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To cite this article: Romala Govender, Michelangelo Bisconti & Anusuya Chinsamy (2016): A late Miocene–early Pliocene baleen whale assemblage from Langebaanweg, west coast of South Africa (Mammalia, Cetacea, Mysticeti), *Alcheringa: An Australasian Journal of Palaeontology*

To link to this article: <http://dx.doi.org/10.1080/03115518.2016.1159413>



Published online: 22 Jun 2016.



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# A late Miocene–early Pliocene baleen whale assemblage from Langebaanweg, west coast of South Africa (Mammalia, Cetacea, Mysticeti)

ROMALA GOVENDER, MICHELANGELO BISCONTI and ANUSUYA CHINSAMY

GOVENDER, R., BISCONTI, M. & CHINSAMY, A., June 2016. A late Miocene–early Pliocene baleen whale assemblage from Langebaanweg, west coast of South Africa (Mammalia, Cetacea, Mysticeti). *Alcheringa* 40, xxx–xxx. ISSN 0311-5518

Knowledge of post-Eocene cetaceans from Africa is very poor with almost nothing known about this group from southern Africa except for the diverse trawled ziphiids. Langebaanweg, a locality yielding prolific Miocene–Pliocene fossils on the southwestern Cape coast of South Africa, preserves terrestrial and marine biotas in juxtaposition. Palaeoenvironments vary from a marine shoreline to a lagoon and estuary and later a shallow marine environment and include several microhabitats. Fragmentary preservation of the cetacean skeletons suggests that they were transported before burial. This first detailed analysis of the Mio-Pliocene mysticete fossils from Langebaanweg uses the petrotympanic region to taxonomically identify specimens. Three un-named species of balaenopterid Mysticeti represent a *Plesiobalaenoptera*-like form, but it is premature to erect a new taxon based on this fragmentary material. The remaining material is too poorly preserved to be identified with confidence.

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Key words: Balaenopteridae, *Plesiobalaenoptera*, petrotympanic, *Balaenoptera*, Varswater Formation.

THE EXTANT cosmopolitan cetacean community along the South African coast includes pelagic and coastal mysticetes, odontocetes and beaked whales, with the best known being *Eubalaena australis* (southern right whale). *Eubalaena australis* and *Megaptera novaeangliae* (humpback whale) migrate along the east and west coasts to their calving and mating grounds, and then return to their feeding grounds in the Antarctic (Cummings 1985, Winn & Reichley 1985, Best 2007). *Balaenoptera brydei*/*B. edeni* (Bryde's whale) and numerous dolphin species live offshore year round, and occasional transient *Orcinus orca* (killer whales) are also seen off the South African coast (see Best 2007).

As a whole, our knowledge of the past diversity and evolution of African cetaceans is poor. The Eocene fossil cetaceans from Egypt have certainly played an important role in understanding the early evolution of whales (Barnes & Mitchell 1978, Gingerich 2008, 2010), but the post-Eocene cetacean record is not well known (see Barnes & Mitchell 1978, Gingerich 2010). The only exception is the trawled beaked whales (Ziphiidae) from South Africa, which revealed previously unrecognised diversity in Southern Hemisphere

beaked whales (Bianucci *et al.* 2007, 2008). Additionally, a beaked whale from freshwater deposits in northern Kenya was linked to the extant *Mesoplodon* and *Hyperoodon* (Mead 1975, Barnes & Mitchell 1978, Wichura *et al.* 2015). Two new fossil mysticete taxa from Angola are closely related to *Caperea*, which triples the known diversity of the Neobalaenidae (Graf *et al.* 2011). These taxa extend the range of the neobalaenids into the Miocene phase of the Benguela Large Marine Ecosystem (Graf *et al.* 2011).

