Fragilicetus velponi: a new mysticete genus and species and its implications for the origin of Balaenopteridae (Mammalia, Cetacea, Mysticeti)

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A new extinct genus, **Fragilicetus gen. nov.**, is described here based on a partial skull of a baleen-bearing whale from the Early Pliocene of the North Sea. Its type species is **Fragilicetus velponi sp. nov.** This new whale shows a mix of morphological characters that is intermediate between those of Eschrichtiidae and those of Balaenopteridae. A phylogenetic analysis supported this view and provided insights into some of the morphological transformations that occurred in the process leading to the origin of Balaenopteridae. Balaenopterid whales show specialized feeding behaviour that allows them to catch enormous amounts of prey. This behaviour is possible because of the presence of specialized anatomical features in the supraorbital process of the frontal, temporal fossa, glenoid fossa of the squamosal, and dentary. **Fragilicetus velponi gen. et sp. nov.** shares the shape of the supraorbital process of the frontal and significant details of the temporal fossa with Balaenopteridae but maintains an eschrichtiid- and cetotheriid-like squamosal bulge and posteriorly protruded exoccipital. The character combination exhibited by this cetacean provides important information about the assembly of the specialized morphological features responsible for the highly efficient prey capture mechanics of Balaenopteridae.

INTRODUCTION

Baleen-bearing whales are large-sized, filter-feeding cetaceans with a long evolutionary history and four living families (Fordyce, 2009). Current evidence supports the hypothesis that they originated in the Oligocene epoch from toothed ancestors (Fitzgerald, 2006, 2010; Deméré *et al.*, 2008) and, over time, underwent extensive diversification, giving rise to tens of genera and species in several families, most of which are now extinct (Fordyce & de Muizon, 2001).

Balaenopteridae Gray, 1864 (rorqual and humpback whales) are the most successful mysticetes (amongst the extant taxa) in terms of species number

as they include eight living species in two genera, *Balaenoptera* Lacépède, 1804, and *Megaptera* Gray, 1846 (Deméré, Berta & McGowen, 2005). One of the probable reasons for the evolutionary success of rorquals and humpbacks is their ability to catch enormous quantities of agile prey by gulp feeding (Pivorunas, 1979; Sanderson & Wassersug, 1993; Goldbogen, Pyenson & Shadwick, 2007). The mechanics of rorqual feeding has been the subject of numerous experiments and studies and is based on the presence of peculiar fibrocartilage fibres at the craniomandibular joint that are able to incorporate mechanical energy during the opening of the mouth (Lambertsen, Ulrich & Straley, 1995); that energy is then released during the closure of the mouth (Lambertsen, 1983; Lambertsen *et al.*, 1995). As the opening of the mouth is principally the result of the force exerted by the entering water, the whole process is mostly passive (Sanderson & Wassersug, 1993). The

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entering water fills an enormous mouth cavity that is expanded by the distension of ventral throat grooves. During this process, a specialized organ located anteriorly between the mandibular rami is thought to provide inputs to the brain to adjust the position of the mandibular rami at each moment (Pyenson *et al*., 2012).

This feeding mechanism is also possible because the muscular and skeletal systems of rorquals and humpbacks possess specialized skeletal and soft tissue features. These include a specialized craniomandibular joint; abruptly depressed and wide supraorbital process of the frontal with the orbitotemporal crest located at its anterior border; temporal crest extended laterally to form a partial roof of the temporal fossa so that the medial wall of the temporal fossa cannot be observed in dorsal view; anteriorly placed lambdoid crest; reduced angular and coronoid processes of the dentary; reduced postcoronoid fossa; and highly concave glenoid fossa of the squamosal (Sanderson & Wassersug, 1993; Bisconti, 2010c). The way in which these characters developed in the balaenopterid skull during the evolution of the family is still poorly understood; in part, this is because of the lack of clear agreement about the topology of the balaenopterid phylogenetic tree (e.g. Deméré *et al*., 2005; Marx, 2011; Bisconti, 2010a,b).

Morphological analyses of the skeleton and internal organs (Deméré *et al*., 2005; Bisconti, 2007a, 2010c; Marx, 2011) suggest that balaenopterid whales are closely related to the gray whale *Eschrichtius robustus* Van Beneden & Gervais, 1868, which is assigned to its own family (Eschrichtiidae Ellerman & Morrison-Scott, 1951). Most of the work carried out on the fossil record supports this view (but see Steeman, 2007, and Bisconti, 2008, for alternative hypotheses). Recent molecular analyses of mitochondrial cytochrome *b* DNA found that *Eschrichtius robustus* is well nested within Balaenopteridae and that *Balaenoptera* is not monophyletic as both *Eschrichtius* and *Megaptera* are included within it (Price, Bininda-Emonds & Gittleman, 2005; Sasaki *et al*., 2005; May-Collado & Agnarsson, 2006). This result generated a conflict between morphological and molecular approaches. Unfortunately, up to now, the fossil record has been of little help in resolving this situation as very few fossil eschrichtiids have been described and the evolutionary history of the gray whale is still scarcely understood (Bisconti & Varola, 2006; Ichishima *et al*., 2006; Bisconti, 2008). Only a few molecular studies have supported the monophyly of both Balaenopteridae and Eschrichtiidae (e.g. Steeman *et al*., 2009; Yang, 2009).

In this paper, a new fossil baleen-bearing whale is described that shows a suite of morphological characters that are intermediate between eschrichtiid and balaenopterid whales. It is named *Fragilicetus velponi* gen. et sp. nov. and is considered to be a stem balaenopterid whale. The comparative analysis of its skeletal anatomy together with a comprehensive phylogenetic analysis place it as the sister group of later-diverging Balaenopteridae to the exclusion of Eschrichtiidae. This phylogenetic result reinforces the monophyly of both Eschrichtiidae and Balaenopteridae and provides evidence about the path of the morphological transformations that occurred during the early part of the evolution of balaenopterids. In a phylogenetic context, *F. velponi* can help in deciphering the emplacement of the morphological features responsible for the specialized feeding behaviour of Balaenopteridae and provides insights into the morphological changes of the rorqual skull during the early stages of balaenopterid evolution.

ANATOMICAL TERMINOLOGY

Anatomical terms follow Mead & Fordyce (2010). Terms from Schaller (1999), Nickel, Schummer & Seiferle (1991), and Kellogg (1965) were also used to supplement those of Mead & Fordyce (2010). It was necessary to include additional reference texts for anatomical terminology as Mead & Fordyce (2010) mainly focused on odontocetes and we found that some mysticete characters commonly used in the previous literature were not clearly defined in their book.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; NBC, Naturalis Biodiversity Center, Leiden, The Netherlands; NMR, Natuurhistorisch Museum Rotterdam, The Netherlands; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SDSU, San Diego State University, San Diego, USA; USNM, United States National Museum, Smithsonian Institution, Washington, USA.

SYSTEMATIC PALAEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER CETACEA BRISSON, 1762

SUBORDER MYSTICETI COPE, 1891

CHAEOMYSTICETI MITCHELL, 1989

BALAENOMORPHA GEISLER & SANDERS, 2003

SUPERFAMILY THALASSOTHERII BISCONTI, LAMBERT & BOSSELAERS, 2013

EPIFAMILY BALAENOPTEROIDEA FLOWER, 1864

FAMILY BALAENOPTERIDAE GRAY, 1864

FRAGILICETUS GEN. NOV.

Diagnosis: The diagnosis of *Fragilicetus* includes the presence of eschrichtiid-like and balaenopterid-like features in the same individual. *Fragilicetus* is

distinguished from the other nonbalaenopterid mysticete families based on the presence, in the same individual, of a squamosal bulging into the temporal fossa; posterior projection of the posterolateral corner of the exoccipital; anterior placement of the posterior apex of the lambdoidal crest; squamosal cleft present and v-shaped (turning ventrally at its lateral end); abruptly depressed and flat supraorbital process of the frontal; anterior portion of temporal crest transversely elongated and forming a dorsal roof to the anterior portion of the temporal fossa; very short intertemporal region; infraorbital region of the frontal exposed dorsally between the ascending processes of the maxillae; anterior end of the parietal located more anteriorly than the posterior ends of the ascending process of the maxilla; descending suprameatal surface from the central portion of the periotic to the superior rim of the internal acoustic meatus; endocranial opening of the facial canal separated from the internal acoustic meatus by a thick crista transversa but not prolonged into a groove; triangular anterior process of the periotic; anterior process of the periotic and central portion of periotic on the same plane; groove for VII cranial nerve in posterior process reduced; anteroposteriorly short and flattened posterior process of the periotic.

Discussion: Fragilicetus velponi belongs to Balaenopteroidea (*sensu* Geisler & Sanders, 2003: Balaenopteroidea is defined as the clade including Eschrichtiidae and Balaenopteridae, their common ancestor, and all the descendants of this ancestor; see Deméré *et al.*, 2005 for further details) because it has a long and definite ascending process of the maxilla, reduced interorbital region of the frontal, depressed supraorbital process of the frontal, and pars cochlearis of the periotic elongated along both the anteroposterior and transverse axes. The type of the depression of the supraorbital process of the frontal is different in Eschrichtiidae and Balaenopteridae; although it is generally accepted that both families have a depressed supraorbital process of the frontal, the degree of development of the depression is in fact greater in Balaenopteridae. In Balaenopteridae the supraorbital process of the frontal is abruptly depressed over its whole longitudinal length but in the living *Eschrichtius robustus*, the depression is evident at the posterior portion of the supraorbital process whereas the more anterior portion is only slightly depressed. The depression of the supraorbital process of the frontal is more balaenopterid-like in the fossil *Eschrichtioides gastaldii*, in which the supraorbital process of the frontal is abruptly depressed in a manner that resembles very closely the condition observed in Balaenopteridae. Some Cetotheriidae Brandt, 1872, such as *Mixocetus elysius* Kellogg, 1934b (our observations on *Mi. elysius* are based

on the photographic illustrations provided by Kellogg, 1934b, in which the reconstructed portions are clearly evident), share the condition observed in *Eschrichtius robustus* but most of the cetotheriids and basal thalassotherians show a gently descending supraorbital process of the frontal. Hereafter, we use Cetotheriidae to mean Cetotheriidae *s.s.* of Bouetel & de Muizon (2006); see also El Adli, Deméré & Boessenecker (2014) and Bisconti (2014) for discussions on this taxon. *Fragilicetus velponi* differs from later-diverging Balaenopteridae in having a well-developed squamosal bulge, strongly developed exoccipital that projects posterolaterally, and in the lack of a posterior projection of the postglenoid process of the squamosal. *Fragilicetus velponi* differs from Eschrichtiidae in having a wide supraorbital process of the frontal, anteriorly compressed supraoccipital, and in the lack of dorsal tubercles on the supraoccipital. It is clearly different from Cetotheriidae in the following characters: (1) the posterior ends of its maxillae do not meet along the midline posteriorly and (2) the posterior ends of its maxillae are not superimposed onto the interorbital region of the frontal.

Etymology: Fragilis, Latin, fragile, in reference to the extreme fragility of the holotype skull. *Cetus*, Latin, whale.

Type species: Fragilicetus velponi sp. nov. This is currently the only included species.

FRAGILICETUS VELPONI SP. NOV.

Holotype: Item no. NMR 999100007727, housed at the Natuurhistorisch Museum Rotterdam, The Netherlands (hereinafter, NMR).

Type locality: The specimen was found along the southwest border of the Deurganckdock, approximately 12 km north-west of Antwerp city centre and 4 km north of the village of Kallo (Fig. 1). The Deurganckdock is an artificial excavation located on the left side of the Scheldt River. The geographical coordinates of the discovery site are 51°17′05″N, 4°15′30″E.

