

"*Balanoptera*" *ryani* Hanna and McLellan, 1924

Balaenoptera ryani, Hanna and McLellan, 1924; Zeigler, Chan, and Barnes, 1997, pp. 131,132.

Type: CASG 1733, a partial cranium missing the SOPF and zygomatic processes of squamosals.

Locality: Five miles east of Monterey, Monterey Co., California, USA.

Stratigraphy: "Monterey" Formation (Hanna and McLellan [1924] are equivocal regarding stratigraphy at the type locality).

Age: early late Miocene (Tortonian Stage).

Nomenclatural summary: Although Zeigler *et al*. (1997) referred this taxon to the "Cetotheriidae," we feel that it represents a basal balaenopterid outside of *Balaenoptera*, which should be assigned to a new genus.

Discussion: Balaenopterid characters of this taxon include SOPF abruptly depressed below vertex, parietals overlapping posteromedial corner of SOPF, sinuous and horizontally oriented squamosal cleft, lambdoidal crests broadly overhanging temporal fossa, and petrosal with triangular anterior process. Cetotheriid-grade characters include: sharply triangular SOS, parietal narrowly exposed on vertex, and no AWP/APM overlap.

"*Balaenoptera*" *gastaldii* (Strobel, 1875)

Cetotherium cortesi, Brandt, 1873, plate 21, figs. 1–10.

Cetotherium gastaldii Strobel, 1881, p. 13, plate 1, fig. 6.

Balaenoptera gastaldii; Portis, 1885.

Type: MGPT 13802, partial skeleton collected in 1862 by M. Gastaldi and now housed at the Museo di Torino.

Locality: Cortandone, Italy.

Stratigraphy: Sabbie d'Asti.

Age: late Pliocene (Piacenzian Stage).

Referred Specimens: MGB 8925, partial mandibles missing condyles and anterior half of horizontal rami.

Nomenclatural summary: Although assigned to *Balaenoptera* by Portis (1885), this taxon is not closely aligned with balaenopterids and instead appears to represent a new genus of basal eschrichtiid (Bisconti, 2003; this study).

Discussion: The incomplete skull of the Cortandone specimen described and illustrated by Portis (1885) is of small size (ZW = approximately 68 cm). Cranial suture closure evidence suggests that the holotype is an adult individual. The skull preserves a mosaic

of primitive and derived mysticete character states. Balaenid grade features include a posteriorly directed pterygoid fossa and possibly palatal maxillary windows. Eschrichtiid grade features include a mandible with a low rounded coronoid crest in front of a low saddle-like neck, a tall posterodorsally directed mandibular condyle, a dorsal swelling above the ligamental groove at the anterior tip of the mandible, a short braincase with rugose muscle attachments on the steeply inclined SOS, and a parietal/frontal suture positioned posterior to the SOPF. Balaenopterid grade features include deeply interdigitating median rostral elements and frontal, abruptly depressed SOPF, and a strongly laterally and dorsally bowed mandible. The palate of this enigmatic taxon is still somewhat mysterious in its dorsoventrally flattened profile. It appears that the vomer has been crushed dorsoventrally. The palate itself is rather transversely broad and has a bilaterally symmetrical pair of long and deep medial palatal grooves. The vomer as preserved is rather cylindrical and enclosed above by premaxillae that meet at the midline (an aetiocetid grade feature). Additional mechanical preparation of the holotype skull and removal of adhering matrix would help resolve current morphological questions.

Cetotheriophanes capellinii (Brandt, 1873)

Cetotherium (*Cetotheriophanes*) *capellinii*; Brandt, 1873, pl. 20, figs. 13–16.
Cetotherium (*Cetotheriophanes*) *capellinii*; Strobel, 1881, p. 11, plate 1, fig. 4.
Cetotheriophanes capellinii; Capellini, 1875, plates 2–3.
Type: MGB 9060, partial skeleton with dentary collected in 1862 by G. Capellini now housed at Museo Geopaleontolgico "Giovanni Capellini," Bologna, Italy.
Locality: San Lorenzo, Italy.
Stratigraphy: argille turchine.
Age: late Pliocene (Piacenzian Stage).
Nomenclatural summary: Brandt (1873) designated *C. capellinii* as the type of the subgenus *Cetotheriophanes*. Capellini (1875) later elevated *Cetotheriophanes* to generic rank. Based on priority, the generic name *Cetotheriophanes* is retained here pending completion of on-going restudy of the holotype.
Discussion: This basal balaenopterid shares many features with the holotype of "*Balaenoptera*" *cortesii* var. *portisii* including a narrowly rounded SOS apex, long exposure of parietal and frontal on narrow intertemporal vertex, elongate and narrow rostrum, large temporal fossa, elongate and slender zygomatic processes, and relatively small tympanic bulla. Balaenopterid characters include SOPF abruptly depressed below vertex, auditory bulla with simple main ridge, and mandible with sinuous longitudinal outline. Ongoing study of these fossils suggests that "*Balaenoptera*" *cortesii* var. *portisii* and *Cetotheriophanes capellinii* may be congeneric or even conspecific (Bisconti and Deméré, in preparation).

Eobalaenoptera harrisoni Dooley *et al*., 2004

Eobalaenoptera harrisoni, Dooley *et al*., 2004.
Type: VMNH 742, partial skeleton consisting of a fragmentary cranium, portions of both petrosals, a partial right tympanic bulla, incomplete axial skeleton (cervical, thoracic, and lumbar vertebrae), and most of both forelimbs.
Locality: Carmel Church Quarry, Caroline County, Virginia, USA.

Stratigraphy: Calvert Formation (probably beds 14–16).

Age: middle Miocene (Serravallian Stage).

Nomenclatural summary: Dooley *et al*. (2004) consider *Eobalaenoptera harrisoni* to be the earliest diverging member of the balaenopteroid clade. As discussed below, however, we question this assignment and suggest that this taxon is a mysticete of uncertain taxonomic affinities.

Discussion: Dooley *et al*. (2004) relied almost solely on characters of the petrosal (i.e., elongate pas cochlearis, tubular internal auditory meatus, greater petrosal nerve foramen on tympanic side, stylomastoid fossa extending onto posterior process, and no promontorial groove) in diagnosing *Eobalaenoptera harrisoni*. Although the mysticete petrotympanic complex does preserve phylogenetically important morphological features, it has not been demonstrated that the supposed balaenopteroid petrosal synapomorphies proposed by Dooley *et al*. (2004) are not applicable at higher levels of universality. In other words character states like the extension of the stylomastoid fossa onto the posterior process may actually be a more generally distributed synapomorphy that is sympleisiomorphic for balaenopteroids. Another problem is that some of the purported balaenopteroid petrosal synapomorphies of *E. harrisoni* are not correctly interpreted or are not clearly homologous with conditions in balaenopteroids. For example, the portion of the petrosal considered by Dooley *et al*. (2004) to represent an elongate pars cochlearis does not appear to actually correspond to the region containing the semicircular canals and bony labyrinth (i.e., it is not homologous with the transversely elongate pars cochlearis of *Balaenoptera* and *Eschrichtius*). Instead, this elongation represents a dense dorsolateral projection of the main suprameatal portion of the petrosal. The promontorium itself is transversely short in *E. harrisoni* and the region housing the internal auditory meatus and the cerebral opening for the facial nerve are positioned close to the level of the fenestra rotunda. In modern and fossil balaenopterids the promontorium is transversely elongated and the region housing the internal auditory meatus and opening for the facial nerve are positioned distinctly medial to the fenestra rotunda.