Langebaanweg is an important palaeontological locality on the west coast of South Africa and yields a diverse vertebrate fauna (Hendey 1981, 1989, Roberts *et al.* 2011). Studies of the marine mammals (Govender *et al.* 2011, 2012, Govender & Chinsamy 2013, Govender 2015), sharks (Tulu & Chinsamy-Turan 2011) and other marine vertebrates have been undertaken that offer to greatly expand the fossil record of these groups in Africa. The fossil cetacean assemblage from 'E' Quarry incorporates taxa that were living along South Africa's coast during the Messinian to Zanclean. This study presents the first detailed investigation of mysticete fossils from Langebaanweg. Fragmentary unidentified odontocete remains are not examined here. The material constitutes well-preserved tympanic bullae, petrosals and other cranial elements, which represent both

adults and young animals. The fauna is compared with assemblages from other sites in the Southern Hemisphere to understand the taxonomic composition of mysticete communities in the Miocene and Pliocene.

*Institutional Abbreviations.* AMNH, American Museum of Natural History, New York; MSNT, Museo di Storia Naturale e del Territorio, Università di Pisa; RBINS M., Royal Belgian Institute of Natural Sciences, Brussels; SAM-PQL, South African Museum Quaternary Palaeontology Langebaanweg; SAM-MBK-ZM, South African Museum Marine Biology Collections.

## Geological setting

Langebaanweg (32°57'19.4"S, 18°6'49.9"E) is located on the stable platform of the South African west coast, 13 km inland of the current coastline (Roberts *et al.* 2011; Fig. 1A, B). The Varswater Formation at 'E' Quarry, spans the middle Miocene (Langhian) to lower Pliocene (Zanclean; Tankard 1974, Hendey 1989, Roberts *et al.* 2006, Roberts *et al.* 2011; Fig. 1B, C). The fossil-rich Langeberg Quartzose Sand Member and Muishond Fontein Pelletal Phosphorite Member are concentrated within an "abbreviated" (Roberts *et al.* 2011, p. 208) stratigraphic interval of *ca* 26–30 m above sea level (Roberts *et al.* 2011; Fig. 1B, C) and are associated with numerous transgressive-regressive episodes (Tankard 1974, Hendey 1989, Roberts *et al.* 2006, 2011). The 'E' Quarry bone bed is at the base of the Muishond Fontein Pelletal Phosphorite Member within a channel fill that has eroded into the Langeberg Quartzose Sand Member (Fig. 1C; Smith & Haarhoff 2006, Roberts *et al.* 2011).

The palaeoenvironmental history of Langebaanweg included a high-energy shallow marine system during the late Miocene (Messinian), incorporating sandy and rocky beaches represented by the Konings Vlei Gravel Member (Kensley 1972, Roberts *et al.* 2011). Later, in the early Pliocene (Zanclean), the Langeberg Quartzose Sand Member was deposited in a lagoon or estuarine setting protected from wave action but open to the sea (Kensley 1977).

The Muishond Fontein Pelletal Phosphorite Member accumulated in a shallow embayment sheltered from the open ocean by granitic islands during the early Pliocene transgression (Smith & Haarhoff 2006). This transgressive cycle is slightly younger than the global sea level cycle T7, which provides a general age estimate of *ca* 5.15 Ma for the Langeberg Quartzose Sand Member and Muishond Fontein Pelletal Phosphorite Member at Langebaanweg (Roberts *et al.* 2011, and references therein).

## Materials and methods

Thirteen curated cetacean fossils form the basis for the descriptions (Table 1). The sampled deposits extend over 0.28 km<sup>2</sup> and specimens were collected from 1970

to 1976 from all fossiliferous beds within the Varswater Formation (Hendey 1976). The various assemblages may also include specimens from older strata. In particular, the fluvial deposits (bed 3aS and 3aN) may include material reworked from the LQSM deposits upstream (Hendey 1981; Fig. 1C).

Fossils were collected from the surface and small sediment samples screened in the field or in the laboratory using 5 mm and 10 mm mesh, as well as bulk sediment samples screened in the field (Hendey 1976, 1981, 1989). Material exposed by mining yielded specimens that are out of stratigraphic context, damaged and disassociated (Hendey 1981). Some exposed remains might be associated (Hendey 1981). Excavations in 1966, 1969, 1970, 1975 and 1976 processed a few to around several hundred cubic metres of sediment (Hendey 1981). The small-scale uncontrolled excavations centred around significant fossils found on the surface (Hendey 1981).

