# THE EARLIEST KNOWN MEMBER OF THE RORQUAL—GRAY WHALE CLADE (MAMMALIA, CETACEA)

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ABSTRACT—*Eobalaenoptera harrisoni*, gen. et sp. nov., is described from a partial skeleton collected from the middle Miocene Calvert Formation of Virginia. Characteristics of this taxon, particularly of the petrosal, indicate that the new whale is a member of the clade that includes the Balaenopteridae (rorquals) and Eschrichtidae (gray whales) to the exclusion of "cetotheres" and the Balaenidae (right whales). Some of the probable synapomorphies of this clade include an elongate pars cochlearis, a tubular internal auditory meatus, the greater petrosal nerve foramen on the tympanic side of the petrosal, the stylomastoid fossa extending onto the posterior process of the petrosal, no medial groove on the pars cochlearis, four digits on each forelimb, depressed supraorbital processes, and ascending processes of maxillae extending onto the vertex. The approximate 14-million-year age of the specimen makes it the oldest known member of the clade by some 3 to 5 million years, and extends the fossil record of this clade closer to the divergence time estimated by some recent molecular studies.

#### INTRODUCTION

The Miocene (23-5 Ma) witnessed the emergence of extant families of mysticetes (baleen whales) and the decline of the archaic "cetotheres," a diverse group of extinct mysticetes (Fordyce and Barnes, 1994; Gottfried et al., 1994; Whitmore, 1994; Messenger and McGuire, 1998) that are almost certainly paraphyletic (Gottfried et al., 1994; Geisler and Luo, 1996). Mysticetes attained their greatest diversity during the Miocene, with over 20 recognized genera in comparison to only six living genera. This dramatic turnover of cetacean faunas (Fordyce, 1980, 1992; Fordyce and Barnes, 1994; Gottfried et al., 1994; Whitmore, 1994; Geisler and Luo, 1996) is thought to be correlated with major changes in ocean currents and sea temperatures (Fordyce, 1980, 1992; Whitmore, 1994). The assessment of this faunal turnover requires an accurate determination of the timing of the first appearance of major living clades, and a rigorous phylogeny of the relevant taxa.

It is widely agreed that the modern families of mysticetes originated some time during the Oligocene or Miocene, but their relationships to more primitive mysticetes and the timing of their earliest diversification are unclear. The relationship of the Eschrichtiidae to other extant mysticetes is controversial. Traditionally, the Eschrichtiidae was regarded as the most primitive family of modern mysticetes (Barnes and McLeod, 1984). A later study (McLeod et al., 1993), focusing on cranial characters, suggested a close relationship of Eschrichtiidae and Balaenidae. On the basis of petrosal characters, Geisler and Luo (1996) and Kimura and Ozawa (2002) suggested that Eschrichtiidae is closer to Balaenopteridae than to Balaenidae. Several molecular studies (Milinkovitch, Ortí, and Meyer, 1993; Milinkovitch, Meyer, and Ortí, 1994; Árnason and Gullberg, 1994; Gatesy, 1998; Messenger and McGuire, 1998) indicated that Eschrichtius falls within the Balaenopteridae.

A variety of divergence times for extant mysticete clades have also been suggested. Some molecular studies (e.g., Milinkovitch, Ortí, and Meyer, 1993; Milinkovitch, Meyer, and Ortí, 1994) have indicated that the Balaenopteridae and sperm whales diverged as recently as 10 Ma, while others (Nikaido et al., 2001; Cassens et al., 2000) suggested that the modern balaenopterid species were already distinct 15–20 Ma. The fossil record has not thus far been able to resolve this issue. The mysticetes have a long fossil record extending back to the Oligocene (thus ruling out a 10 Ma divergence time), but the age of the oldest known balaenopterid, "*Megaptera*" *miocaena* (Kellogg, 1922) is a little unclear. While some authorities (Fordyce and Barnes, 1994; Whitmore, 1994), consider it to be 10 to 12 million years old, Repenning and Tedford (1977:24) imply that the age of this specimen may be only 9 to 10 Ma. Here we report on a new fossil mysticete from the Miocene of Virginia that provides strong support for a clade comprising Eschrichtiidae and Balaenopteridae, consistent with at least one recently proposed molecular phylogeny (Cassens et al., 2000). The 14-million-year age of this new mysticete is definitely older than "*M*." *miocaena*.