Compounding the problem of questionable utility of petrosal character states is the incompleteness of the holotype skeleton of *E. harrisoni*. The other regions of the skull traditionally used to characterize/diagnose fossil and modern mysticetes (e.g., degree of intertemporal exposure of parietal and frontal, position of SOPF, extent of rostral/cranial interdigitation, development of ascending process of maxilla, morphology of the nasals, basicranial features of the pterygoid sinus, and features of the mandible) are not preserved in the incomplete holotype skeleton. Although Dooley *et al*. (2004) use some postcranial elements (i.e., vertebrae and ribs) to further characterize this new species, it is questionable whether the selected characters are really diagnostic at the species, genus, or even family level. Of course these shortcomings are not unique to this taxon, but without a broader morphological diagnosis using more traditional characters from the skull and mandible it is difficult to make useful comparisons between *E. harrisoni* and other fossil and modern balaenopteroids.

Based on the issues discussed above we feel that *Eobalaenoptera harrisoni*, as currently diagnosed, cannot be unambiguously shown to be a basal balaenopteroid. Until more complete skull and mandibular material is available for this taxon, it should be considered a mysticete of uncertain taxonomic affinity.

"Megaptera" hubachi Dathe, 1983

Megaptera hubachi, Dathe, 1983.

Type: MB Ma 28570 nearly complete skeleton with damaged portions of cranium, rostrum, and mandibles, and associated axial skeleton and pectoral elements.

Locality: Bahia de Guayacan, northern Chile.

Stratigraphy: Pliocene marine sandstones (no formal stratigraphic unit given by Dathe, 1983).

Age: Pliocene (?) (Piacenzian Stage).

Nomenclatural summary: As discussed below this balaenopterid taxon is not a species of *Megaptera* and, pending additional study, should be placed in a different genus.

Discussion: A relatively small species of balaenopterid (CBL = approximately 157 cm; ZW = 85 cm) falling within the size range of *Balaenoptera acutorostrata*. Cranial suture closure evidence suggests that the holotype is an adult individual. Although originally assigned to *Megaptera*, the holotype does not possess any of the autapomorphies of the extant humpback whale. The nasal processes are not sharply extended anteriorly at the midline, there is no invasion of the posterior portion of the nasals by a narrow finger of the frontal, the coronoid process of the mandible is large and triangular in shape, and the scapula possesses strong acromion and coracoid processes. Although, as in modern *Megaptera novaeangliae*, the zygomatic processes of the squamosal diverge laterally and there is no squamosal crease *sensu* Kellogg (1924), in the context of this study divergent zygomatic processes are viewed as the primitive condition. Balaenopterid features include: apex of SOS bluntly truncated, SOPF abruptly depressed below the level of the vertex, distinct AWP/APM overlap, prominent squamosal cleft, and SOPF/maxillary suture marked by characteristic balaenopterid "pocket." The ascending processes of the maxillae are narrowly triangular as in *Balaenoptera davidsonii*, however, the horizontal ramus of the mandible is distinctly thicker transversely than in the latter taxon.

"Megaptera" miocaena Kellogg, 1922

Megaptera miocaena, Kellogg, 1922.

Type: USNM 10300, incomplete skull.

Locality: Three miles east of Lompoc, Santa Barbara Co., California, USA.

Stratigraphy: Monterey Formation.

Age: early late Miocene (Tortonian Stage).

Referred Specimens: Oishi and Hasegawa (1995) list a tentatively referred specimen of this taxon from the Funakawa Formation (upper Miocene) of Akita, Japan. Isolated tympanic bullae from the Tatsunokuchi and Na-arai formations (Lower Pliocene) of northeastern Honshu, Japan were also tentatively referred to this taxon.

Nomenclatural summary: As discussed below this basal balaenopterid taxon is not a species of *Megaptera* and, pending additional study, should be placed in a new genus.

Discussion: A fossil balaenopterid of moderate size (ZW = 127 cm) and intermediate between *Balaenoptera acutorostrata* and *B. borealis*. Cranial suture closure evidence suggests that the holotype is an adult individual. Although originally assigned to *Megaptera*, the holotype does not possess any of the autapomorphies of the extant humpback whale. The nasals are relatively short and rectangular (not triangular and sharply extended anteriorly at the midline) and there is no invasion of the posterior portion of the nasals by a narrow finger

of the frontal. Although there is no squamosal crease and the zygomatic processes of the squamosal do diverge laterally as in modern *Megaptera novaeangliae*, in the context of this study divergent zygomatic processes are viewed as the primitive condition. Balaenopterid features of "*M.*" *miocaena* include: apex of SOS bluntly truncated, no exposure of frontal or parietal on vertex, parietals overlapping posteromedial corner of SOPF, SOPF abruptly depressed below the level of the vertex, lambdoidal crests broadly overhanging temporal fossa, and triangular anterior process of petrosal. The degree of interdigitation of cranial and rostral elements is intermediate between that of derived balaenopterids and cetothere-grade taxa as evidenced by very short AWP that have an extremely short overlap of the short and triangular APM. Additional noteworthy characters include SOPF/maxillary suture marked by incipient balaenopterid "pocket" and tympanic bulla with large and bulbous dorsal posterior prominence. Although the latter feature resembles somewhat the condition in extant *Megaptera novaeangliae*, the humpback bulla is more inflated ventrally than in "*M.*" *miocaena*.

Megapteropsis robusta Van Beneden, 1872

Megapteropsis robusta, Van Beneden, 1872, p. 15.
Megaptera affinis, Van Beneden, 1880, pp. 39–45, plates 40–45.
Type: None designated.
Locality: Antwerp, Belgium.
Stratigraphy: Diest Formation (sablesmoyens d'Anvers).
Age: late late Miocene (Messinian Stage).
Nomenclatural summary: Van Beneden (1872) originally used the binomen *Megapteropsis robusta*, but later (Van Beneden, 1880) suppressed that name and assigned a new binomen, *Megaptera affinis*. Apparently this was done to emphasize the perceived similarity between the fossil species and the extant humpback. This is not a valid reason for a name change and, based on priority, the original binomen should be retained. As discussed below, this taxon may represent a fossil eschrichtiid.

Discussion: In his description of this new species Van Beneden (1880) did not discuss any diagnostic features and instead merely provided a general listing of the kinds of fossil elements in the collections of the IRSNB that he assigned to this taxon. As is typical of the Antwerp fossil material there was no holotype designated and no discussion as to whether any of the fossil elements were associated and from the same individual. Later, Van Beneden (1882; plates 66–75) illustrated numerous elements assigned to this taxon including a complete mandible, a partial premaxilla, an isolated petrosal, an isolated tympanic bulla, and isolated cervical, thoracic, and lumbar vertebrae. Because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unequivocally diagnose this taxon. In addition the disparate referred specimens may represent taxa belonging to different genera and even different families. The large mandible (IRSNB 810) referred to this taxon by Van Beneden (1882) is very unusual and shares a number of features with *Eschrichtius robustus* including a mandibular condyle oriented posterodorsally; an angle equal to or slightly larger than the condyle in vertical diameter; an anteroventrally oriented mandibular foramen, and a dorsally concave dorsal margin of the mandibular neck between the coronoid region and the mandibular condyle. Unfortunately, this specimen has been badly damaged and its morphology is currently

difficult to interpret. It is possible, however, to confirm the unique morphological features noted above.