Anatomical terms follow Mead & Fordyce (2009) for odontocetes with amendments cited in the text.

## Taphonomy and preservation

The cetacean vertebrae have cracked surfaces resembling weathering stages 3–5 of Behrensmeyer (1978), indicating that they were exposed for some time before burial with cracking and splintering occurring *in situ*. Skeletal elements from the dig site also show evidence of point compression fractures on long bones, together with greenstick fractures that are the result of trampling by hooved animals during or immediately after burial in unconsolidated sediment (Smith & Haarhoff 2006). Some fossils may have been deposited by flooding or as a consequence of the scour pools being used as watering holes (Smith & Haarhoff 2006).

Tooth marks on the cetacean fossils demonstrate scavenging by sharks (Govender & Chinsamy 2013). There is also evidence of bone damage consistent with terrestrial carnivores (RG unpublished data). These could be the result of bones being moved from the beach or estuary to more secure areas for consumption. The surface modifications on the bone include scratches, cracking and fractures that indicate that deposition occurred after exposure to the elements (Smith & Haarhoff 2006).

## Description of selected mysticete specimens

Several mysticete ear and skull bones were found in members of the Varswater Formation at 'E' Quarry, Langebaanweg, Western Cape, South Africa (Table 1). The taxonomic assignment of these specimens is hampered by poor preservation.

Most of the specimens are represented by tympanic bullae. According to Oishi & Hasegawa (1994) and Bisconti (2010a), it is almost impossible to use this