The new mysticete was collected from the Carmel Church Quarry, Ruther Glen, Virginia, near the western margin of the western Atlantic Coastal Plain. Here five distinct Tertiary beds are found in a 10 m-thick section (Fig. 1). Molds of invertebrate fossils found in the uppermost unit indicate that it correlates with the late Miocene Eastover Formation (Ward, 1992; Marr and Ward, 1993). Immediately below the Eastover is a bluegray silty clay, containing some vertebrate remains. Lithologically, this unit is consistent with bed 19 of the Choptank Formation as described in Ward (1984, 1992). Below this is an olive-colored, clayey silt. This lithology is typical of beds 10-16 of the upper part of the Calvert Formation, and is not seen in other units along the Virginia Coastal Plain (Ward, 1992). At the base of this bed is a coarse conglomerate in intimate association with an extremely rich bonebed. Andrews (1985) reported the following diatoms from this unit: Actinoptychus marylandicus, Actinoptychus virginicus, Delphineis biseriata, Delphineis novaecaesaraea, Rhaphoneis amphiceros, Rhaphoneis lancettula, and Rhaphoneis scutula. These diatoms correlate with East Coast Diatom Zone (ECDZ) 6 of Andrews (1988), equivalent to beds 14-16 of the Calvert Formation together with beds 17-18 of the Choptank Formation. ECDZ 6 is considered to be middle Serravalian, 13 to 14 Ma (Andrews, 1988). The lithology of this unit is consistent with beds 14-16 of the Calvert Formation rather than with beds 17-18.

Underlying the conglomerate is a green, glauconitic sand containing occasional shark teeth. Lithologically, this is similar to the early Eocene Nanjemoy Formation. The unconformable Nanjemoy-Calvert contact is the typical relationship observed between these units in the western part of the Virginia Coastal Plain (Ward, 1992).



FIGURE 1. **A**, Map of Virginia showing the location of the Carmel Church Quarry. **B**, Stratigraphic section of the Tertiary beds at the Carmel Church Quarry (adapted from Marr and Ward, 1993).

Underlying the Nanjemoy is a fine-grained sand which appears to correlate with the Paleocene Aquia Formation.

The bonebed produces fossils of a large number of cetaceans (e.g., *Diorocetus, Hadrodelphis*), sharks (e.g., *Odontaspis, Carcharias, Carcharhinus, Isurus, Galeocerdo, Hemipristis, Notorynchus*) and bony fish (e.g., *Mola, Tautoga, Pogonias*), as well as sirenians (*Metaxytherium*?), seals, crocodilians (*Thecachampsa*), turtles (*Syllomus*), birds, and land mammals (horse, peccary) (Dooley, 1993; Fraser and Dooley, 2000). Among the cetaceans recovered are remains of at least three taxa of baleen

whales, the cetothere-grade *Diorocetus hiatus* and? *Aglaocetus* sp., and the new taxon described here.

# MATERIALS AND METHODS

The holotype of the new taxon described here consists of a partially articulated skeleton that was recovered with its ventral side facing uppermost, and comprises the back part of the skull, including parts of the petrosals and tympanic bullae, the first 28 vertebrae, some ribs and the majority of both forelimbs. This new taxon was compared to specimens of Diorocetus hiatus and "Mesocetus" siphunculus housed in the collections of the Virginia Museum of Natural History, as well as to specimens of Parietobalaena palmeri, Diorocetus hiatus, Pelocetus calvertensis, Herpetocetus sp., "Megaptera" miocaena and "Mesocetus" siphunculus housed in the United States National Museum of Natural History (Smithsonian Institution), and to modern specimens of Balaenoptera, Megaptera, Eschrichtius, and Eubalaena. Comparisons were also made to published photographs and descriptions of Thinocetus arthritus, Isanacetus laticephalus, and Parabalaenoptera baulinensis, as well as the taxa listed above. Uses of published measurements of particular specimens are cited individually. Petrosal terminology follows Geisler and Luo (1996), while tympanic bulla terminology follows Oishi and Hasegawa (1994).

**Institutional Abbreviations**—**VMNH**, Virginia Museum of Natural History, Martinsville; **USNM**, National Museum of Natural History, Smithsonian Institution.

Anatomical Abbreviations—aes, anteroexternal sulcus; ap, anterior process; aplp, lateral projection of anterior process; apmp, medial projection of the anterior process; app, pedicle of the anterior process; apvf, ventral facet of anterior process; bo, basioccipital; Ce, cervical vertebra; ctpp, caudal tympanic process of petrosal; dpp, dorsal posterior prominence of the tympanic bulla; elf, endolymphatic foramen; eo, exoccipital; fm, fossa for head of malleus; fom, foramen magnum, fr, fenestra rotunda; fst, fossa for stapedial muscle; fv, fenestra vestibuli; gl, glenoid fossa; gtt, groove for tensor tympani; het, hiatus epitympanicus; Hu, humerus; iam(vii), internal auditory meatus canal for facial nerve; iam(viii), internal auditory meatus canal for cochlear nerve; L, lumbar vertebrae, mx, maxilla; npp, neck of posterior process; oc, occipital condyle; pal, palatine; pmx, premaxilla; pp, posterior process; ppp, pedicle on posterior process of petrosal; pr, promontorium; pt, pterygoid; Ra, radius ; sm, stylomastoid notch (for hyomandibular branch of VII); soc, suproorbital process; sq, squamosal; sqflg, squamosal flange of posterior process; stfo, stylomastoid fossa; T, thoracic vertebra; **ttsp**, tegmen tympani (=superior process); **v**, vomer; vii, facial nerve canal; vk, ventral keel of the tympanic bulla; zg, zygomatic process of the squamosal.