Parabalaenoptera baulinensis Zeigler *et al*., 1997

Parabalaenoptera baulinensis, Zeigler *et al*., 1997.
Type: CASG 66660; partial associated skeleton (cranium, petrosal, bulla, mandible, scapula, humerus, vertebrae, ribs).
Locality: Near Bolinas Point, Point Reyes Peninsula, Marin Co., California, USA.
Stratigraphy: Santa Cruz Mudstone.
Age: late late Miocene (6.0–6.8 Ma) (Messinian Stage).
Nomenclatural summary: This taxon represents a balaenopterid distinct from any nominal species of fossil and modern *Balaenoptera*.
Discussion: A fossil species of moderate size (CBL = 224 cm; ZW = 98 cm), similar in size to *Eschrichtius robustus*. Cranial suture closure evidence suggests that the holotype is an adult individual. Unique features include: slenderly elongate nasals and extremely long overlap of the APM and AWP. Balaenopterid features include: SOPF abruptly depressed below vertex; maxilla/frontal contact marked by frontal "pocket;" elongate and dorsally oriented APM; anterior margin of SOPF expanded anteromedially, parietals overlapping posteromedial corner of SOPF, bluntly triangular SOS, lambdoidal crests broadly over-hanging temporal fossa, mandible with broadly sinuous longitudinal outline, posteriorly directed mandibular condyle, and small and elevated mandibular foramen. Primitive char-acters of this taxon include: narrow and elongate intertemporal region, narrowly elongate nasals, elongate squamosal fossa, and straight lateral margin of SOS.

Plesiocetus garopii Van Beneden, 1859

Plesiocetus garopii; Van Beneden, 1859.
Plesiocetus garopii; Van Beneden, 1872.
Plesiocetus garopii; Van Beneden and Gervais 1868–1879, pp. 285–287, pl. 16, figs. 1–9.
Balaenoptera musculoides Van Beneden, 1880, p. 15.
Balaenoptera musculoides; Van Beneden, 1882, pp. 65–71, plates 52–65.
Plesiocetus garopii; Kellogg, 1931, pp. 312–313.
Balaenoptera garopii; Deméré, 1986, p. 290.
Type: No type specimen designated.
Type Locality: Antwerp, Belgium.
Stratigraphy: Kattendijk and Lillo formations (Sable Superieur d'Anvers).
Age: early Pliocene (Zanclian Stage).
Nomenclatural summary: Van Beneden (1859) originally named this taxon *Plesiocetus garopii* and later (Van Beneden, 1872) made it the sole member of the genus *Plesiocetus*, which he felt was a balaenopterid. In 1880 Van Beneden renamed this species *Balaenoptera musculoides*, presumably creating the new binomen because in his opinion the fossil closely resembled the living fin whale (*Balaenoptera physalus*), which was known by Van Beneden as *Balaenoptera musculus*. Thus he apparently wanted to emphasize that relationship by giving the fossil a similar name and suppressing usage of the earlier binomen. He seems to have used the same criteria for establishing *Balaenoptera borealina*, *Balaenoptera*

rostratella, *Balaenoptera sibbaldina*, and *Megaptera affinis*. Interestingly, Van Beneden (1880) later changed his opinion concerning the relationships of *Plesiocetus*, concluding that this taxon represented a genus of cetotheriid.

Kellogg (1931), relying on the conclusions of Van Beneden (1872), called this taxon *Plesiocetus garopii* and noted that it should be considered the type of the genus *Plesiocetus* based on statements made by Van Beneden (1872, p. 15) that the genus name should be reserved solely for this large species of fossil balaenopterid.

Discussion: Van Beneden (1880) does not provide any useful discussion of the morphology of this taxon, but rather gives unreferenced general listings (no specimen numbers) of the skeletal elements assigned to it. There is no discussion of individual specimens and no mention as to whether any of the specimens were associated. For *Balaenoptera musculoides* Van Beneden (1880) noted that the Royal Museum collection contains a mandible, earbones, skull fragments, a partial vertebral column, and some ribs. In his later monograph Van Beneden (1882) listed and illustrated a complete left mandible, isolated tympanic bullae and petrosals, isolated cervical, thoracic, lumbar, and caudal vertebrae, isolated ribs, and several pectoral elements. Because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon.

PHYLOGENETIC ANALYSIS

The ingroup consists of 28 extinct and extant mysticetes including one aetiocetid (*Aetiocetus weltoni*), one eomysticetid (*Eomysticetus whitmorei*), eight "cetotheres" (*Diorocetus hiatus*, *Aglaocetus patulus*, *Cophocetus oregonensis*, *Cetotherium rathkii*, *Mixocetus elysius*, *Isancetus laticephalus*, *Pelocetus calvertensis*, and *Parietobalaena palmeri*), the neobalaenid (*Caperea marginata*), and two balaenids (*Balaena mysticetus* and *Eubalaena glacialis*). The following balaenopteroids were included in the analysis: *Balaenoptera acutorostrata*, *B. borealis*, "*B.*" *portisi*, *B. davidsonii*, a representive of the *B. edeni* species complex, *B. musculus, B. physalus, B. siberi*, "*B.*" *gastaldi, Eschrichtius robustus, Megaptera novaeangliae*, "*M.*" *hubachi*, "*M.*" *miocaena, Parabalaenoptera baulensis*, and SDSNH 90517 (Appendix 1 and text). Selection of ingroup fossil taxa was mainly based on relative completeness of fossil material and access to collections. The outgroups used included three basal odontocetes, *Physeter macrocephalus, Tasmacetus shepherdi* (the most basal ziphiid according to Geisler and Sanders, 2003) and *Agorophius* sp. (ChM 5852).

Phylogenetic analysis of the morphological character dataset is based on 85 craniodental, postcranial and soft anatomical characters (32 binary and 53 multistate; Appendices 2, 3). Multistate characters were treated as unordered. The morphological data set (Appendix 3) was analyzed using PAUP* v4b10 (Swofford, 2001) with a maximum parsimony optimality criterion. All characters and character-state transformations were unweighted. All gaps in the molecular data were treated as missing. Because of the large number of taxa (28), a heuristic search and random stepwise addition (branch swapping: tree bissection-reconnection) was performed with 5000 replicates. Zero length branches were collapsed using the "amb-" option. This has been suggested when running analyses containing a significant amount of missing data as it suppresses ambiguous reconstructions due to question marks (Kearney and Clark, 2003). One thousand bootstrap replicates with ten random stepwise addition heuristic searches per replicate were also performed. Branch

support (BS) values for each branch (Bremer, 1988, 1994) were calculated using TreeRot v. 2 (Sorenson, 1999) and PAUP* v4b10 (Swofford, 2001).

In addition to a morphological analysis, a simultaneous or "total evidence" analysis was performed using sequences of three mitochondrial genes (cytochrome *b*, ND4, and ND4L) and one nuclear gene (α-lactalbumin). All ND4, ND4L, and α-lactalbumin were obtained from Rychel *et al*. (2004). These included new as well as published sequences. GenBank accession numbers and references are included in Table I of Rychel *et al*. (2004). All cytochrome *b* data were obtained from Arnason and Gulberg (1994), except that of *Eubalaena glacialis* which was obtained from Rychel *et al*. (2004). The molecular data set included a total of 4001 characters. Alignments are those of Rychel *et al*. (2004). Sequences not representing ingroup and outgroup taxa in this study were excluded. Due to the absence of sequence data for *Tasmacetus shepherdi*, those of *Ziphius cavirostris* were substituted. Both *Ziphius cavirostris* and *Tasmacetus shepherdi* are ziphiid odontocetes, and their close relationship is highly supported by morphological and molecular data (Hamilton *et al*., 2001; Dalebout *et al*., 2002; Geisler and Sanders, 2003).