Formation and age: The specimen was found *in situ* in the Kattendijk Sand Member of the Kattendijk Sands Formation (Early Pliocene, Zanclean), about 3 m above the basal gravel, at a depth of about 21.5 m below the Tweede Algemene Waterpassing (TAW; Fig. 2). TAW is the standardized (rectified) second general water level (main level of the sea at Ostend at low tide). The Belgian standard TAW is 2.33 m lower than the Dutch, German, and French standards. At the discovery site, the basal gravel of the Kattendijk Sand Member is in contact with and on top of the Rupel clay (Oligocene,
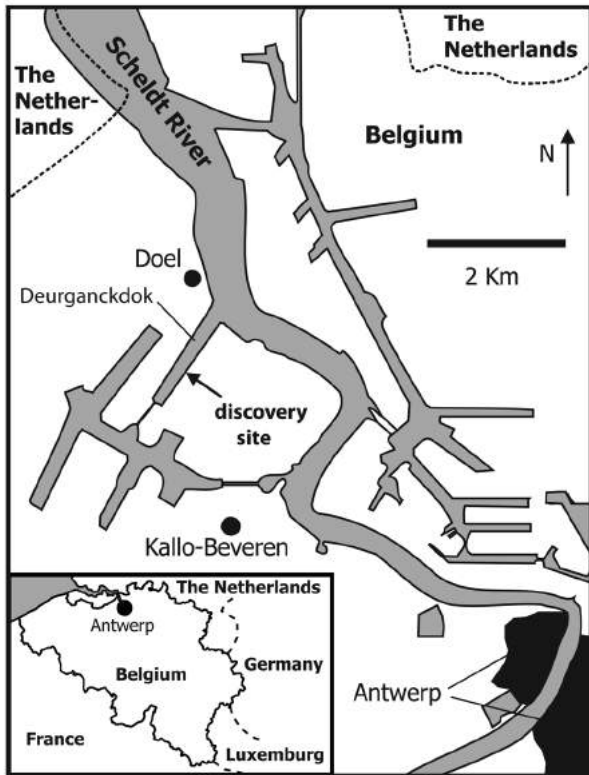
Figure 1. Map showing the discovery site of the holotype of ***Fragilicetus velponi*** **gen.** et **sp. nov.** near the city of Antwerp, Belgium.

Rupelian) at a depth of about 24.6 m (Fig. 2). At the top, the Kattendijk sands are unconformably overlain by the basal gravel of the Oorderen Sand Member (Middle Pliocene, Piacenzian). The Kattendijk Sand Member is about 6 m thick at the discovery site. At about the level of the fossil, in the Kattendijk sands, one occasional and two (almost) continuous shell layers occur. The upper layer mainly consists of single valves of *Glycymeris obovata ringelei* (Moerdijk & van Nieulande, 2000) (Bivalvia, Glycymeridae); the lower level consists of single valves of *Paliolum gerardi* (Nyst, 1835) (Bivalvia, Pectinidae). Intermixed between these levels, it is sometimes possible to observe an occasional layer mainly formed by duplets of *Plyothirina sowerbyana* (Nyst, 1843) (Brachyopoda). The estimated age of the Kattendijk Formation has been constrained between *c.* 5.0 and 4.4 Mya (Louwye, Head & De Schaepper, 2004). The Kattendijk Formation was correlated with the standard sequence 3.4 (Vandenberghe *et al.*, 1998), and the base of this formation with the sequence boundary at 5.5 Mya (Haq, Hardenbol & Vail, 1987), which is now regarded as sequence boundary Me2 at 5.73 Mya (Hardenbol *et al.*, 1998). The correlation of the Kattendijk Formation with standard sequence 3.4 (5.73–4.37 Mya) was con-

firmed by Louwye *et al.* (2004). Based on these correlations, the estimated age of the holotype skeleton of *F. velponi* is approximately 5 Mya.

Diagnosis: As for genus.

Etymology: Velpon is the brand of the glue used in the preparation of the holotype skull.

COMPARATIVE ANATOMY

The specimen consists of a partial skull with associated periotics. The rostral bones, tympanic bullae, dentary, and most of the postcranial skeleton were not found at the excavation site and are thus missing. Only five rib fragments were found that represent the postcranial skeleton. Measurements are provided in Supporting Information Table S1. The skull shows several bite marks in the posterior part of the right side (Fig. 3). The bites are orientated dorsoventrally and are located on the right temporal fossa; eight bite signs occur in the right squamosal and three in the parietal.

VOMER

A 320-mm-long fragment of the vomer represents the rostrum; it is dorsally concave and its ventral border forms a transversely rounded keel. This fragment is poorly preserved and does not allow detailed comparisons.

FRONTAL

Only the interorbital region and the posterior parts of the supraorbital processes of the frontal are preserved in the holotype skull. The interorbital region of the frontal is small and dorsally flat; the sagittal suture is not fused (Fig. 4). Posteriorly, the interorbital region of the frontal is bordered by the parietal.

Lateral to the interorbital region, grooves for the articulation of the posteromedial elements of the rostrum are observed that show that the ascending process of the maxilla did not meet along the midline posteriorly to the nasofrontal suture. A part of the interorbital region, that was about 80 mm in length, is exposed dorsally between the medial borders of the ascending processes of the maxillae and premaxillae.

Lateral to the interorbital region, the frontal descends abruptly towards the emergence of the supraorbital process of the frontal. Only the ventral face of the supraorbital process of the frontal is well preserved as most of the dorsal face has eroded. The ventral face is flat and is crossed by the optic canal that is located in the posterior-most portion. The posterior border of the supraorbital process of the frontal is straight to
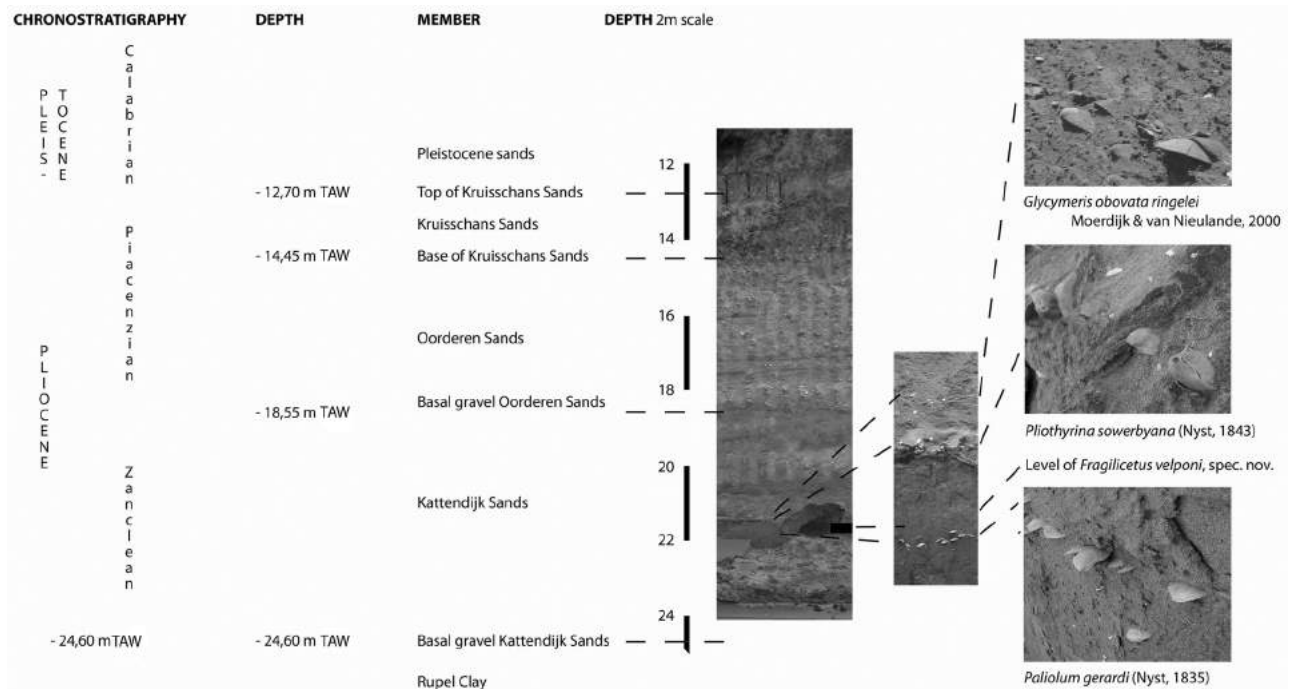
Figure 2. Stratigraphical information for the discovery site with the position of the holotype of *Fragilicetus velponi* **gen.** et **sp. nov.** indicated. The specimen is from the Zanclean of Belgium; it is from the Kattendijk Sands Formation and was found at a height of approximately 22 m below the main level of the sea at Ostend at low tide (Tweede Algemene Waterpassing: see text for explanation). Additional finds at the site include *Glycymeris obovata ringelei*, *Pliothyrina sowerbyana*, and *Paliolum gerardi* mollusc species.
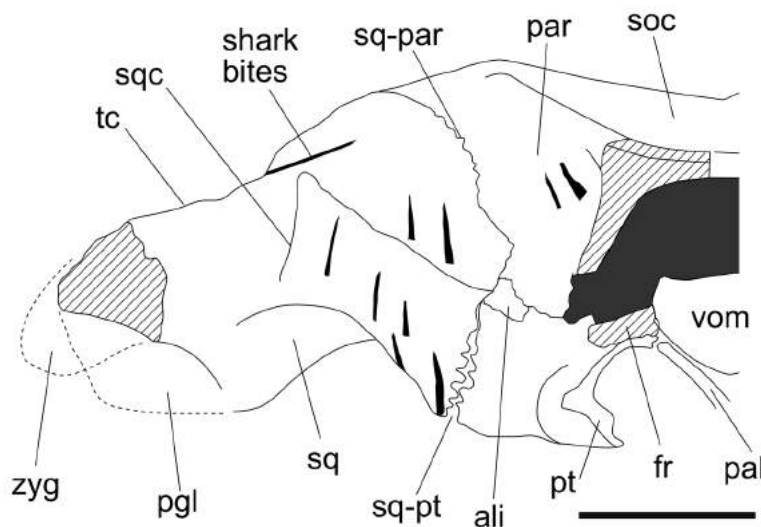