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758 Order CETACEA Brisson, 1762 Suborder MYSTICETI, Gray, 1864 Family? BALAENOPTERIDAE Lacépède, 1804 *EOBALAENOPTERA*, gen. nov.

**Type and Only Known Species**—*Eobalaenoptera harrisoni*, sp. nov.

**Diagnosis**—As for the type species.

**Etymology**—*Eobalaenoptera* is derived from the Greek, eos, meaning dawn together with *Balaenoptera* (from the Latin balaena, whale, and Greek pteron, wing or fin), and is a reference to the early appearance of the new taxon in the clade that includes Balaenopteridae.



FIGURE 2. A, reconstruction of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742). Shaded areas represent recovered elements. **B**, schematic reconstruction of a "cetothere" skull, ventral view, to show the orientation of the petrosal, after Geisler and Luo, 1996. For abbreviations, see text.

#### EOBALAENOPTERA HARRISONI, sp. nov.

**Holotype**—VMNH 742; partial skeleton comprised of skull fragments, including most of the supraoccipital, with the basioccipital, occipital condyles, and portions of the squamosals, portions of both petrosals, a portion of the right tympanic bulla, the first 28 vertebrae in articulation, part of the glenoid region of one scapula, both forelimbs proximal to the phalanges, and numerous rib fragments (Fig. 2A); collected in 1991 and 1992.

**Referred Specimen**—VMNH 3483, an isolated left tympanic bulla, Carmel Church Quarry; collected by A. Dooley in 1992.

Locality and Horizon—The Martin Marietta Carmel Church Quarry (Dooley, 1993), Caroline County, Virginia, USA; Calvert Formation, middle Miocene (Serravalian). Based on paleontological and lithological data, the Calvert at this locality is correlated with beds 14–16 of the Calvert Formation elsewhere (Ward, 1992; Gottfried et al., 1994), yielding an age of approximately 14 Ma (Andrews, 1985; Ward, 1992; Marr and Ward, 1993).

**Diagnosis**—A mysticete that differs from all known "cetotheres" in having the following characters: pars cochlearis transversely elongate with a tubular internal auditory meatus; greater

petrosal nerve foramen on tympanic side of pars cochlearis; stylomastoid fossa extending onto posterior process, and no medial groove on pars cochlearis; long lateral projection of the anterior process, directed anterolaterally; cervical vertebrae contribute less than 11% of the length of the pre-caudal vertebral column; capitulum and tuberculum on first rib joined by a bony lamina. It differs from all Balaenopteridae and Eschrichtiidae in exhibiting the following: posterior process of the petrosal massive, elongate and tapering distally; dorsoventrally deep tegmen tympani; lateral process projection of the anterior process of the petrosal directed anterolaterally; tympanic bulla small. It shares with *Megaptera* and *Isanacetus* a tympanic bulla with a swollen dorsal posterior prominence and a pronounced keel.

**Etymology**—*harrisoni* honors Mr. Carter Harrison, whose volunteer work and contributions have been a great support to the ongoing excavations at the Carmel Church Quarry.

## DESCRIPTION

Relatively little of the skull of *Eobalaenoptera* is preserved, but a major part of the occipital region is present, including the petrosal and tympanic bulla. The supraoccipital is very rugose, with



FIGURE 3. Left petrosal of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742), **A**, dorsal. **B**, anteromedial. **C**, anterior. **D**, ventral. **E**, posterolateral and **F**, posteroventral views. Area A represents the broken surface of the spongy bone posterior to the "crater" of the internal acoustic meatus. For other abbreviations, see text.



prominent lambdoidal crests. A longitudinal ridge was apparently present, but as the bone is broken along the midline, this cannot vertice confirmed. The occipital condyles are prominent and the foramen magnum is nearly circular. Invertebrate borings on the broken surfaces of the exoccipitals and supraoccipital indicate that the

skull became disarticulated before complete burial. The petrosal (Figs. 2B, 3) has a broad, flat external (tympanic) surface of the tegmen tympani that has a partially compressed anterior process. The opening for the greater petrosal nerve is situated on the tympanic side of the bone. There is no medial groove of the pars cochlearis, and the stylomastoid fossa extends onto the posterior surface. Some incipient development of pachyostosis (hypertrophy of spongy bone) is clearly apparent on the cranial side of the pars cochlearis as indicated by a porous and eroded area. But the most distinctive feature is the elevated ('volcano-like') rim for the acousto-vestibular (VIII) nerves (Fig. 4), coupled with the position of the primary facial foramen (entry of VII into the par cochlearis) outside this elevated rim. There is a prominent lateral projection of the anterior process, which is directed anterolaterally. The posterior process of the petrosal is not expanded distally.