A simultaneous or "total evidence" analysis represents one of the only ways that fossil taxa and genetic data from extant organisms can be combined. However, the logic of combining data from different sources (i.e. mitochondrial, nuclear, and morphological) has been hotly debated in the systematic literature (Huelsenbeck *et al*., 1996; Wiens, 1998). Wiens (1998) argued that combining data increases phylogenetic accuracy and therefore should not be dismissed a *priori*. He suggested running separate analyses for each individual data partition and then performing a combined analysis to assess which parts of the tree are well-supported by all relevant data. Separate analyses of cytochrome b, ND4/ND4L, and α-lactalbumin have already been published in Rychel *et al*. (2004).

The simultaneous or "total evidence" analysis of the concatenated morphological and molecular data was conducted using the same procedure outlined for the morphological analysis. Gaps were treated as missing data. In addition to branch support values, partitioned branch support (PBS) values (Baker and DeSalle, 1997; Baker *et al*., 1998) were computed for each gene and the morphological data set to assess the relative contribution of each partition in the simultaneous analysis. Partitioned branch support values were calculated using TreeRot v. 2 (Sorenson, 1999) and PAUP* v4b10 (Swofford, 2001).

RESULTS

Analysis of the morphological data set yielded 21 equally parsimonious trees of 302 steps (CI = 0.5397; RI = 0.7146; RC = 0.3857). The strict consensus of those trees is shown in Fig. 3 with bootstrap values above and branch support values below each relevant node. Mysticetes are highly-supported (bootstrap = 100%, branch support = 9). A monophyletic Balaenoidea and Balaenidae are also highly-supported (balaenoids: bootstrap = 99%, branch support = 10; balaenids: bootstrap = 100%, branch support = 9). Balaenopteroids are well-supported (bootstrap = 88%, branch support = 6), but a monophyletic Balaenopteridae and Eschrichtiidae are not. Relationships among balaenopterids remain weakly-supported.

The position of the "cetotheres" is basal to all modern mysticetes as suggested by Geisler and Sanders (2003). This differs from the analysis of Kimura and Ozawa (2002), in which "cetotheres" were more closely related to balaenopteroids. Relationships among
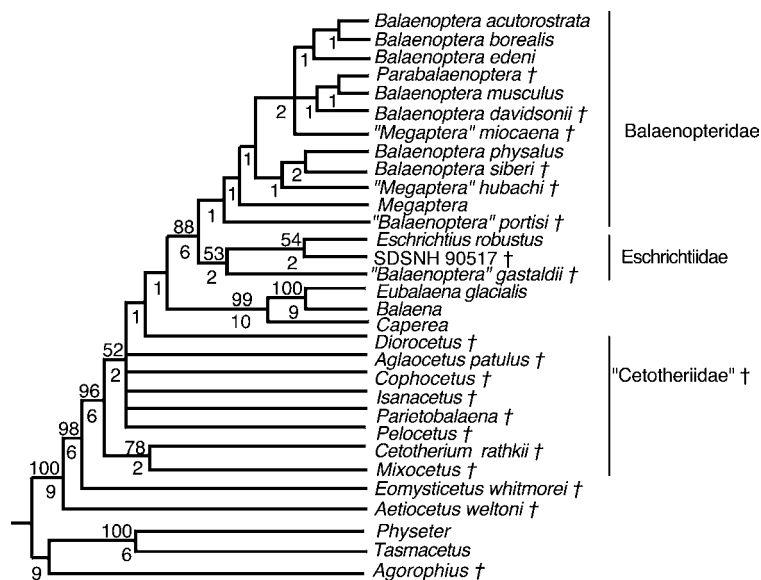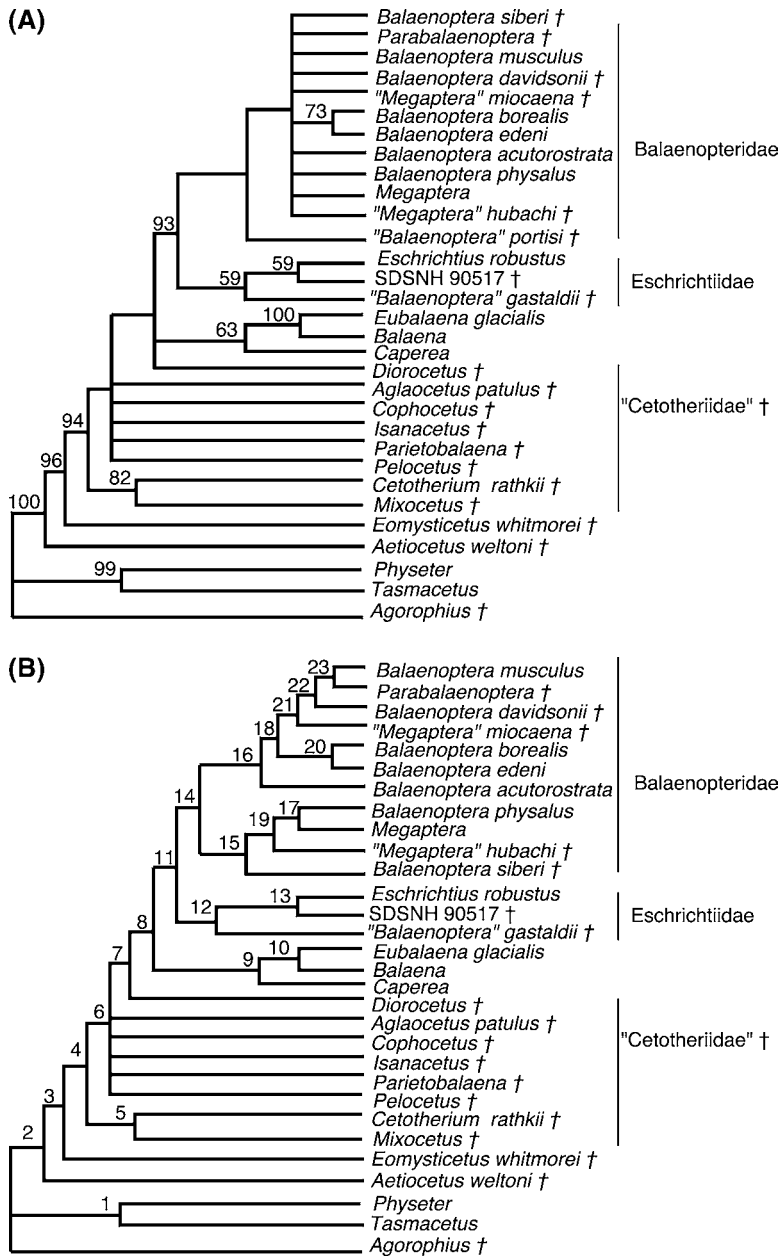
Fig. 3. Strict consensus of 21 most parsimonious trees for the matrix of 28 extinct and extant taxa coded for 85 morphological characters. Bootstrap and Bremer support values are indicated above and below the nodes, respectively.

"cetotheres" remain unresolved. Several manipulations of the data were done to assess the influence of "cetotheres" on the topology. When the analysis was repeated with the deletion of three less well-represented "cetotheres" (*Aglaocetus*, *Isanacetus*, and *Cophocetus*) 484 equally most-parsimonious trees were found. Although the analysis recovered the Balanopteroidea, Balaenoidea, Balaenopteridae and Eschrichtiidae, relationships among the balaenopterid species were mostly unresolved. Another data run in which we deleted all "cetotheres" resulted in 109 equally parsimonious trees. Again the aforementioned major clades were recovered although relationships of taxa within them were considerably less well resolved than in the initial analysis.