Figure 3. Localizations and orientations of shark bite marks on the holotype skull of *Fragilicetus velponi* **gen.** et **sp. nov.** as seen from the anterior view. The shark bite marks are in solid black. The skull is in anterior view; only the right side of the skull is shown because it is that part that bears the shark bite marks. Abbreviations: ali, alisphenoid; fr, frontal; pal, palatine; par, parietal; pgl, postglenoid process of squamosal; pt, pterygoid; soc, supraoccipital; sq, squamosal; sqc, squamosal cleft; sq-par, squamosal–parietal suture; sq-pt, squamosal-pterygoid suture; tc, temporal crest; vom, vomer; zyg, zygomatic process of the squamosal. Scale bar = 100 mm.
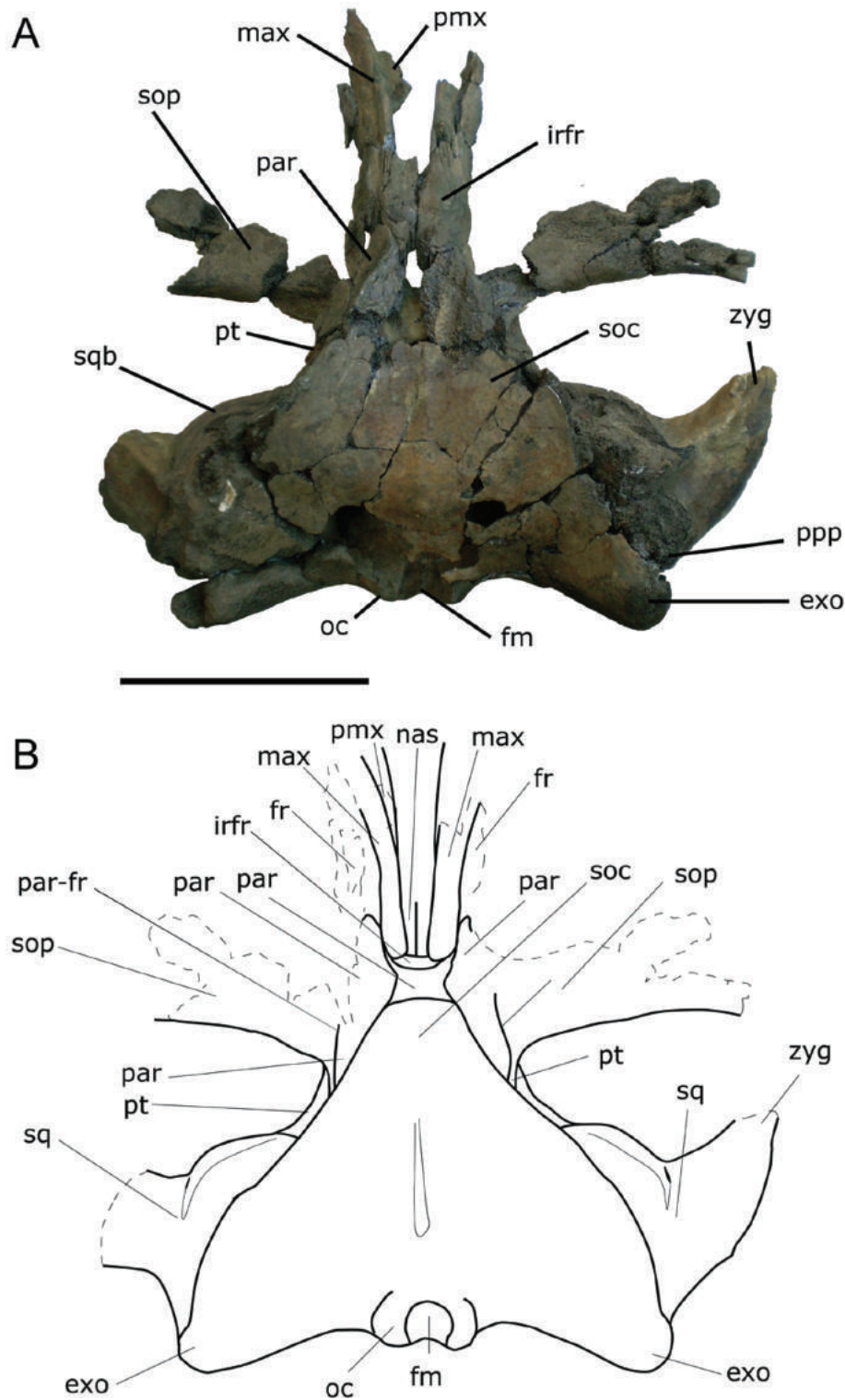
Figure 4. Holotype skull of *Fragilicetus velponi* **gen.** et **sp. nov.** in dorsal view. A, photographic representation; B, interpretative representation. Abbreviations: exo, exoccipital; fm, foramen magnum; fr, frontal; irfr, interorbital region of the frontal; max, maxilla; nas, nasal; oc, occipital condyle; par, parietal; par-fr, frontoparietal suture; pmx, premaxilla; ppp, posterior process of the periotic; pt, pterygoid; soc, supraoccipital; sop, supraorbital process of the frontal; sq, squamosal; sqb, squamosal bulge; zyg, zygomatic process of the squamosal. Scale bar = 300 mm.
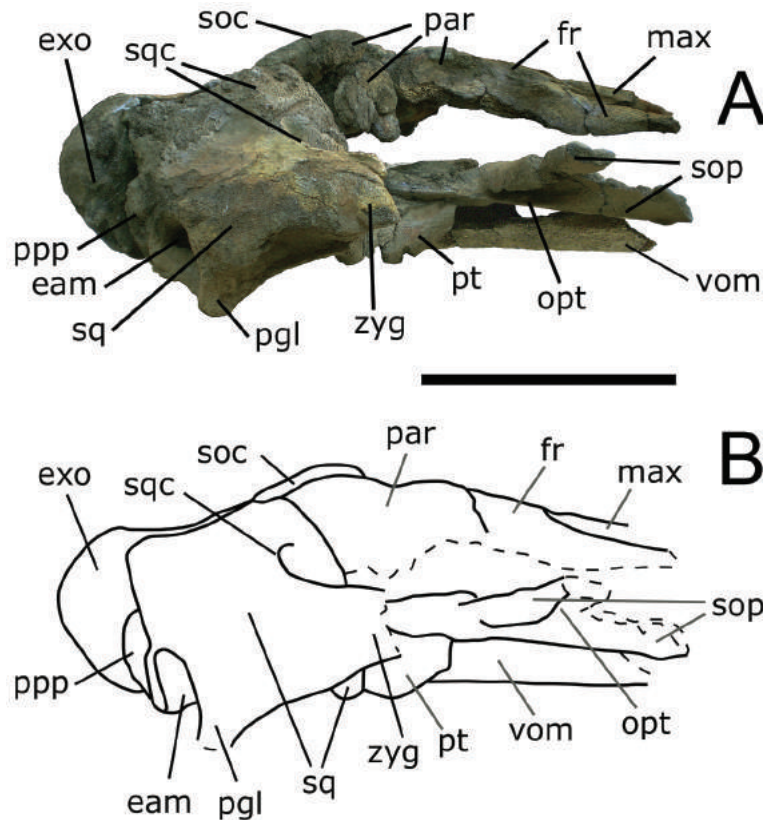
Figure 5. Holotype skull of ***Fragilicetus velponi* gen.** et **sp. nov.** in lateral view. A, photographic representation; B, interpretative representation. Abbreviations: eam, external acoustic meatus; exo, exoccipital; fr, frontal; max, maxilla; opt, optic channel; par, parietal; pgl, postglenoid process of squamosal; ppp, posterior process of the periotic; pt, pterygoid; soc, supraoccipital; sop, supraorbital process of the frontal; sq, squamosal; sqc, squamosal cleft; vom, vomer; zyg, zygomatic process of the squamosal. Scale bar = 300 mm.

slightly concave (posterior concavity) and projects anteriorly and laterally in dorsal view (Figs 4–6).

The frontal of *F. velponi* does not show significant differences with respect to those of other living and fossil Balaenopteridae. The abruptly depressed supraorbital process of the frontal is longitudinally elongated and transversely expanded, resembling that of the typical balaenopterid whales (Figs 4, 5). Only in the living *Balaenoptera musculus* Linnaeus, 1758, does the posterior border of the frontal project anterolaterally; in all the other living balaenopterids the posterior border of the supraorbital process of the frontal projects transversely or posterolaterally. The anterolateral projection of the posterior border of the supraorbital process of the frontal seems to be a primitive feature of Balaenopteridae as it is observed in archaic taxa such as *Archaebalaenoptera castriarquati* Bisconti, 2007a, *Protororqualus cuvieri* Bisconti, 2007b, and *Parabalaenoptera baulinensis* Zeigler *et al*., 1997. *Balaenoptera bertae* Boessenecker, 2013, has a peculiar concavity in the medial portion of the posterior border of the supraorbital process of the frontal that

is not observed in other balaenopterid species. Only *Balaenoptera edeni* Anderson, 1878, has a concavity in the posterior border of the supraorbital process of the frontal in the same position but this concavity is less developed (Cummings, 1985).

The frontal of Balaenopteridae differs greatly from those of Eschrichtiidae and Cetotheriidae. In Eschrichtiidae and some Cetotheriidae (e.g. *Piscobalaena nana* Pilleri & Siber, 1989), the supraorbital process of the frontal may be depressed from the interorbital region of the frontal and projects laterally and ventrally. In other Cetotheriidae and basal thalassotherian taxa (e.g. *Parietobalaena palmeri* Kellogg, 1924; *Diorocetus hiatus* Kellogg, 1968b) it gently descends from the interorbital region of the frontal. The degree of the depression of the supraorbital process of the frontal differs amongst eschrichtiid species. For example, in the living gray whale the supraorbital process projects laterally and ventrally, whereas in the fossil *Eschrichtioides gastaldii* the supraorbital process of the frontal is much more balaenopterid-like and projects sharply laterally (Bisconti, 2008). In Balaenopteridae, the supraorbital process of
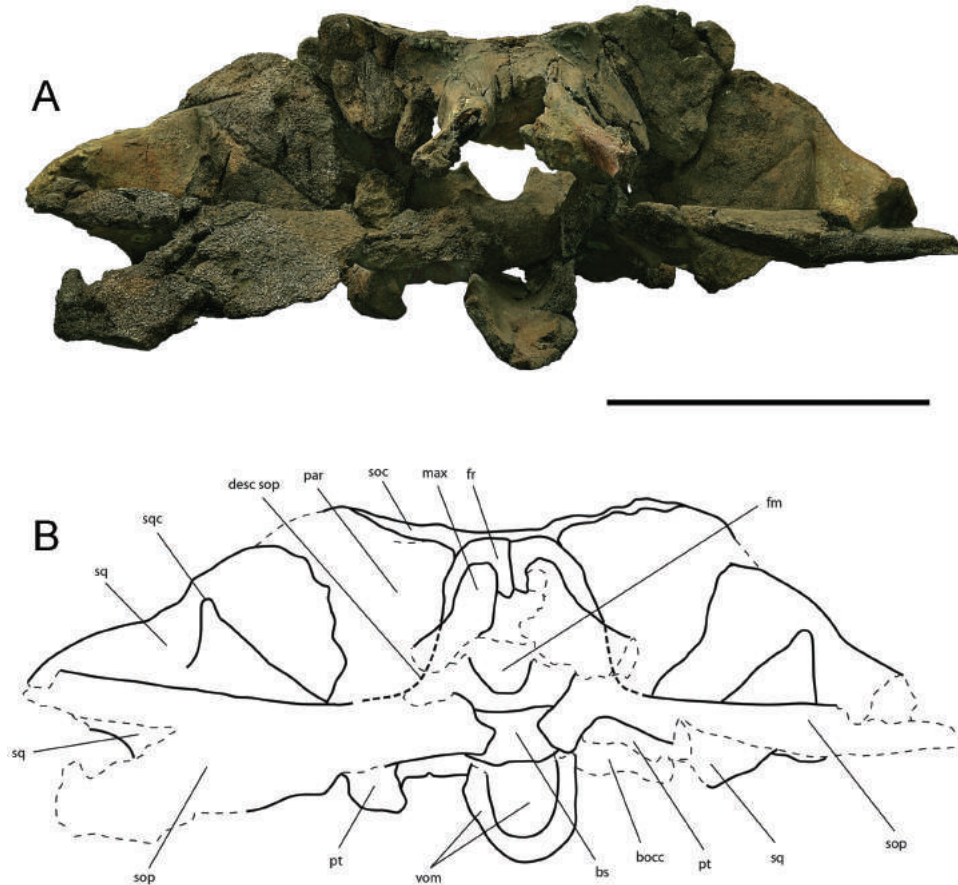
Figure 6. Skull of ***Fragilicetus velponi*** **gen.** et **sp. nov.** in anterior view. A, photo; B, line drawing. Abbreviations: bocc, basioccipital; bs, basisphenoid; desc sop, descending part of supraorbital process of the frontal; fm, foramen magnum; fr, frontal; max, maxilla; par, parietal; pt, pterygoid; soc, supraoccipital; sop, supraorbital process of the frontal; sq, squamosal; sqc, squamosal cleft; vom, vomer. Scale bar = 300 mm.

the frontal projects laterally, forming an approximately right angle with the lateral surface of the interorbital region of the frontal. Additional information on this point is provided in the Discussion.

PARIETAL AND INTERPARIETAL

The frontal border of the parietal reaches a boss located a few mm anterior to the posterior end of the ascending process of the maxilla. The anterior portion of the external surface is transversely concave and is dorsally covered by the temporal crest formed by the supraoccipital border of the parietal and the lateral border of the supraoccipital. The coronal suture between the frontal and parietal is anteriorly concave. Posteriorly, the parietal is externally concave approaching the squamous border. There is no postparietal foramen (Fig. 5).

The dorsal exposure of the parietal cannot be assessed properly as most of this bone is missing from the cranial vertex (Fig. 4). Judging from the relative positions of the anterior border of the supraoccipital and the posterior border of the interorbital region of the frontal, the dorsal exposure of the parietal would have been wide and long in *F. velponi*. For this reason, the vertex of this whale would differ from that of living and fossil Balaenopteridae, in which the dorsal exposure of the parietal is small and anteroposteriorly short (Fig. 4).

The presence of the interparietal cannot be confirmed as the area where the interparietal should be present is badly worn (Fig. 4). It is possible to exclude the presence of an interparietal of the same shape as that exhibited by *Eschrichtius robustus* (*sensu* Tsai *et al.*, 2014) because in the latter the interparietal appears as an anteroventral protrusion from the anteroventral surface of the supraoccipital (see Tsai *et al.*, 2014 for a preliminary discussion on this point). As this kind of interparietal is absent in the reasonably

well-preserved supraoccipital of *F. velponi*, we may exclude its presence.

VERTEX

The vertex is not preserved as a whole; thus it is not possible to determine the relative exposure of the parietal at the cranial vertex (Fig. 4). However, given the arrangement of the surrounding bones, if it was exposed, its exposure was limited to a few mm along the sagittal axis; parasagittally, a triangular exposure of the parietal was certainly present and can be observed in the holotype specimen.

Judging from the preserved bones, as a whole, the vertex of *F. velponi* was balaenopterid-like. In this species, the vertex is characterized by a narrow interorbital region of the frontal laterally bordered by long ascending processes of the maxillae. It is not clear whether the premaxillae also bordered the interorbital region of the frontal. The parietal is interdigitated with the posteromedial elements of the rostrum described above and separated the supraoccipital from the interorbital region of the frontal. As in more advanced balaenopterids, the supraorbital process of the frontal is abruptly depressed from the interorbital region of the frontal.