The tympanic bulla (Fig. 5) of *Eobalaenoptera* has a swollen dorsal posterior prominence, similar to that of *Megaptera* and *Isanacetus* (Oishi and Haseagwa, 1994; Kimura and Ozawa, 2002) (Fig. 5). A distinct keel on the ventral surface extends from the anteromedial corner to the posterolateral edge.

The postcranial skeleton is well preserved anterior to the caudal region. The length of the precaudal vertebral series is approximately 3 m. The epiphyses are entirely fused to the centra throughout the length of the column, indicating a fairly mature individual. In situ, the specimen was preserved ventral side uppermost and, apparently as a consequence, many of the neural arches are crushed or even completely broken off. Some of the vertebrae exhibit deep excavations, almost certainly the result of invertebrate borings after the skeleton came to rest on the bottom of the sea floor. Scratches caused by sharks biting into the carcass are common on the surfaces of the vertebrae and ribs.

The cervical series of *Eobalaenoptera* is short relative to the length of the precaudal vertebrae. There is no fusion of the cervical vertebrae. The cervicals make up less than 11 percent of the preserved pre-caudal vertebral column length and possibly even less than 10 percent. Because no caudal vertebrae have been preserved it is conceivable that additional lumbars are missing. Indeed this seems likely in view of the relatively low number of lumbars (nine). The axis and atlas (Fig. 6) are both rather massive elements, and the transverse processes on the atlas are particularly prominent.

Most of the ribs were draped over the conglomerate, badly crushed and broken, and few were complete. The first rib in *Eobalaenoptera* (Fig. 7A) has the capitulum and tuberculum joined by a bony lamina, so that the proximal end of the rib is triangular in outline. This feature, although common in modern mysticetes, has not been reported in any Miocene "cetothere."

The proximal portion of the left scapula is preserved with part of the glenoid. Only the base of the coracoid process is present, but it appears to have been narrow with a sub-circular cross-section rather than being blade-like.

Large portions of both forelimbs are preserved (Fig. 8). The humerus is very similar to that of *Pelocetus calvertensis* in size and shape. As in *Pelocetus*, the humerus has a large, rugose radial tuberosity. The humerus is shorter relative to the radius, and the forelimb is shorter relative to the length of the body, than in *Pelocetus* (Table 1). Four digits were preserved on each forelimb.



FIGURE 5. Tympanic bullae. **A–B**, right tympanic bulla of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742), **A**, ventral, **B**, medial views. **C–D**, Left tympanic bulla referred to *Eobalaenoptera harrisoni*, gen. et sp. nov. (VMNH 3483), **C**, ventral, **D**, medial views.

## DISCUSSION

Eobalaenoptera is unusually large compared to the baleen whales previously described from the Calvert Formation, and shows significant differences from contemporaneous "cetothere" species, particularly in the ear region and postcranial skeletal proportions. Eobalaenoptera shares a number of features with modern rorquals, "Megaptera" miocaena, and the gray whale, with the petrosal in particular exhibiting some remarkably derived features. These include the loss of the medial groove of the pars cochlearis, a broad and flat external (tympanic) surface of the tegmen tympani, the stylomastoid fossa extending onto the posterior surface, a partially compressed anterior process of the tegmen tympani, and the opening for the greater petrosal nerve situated on the tympanic side of the bone. Perhaps the most significant feature is the volcano-like rim surrounding the internal acoustic meatus for the acousto-vestibular nerves, a feature that we consider unique to balaenopterids and eschrichtiids. Unlike the Miocene-Pliocene balaenids and "cetotheres," there is no shared depression or funnel for the facial nerve and the acoustovestibular nerves. The posterior process of the petrosal is not expanded distally, and this contrasts markedly with the condition in all described "cetotheres."

The characters listed above are also found in "Megaptera" miocaena. However, the petrosal of Eobalaenoptera clearly differs from that of "M." miocaena in the anterolateral orientation of the lateral projection of the anterior process, its unusual thickness, and its large size relative to the skull. While Kellogg (1922) considered the petrosal of "M." miocaena to be very similar to the modern Megaptera novaeangliae, we find the likeness to be no closer than between "M." miocaena and Ba-

*laenoptera*. Due to the absence of forelimb characters in "*M*." *miocaena*, together with the presence of a broader rostrum (also noted by Kellogg, 1922), we consider the referral of "*M*." *miocaena* to *Megaptera* to be unjustified. Further discussion of the systematic position of "*M*." *miocaena* is beyond the scope of the present paper and will be addressed in future studies.

The presence of a keel on the tympanic bulla of *Eobalaen*optera is another derived character. While it is less pronounced than in *Eschrichtius*, *Balaenoptera*, and *Megaptera*, it is similar to that described in *Isanacetus* (Kimura and Ozawa, 2002). Again, this contrasts with most "cetotheres," in which the keel is absent or very indistinct.

The tympanic bulla of *Eobalaenoptera* also possesses a pronounced dorsal posterior prominence, a feature shared with *Megaptera*, "*M*." *miocaena*, and *Isanacetus*, but not with other "cetotheres" (Kellogg, 1965, 1968a, b, 1969). The tympanic bulla is quite small compared to the petrosal; while the petrosal of *Eobalaenoptera* is larger than that of "*M*." *miocaena*, its tympanic bulla is much smaller.