The "total evidence" analysis of all taxa resulted in 18 most-parsimonious trees of 2418 steps (CI = 0.584; RI = 0.481; RC = 0.281). Figure 4(A) shows the strict consensus tree of these 18 trees with bootstrap values above each relevant node. The consensus tree produced little resolution within Balaenopteridae, but showed similar support for nodes supported by the strict consensus tree of the morphological characters (Fig. 3).

Wilkinson (2003) discussed the problem of low resolution in relation to large numbers of trees sometimes encountered in analyses with significant amounts of missing data. Here we have encountered a similar problem on a much smaller scale and are able to explore the data in much greater detail. Wikinson (1994, 2003) suggested the use of reduced consensus methods in analyses with a great number of most-parsimonious trees in order to tease apart relationships among taxa that may indeed be strictly supported. In this study we were able to do this manually.

When the 18 most-parsimonious trees were investigated further, two underlying topologies were discovered representing two separate islands (Fig. 5). The first (Fig. 5(A))

Fig. 4. (A) Unrooted strict consensus of 18 most parsimonious trees for the combined mor-
phological and molecular data sets. (B) Unrooted strict consensus of 18 most parsimonious
trees for the combined morphological and molecular data sets, but with "*Balaenoptera*"
portisi excluded. Nodes are labeled to identify bootstrap, partitioned branch support, and
Bremer support values from each analysis reported in Table II.
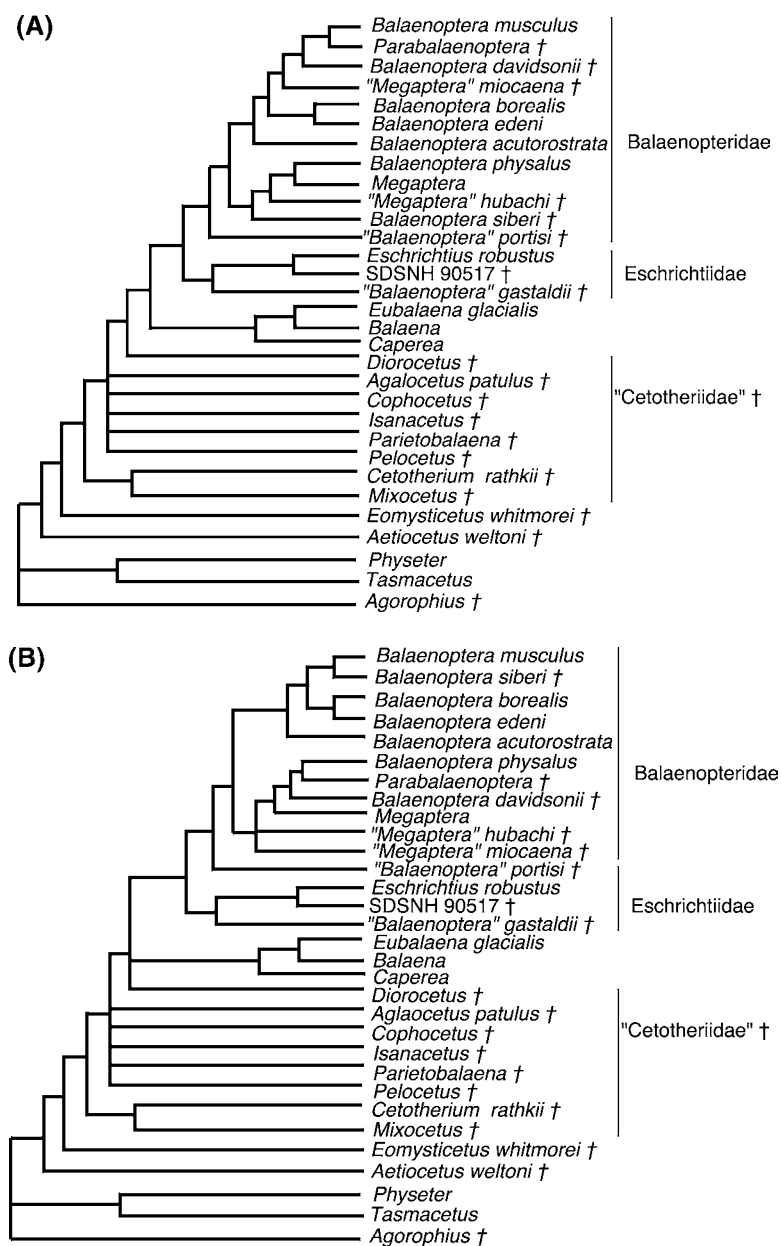
Fig. 5. (A) Unrooted consensus tree for the combined morphological and molecular data sets (see Fig. 3), island 1 (trees 1–6) with "*Balaenoptera*" *portisi* included. (B) Unrooted consensus tree for the combined morphological and molecular data sets (see Fig. 3), island 2 (trees 7–18) with "*Balaenoptera*" *portisi* included.

is a consensus of the six trees of "Island 1." The second (Fig. 5(B)) is a consensus of the 12 trees of "Island 2." These two topologies are similar in the relationships among non-balaenopterids, but are highly divergent when comparing relationships within balaenopterids. However, relationships of the extant balaenopterids to one another are conserved between both topologies and two clades of extant balaenopterids emerge (although not supported by high bootstrap values): *Megaptera + Balaenoptera physalus* and *Balaenoptera acutorostrata + B. musculus + B. borealis + B. edeni*. The fossil taxon *"Megaptera" hubachi* is stable in its grouping with the *Megaptera + B. physalus* clade in both trees. Other fossil taxa are notably inconsistent in their position between the two trees. However, the position of each fossil taxon is stable within each island. Thus it can be noted that the addition of fossil taxa obscures the relationship between extant taxa in the consensus tree, but also supports two underlying most-parsimonious phylogenies.

Removal of *"Balaenoptera" portisi*, the most basal balaenopterid in both morphological and "total evidence" analyses (although not well-supported), produced a well-resolved strict consensus tree (Fig. 4(B)) of six most-parsimonious trees of 2414 steps (CI = 0.585; RI = 0.479; RC = 0.280). The strict consensus tree in Fig. 4(B) is the same as the consensus tree of "Island 1" in Fig. 5(A) with the exception of the removal of *"Balaenoptera" portisi*. These results should be interpreted cautiously. The removal of *"B." portisi* has produced a more resolved consensus tree that shows the same relationships as six out of 18 most-parsimonious trees of the analysis with *"B." portisi*. However, this does not mean that the removal of *"B." portisi* has produced a tree with greater phylogenetic accuracy.