Based on what is preserved, the vertex of *F. velponi* is clearly different from that of typical cetotheriids in that in *F. velponi* the posterior ends of the ascending processes of the maxillae do not meet along the midline posteriorly to the interorbital region of the frontal. Furthermore, in *F. velponi* the supraorbital processes of the frontal are abruptly depressed from the interorbital region of the frontal. The vertex of *F. velponi* also differs from that of Eschrichtiidae because it does not have a wide interparietal projected from the anteroventral surface of the supraoccipital, and because the supraorbital processes of the frontal are more abruptly depressed than those of *Eschrichtius robustus*. In the Pliocene *Eschrichtioides gastaldii* Strobel, 1881, the supraorbital processes of the frontal are abruptly depressed but their extension is shorter along both the longitudinal and transverse axes. In the living balaenopterid species, the cranial vertex is characterized by wide and long ascending processes of the maxilla that, in most of the species, have squared posterior ends. This character is not observed in the fossil *Ar. castriarquati*, *Para. baulinensis*, *Plesiobalaenoptera quarantellii* Bisconti, 2010b, *Pr. cuvieri* Fischer, 1829, or '*Megaptera*' *hubachi* Dathe, 1983, in which the posterior ends of the ascending processes of the maxillae are rounded or pointed. Judging from the preserved grooves for the articulation with the maxilla that are observed on the interorbital region of the frontal, the posterior ends of the ascending processes of the maxilla in *F. velponi* were transversely narrow. It is difficult to understand if they were rounded or squared but they were certainly narrower, in comparative terms, than those observed in the living balaenopterid species and '*Balaenoptera*' *siberi* Pilleri, 1989.

SQUAMOSAL

Starting from its parietal margin, the temporal surface of the squamosal plate is convex and protrudes into the temporal fossa forming a large and round bulge (Fig. 4). Laterally, this bulge is bordered by a vertical groove running medially to the zygomatic process of the squamosal; this groove corresponds to the squamosal crease. The squamosal cleft runs from the posteroventral corner of the alisphenoid towards the squamosal–pterygoid suture up to the groove located laterally to the squamosal bulge. It then turns ventrally. The lambdoid crest is low and does not project more posteriorly than the occipital condyles. The zygomatic process is short and robust but, as its anterior apex is lacking, it is not possible to know its total length (Fig. 5). The postglenoid process projects ventrally but not posteriorly. Anterior to the glenoid process, the glenoid fossa is not preserved. The external acoustic meatus is wide.

The foramen ovale is not preserved as a whole but its dorsal roof is observed when the skull is in ventral view (Fig. 7). The roof of the foramen ovale runs from the posterolateral termination of the pterygoid to the ventromedial border of the squamosal, suggesting that it was located between the squamosal and the pterygoid.

In ventral view, the postglenoid process is located anterolaterally to the posterolateral corner of the exoccipital (Fig. 7); even based on the preserved portion of the postglenoid process in the holotype skull, it appears that there should be a relatively wide distance between the postglenoid process and the posterolateral corner of the exoccipital. Such a distance is not present in the living Balaenopteridae as their postglenoid process projects posteriorly and ventrally, giving the glenoid fossa of the squamosal a crescent shape. In ventral view, in the living Balaenopteridae, the postglenoid process of the squamosal has an apex that is located more posteriorly than the posterolateral corner of the exoccipital; the exoccipital is not as robust as that observed in Cetotheriidae, Eschrichtiidae, and *Fragilicetus* (True, 1904).

We were unable to observe a squamosal bulging in any of the living and fossil Balaenopteridae that we were able to examine. Moreover, we were unable to find a reference to the presence of this character in Balaenopteridae in the literature. For these reasons, we conclude that a squamosal bulge is absent in Balaenopteridae. Potential exceptions are discussed below.
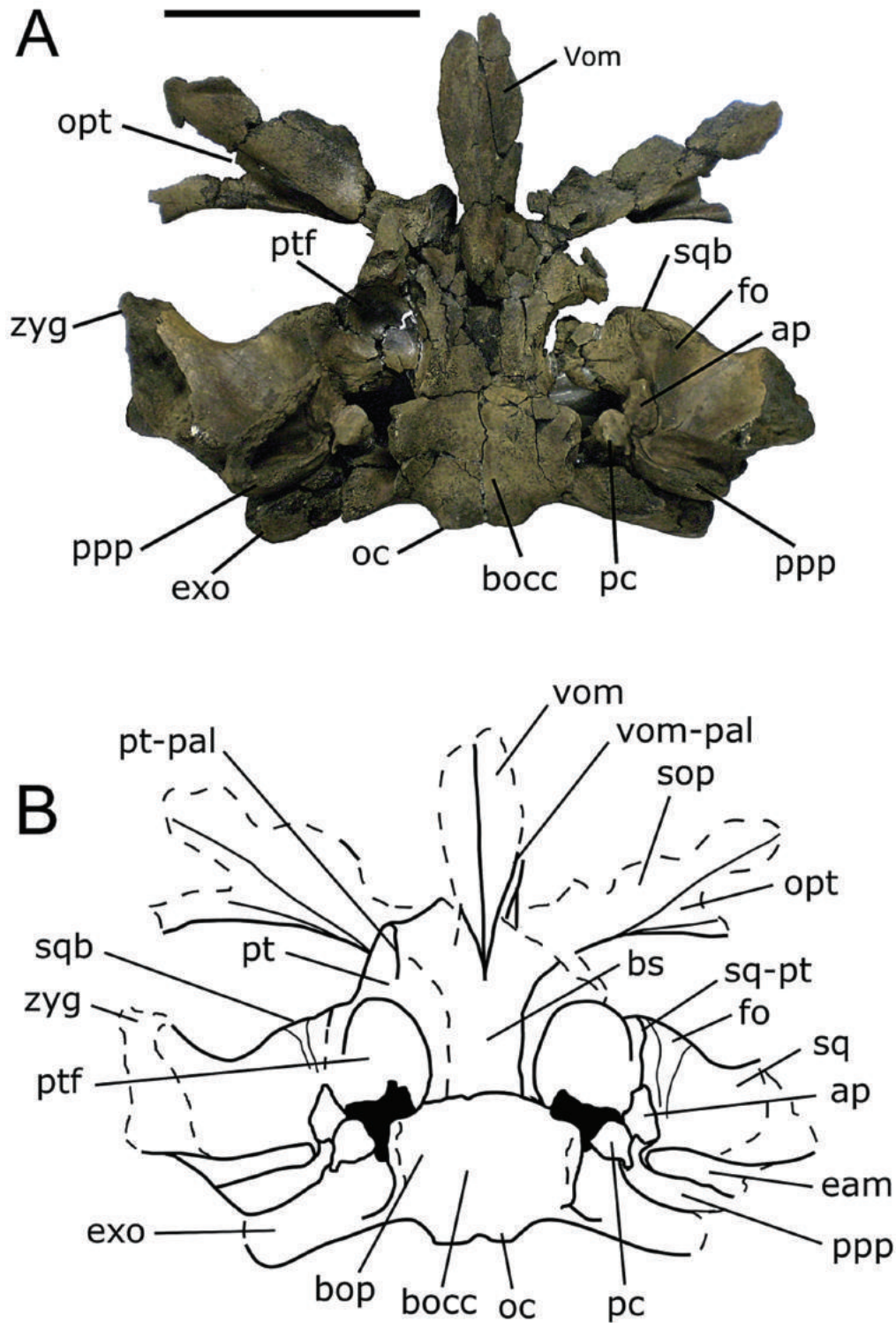
Figure 7. Skull of *Fragilicetus velponi* **gen.** et **sp. nov.** in ventral view. A, photo; B, line drawing. Abbreviations: ap, anterior process; bocc, basioccipital; bop, descending process of the basioccipital; bs, basisphenoid; eam, external acoustic meatus; exo, exoccipital; fo, foramen ovale; oc, occipital condyle; opt, optic channel; pc, pars cochlearis; ppp, posterior process of the periotic; pt, pterygoid; ptf, pterygoid fossa; pt-pal, pterygoid–palatine suture; sop, supraorbital process of the frontal; sq, squamosal; sqb, squamosal bulge; sq-pt, squamosal-pterygoid suture; zyg, zygomatic process of the squamosal; vom, vomer; vom-pal, vomer–palatine suture. Scale bar = 300 mm.

The posterior wall of the temporal fossa is usually anteriorly concave or flat but never convex. In *Balaenoptera borealis* Lesson, 1828, there is a dorsoventral groove (squamosal crease) running medially to the emergence of the zygomatic process where the terminal portion of the squamosal cleft is located; this groove is morphologically close to that observed in *Eschrichtius robustus* and *F. velponi* in the same position. However, in *B. borealis* the portion of the squamosal that is medial to this groove is not convex and does not bulge into the temporal fossa. Moreover, as pointed out by Bisconti (2008), the groove is only present in some specimens of *B. borealis*, suggesting that this character is subject to individual variation (M. Bisconti, pers. observ. in specimens USNM 504699, 504698, 504701, 504244, 486174). The squamosal bulge is a character typically observed in *Eschrichtius robustus* and Cetotheriidae such as *Mi. elysius* Kellogg, 1934b, *Metopocetus durinasus* Cope, 1896, *Herpetocetus transatlanticus* Whitmore & Barnes, 2008, and *Herpetocetus bramblei* Whitmore & Barnes, 2008.

The squamosal cleft occurs in living Balaenopteridae and *Eschrichtius robustus*, in which it is v-shaped. Recently, Bisconti (2014) showed the presence of the squamosal cleft in the cetotheriid *Herentalia nigra* Bisconti, 2014; in this whale, the squamosal cleft is straight. A squamosal cleft is also observed in several undescribed cetotheriid-like specimens from Holland and Belgium (authors' pers. observ.), suggesting that this feature could be a symplesiomorphy of the clade including Cetotheriidae *s.s.* and Balaenopteroidea. However, a full description of this undescribed material is necessary to get a well-grounded assessment of this character.

In *Eschrichtius robustus*, the squamosal cleft starts from the alisphenoid–squamosal suture approximately at the middle of the suture (NBC specimens St20079, RGM13130, and RGM630 and AMNH specimen no. 34270) or from the parietal–squamosal suture (AMNH specimen no. 181374). In balaenopterid species, the squamosal cleft may start from the squamosal–pterygoid suture (*B. musculus*: AMNH 234949; *B. borealis*: NBC 31164, AMNH 34871; *B. edeni*: ISAM, Iziko South African Museum, Cape Town, South Africa ZM12962, ZM40482; *Balaenoptera acutorostrata* Lacépède, 1804: ISAM EL 77, ZM15269; NBC RGM 1428; *Megaptera novaeangliae* Brisson, 1752: ISAM ZM2288), from the squamosal–alisphenoid suture (*B. musculus*: AMNH 34869), or from the squamosal–parietal suture (*Meg. novaeangliae* juvenile: ISAM ZM39781; *Balaenoptera physalus* Linnaeus, 1758: ISAM ZM13900). In *Caperea marginata* Gray, 1846, the squamosal cleft starts from the squamosal–pterygoid suture (AMNH 36692; ISAM ZM41126, ZM40626; RBINS 1536). In the fossil '*Meg.*' *hubachi* the squamosal cleft is present but it is unclear whether it starts from the pterygoid or from the alisphenoid; in '*Balaenoptera*' *ryani* Hanna & McLellan, 1924, the squamosal cleft starts from the squamosal–alisphenoid suture. After this review, it is hard to state which is the plesiomorphic condition of the squamosal cleft. Judging from the cladistic results of Bisconti (2010c), and from the assumption that Eschrichtiidae is the sister group of *Fragilicetus* + Balaenopteridae, the primitive condition of the anterior starting point of the squamosal cleft should be from the alisphenoid–squamosal suture. Further discussion on this point is provided in the Phylogenetic analysis section.

In living Balaenopteridae, the foramen ovale is located between the squamosal and the pterygoid (Fraser & Purves, 1960); in *Eschrichtius robustus* the foramen ovale is located within the squamosal (M. Bisconti, pers. observ. on specimens NBC RGM 13130, RGM 630) or between the squamosal and the pterygoid (M. Bisconti, pers. observ. on specimens AMNH 181374, SDSU S-974, NBC St 20079). In *Ca. marginata*, the foramen ovale is located within the pterygoid (Bisconti, 2012). In basal thalassotherian taxa and Cetotheriidae the foramen ovale is located in the squamosal or between the squamosal and the pterygoid; it is usually joined to the squamosal–pterygoid suture through an internal suture running within the foramen ovale itself (see images in Kellogg, 1934a, b, 1965, 1968b–d; Packard & Kellogg, 1934).