In general terms, the skeleton of *Eobalaenoptera* is larger than those of "cetotheres." For example the length of the precaudal series of vertebrae is just over 3.0 m, which is considerably larger than *Pelocetus* (Kellogg, 1965) at 2.54 m, and also the younger, Choptank Formation "cetothere" *Thinocetus* at 2.76 m (Kellogg, 1969) (Table 1).

*Eobalaenoptera* has a relatively short neck that compares closely with that of modern rorquals. From the available material, the neck of *Eobalaenoptera* is certainly less than 11 percent of the length of the pre-caudal vertebral column length, and more likely closer to 10 percent. In the modern genus *Ba*-



FIGURE 6. A, B, atlas, and C, D, axis of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742). A and C, anterior and, B and D, posterior views.

*laenoptera*, the neck makes up 8–10 percent of the pre-caudal column, depending on species, while in *Eschrichtius* it is approximately 12 percent (Tomilin, 1957). By comparison, this value is 13 percent in *Pelocetus calvertensis* (USNM 11976; Kellogg, 1965) and *Thinocetus arthritus* (USNM 23794; Kellogg, 1969) and 14.6 percent in *Parietobalaena palmeri* (USNM 23203; Kellogg, 1968b).

The humerus of *Eobalaenoptera* is about the same size as in *Pelocetus*, making it shorter relative to the length of the vertebral column. However, the radius of *Eobalaenoptera* is longer than in either *Pelocetus* or *Thinocetus*, and consequently would have contributed more to the length of the flipper than would the humerus (Table 1).

# PHYLOGENETIC ANALYSIS

A phylogenetic analysis was performed on a data matrix of 42 characters from 18 different taxa (Appendices 1, 2). The taxa included two archaeocetes, five odontocetes, and ten mysticetes, in addition to *Eobalaenoptera*. Characters were chosen for this analysis to reveal the relationships of *Eobalaenoptera*, rather than to undertake a comprehensive analysis of all mysticetes. The analysis was performed using PAUP 4.0b10 (Swofford, 1998) using both the heuristic and branch-and-bound search options. All characters were unordered. Each analysis resulted in 21 equally parsimonious trees, each with 92 steps, a consistency index of 0.7283, and a retention index of 0.8596. The resulting strict consensus tree is shown in Figure 9.

Balaenopteridae and Eschrichtiidae share derived features of the petrosal relative to "cetotheres" and balaenids (Geisler and

Luo, 1996), and many of these are present in Eobalaenoptera (Figs. 2B, 3). These include: elongate pars cochlearis, tubular internal auditory meatus, greater petrosal nerve foramen on tympanic side, stylomastoid fossa extending onto posterior process, and no medial groove on the pars cochlearis. These synapomorphies support a clade composed of Balaenopteridae, Eschrichtiidae, Parabalaenoptera baulinensis, "Megaptera" miocaena and Eobalaenoptera harrisoni. This clade is nested within the paraphyletic "cetotheres" (Fig. 9), consistent with the view that balaenopterids had a "cetothere" ancestry (Barnes and McLeod, 1984). Our tree includes a diverse range of extinct and living taxa, and is consistent with the close relationship of Eschrichtius and Balaenopteridae, to the exclusion of Balaenidae, as previously indicated by morphologic studies (Kimura and Ozawa, 2002), cytochrome b DNA sequences (Árnason and Gullberg, 1994), mitochondrial ribosomal DNA studies (Milinkovitch, Meyer, and Ortí, 1994), and by the latest analyses combining all molecular data (Messenger and McGuire, 1998; Gatesy, 1998).

*Parabalaenoptera baulinensis*, from the late Miocene of California, appears to be closely related to the balaenopterids based on a variety of skull characters (Zeigler et al., 1997). Unfortunately, the petrosal of *Parabalaenoptera* has not been described, making a direct comparison to *Eobalaenoptera* difficult.

The strict consensus cladogram (Fig. 9) indicates an unresolved node comprising *Balaenoptera* + *Megaptera*, *Eschrichtius*, *Parabalaenoptera*, "*Megaptera*" *miocaena*, and *Eobalaenoptera*. Certain synapomorphies of this clade, in particular the depression of the frontals and the presence of posterior max-



FIGURE 7. Partial first and second right ribs of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742). **A**, first rib, and **B**, second rib.

illary processes, are not preserved in *Eobalaenoptera*. Nevertheless, at least one character, the shortened cervical vertebrae relative to the precaudal series, suggests that *Eobalaenoptera* is closer to the balaenopterids than to *Eschrichtius*. The cervicals of *Eobalaenoptera* are relatively shorter than those of *Eschrichtius*, but are similar in relative length to those in *Balaenoptera acutorostrata*, and is the reason for our tentative referral of *Eobalaenoptera* to the Balaenopteridae. The vertebral columns for *Parabalaenoptera* and "*Megaptera*" miocaena are imperfectly known, and therefore we cannot comment on the proportional length of their cervical series.