Bootstrap, branch support, and partitioned branch support values for the consensus tree excluding *"B." portisi* (Fig. 4(B)) are shown in Table III. Similar results were obtained for the consensus tree including *"B." portisi* (Fig. 4(A)). Basal nodes of the "total evidence" tree have similar bootstrap and branch support values to the morphology tree. Support for Balaenoidea is substantially reduced in the "total evidence" analysis (99% morphology; 63% "total evidence"). This is due to the incongruence between the morphological and DNA data. Partioned branch support values at Node 9 (Balaenoidea) for ND4 and ND4L sequences are −10 and −6.99 respectively (Table III). Indeed, *Caperea marginata* is more closely related to balaenopteroids in the ND4/ND4L gene tree (Rychel *et al*., 2004). Bootstrap values for Balaenopteroidea increased slightly (89% without *"B." portisi* and 93% with *"B." portisi*). Relationships within Balaenopteroidea remain weakly supported except for the strong relationship between *Balaenoptera borealis* and *B. edeni*. The position of *Balaenoptera acutorostrata* differs significantly between morphology/total evidence trees and the molecular trees (Rychel *et al*., 2004). In the morphology and "total evidence" trees this taxon is included in a clade with *B. musculus + B. edeni + B. borealis*. In the combined molecular trees of Rychel *et al*. (2004), *B. acutorostrata* is the most basal balaenopteroid.

DISCUSSION

We have identified three major well-supported clades: Mysticeti, Balaenoidea (Balaenidae + Neobalaenidae), and Balaenopteroidea (Balaenopteridae + Eschrictiiidae). The focus of the following discussion is on those clades with robust bootstrap values. A monophyletic Mysticeti is highly supported (100%) and diagnosed by seven unequivocal synapomorphies: 5 (0 ≥ 1) lateral margin of maxillae thin, 17 (2 ≥ 1) descending process of maxilla present, 44 (0 ≥ 1) posterior portion of vomer exposed on basicranium and

Table III. Bootstrap, Partitioned Branch Support, and Bremer Support[a]

Node	Bootstrap	Bremer support	Partitioned branch support				
			cytb	ND4	ND4L	α-lac	Morph
1	99	6	0	0	0	0	6
2	99	9	0	0	0	0	9
3	94	6	0	0	0	0	6
4	92	5	0	0	0	0	5
5	76	2	0	0	0	0	2
6	<50	2	0	0	0	0	2
7	<50	1	0	0	0	0	1
8	<50	1	0	0	0	0	1
9	63	4	0.01	−10	−6.99	3	17.97
10	100	19	0	0	0	0	19
11	89	6	0	0	0	0	6
12	55	2	0	0	0	0	2
13	57	2	0	0	0	0	2
14	<50	2	−0.72	−0.48	−0.48	0.72	2.96
15	<50	1	0	0	0	0	1
16	<50	1	−0.08	0	0.04	0	1.04
17	<50	1	0	0	0	0	1
18	<50	1	0	0	0	0	0
19	<50	1	0	0	0	0	1
20	81	1	0	0	0	0	1
21	<50	1	0	0	0	0	1
22	<50	1	0	0	0	0	1
23	<50	1	0	0	0	0	1

[a]Support values are for combined data analyses excluding "*Balaenoptera*" *portisi*. Decimals rounded to the nearest hundredth.

covering basisphenoid/basioccipital suture, 45 (0 ≥ 1) basioccipital crest, 57 (0 ≥ 1) mandibular symphysis unfused with only a ligamental or connective tissue attachment, marked by anteriorposterior groove, 58 (0 ≥ 1) mandibular symphysis short with large boss dorsal to groove, and 61 (0 ≥ 1) dorsal aspect of mandible curved laterally.

The parsimony analysis of the morphological evidence alone strongly supported (99%) monophyly of the Balaenoidea (Balaenidae + Neobalaenidae). This clade is diagnosed by seven unequivocal synapomorphies: 35 (0 ≥ 1) squamosal, glenoid fossa, and zygomatic process depressed, 40 (0 ≥ 1) maxillary window of palate present and extending to posterior margin, 43 (0 ≥ 1) anterior margin of palatines W-shaped, 47 (0 ≥ 1) medial margin of tympanic bulla flattened dorsoventrally, 60 (1 ≥ 0) ventromedial groove present on mandible, 63 (0 = 1) mandibular condyle directed dorsally, and 67 (0 ≥ 1) cervical vertebrae fused.

A well-supported (88% morphology; 89% "total evidence") Balaenopteroidea includes the most recent common ancestor of Balaenopteridae and Eschrichtiidae and all its descendants but excludes Aetiocetidae, Eomysticetidae, Balaenidae, and Neobalaenidae. This clade is diagnosed by six synapomorphies: 9 (1 ≥ 3) nasals extremely broad, 33 (0 ≥ 1) squamosal fossa reduced to absent, 34 (0 ≥ 3) squamosal cleft present, contacts parietal, 54 (0 ≥ 1) petrosal endocranial surface angular and separated from ventral surface of elongated promontorium, 56 (1 ≥ 2) petrosal with circular endocranial opening of facial nerve, and 62 (0 ≥ 1) mandibular foramen small.

Two additional clades received less support the Balaenopteridae and the Eschrichtiidae. The Balaenopteridae are united by three unequivocal synapomorphies: 73 (1 ≥ 3) ventral grooves extend as far posterior as the umbilicus, 74 (0 ≥ 1) ventral throat pouch present, and 78 (0 ≥ 1) frontomandibular stay present. A monophyletic Eschrichtiidae includes the extant *Eschrichtius robustus* and the extinct taxa "*Balaenoptera*" *gastaldi* and SDSNH 95017. This clade is diagnosed by four unequivocal synapomorphies: 58 (1 ≥ 2) mandibular symphysis short with large boss dorsal to groove, 63 (0 ≥ 2) mandibular condyle directed posterodorsally, 72 (1 ≥ 3) dorsal humps present, and 75 (2 ≥ 1) baleen plates few and thick. The inclusion of "*Balaenoptera*" *gastaldi* and SDSNH 95017 within the Eschrichtiidae extends the fossil record of the family back to the late Pliocene. Previously, eschrichtiids had only been known from the late Pleistocene (Barnes and McLeod, 1984).

The addition of new morphological data corroborates most previous cladistically based morphological hypotheses in supporting a monophyletic Balaenoidea, Balaenopteroidea, and a basal position for "cetotheres" among all modern mysticetes (Geisler and Sanders, 2003). This result is also supported by total evidence analyses reported in this study. Recent molecular analyses of extant taxa (Rychel *et al.*, 2004) differ only in positioning *Caperea* as closer to the balaenopteroids than to balaenids. Evidence also suggests a monophyletic Balaenopteridae and Eschrichtiidae, but this is not well-supported. Taxonomic relationships within balaenopterids are hindered by a lack of resolution. Future work should be directed toward clarifying the taxonomic status and evolutionary relationships among balaenopterid species (e.g., *B. brydei-edeni-borealis-omurai* complex). Work in progress includes the description of new fossil balaenopteroids and their incorporation into phylogenetic analysis, expansion and refinement of the morphological character matrix, and addition of nuclear genes to the molecular dataset (Gatesy, unpublished). Only then will a broader, more inclusive phylogenetic hypothesis of extinct and extant mysticetes be available.

APPENDIX 1. SPECIMENS AND REFERENCES

The following specimens and/or published literature were used to code three odontocete and 21 mysticete taxa for 85 morphological characters. Fossil balaenopterids are listed in text. For institutional abbreviations see Materials and Methods section.