ALISPHENOID

In the temporal fossa, a squared alisphenoid can be observed (Fig. 3); it is located between the squamosal and the parietal. From its posteroventral corner, the squamosal cleft starts to develop posteriorly. Amongst the living balaenopterid species, only in *Meg. novaeangliae* is the alisphenoid not exposed in the temporal fossa. In *B. physalus* (NBC RGM 31163, AMNH 35026), *B. acutorostrata* (AMNH 181411, 35680), *Balaenoptera brydei* (NBC RGM 17712), and *B. borealis* (NBC RGM 31164, AMNH 34871), the alisphenoid is located between the parietal and pterygoid and is not in contact with the frontal. In these species the contact with the squamosal is reduced to a point located at the posterior end of the alisphenoid. It is hard to assess the alisphenoid exposure in fossil balaenopterid species (e.g. *Ar. castriarquati*, *Pr. cuvieri*, *B. bertae*) and comparisons may be carried out only with '*B.*' *ryani* and '*Meg.*' *hubachi*, in which the alisphenoid is exposed between the parietal, squamosal, pterygoid, and frontal (Hanna & McLellan, 1924; Bisconti, 2010c). In *Diunatans luctoretemergo* Bosselaers & Post, 2010, the alisphenoid is located between the squamosal, parietal, and pterygoid.

In cetotheriid species, the alisphenoid may have different positions: in *Mi. elysius* it is located between the

pterygoid, squamosal, and parietal (Kellogg, 1934b); in *Met. durinasus* the alisphenoid is included between the squamosal and parietal but it is not clear whether the alisphenoid is in contact with the frontal (Kellogg, 1968a); in *Pi. nana* the alisphenoid is present only in juvenile individuals and then disappears in adult as it is covered by superficial expansions of the surrounding bones (Bouetel & de Muizon, 2006); in *Here. nigra* it is included between the squamosal and parietal (Bisconti, 2014); in *Cetotherium riabinini* and *Herpetocetus morrowi* it is included between the parietal, squamosal, pterygoid, and frontal (El Adli *et al.*, 2014; Gol'Din, Startsev & Krakhmalnaya, 2014). In more advanced thalassotherian taxa that, according to Bisconti *et al.* (2013), form the balaenopteroid stem group (comprising *Aglaocetus moreni*, *Titanocetus sammarinensis*, and *Cophocetus oregonensis* Packard & Kellogg, 1934), the alisphenoid may occupy different positions. Amongst these taxa, in *Ag. moreni* it is located between the parietal, pterygoid, squamosal, and frontal (Kellogg, 1934a), in *Co. oregonensis* the alisphenoid is not exposed in the temporal fossa, and in *T. sammarinensis* it is unclear whether the alisphenoid, which is included between the parietal, pterygoid, and squamosal, is in contact with the frontal. In *Eschrichtius robustus* the alisphenoid may be included between the parietal, pterygoid, squamosal, and frontal (NBC St 20079, AMNH 181374) or it may be separated from the frontal by the interposition of both the pterygoid and parietal (NBC RGM 13130, AMNH 34260).

PTERYGOID

The pterygoid appears dorsoventrally crushed. Its ventral portion is broken off and is not preserved in the skull. The pterygoid fossa is anteriorly rounded; its transverse diameter is relatively wide as it reaches 210 mm; the fossa is relatively shallow, being 30 mm in dorsoventral height (as preserved). The dorsolateral border of the pterygoid is exposed in the temporal fossa and it is bounded by the alisphenoid dorsally and by the squamosal posteriorly. Additional information on the pterygoid is provided in the Basicranium section.

OCCIPITAL REGION

The supraoccipital is posteriorly wide but its transverse diameter decreases approaching its anterior apex (Figs 4, 8). The apex itself is damaged but the overall curve of the supraoccipital border and the imprint in the parietal suggest that it was rounded and not pointed. Its lateral borders covered the temporal fossa anterodorsally but the posterior wall of the temporal fossa is visible in dorsal view as the squamosal bulges into it. The dorsal surface of the supraoccipital is transversely concave and anteroposteriorly convex; neither
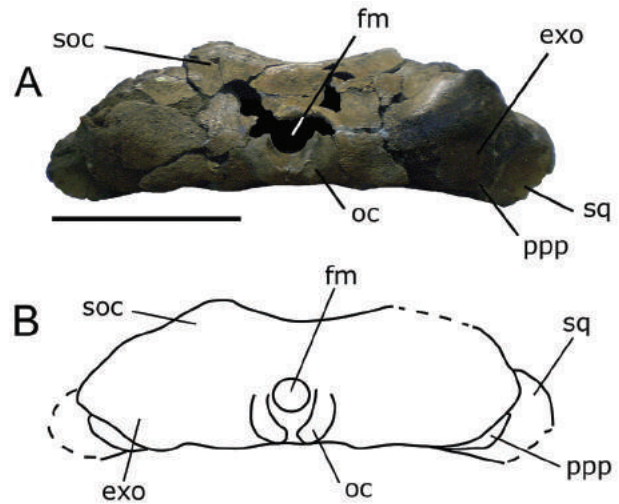

Figure 8. Skull of ***Fragilicetus velponi*** **gen.** et **sp. nov.** in posterior view: A, photo; B, line drawing. Abbreviations: exo, exoccipital; fm, foramen magnum; oc, occipital condyle; ppp, posterior process of the periotic; soc, supraoccipital; sq, squamosal. Scale bar = 300 mm.

sagittal crest nor tubercles for attachment of the neck muscles are present. Around 70 mm from the dorsal border of the foramen magnum there is a boss on the supraoccipital; a rounded relief is developed along the midline anteriorly to the boss. Anterior to the boss, the supraoccipital is nearly horizontal but it is more inclined posteriorly behind the boss itself.

The exoccipital is wide and broadly squared in posterior view (Fig. 8). The external corner of the exoccipital is rounded and projects more posteriorly than the occipital condyles. The occipital condyles are kidney-shaped and small in size. The foramen magnum is transversely compressed and dorsoventrally elongated, and appears small in size compared with the overall size of the skull.

Bisconti (2007b) compared the supraoccipital shape in several balaenopterid taxa. From his analysis, it is clear that a sort of transverse constriction occurs in most of the living balaenopterids but that such a constriction is much more marked in fossil species such as *Ar. castriarquati*, '*Meg.' hubachi*, '*B.' ryani*, and '*Plesiocetus' cortesii* var. *portisi*. In the living species, the anterior border of the supraoccipital is usually squared and transversely wider than what can be observed in the fossil species mentioned above or in *F. velponi*. As a whole, the supraoccipital appears to be more transversely expanded anteriorly in the living species. *Balaenoptera bertae* has a narrow and squared anterior end of the supraoccipital with the transverse constriction located more anteriorly than what can be seen in the other balaenopterid taxa (Boessenecker, 2013). Amongst fossil balaenopterids,

only *Diu. luctoretemergo* exhibits an approximately squared anterior border of the supraoccipital that is transversely expanded (Bosselaers & Post, 2010). 'Balaenoptera' siberi shows a rounded and wide anterior border of the supraoccipital (Pilleri, 1989).

In the living balaenopterids and in the described fossil taxa, the squamosal does not bulge into the temporal fossa; therefore, the posterior wall of the temporal fossa cannot be observed in dorsal view. As discussed above (see Squamosal section), the bulging of the squamosal is a plesiomorphic character observed in advanced archaeocetes such as *Saghacetus osiris* Dames, 1894 (taxonomy according to Uhen, 1998), toothed mysticetes such as *Chonecetus* Russell, 1968 and *Aetiocetus* Emlong, 1966, Eschrichtiidae, and archaic mysticetes such as Cetotheriidae and *Titanocetus* Bisconti, 2006. In living and fossil balaenopterid species the squamosal bulge is absent, the posterior wall of the temporal fossa is not visible in dorsal view, and the temporal fossa is dorsomedially covered by a transverse extension of the supraoccipital border of the parietal and of the lateral border of the supraoccipital forming the temporal crest. The presence of a squamosal bulge in *F. velponi* supports the view of this taxon as an archaic, prebalaenopterid species.

BASICRANIUM

In ventral view, the basisphenoid and the presphenoid are fused, as are the basisphenoid and the basioccipital. The sella turcica is wide (anteroposterior diameter, 80 mm; transverse diameter, 80 mm) and its posterior border is marked by a strong relief. The alisphenoid is anteroposteriorly short and is part of the skeletal mosaic forming the temporal fossa (Fig. 7).

The posterior lacerate foramen is wide and has parallel lateral and medial borders. Its transverse diameter is lower anteriorly. Jugular and condyloid foramina are absent. The medial border of the posterior lacerate foramen is bordered by the flat and protruding descending process of the basioccipital and the anterior border is anteriorly delimited by the posterior end of the pterygoid fossa. Only a small portion of the medial and dorsal laminae of the pterygoid are preserved, showing the internal surface of the pterygoid fossa that is concave and comparatively wide.

It is hard to provide detailed comparisons of the basicranium amongst taxa because of the poor preservation of that of *F. velponi*. The most striking character is the protrusion of the posterior part of the exoccipital with respect to the postglenoid process. In *F. velponi* the posterolateral corner of the exoccipital is located more posteriorly than the postglenoid process, as also seen in Eschrichtiidae and Cetotheriidae. In basal thalassotherian taxa and living Balaenopteridae the exoccipital is thinner and the postglenoid process

is located at the level of the posterior border of the exoccipital or more posteriorly. In other basal Balaenopteridae (e.g. *Ar. castriarquati* and *Pr. cuvieri*), the posterior protrusion of the exoccipital is similar to that observed in *F. velponi*. *Balaenoptera bertae* and *Diu. luctoretemergo* show an intermediate condition resembling that of more archaic mysticetes (e.g. *Eomysticetus* Sanders & Barnes, 2002, *Yamatocetus* Okazaki, 2012, *Dio. hiatus*): in these species the exoccipital is posteriorly protruded but the posterolateral corner is located much more medially than the postglenoid process, whereas in Cetotheriidae, Eschrichtiidae, basal balaenopterids, and *Fragilicetus* it is located slightly medially (Bosselaers & Post, 2010; Boessenecker, 2013).

PERIOTIC

The posterior process of the right periotic is located between the exoccipital and the squamosal. This process is robust but relatively flattened, and is at a right angle with respect to the orientation of the anterior process. The stylomastoid fossa is long and nearly flat, resembling that of the fin whale *B. physalus* (Bisconti, 2001; Ekdale, Berta & Deméré, 2011; Figs 9, 10). There is not an evident groove for the VII cranial nerve on the posterior process. The borders of the anterior process converge anteriorly, giving the process a nearly triangular shape in dorsal view. A wide epitympanic hiatus is located between two tuberosities located laterally and posteriorly to the anterior process. The anterodorsal angle of the periotic (*sensu* Mead & Fordyce, 2010, p. 187) is small as the anterior process does not descend from it; instead, both are on the same plane. The dorsal crest is well developed; a flat cranial surface descends from it to the plane where the internal acoustic meatus and the foramen singulare are located. These are closely placed but are well separated by a thick crista transversa. The endocranial opening of the facial canal is not prolonged into a groove. The endolymphatic duct is located within a wide and triangular fossa; the cochlear window is confluent into the perilymphatic duct and is separated from the endolymphatic duct by a thick crest. The pars cochlearis is elongated both anteroposteriorly and transversely; the groove for the tensor tympani muscle is located more anteriorly than the anterior border of the pars cochlearis. A deep groove is observed under the internal acoustic meatus and foramen singulare.

Balaenopteroid characters of the periotic of *F. velponi* are the transverse and anteroposterior elongations of the pars cochlearis. The shape of the anterior process of the periotic of *F. velponi* matches the shape observed in at least one individual of *Eschrichtius robustus* (NBC RGM 630) although in others the anterior process appears more triangular (Ekdale *et al.*, 2011).
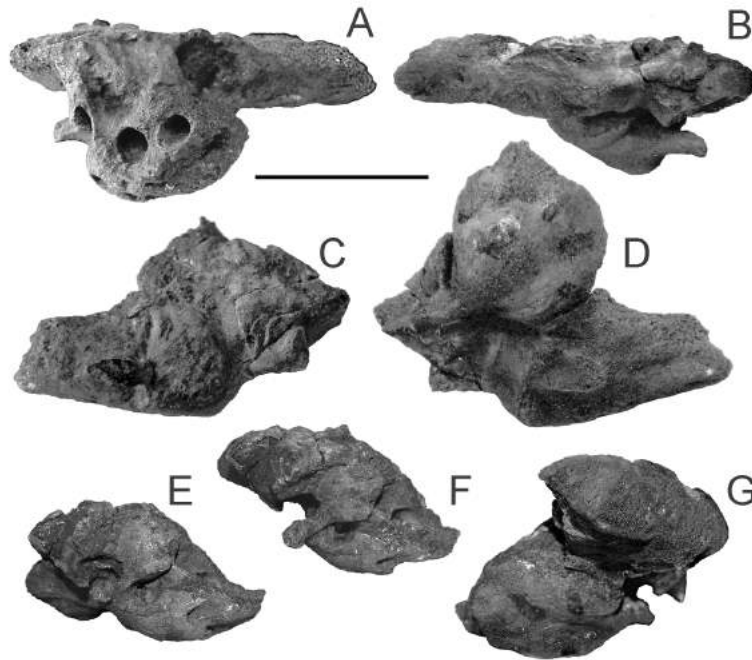
Figure 9. Left periotic of the holotype of ***Fragilicetus velponi*** **gen.** et **sp. nov.** Views as follows: A, cranial; B, lateral; C, dorsal; D, ventral; E, posterior; F, posterodorsal; G, anterior. Scale bar = 50 mm.