The placement of *Eobalaenoptera* in a clade that includes eschrichtiids and balaenopterids extends the minimal timing of the first appearance of these groups. Some previous molecular studies suggest that the Balaenopteridae diverged from sperm whales as recently as 10 Ma based on ungulate molecular divergence rates (Milinkovitch, Ortí, and Meyer, 1993; Milinkovitch, Meyer, and Ortí, 1994), (but see Geisler and Luo, 1996, and Messenger and McGuire, 1998). The very short fossil record for the Eschrichtiidae, about 100,000 years (Barnes and McLeod, 1984; Fordyce and Barnes, 1994), and the relatively short fossil record of the Balaenopteridae (certainly not more than 12 Ma, (Fordyce and Barnes, 1994; Whitmore, 1994), and probably only 9 to 10 Ma (Repenning and Tedford, 1977) has led to continued support for this view (Li, 1997). More recent molecular studies (Nikaido et al., 2001; Cassens et al., 2000) have indicated a much older divergence time for the Mysticeti, with the Balaenopteridae appearing at least 15 to 20 Ma. The presence of Eobalaenoptera in the Calvert Formation demonstrates that the crown clade of Balaenopteridae-Eschrichtiidae had split from all other whales by at least 14 Ma. This is much closer to the divergence estimates of Nikaido et al. (2001) and Cassens et al. (2000) than the 9 to 10 Ma age of "Megaptera" miocaena. Furthermore, the first appearance of balaenopterids predates the decline of the archaic "cetotheres."



FIGURE 8. Partial reconstructed forelimbs of *Eobalaenoptera harrisoni*, gen. et sp. nov. (holotype, VMNH 742), lateral view. A, right forelimb, and B, left forelimb.

TABLE 1. Comparative measurements of Miocene mysticetes. All measurements are lengths, in mm, with the exception of oc and fom, which
are the distance between the outer margins of the occipital condyles and the width of the foramen magnum, in mm, respectively. Eobalaenoptera
measurements based on VMNH 742, Pelocetus based on USNM 11976, except L1 and L2, which are based on USNM 23058, Thinocetus based
on USNM 23794. Measurements in italics are estimates, where the centrum is unknown.

	ос	fom	Hu	Ra	Ce1		Ce2	Ce3	Ce4	Ce5	Ce6	Ce7
Eobalaenoptera	169	52	265	410	80		52	38	38	40	45	55
Pelocetus	183	48	266	397	96		70	35	36	37	38	38
Thinocetus	176	56	260	385	97		95	36	32	32	34	40
	T1	T2	Т3	T4	T5	T6	T7	Т8	Т9	T10	T11	T12
Eobalaenoptera	60	72	79	86	96	105	117	125	133	137	149	145
Pelocetus	42	47	58	67	70	74	81	90	104	104	107	119
Thinocetus	45	54	60	67	68	72	76	83	93	99	103	106
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12
Eobalaenoptera	152	159	168	185	177	178	190	187	195	_		
Pelocetus	115	116	116	118	121	120	120	132	131	137		
Thinocetus	108	109	111	114	117	120	124	126	132	134	136	138

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FIGURE 9. Strict consensus cladogram showing phylogenetic relationships of *Eobalaenoptera*. Taxa denoted by an "\*" are typically assigned to the "Cetotheriidae."

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#### **APPENDIX 1**

Character matrix for phylogenetic analysis. Character state descriptions are in Appendix 2. Missing or unknown data are indicated with "?." Specimens and principal references are as follows: *Basilosaurus*,