Odontoceti
  Physeter macrocephalus, Flower, 1869
  Tasmacetus shepardi, USNM 484878
  Agorophius sp., ChM 4256, 5852
Mysticeti
  Aetiocetus weltoni, UCMP 122900
  Eomysticetus whitmorei, ChM PV 4253
  Diorocetus hiatus, USNM 16783, 23494
  Cetotherium rathkii, Brandt, 1873
  Aglaocetus patulus, USNM 23690
  Cophocetus oregonensis, Packard and Kellogg, 1934
  Isanacetus laticephalus, Kimura and Ozawa, 2002
  Mixocetus elysius, LACM 882
  Parietobalaena palmeri, USNM 10668, 10677, 16119, 12697
  Pelocetus calvertensis, USNM 11976

Balaena mysticetus, LACM 55479, 55475
Balaenoptera acutorostrata, LACM 54598, USNM 571236, MSNT 260
Balaenoptera borealis, USNM 504244
Balaenoptera edeni, LACM 84024, MSNT 250
Balaenoptera musculus, LACM 72562
Balaenoptera physalus, MSNT 251, LACM 80620
Eubalaena glacialis, LACM 57763, MSNT 303, LACM 86020
Megaptera novaeangliae, LACM 72562, MSNT 263
Eschrichtius robustus, LACM 86047, 84190
SDSNH 90517
Caperea marginata, USNM 550146, IRSN 1536,

APPENDIX 2. MORPHOLOGICAL CHARACTER LIST

Cranial Characters

1. *Rostral curvature in lateral aspect.*
0 = straight or slightly upturned, 1 = arched slightly dorsoventrally, 2 = arched
  moderately dorsoventrally, 3 = arched extremely dorsoventrally (Barnes and McLeod,
  1984; Jefferson *et al.*, 1993; Messenger and McGuire, 1998).
2. *Rostral transverse width relative to CBL.*
0 = narrow (15–22%), 1 = very narrow (5–12%), 2 = broad (24–31%), and 3 = very
  broad (>31%) (Uhen, 1999).
3. *Rostral length relative to CBL.*
0 = less than 60% of CBL, 1 = greater than 60% of CBL (Gingerich *et al.*, 1995).
4. *Transverse slope of maxilla at midpoint.*
0 = vertical (90°), 1 = flat (0° to 10–20°), 2 = sloped (20–35°), 3 = steep (>45°).
5. *Lateral margins of maxillae.*
0 = thick, 1 = thin (Barnes, 1990; McLeod *et al.*, 1993).
6. *Premaxillary-maxillary suture.*
0 = fused dorsally along midline, 1 = no fusion (Geisler and Sanders, 2003).
7. *Position of narial fossa on rostrum.*
0 = well anterior to antorbital notch, 1 = at or behind antorbital notch, 2 = well posterior
  to antorbital notch.
8. *Nasals, length.*
0 = long (17–25% of CBL), 1 = moderate (10–16%), 2 = short (5–10%) (McLeod *et al.*,
  1993).
9. *Nasals, width.*
0 = slender (15–25% of length), 1 = broad; (26–45%), 2 = very broad (46–70%), 3 =
  extremely broad (>71%).
10. *Nasals, anterior margin.*
0 = U- or V-shaped (posteriorly directed), 1 = straight, 2 = V-shaped (anteriorly directed)
11. *Nasals, posterior margin.*
0 = frontals extend into nasals (W-shaped), 1 = frontals extend into nasals
  (finger-shaped), 2 = frontals extend into nasals (U-shaped), 3 = straight or nearly
  straight margin, 4 = nasals extend into frontals (M-shaped), 5 = frontals extend into
  nasals (U or V shaped).

12. *Nasals, dorsal surface*.

0 = flattened, 1 = keeled medially entire length, 2 = keeled medially anterior half

13. *Nasals, position of posteriormost margin*.

0 = anterior to SOPF, 1 = anterior half of SOPF, 2 = posterior half of SOPF, 3 = zygomatic process, 4 = posterior temporal fossa.

14. *Premaxillary, posterior process*.

0 = no contact with frontals, 1 = contacting frontals, 2 = contacting frontal and forming robust ascending process (Miller, 1923).

15. *Posteriormost end of ascending process of premaxilla*.

0 = anterior to SOPF, 1 = anterior border of SOPF, 2 = posterior border of SOPF, 3 = zygomatic process, 4 = posterior temporal fossa (Geisler and Sanders, 2003).

16. *Posteriormost edge of the ascending process of maxilla*.

0 = anterior to SOPF, 1 = anterior border of SOPF, 2 = posterior border of SOPF, 3 = zygomatic process, 4 = posterior temporal fossa.

17. *Descending process of maxilla*.

0 = present, 1 = present as infrorbital plate, 2 = absent (modified from McLeod *et al*., 1993).

18. *Maxilla/frontal suture*.

0 = abutting, 1 = overriding anteromedial corner of supraorbital process without pocket, 2 = overriding anteromedial corner of supraorbital process with pocket, 3 = overriding entire supraorbital process as broad plate.

19. *Ascending process of maxilla*.

0 = bluntly triangular posteromedial corner of maxilla, 1 = broad and finger-like, exposed dorsally, 2 = narrow and finger-like, exposed laterally, 3 = small overlap or 90° corner between medial and posterior maxillary margins, 4 = broadly elongate, 5 = maxilla broadly covers frontal.

20. *Maxilla, posteromedial corner*.

0 = contacts nasal, 1 = contacts frontal, 2 = contacts premaxilla (Uhen and Gingerich, 2001).

21. *Lachrymal*.

0 = exposed dorsally, 1 = covered by frontal.

22. *Ascending process of maxilla/anterior wing of parietals*.

0 = separate, 1 = touching or nearly touching, 2 = short overlap, 3 = long overlap, 4 = overlying.

23. *Frontal, postorbital process*.

0 = well separated from zygomatic process, 1 = touching or nearly touching zygomatic process, (Fordyce, 1984; Barnes, 1990; McLeod *et al*., 1993; Uhen, 1998; Kimura and Ozawa, 2002).

24. *Frontal, supraorbital processes*.

0 = broad anteroposteriorly and short transversely, 1 = moderately broad anteroposteriorly and moderately elongate transversely, 2 = very narrow anteroposteriorly and very elongate transversely (Miller, 1923).

25. *Frontal, supraorbital processes*.

0 = at level of vertex, 1 = gradually sloping from vertex, 2 = abruptly depressed below vertex (Miller, 1923).

26. *Frontal, exposure on cranial vertex.*
0 = long exposure, 1 = narrow exposure, 2 = very narrow exposure (Lindow, 2002).
27. *Parietal, exposure on cranial vertex.*
0 = long, 1 = short, 2 = parietal excluded (Fordyce, 1984).
28. *Parietal/frontal, interorbital region.*
0 = both large (parietal = frontal), 1 = parietal>frontal, 2 = frontal>parietal, 3 = both reduced.
29. *Occipital shield, position of apex.*
0 = posterior to temporal fossa, 1 = to posterior half of temporal fossa, 2 = to anterior half of temporal fossa, 3 = to orbit, 4 = anterior to orbit.
30. *Occipital shield, anterior margin.*
0 = rounded, 1 = sharply triangular, 2 = bluntly triangular, 3 = broad with straight margins.
31. *Occipital shield, lateral margins.*
0 = convex, 1 = straight, 2 = concave.
32. *Squamosal, zygomatic process.*
0 = parallel, 1 = divergent.
33. *Squamosal fossa.*
0 = large and well developed, 1 = reduced to absent.
34. *Squamosal cleft.*
0 = absent, 1 = present, contacts pterygoid, 2 = present, contacts alisphenoid, 3 = present, contacts parietal.
35. *Squamosal, glenoid fossa and zygomatic process.*
0 = elevated, 1 = depressed (McLeod *et al*., 1993; Messenger and McGuire, 1998).
36. *Squamosal, posterior width.*
0 = intermediate, 1 = wide, 2 = very wide.
37. *Pterygoid and squamosal, continuous exposure*
0 = yes, 1 = no.
38. *Foramen pseudo-ovale, construction.*
0 = squamosal only, 1 = squamosal and pterygoid, 2 = pterygoid only.
39. *Palate, shape.*
0 = flat with no median keel, 1 = median keel dividing palate into right and left concave longitudinal "troughs," (modified from McLeod *et al*., 1993; Messenger and McGuire, 1998).
40. *Palate, maxillary window.*
0 = maxillary window in infraorbital plate absent, 1 = maxillary window present and extending to posterior margin, 2 = maxillary window present and not reaching posterior margin.
41. *Palate, vascularization.*
0 = few palatal foramina, 1 = numerous large foramina opening laterally and anterolaterally into long sulci.
42. *Palatines, extension.*
0 = to internal nares, 1 = short overlap of pterygoids, 2 = long overlap of pterygoids nearly reaching pterygoid fossa.
43. *Palatines, anterior margin.*
0 = blunt or U-shaped, 1 = W-shaped.