In *Eschrichtius robustus* the perilymphatic duct and the round window are confluent as in some fossil balaenopteroid specimens such as '*Balaenoptera*' *rostratella* Van Beneden, 1880 (RBINS M. 794) and '*Balaenoptera*' *musculoides* Van Beneden, 1880 (RBINS M. 752b).

Differing from *Plesiobalaenoptera quarantellii* and the fossil balaenopteroids mentioned above, the dorsal surface of the periotic of *F. velponi* is not highly raised. Rather, it is flat resembling that of *B. acutorostrata* and *B. physalus* (Bisconti, 2001; Ekdale *et al.*, 2011).

As pointed out by Bisconti *et al*. (2013), the separation of the internal acoustic meatus and endocranial opening for the facial canal observed in *F. velponi* is a symplesiomorphy of Thalassotherii. Only in adult Balaenopteridae, Eschrichtiidae, and a small number of basal thalassotherian taxa (i.e. *Pelocetus*, '*Aglaocetus*' *patulus* Kellogg, 1968c, *Isanacetus laticephalus* Kimura & Ozawa, 2002) are the internal opening of the facial canal and the internal acoustic meatus confluent. However, Bisconti (2001) demonstrated that in early juvenile *B. physalus* and *B. acutorostrata* the internal opening of the facial canal and the internal acoustic meatus are separate and then later become incorporated within a single foramen. Additional observations of this developmental process have been made in *B. edeni* (ISAM ZM 40449) and

B. borealis (RBINS Reg. 1538γ) (M. Bisconti, pers. observ.).

PHYLOGENETIC ANALYSIS

INTRODUCTION

Fragilicetus velponi shows a mix of morphological features that is intermediate between Eschrichtiidae and Balaenopteridae. The shape of the posteromedial elements of the rostrum as implied by their articular grooves on the frontal, the morphology of the interorbital region of the frontal, and the abruptly depressed supraorbital process of the frontal prevent its assignment to Eomysticetoidea, Balaenidae, Neobalaenidae, Cetotheriidae, or any of the basal thalassotherian taxa. The lack of strong tubercles on the supraoccipital suggests that it does not belong to Eschrichtiidae (Barnes & McLeod, 1984; Bisconti, 2008). The presence of a squamosal bulge into the temporal fossa excludes it from belonging to Balaenopteridae (Bisconti, 2010b). However, the squamosal bulge and the geometry of the posterolateral corner of the exoccipital with respect to the occipital condyles suggest some affinity with Eschrichtiidae (Bisconti, 2008), whereas the triangular anterior process of the periotic, the small anterodorsal angle of the periotic, the arrangement of the bones surrounding the interorbital region of the frontal, and the shape of
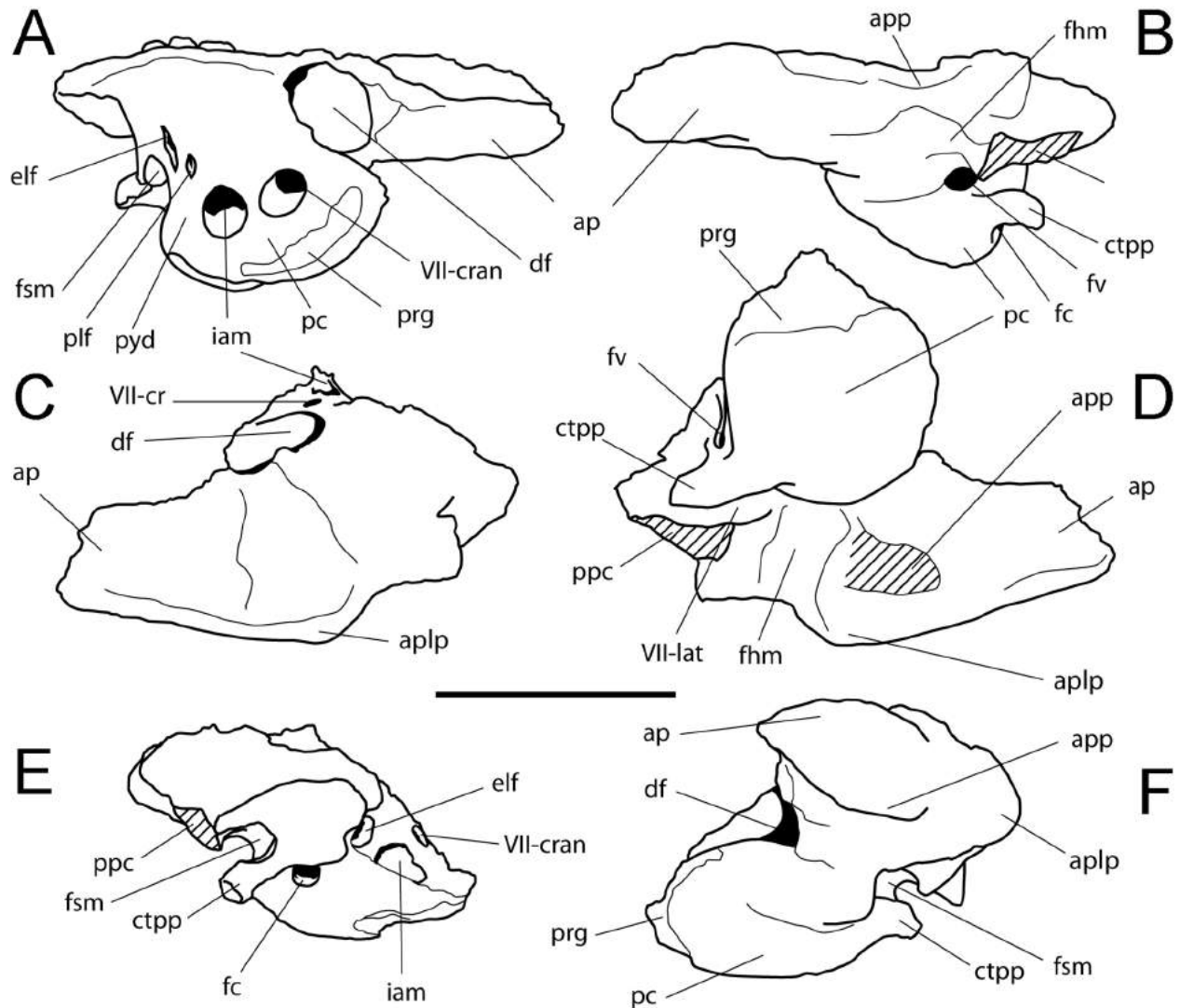
Figure 10. Left periotic of the holotype of *Fragilicetus velponi* **gen.** et **sp. nov.**: A, cranial view; B, lateral view; C, dorsal view; D, ventral view; E, posterior view; F, anterior view. Posterior process not represented. Abbreviations: VII-cran, endocranial opening of the facial canal; VII-lat, lateral opening of the facial canal; ap, anterior process; aplp, lateral projection of anterior process; app, anterior pedicle for tympanic bulla; ctpp, caudal tympanic process; df, dorsal fossa; elf, endolymphatic foramen; fc, fenestra cochleae (round window); fhm, fossa for the head of malleus; fsm, fossa for stapedial muscle; fv, fenestra vestibuli (oval window); iam, internal acoustic meatus; pc, pars cochlearis; plf, perilymphatic foramen; ppc, pedicle for posterior process; prg, promontorial groove; pyd, pyramidal process. Scale bar = 50 mm.

the squamosal cleft suggest some relationship with Balaenopteridae.

Here, a phylogenetic analysis was performed to investigate the relationships of *F. velponi*. The results are discussed in the broader context of mysticete and balaenopterid phylogeny.

METHODS

The phylogenetic analysis was performed by using PAUP 4.0b10 (Swofford, 2002) on the basis of 247 osteological characters and two characters from the baleen scored for 50 taxa. The taxonomic sample included representatives of all the baleen-whale radiations, including five still-undescribed taxa. General information on the undescribed taxa is provided in the Supporting Information. The analysis used the morphological and taxonomic data sets of Bisconti (2010c). The relevant literature used for the character definitions and codings is provided in the Supporting Information. Both the character list and taxon × character matrix are reported in the Supporting Information together with the

list of the specimens examined for comparisons and phylogenetic analysis. Character states were unordered and unweighted under the accelerated transformation character states optimization procedure. The tree bisection-reconnection (TBR) algorithm, with one tree being held at each step during stepwise addition, was used to find the most parsimonious cladograms. Character support at nodes was assessed by a bootstrap analysis with 1000 replicates. A randomization test was performed to evaluate the distance of the cladograms resulting from the TBR search and 10 000 cladograms sampled equiprobably from all the possible cladograms deriving from the matrix (Bisconti, 2005). Morphological transformations at the nodes were reconstructed by the appropriate commands of PAUP.

RESULTS

The TBR search found 13 most parsimonious cladograms whose strict consensus is shown in Figure 11 (tree statistics are provided in the corresponding caption). The principal features of the strict consensus tree are provided in the Supporting Information. Here we focus on the relationships of Eschrichtiidae and Balaenopteridae, with particular emphasis on the relationships of *F. velponi*.

Our results confirm the monophyly of Eschrichtiidae and Balaenopteridae and that they are sister groups. *Fragilicetus velponi* is the most basal balaenopterid species. It is the sister group of the Late Miocene *Plesiobalaenoptera quarantellii* and *Para. baulinensis*, which form a monophyletic clade corresponding to the subfamily Parabalaenopterinae of Zeigler *et al*. (1997). Parabalaenopterinae is the sister group of a clade formed by '*Balaenoptera*' *portisi*, two undescribed Italian taxa (see Supporting Information), and *Pr. cuvieri*. This clade is the sister group of a monophyletic group formed by '*Meg.*' *hubachi* and three additional balaenopterid clades: (1) a clade formed by *Ar. castriarquati* and two undescribed Peruvian taxa; (2) a clade formed by '*B.*' *siberi* and an undescribed Belgian taxon (M. Bisconti & M. Bosselaers, unpubl. data); (3) a clade formed by *Diu. luctoretemergo*, *Meg. novaeangliae*, and the living *Balaenoptera* species. Amongst the living species, *B. musculus* and *B. physalus* are the most basal and *B. borealis* and *B. edeni* are the most derived species, *B. acutorostrata* being the sister group of *B. borealis* and *B. edeni*.

The main results of the 50% majority rule strict consensus tree shown in Figure 12 (tree statistics are provided in the corresponding caption) are provided in the Supporting Information. The bootstrap tree did not distinguish between *Fragilicetus* and Balaenopteridae, suggesting that *F. velponi* is more closely related to later-diverging Balaenopteridae than to Eschrichtiidae.

However, within the *Fragilicetus* + Balaenopteridae clade, the bootstrap tree was only able to distinguish four clades (*B. acutorostrata* + *B. edeni* + *B. borealis*, Parabalaenopterinae, *Pr. cuvieri* + '*B.*' *portisi* + New Belgian taxon 1, and *Ar. castriarquati* + New Peruvian specimen 1). The lack of resolution within Balaenopteridae + *Fragilicetus* suggests that clades in this group are distinguished by limited numbers of characters; therefore, Balaenopteridae is prone to collapse into an unresolved node under a bootstrap approach.

The randomization test found that the mean length of the 10 000 cladograms generated with equal probability from the matrix used for the TBR and bootstrap searches was 2213.0261 steps, which is higher than the 987 steps of the TBR-generated strict consensus tree of Figure 12. The randomization test also found that the mean length of the equiprobable cladograms is higher than the 1144 steps of the 50% majority rule strict consensus tree of Figure 13. In conclusion, the randomization test demonstrated that the matrix used in the present phylogenetic analysis possesses a phylogenetic signal and that the TBR-generated strict consensus tree and the 50% majority rule strict consensus tree are significantly different from chance.