APPENDIX TABLE A1

	Character					
Taxon	1–5	6–10	11–15	16–20		
Basilosaurus	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 1 0 0 1		
Zygorhiza	$0 \ 0 \ 0 \ 0 \ 0$	0 0 0 0 0	$0 \ 0 \ 0 \ 0 \ 0$	0 1 0 0 1		
Physeter	1 0 1 0 1	1 1 0 0 1	$0 \ 0 \ 0 \ 0 \ 0$	0 0 2 0 1		
Mesoplodon	0 0 1 0 1	1 1 0 0 1	$0 \ 0 \ 0 \ 0 \ 0$	0 0 2 0 0		
Tursiops	1 0 1 0 1	0 1 0 0 1	$0 \ 0 \ 0 \ 0 \ 0$	0 0 2 1 0		
Xenorophid	0 0 1 0 1	0 1 0 0 1	0 0 1 1 0	0 0 0 1 0		
Squalodon	0 0 1 0 1	0 1 0 0 1	0 0 1 ? 0	0 0 0 1 0		
Eubalaena	2 0 2 3 0	0 1 0 1 1	1 0 1 2 1	2 1 2 0 0		
Pelocetus	2 1 2 2 0	0 2 0 1 1	$1 \ 0 \ 1 \ 2 \ 1$	2 2 1 0 0		
Herpetocetus	$2 \ 2 \ 2 \ 1 \ 0$	0 1 1 2 1	$1 \ 0 \ 1 \ 1 \ 1$	$1 \ 1 \ 1 \ 0 \ 0$		
Parietobalaena	$2 \ 2 \ 2 \ 1 \ 0$	0 ? 1 1 1	$1 \ 0 \ 1 \ 1 \ 1$	2 2 1 0 0		
Balaenoptera	2 0 2 2 0	0 2 0 1 1	1 1 0 3 1	2 2 2 2 2 2		
Eschricĥtius	2 0 2 2 0	0 2 0 2 1	1 1 0 3 1	2 2 2 2 2 2		
Eobalaenoptera	2 0 2 2 0	0 2 1 1 1	1 1 0 3 1	2 2 2 2 2 2		
Megaptera	2 0 2 2 0	0 2 0 1 1	1 1 0 3 1	2 2 2 2 2 2		
Paraĥalaenoptera	?????	?????	?????	?????		
Isanacetus	2 0 2 2 0	0 2 0 2 1	1 0 1 3 0	2 2 1 0 1		
"Megaptera" miocaena	2 0 2 2 0	0 2 0 1 1	1 1 0 3 1	2 2 2 2 2 2		

Geisler and Luo (1996), Kellogg (1936); Zygorhiza, Geisler and Luo (1996), Kellogg (1936); Physeter, USNM 253051, Geisler and Luo (1996); Mesoplodon, Geisler and Luo (1996), Tomilin (1957); Tursiops, Geisler and Luo (1996), Tomilin (1957), uncatalogued Louisiana State University specimen; xenorophid, Luo and Eastman (1995); Squalodon, Luo and Eastman (1995), USNM 10484, USNM 23527; Eubalaena, Geisler and Luo (1996), Kimura and Ozawa (2002), VMNH uncatalogued specimen; Pelocetus calvertensis, USNM 11976, Kellogg (1965), Kimura and Ozawa (2002); Herpetocetus, Geisler and Luo (1996); Parietobalaena palmeri, USNM 23203, USNM 10677, USNM 11535, Kellogg (1968b); Eobalaenoptera harrisoni, VMNH 742, VMNH 3483, this study; Balaenoptera, USNM 484991, VMNH uncatalogued specimen, Tomilin (1957), Kimura and Ozawa (2002); Megaptera, USNM 269982, Tomilin (1957); Parabalaenoptera, Ziegler et al. (1997); Isanacetus, Kimura and Ozawa (2002); "Megaptera" miocaena, USNM 10300, Kellogg (1922).

#### **APPENDIX 2**

Character descriptions and states for characters used in phylogenetic analysis. Characters 1–28 are based on Fordyce (1994), Luo and Eastman (1995), Geisler and Luo (1996), and Luo and Marsh (1996). Characters 41–42 are based on Fordyce (1994), Oishi and Hasegawa (1994), Geisler and Luo (1996) and original observation of this study. Other skull and postcranial characters are adopted with modification from Kimura and Ozawa (2002) and original observation of this study.

- 1. Length of anterior process relative to promontorium: 60-80% (0); <50% (1); >90% (2).
- 2. Lateral surface of anterior process: convex (0); flat (1); fossa or groove (2).
- 3. Articulation of bulla with anterior process: none or small (0); present, with fovea epitubaria on anterior process (1); fused with ridgelike pedestal (2).
- 4. Lateral projection of anterior process: absent (0); blade-like (1); robust (2); hypertrophied (3).
- 5. Accessory ossicle of the tympanic: absent (0); present (1).
- 6. Fusion of accessory ossicle with anterior process: absent (0); present (1).
- 7. Groove for tensor tympani muscle: enlarged oval fossa (0); groove (1); groove absent or poorly defined (2).
- 8. Hiatus epitympanicus: present (0); absent or poorly developed (1).
- 9. Fossa for the malleus: present (0); partially defined (1); absent (2).
- 10. Fossa incudis: present (0); absent (1).
- 11. Ventrolateral tuberosity: present (0); absent (1).
- 12. Transverse elongation of the pars cochlearis: absent (0); present (1).
- 13. Groove on medial side of pars cochlearis: absent (0); present (1).
- 14. Stylomastoid fossa: absent (0); present (1); enlarged, extending onto posterior side of pars cochlearis (2); enlarged, extending onto posterior process (3).
- 15. Floor of stapedial muscle fossa: fully formed (0); partially formed (1).
- 16. Ventrolateral ridge: absent (0); present (1); present and expanded (2).