44. *Vomer, posterior portion.*

0 = not exposed, 1 = exposed on basicranium and covering basisphenoid/basioccipital suture (Barnes, 1990; McLeod *et al.*, 1993; Messenger and McGuire, 1998).

45. *Basioccipital crests.*

0 = narrow transversely, 1 = wide and delicate, 2 = wide and bulbous (modified from Lindow, 2002).

46. *Paroccipital process, skull in ventral view.*

0 = posterior to occipital condyles, 1 = in line with condyles, 2 = well anterior to condyles (Geisler and Sanders, 2003).

47. *Tympanic bulla, medial margin.*

0 = rounded/inflated dorsoventrally, 1 = flattened dorsoventrally.

48. *Tympanic bulla, shape.*

0 = narrow and long, 1 = wide (Geisler and Sanders, 2003, #251)

49. *Tympanic bulla, median furrow.*

0 = absent, 1 = notch, 2 = broad furrow. (Muizon, 1987; Fordyce, 1994; O'Leary and Geisler, 1999; Geisler and Sanders, 2003, #266).

50. *Petrosal, transverse elongation of pars cochlearis.*

0 = absent, 1 = present (Geisler and Luo, 1996, #12).

51. *Petrosal, lateral projection of anterior process.*

0 = absent, 1 = present, 2 = present and robust, 3 = present and hypertrophied (Geisler and Luo, 1996; Geisler and Sanders, 2002).

52. *Petrosal, groove for tensor tympani muscle*

0 = enlarged fossa, 1 = groove, 2 = groove absent or poorly developed. (Geisler and Luo, 1996; Geisler and Sanders, 2002)

53. *Petrosal, promontorial groove on medial side of pars cochlearis.*

0 = absent, 1 = present (Geisler and Luo, 1996).

54. *Petrosal, endocranial surface.*

0 = rounded and continuous with ventral surface of rounded promontorium, 1 = angular and separated from ventral surface of elongated promontorium.

55. *Petrosal, perilymphatic foramen.*

0 = confluent with fenestra rotunda, 1 = narrowly separated from fenestra rotunda, 2 = widely separated from fenestra rotunda, 3 = very widely separated from fenestra rotunda (Geisler and Luo, 1996; Geisler and Sanders, 2002).

56. *Petrosal, endocranial opening of facial nerve.*

0 = with anterior fissure, 1 = oval-shaped, 2 = circular (Geisler and Luo, 1996; Kimura and Ozawa, 2002; Geisler and Sanders, 2002)

57. *Mandible, mandibular symphysis.*

0 = bony/fused, 1 = unfused with only a ligamental or connective tissue attachment, marked by anteriorposterior groove (Barnes, 1990; McLeod *et al.*, 1993; Messenger and McGuire, 1998).

58. *Mandible, mandibular symphysis.*

0 = long with fusion, 1 = long with smooth surface dorsal to groove, 2 = short with large boss dorsal to groove.

59. *Mandible, neck (dorsal aspect).*

0 = concave laterally, 1 = sinuous neck straight relative to horizontal ramus, 2 = laterally convex without reflexed neck, 3 = laterally convex with reflexed neck

60. *Mandible, ventromedial groove.*
0 = present, 1 = absent.
61. *Mandible, dorsal aspect.*
0 = straight, 1 = medially curved, 2 = laterally curved (Barnes and McLeod, 1984; Deméré, 1986)
62. *Mandible, mandibular foramen.*
0 = large, 1 = small (modified from Barnes, 1990; McLeod *et al.*, 1993).
63. *Mandible, mandibular condyle.*
0 = directed posteriorly, 1 = directed dorsally, 2 = directed posteroventrally (McLeod *et al.*, 1993; Messenger and McGuire, 1998).
64. *Mandible, coronoid ridge/process.*
0 = large and spatulate, 1 = finger-like and laterally deflected, 2 = reduced to coronoid crest, 3 = reduced to knob and low crest (Barnes and McLeod, 1984; McLeod *et al.*, 1993).

Dental Characters

65. *P1, number of roots.*
0 = one or more, 1 = teeth absent (Uhen, 1999).
66. *Upper molars, crowns.*
0 = multicusped, 1 = conical, 2 = teeth absent.

Postcranial Characters

67. *Vertebrae, cervical.*
0 = unfused, 1 = fused (Barnes and McLeod, 1984).
68. *Scapula, acromion process.*
0 = large, 1 = reduced or absent (modified from Barnes and McLeod, 1984).
69. *Scapula, coracoid process.*
0 = present, 1 = absent (Miller, 1923; Muizon, 1987).
70. *Humerus-radius length ratio.*
0 = humerus equal or longer than radius, 1 = humerus 50–75% of length of radius, 2 = humerus < 40% of length of radius (modified Barnes and McLeod, 1984; Kimura and Ozawa, 2002).
71. *Manus, number of digits.*
0 = 5 digits, 1 = 4 digits. (Barnes and McLeod, 1984, Messenger and McGuire, 1998).

Soft Tissue Characters

72. *Dorsal fin.*
0 = absent, 1 = present, prominent, 2 = present, small, 3 = dorsal humps
73. *Ventral grooves.*
0 = absent, 1 = few, confined to throat, 2 = numerous and terminate midbody, 3 = numerous and extend to or posterior to umbilicus (modified from Barnes and McLeod, 1984).
74. *Ventral throat pouch.*
0 = absent, 1 = present.

75. *Baleen plates.*
0 = absent, 1 = few and thick (130–160), 2 = few and thin (200), 3 = numerous and thin (250/260) (modified from Miller, 1923; Heyning, 1997)

76. *Baleen, right and left racks.*
0 = meet at midline, 1 = separated by anterior cleft

77. *Baleen fringes.*
0 = absent, 1 = stiff, 2 = fine.

78. *Frontomandibular stay.*
0 = absent, 1 = present.

79. *Tongue.*
0 = muscle, 1 = connective tissue (Sanderson and Wassersug, 1993).

80. *Pigmentation of jaws/flippers.*
0 = absent, 1 = present.

81. *White band on flippers.*
0 = absent, 1 = present

82. *Asymmetric pigmentation.*
0 = absent, 1 = present on baleen only, 2 = present on baleen and head

83. *Body size (skull length:skeleton (body) length).*
0 = large, 1 = small, 2 = very large

84. *Tubercles/Callosities on rostrum/body.*
0 = no, 1 = yes, tubercles, 2 = yes, callosities

85. *Longitudinal ridges on rostrum.*
0 = absent or indistinct, 1 = one, median, 2 = three, lateral

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