DISCUSSION

SELECTED POINTS ABOUT THE PHYLOGENY OF BALEEN-BEARING WHALES

The present phylogenetic analysis resulted in the most inclusive and well-resolved cladogram depicting phylogenetic relationships amongst baleen-bearing whales available to date (Figs 11, 12). Recently published cladistic analyses of mysticetes have either failed to find well-resolved phylogenetic relationships of Balaenopteridae and thus provided conflicting results about the positions of many mysticete taxa (Deméré *et al*., 2005, 2008; Bisconti, 2010a,b, 2014: 2014; Marx, 2011) or used a reduced taxonomic data set (e.g. Kimura & Hasegawa, 2010; El Adli *et al*., 2014). Most of these conflicts were discussed by Bisconti (2012, 2014), Bisconti *et al*. (2013), and Marx (2011) and are not further discussed here. In this paragraph, we focus on the relationships of Balaenopteridae and Eschrichtiidae and accept the inclusion of *Ca. marginata* within Balaenoidea following Bisconti (2000, 2003, 2012) who thoroughly supported this view.

The sequence of sister groups of Balaenopteroidea is constituted by *Co. oregonensis*, *Ag. moreni*, and *T. sammarinensis*. The positions of these three taxa vary in different cladistic analyses (Bisconti, 2008, 2010b, 2014; Deméré *et al*., 2008; Marx, 2011), probably because they exhibit different intermixings of plesiomorphic and
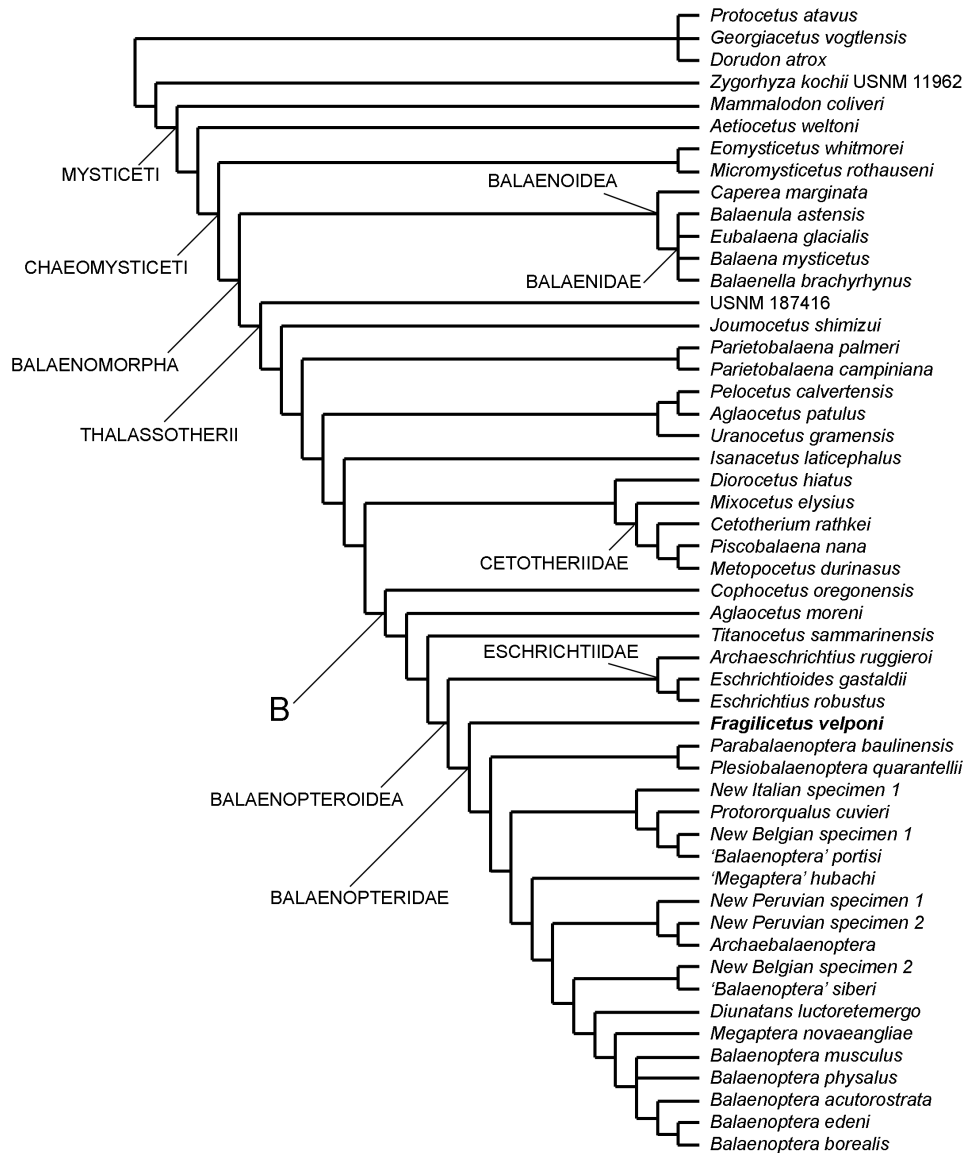
Figure 11. Phylogenetic relationships of ***Fragilicetus velponi* gen.** et **sp. nov.** resulting from the tree bisection-reconnection search. Major mysticete clades are shown. Clade B corresponds to Balaenopteroidea + *Aglaocetus moreni* + *Cophocetus oregonensis* + *Titanocetus sammarinensis* (see text and Supporting Information for further explanation). Tree statistics: tree length = 987; consistency index (CI) = 0.3576; homoplasy index (HI) = 0.6424; CI excluding uninformative characters = 0.3511; HI excluding uninformative characters = 0.6489; retention index = 0.7129; rescaled consistency index = 0.2550.

apomorphic states. All three taxa have a long ascending process of the maxilla that interdigitates with the frontal, and nasal well included within the interorbital region of the frontal. These characters suggest that they are more closely related to the Balaenopteroidea clade. However, the morphologies of the frontal, parietal, and squamosal suggest closer affinity with the basal thalassotherian taxa. Marx (2011) found that *T. sammarinensis* is the sister group of a large clade including Cetotheriidae, *Ca. marginata*, and

Balaenopteroidea. He thus suggested that this species is close in ancestry to a large group of whales that possess the most complicated articulation patterns between the rostrum and frontal (i.e. Cetotheriidae, Eschrichtiidae, and Balaenopteridae), somewhat confirming the results of the present study. Another confirmation is provided by El Adli *et al.* (2014) who found that *Ag. moreni* is the sister group of Balaenopteroidea; they did not include *T. sammarinensis* in their analysis. Their result suggests that *Ag. moreni* is not a typical
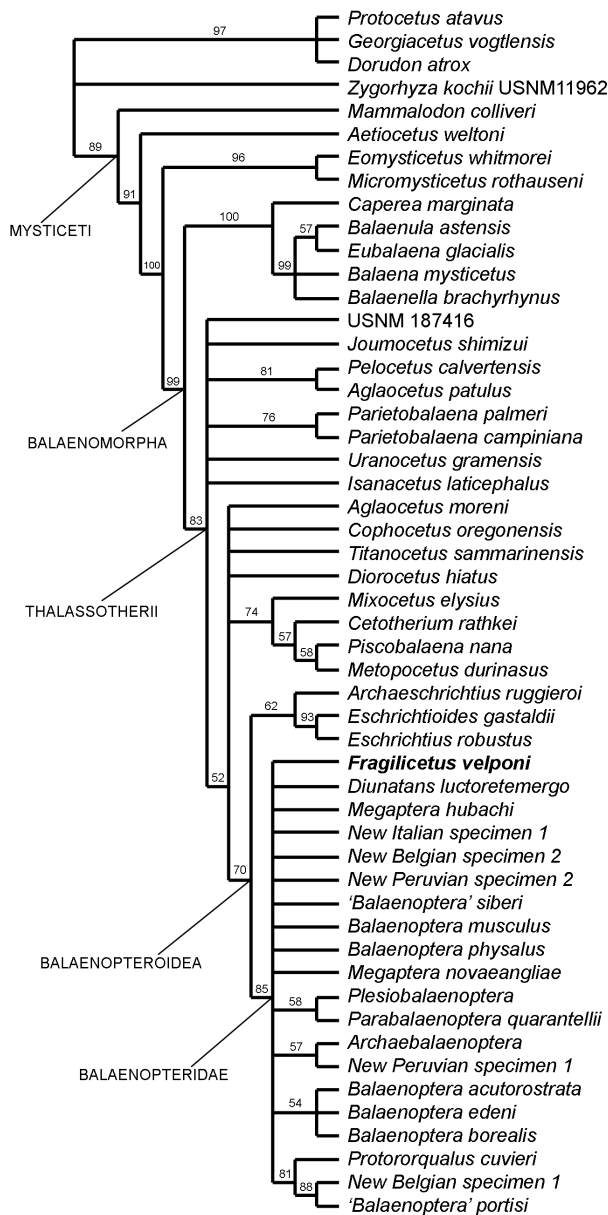
Figure 12. Bootstrap 50% majority rule strict consensus tree. Numbers above the branches are bootstrap support values. See Methods for details. Tree statistics: tree length = 1144; consistency index (CI) = 0.3086; homoplasy index (HI) = 0.6914; CI excluding uninformative characters = 0.3025; HI excluding uninformative characters = 0.6975; retention index = 0.6418; rescaled consistency index = 0.1980.

basal thalassotherian mysticete; rather, it is more closely related to the ancestor of Balaenopteroidea, supporting the hypothesis of relationships provided by Bisconti *et al*. (2013) and the present work. However, further work is certainly needed to better understand the relationships of these interesting species.

Steeman (2007) and Bisconti (2008, 2010c) found morphological evidence of the monophyly of Eschrichtiidae and Cetotheriidae. Steeman (2007) established the superfamily Cetotherioidea Steeman, 2007, to include these two families. After subsequent re-analysis of morphological characters, Bisconti (2010b) rejected the monophyly of Cetotherioidea and found that Cetotheriidae and Balaenopteroidea (including Balaenopteridae and Eschrichtiidae) are sister group to each other. This result was further confirmed by Marx (2011, but note that he found *Ca. marginata* to be the sister group to a clade including Eschrichtiidae and Balaenopteridae), Deméré *et al*. (2008, but note that they also found *Ca. marginata* to be the sister group to a clade including Eschrichtiidae + Balaenopteridae), Bisconti (2012, 2014), Bisconti *et al*. (2013), El Adli *et al*. (2014), and the present work. Based on this series of works, Cetotherioidea is not monophyletic and should be abandoned.

In general, the sister-group relationship of Eschrichtiidae and Balaenopteridae (with or without inclusion of *Ca. marginata*) is well supported in the literature (Deméré *et al*., 2005, 2008; Bisconti, 2010c, 2014; Marx, 2011; Fordyce & Marx, 2012; Bisconti *et al*., 2013; El Adli *et al*., 2014) and the present work confirms this relationship.

The monophyly of Balaenopteridae is not in discussion in morphology-based phylogenetic analyses but it is in molecule-based studies (e.g. Rychel, Reeder & Berta, 2004; May-Collado & Agnarsson, 2006). As reviewed by Deméré *et al*. (2005), in some molecular phylogenies, *Eschrichtius robustus* is well nested within balaenopterid taxa, making Balaenopteridae paraphyletic. The present study supports the placements of *Eschrichtius robustus* and Balaenopteridae in different families, reinforcing the conclusions of other morphology-based works (Barnes & McLeod, 1984; McLeod, Whitmore & Barnes, 1993; Kimura & Ozawa, 2002; Deméré *et al*., 2005, 2008; Marx, 2011; Bisconti, 2010b, 2012, 2014; Bisconti *et al*., 2013; El Adli *et al*., 2014) and thus rejecting the hypothesis of a paraphyletic Balaenopteridae suggested by molecular studies.