- 17. Dorsolateral ridge: present (0); absent (1); swollen and enlarged (2).
- Suprameatal area of petrosal: concave fossa (0); flat (1); convex (2).
- 19. Depth and shape of fundus for internal acoustic meatus: shallow and ovoid (0); shallow and tear-drop shaped (1); deep and ovoid (2).
- 20. Endocranial opening of facial canal: circular (0); with anterior fissure (1); deep and tubular (2).
- 21. Separation of perilymphatic foramen from fenestra rotunda: wide (0); narrow (1); absent (2).
- 22. Orientation of posterior process of petrosal: posterolateral relative to the longitudinal axis of pars cochlearis (0); at right angle to the longitudinal axis of pars cochlearis (1).
- 23. Size of posterior process relative to promontorium: <70% (0); >100% (1).
- 24. Constriction between posterior process of petrosal and pars cochlearis: constricted transversely (0); absent (1); constricted transversely and dorsoventrally (2).
- 25. Contact of posterior process of petrosal with squamosal: corrugated suture (0); smooth surface (1); prominent flange (2).
- 26. Posterolateral extension of facial nerve sulcus: on ventral side of posterior process of tympanic and short (0); absent (1); on ventral surface of compound posterior process and long (2).
- 27. Articulation of the posterior process of petrosal to posterior process of tympanic: suture (0); suture in juveniles, fused in adults (1).
- Posterior end of posterior process of petrosal: exposed in mastoid region (0); not exposed (1).
- 29. Supraorbital process abruptly depressed relative to vertex absent (0); present (1).
- 30. Coronoid process of mandible: prominent (0); reduced (1).
- 31. Nasals: narrower than proximal end of premaxilla (0); wider than proximal end of premaxilla (1).
- 32. Ascending processes of maxillae on vertex: absent (0); small (1); prominent (2).
- 33. Skull arch: absent (0), <5 degrees (1); 10–20 degrees (2); >20 degrees (3).
- 34. Dorsal margin of mandible: straight (0); moderately arched (1); strongly arched (2).
- 35. Number of digits: five (0); four (1).
- 36. Cervical vertebrae: all free (0); partially fused (1); all fused (2).
- 37. Contact of maxilla with supraorbital process: suture (0); maxilla projects over supraorbital process (1); fissure with only partial contact (2).
- 38. Exposure of frontals on midline: present (0); absent (1).
- 39. Length of cervical series relative to precaudal series:  $\leq 10\%$  (0); >10% (1).
- 40. Humerus length relative to radius: >100% (0); approximately 100% (1); 80%-50% (2); <50% (3).
- 41. Swollen dorsal posterior prominence of tympanic bulla: absent (0); present (1).
- 42. Keel on tympanic bulla: absent (0); present (1).

APPENDIX TABLE A1 (extended)

			Character		
Taxon	21–25	26–30	31–35	36–40	41-42
Basilosaurus Zugarkiza	$   \begin{array}{ccccccccccccccccccccccccccccccccccc$	1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	0 0
Physeter	1 1 0 0 1	$     \begin{array}{c}       1 & 0 & 0 & 0 & 0 \\       0 & 0 & 1 & 0 & 0   \end{array} $	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 1 0 0 2	0 0 0
Mesoplodon	1 0 0 0 1	$0 \ 0 \ 1 \ 0 \ 0$	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$1 \ 1 \ 0 \ 0 \ 2$	0 0
Xenorophid	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 1 0 0 2 0 0 0 ? ?	
Squalodon	0 0 0 0 0	0 0 1 0 0	0 0 0 0 0	0 1 0 0 2	0 0
Eubalaena Pelocetus	$1 1 1 0 0 \\ 1 0 1 2 0$	$\begin{array}{c} 2 & 1 & 0 & 0 & 1 \\ 2 & 1 & 0 & 0 & 0 \end{array}$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$   \begin{array}{c}     0 & 1 \\     0 & 0   \end{array} $
Herpetocetus	$\begin{array}{cccccccccccccccccccccccccccccccccccc$		0 0 0 0 0 ?	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	0 0
Parietobalaena	$1 \ 0 \ 1 \ 2 \ 0$	2 1 0 0 0	0 0 0 0 ?	$0\ 2\ 0\ 1\ 2$	0 0
Eschrichtius	$\begin{array}{c} 7 & 0 & 1 & 2 & 0 \\ 2 & 0 & 1 & 2 & 0 \end{array}$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 0 & 1 \\ 0 & 1 \end{array}$
Eobalaenoptera Megaptera	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 2 & 1 & 0 & ? & ? \\ 2 & 1 & 0 & 1 & 0 \end{array}$	??????	0??12 02103	11
Parabalaenoptera	$\begin{array}{c} 0 & 1 & 2 & 0 \\ 2 & 2 & 2 & 2 & 2 \\ 1 & 0 & 1 & 2 & 0 \end{array}$	2 1 0 1 0 ? ? ? 1 0	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	??
"Megaptera" miocaena	? 0 1 2 0	2 1 0 0 ? 2 1 0 1 ?	$0\ 0\ 1\ 0\ ?$ $0\ 2\ 0\ ?\ ?$	$\begin{array}{c} 0 & 2 & 0 & 7 & 7 \\ 2 & 2 & 1 & 7 & 7 \end{array}$	1 1 1 1