By using appropriate commands in PAUP, it was possible to find that seven character states show transformations at the Balaenopteridae node. Unfortunately, all of these character states have consistency index < 1, suggesting that they are homoplastic (Balaenopteridae synapomorphies found by PAUP are listed in the Supporting Information). This finding demonstrates that there is a high amount of homoplasy in at least some parts of the mysticete phylogenetic tree, suggesting that recurring evolution of character states is a normal phenomenon in these mammals. The large amount of homoplasy in the morphological data set could be one of the reasons for the different topological results found by different authors with respect to the phylogenetic
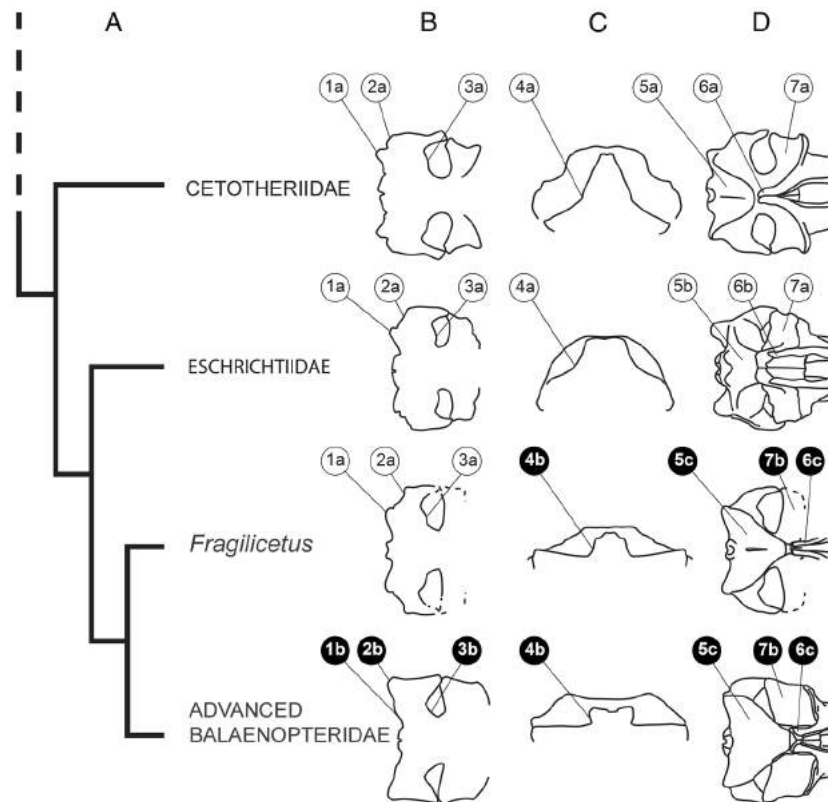
Figure 13. Schematic diagram showing the phylogenetic relationships of *Fragilicetus velponi* **gen.** et **sp. nov.** and some morphological transformations as reconstructed from the cladistic analysis presented in the Supporting Information. A, phylogenetic relationships of Cetotheriidae, Eschrichtiidae, *Fragilicetus* **gen. nov.**, and later Balaenopteridae. B, outlines of skulls in ventral view to show the morphology of the respective families. C, outlines of skulls in anterior view. D, schematic diagram showing dorsal skull architectures. Numbers in black circles correspond to typical balaenopterid character states. Numbers in white circles correspond to cetotheriid and eschrichtiid character states. Numbers correspond to the following: 1, protrusion of posterolateral corner of exoccipital (a, strong; b, slight); 2, posterior projection of postglenoid process of squamosal (a, no; b, yes); 3, squamosal bulges into the temporal fossa (a, yes; b, no); 4, supraorbital process of the frontal abruptly depressed from the interorbital region (a, no; b, yes); 5, shape of supraoccipital (a, triangular with narrow anterior border; b, triangular with broad anterior border; c, posterior portion widely expanded and lateral borders highly converging anteriorly); 6, articulation of rostrum and frontal (a, maxilla superimposed onto the interorbital region of the frontal, maxilla converging towards the midline posteriorly, premaxilla absent; b, premaxilla strongly superimposed onto the interorbital region of the frontal and maxilla reduced; c, maxilla superimposed onto the interorbital region of the frontal, premaxilla present); 7, supraorbital process of the frontal (a, gently descending or slightly depressed; b, abruptly depressed from the interorbital region of the frontal). Not to scale.

relationships of Balaenopteridae. Additional reasons were discussed by Deméré *et al.* (2005) and Marx (2011) and concern taxonomic uncertainties about the status of the *Balaenoptera brydei–omurai–edeni–borealis* complex.

PHYLOGENETIC RELATIONSHIPS OF
FRAGILICETUS VELPONI

Skull morphology provides most of the characters used in morphology-based studies of the phylogenetic relationships of mammals, and mysticetes are no exception (e.g. Bouetel & de Muizon, 2006; Whitmore &

Barnes, 2008). For this reason, the availability of reasonably complete skulls with petrosals can be of great help in deciphering the evolution of lineages of the Mysticeti tree.

The discovery of *F. velponi* has helped to decipher the phylogenetic relationships of gray whales and rorquals as it shows a mix of morphological features that is intermediate between them. Its inclusion in the comprehensive phylogenetic analysis presented here confirmed the monophyly of both Eschrichtiidae and Balaenopteridae, and the sister-group relationship of these families to the exclusion of Cetotheriidae. The inclusion of *F. velponi* and additional balaenopterid taxa

under description led to a well-resolved hypothesis of the phylogeny of Balaenopteridae in which several new and undescribed balaenopterid clades are included for the first time. The consequences of this phylogenetic hypothesis for the systematics, taxonomy, and paleobiogeography of Balaenopteridae will be fully analysed elsewhere.

Deméré *et al*. (2005) and Marx (2011) both obtained high levels of resolution within Balaenopteridae but the relationships that they illustrated differed from each other and were also different from the relationships presented by Bisconti (2010c), Bisconti *et al*. (2013), and the present work. Deméré *et al*. (2005) found a paraphyletic *Balaenoptera*, a result that was not confirmed by either Marx (2011) or the present work. Marx (2011) and Boessenecker (2013) found evidence for a monophyletic *Megaptera* including *Meg. novaeangliae*, '*Megaptera*' *miocena*, and '*Meg.*' *hubachi*, but this result was in disagreement with Deméré *et al*. (2005) and Bisconti *et al*. (2013), who found that *Megaptera* (including the above taxa) is polyphyletic. As pointed out by Deméré *et al*. (2005) and Marx (2011) it will be difficult to find a consensus about the relationships of living Balaenopteridae as an amount of uncertainty exists about the taxonomic status and morphological differentiation within the *Balaenoptera omurai*–*brydei*–*borealis*–*edeni* complex. Additionally, as pointed out by Bisconti *et al*. (2013) and this work, such a consensus is likely to be prevented by the large amount of homoplasy present in the morphological data set.

By means of the present phylogenetic results, *F. velponi* can be considered as a stem balaenopterid whale still retaining archaic characters. Given its position in the hypothesis of phylogeny presented here, its morphology should be considered close to that of the ancestor of Balaenopteridae. *Fragilicetus velponi* cannot be considered to be the common ancestor of later Balaenopteridae with certainty because it lived around 5 Mya and Balaenopteridae originated around 12 Mya (Deméré *et al*., 2005). However, it may reveal details of the morphological transformations that led to the more advanced balaenopterid morphotype (Fig. 13). In particular, *F. velponi* shows an intermediate condition between Eschrichtiidae and later balaenopterids as it exhibits apomorphic balaenopterid characters (transverse expansion of the anterior part of the temporal crest that forms a dorsal roof of the anterior portion of the temporal fossa, more anterior placement of the posterior apex of the lambdoid crest, transverse reduction of the distance between the zygomatic process of the squamosal and the medial wall of the temporal fossa, abruptly depressed supraorbital process of the frontal) intermixed with eschrichtiid characters (squamosal bulge, transverse projection of the temporal crest, anterior placement of the posterolateral corner of the exoccipital).

PAUP found that 23 character states show changes at the Balaenopteridae node but all of them had a consistency index < 1 (see Supporting Information). This means that all the diagnostic features of this clade are affected by homoplasy and, probably, this fact is the reason for the collapse of the Balaenopteridae node into an unresolved polytomy in the bootstrap tree (Fig. 13). In our opinion, researchers should realize that the levels of homoplasy observed within the Balaenopteridae will be a major problem in future phylogenetic analyses of this clade and will represent a difficult obstacle to overcome in attempts to determine the true relationships of living and fossil rorquals and humpbacks. Critical to removing this obstacle will be: (1) a complete re-examination of the morphological characters used in phylogenetic analyses; (2) a reassessment of the taxonomy of living and fossil taxa. As a whole, these tasks will probably take years to be accomplished.

FUNCTIONAL IMPLICATIONS IN THE ORIGIN OF BALAENOPTERID FEEDING BIOMECHANICS

The availability of a well-resolved phylogenetic hypothesis of relationships for Balaenopteroidea (Fig. 11) allows a preliminary reconstruction of the sequence of the morphological transformations that occurred during the origin of Balaenopteridae. The discovery of *F. velponi* helps in determining which transformations occurred at earlier stages and which at later stages of balaenopterid origin. As shown in Figure 13, *F. velponi* retains a posteriorly protruding exoccipital and squamosal bulge, which give the posterior portion of its skull an eschrichtiid-like or cetotheriid-like shape. The more anterior portion is more balaenopterid-like as it shows an abruptly depressed and horizontal supraorbital process of the frontal, transversely unexpanded anterior end of the supraoccipital, and transversely extended temporal crests covering the medial wall of the temporal fossa in dorsal view.

Some of these characters have important functional implications. As far as the exoccipital is concerned, it must be noted that the differential extension of this bone is probably related to the attachment sites for the obliquus capitis superior, the trachelo-occipitalis, and the longissimus muscles, which are related to neck movements (Barnes & McLeod, 1984). The reduction of the exoccipital protrusion in Balaenopteridae is probably related to the reduction in the functions of these muscles. As *F. velponi* preserves wide and robust attachment sites for the neck muscles, it is hypothesized that it was able to perform a certain degree of lateral head rotation.

Functional implications can also be inferred from the morphology of the anterior portion of the temporal fossa and of the supraorbital process of the frontal. The presence of a flat supraorbital process of the frontal, a

dorsally covered anterior portion of the temporal fossa, and a more anterior location of the lambdoid crest in the ancestor of Balaenopteridae suggest that the rearrangement of the temporal muscle played a crucial role in the origin of balaenopterid whales. This is not surprising as several scholars have hypothesized that the key innovation of Balaenopteridae is a novel and more advanced capacity for mass predation using gulp feeding (e.g. Lambertsen *et al.*, 1995; Goldbogen *et al.*, 2007); this feeding mode is associated with peculiar characters of the temporalis muscle, including the presence of its tendinous part, known as the frontomandibular stay, and the frontal (Lambertsen *et al.*, 1995; Croll & Tershy, 2002). The origin of an abruptly depressed and flat supraorbital process of the frontal played a crucial role in the evolution of balaenopterid gulp feeding because it works as the principal attachment site for the frontomandibular stay, which enhances and strengthens the mechanical linkage between the skull and the lower jaw (Lambertsen *et al.*, 1995). Here it is thus speculated that changes in the morphology and function of the temporal fossa triggered the process that led to the origin of Balaenopteridae. This process occurred more than 12 Mya. The survival of *F. velponi* up to *c.* 5 Mya implies the existence of a *c.* 7-Myr-long ghost lineage starting from the common ancestor of Balaenopteridae; the existence of this ghost lineage was unknown to science up to the discovery of *F. velponi*.

Even though *F. velponi* has helped in the understanding of some aspects of the origin of Balaenopteridae, it is still not possible to dismantle this process into smaller steps and understand how and when the optimized biomechanics of balaenopterid feeding was fully realized. Several new fossil balaenopterids are under study and it is to be hoped that they will be of help in understanding the evolution of this intriguing marine mammal group.

CONCLUSIONS

The new genus *Fragilicetus* is established based on the new fossil species *F. velponi*. *Fragilicetus* is the sister group of later Balaenopteridae; Eschrichtiidae is the sister group of the Balaenopteridae clade. *Fragilicetus velponi* shares several characters with Eschrichtiidae, e.g. the prominent bulge of the squamosal into the temporal fossa and the posterior protrusion of the posterolateral corner of the exoccipital; it shares with later Balaenopteridae the shape of the abruptly depressed supraorbital process of the frontal, details of the articulation of the rostrum with the frontal, and the shape of the supraoccipital. A phylogenetic analysis revealed that *F. velponi* is closer to Balaenopteridae than to Eschrichtiidae. The phylogenetic analysis also revealed high levels of homoplasy in the Balaenopteroidea clade but these did not prevent the construction of a highly resolved strict consensus tree. However, the high levels of homoplasy prevent unambiguous diagnoses of the internal nodes of Balaenopteridae. The morphological characters observed in *F. velponi* showed that the appearance of a wide and flat, abruptly depressed supraorbital process of the frontal and an anteriorly constricted supraoccipital preceded the loss of the

Figure 14. Artistic interpretation of possible interaction between a large shark and ***Fragilicetus velponi* gen.** et. **sp. nov.** as suggested by the shark bite marks on the skull of the holotype specimen shown in Figure 3. The human in the upper right corner serves as a size reference. Illustration by Mark Bosselaers.

squamosal bulge and the loss of strong attachment sites for neck muscles in the evolutionary process leading to the balaenopterid lineage. These characters have functional implications respectively related to the anterior placement of the attachment for the temporalis muscle and to the preservation of a mobile head in the earliest phases of balaenopterid evolution.

Finally, the fossil described in the present paper is a demonstration of direct interaction between sharks and mysticetes in the Pliocene; an illustration of this interaction is shown in Figure 14.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Measurements of the holotype skull.
Table S2. Institutional abbreviations.