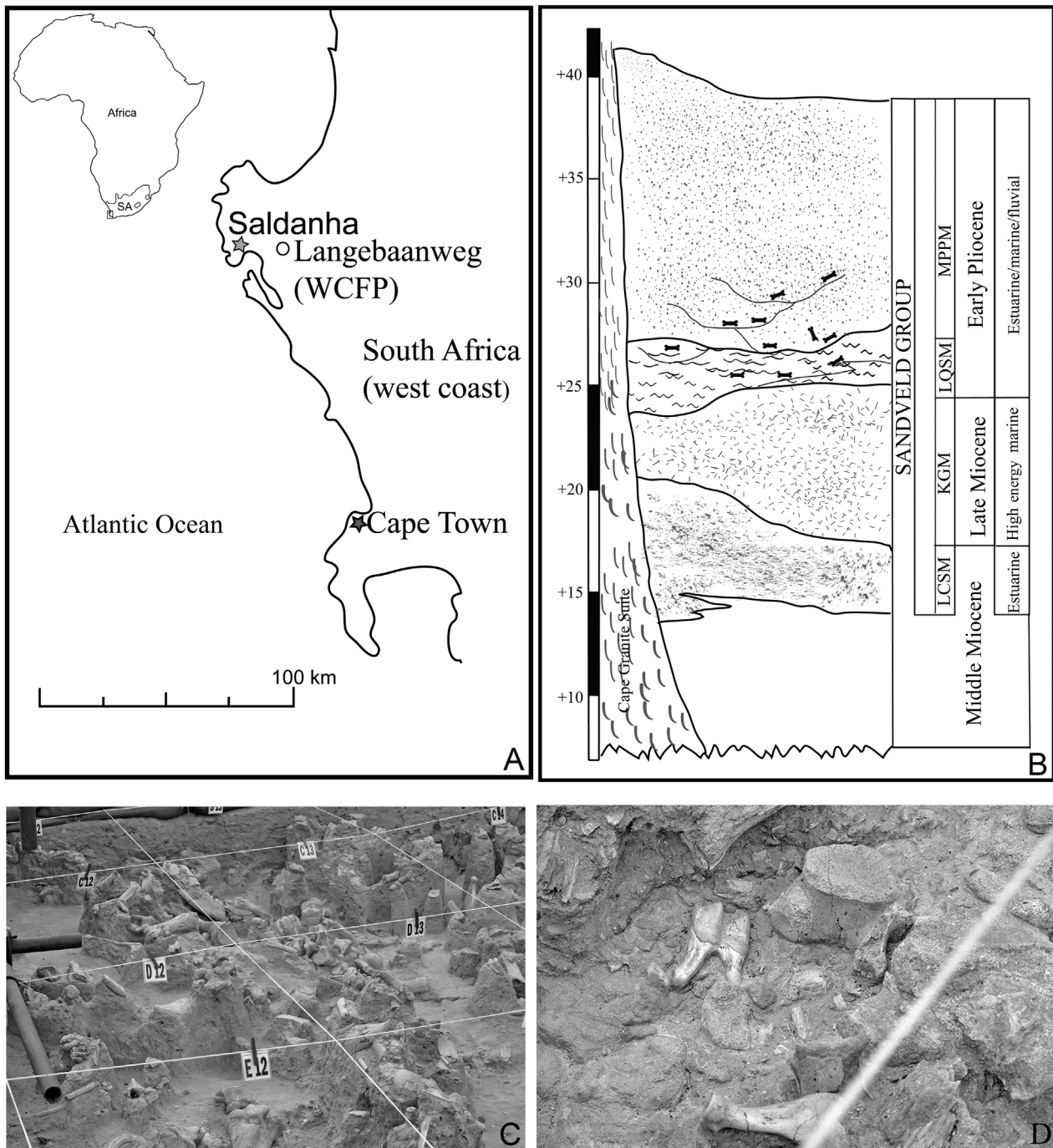


Fig. 1. Map showing the locality of the discovery at Langebaanweg. **A**, Position of Langebaanweg (WCFP – West Coast Fossil Park) along South Africa’s west coast. **B**, Stratigraphic section of Langebaanweg [Langeenheid Clayey Sand (LCSM), Konings Vlei Gravel (KGM), Langeberg Quartz Sand (LOSM) and Muishond Fontein Pelletal Phosphorite Members (MPPM)] (after Roberts *et al.* 2011) (m above sea level). **C**, Fossils in the lag deposit at Langebaanweg (West Coast Fossil Park). **D**, Juxtaposition of the marine (whale vertebrae; seal radius in foreground) and terrestrial vertebrate fossils.

anatomical region for accurate species-level assignment, although it may be used to distinguish families and, in some cases, genera.

The tympanic bullae from ‘E’ Quarry are consistent with balenopterids (see below), with three elements (SAM-PQL-20482, SAM-PQL-55001, and SAM-PQL-21230) associated with petrosals. Specimens,

SAM-PQL-40089 (left bulla), SAM-PQL-14239 (left bulla), SAM-PQL-28776 (left bulla), SAM-PQL-52004 (left bulla), SAM-PQL-69797 (right bulla), are too poorly preserved to allow detailed descriptions and comparisons.

SAM-PQL-20482 (Figs 2, 3)

Taxa	Specimen	Anatomical part	Discovery site	Approximate age
<i>Plesiobalaenoptera</i> -like taxa	SAM-PQL20482	Left tympanic bulla and periotic	Konings Vlei Gravel Member. South end of East area, bed 1 (coarse grit)	Late Miocene
	SAM-PQL-55001	Right tympanic bulla, left and right incomplete periotics and skull fragments	?LQSM	?Earliest/early Pliocene
	SAM-PQL-21230	Left tympanic bulla and incomplete periotic and skull fragments including occipital condyles	Either bed 1 (KGM) or bed 2 (LQSM)	Late Miocene or earliest/early Pliocene
<i>Balaenopteridae</i> gen. et sp. indet.	SAM-PQL40089	Left tympanic bulla	BCW Cut 1. MPPM	Early Pliocene
	SAM-PQL-52004	Left tympanic bulla	Pickup Rock Platform. ?LQSM or MPPM	?Earliest/early Pliocene
	SAM-PQL-2686	Right tympanic bulla	MPPM Bed 3aS	Early Pliocene
	SAM-PQL-14239	Right tympanic bulla	B Elephant site, west of road, LQSM	Earliest/early Pliocene
	SAM-PQL28776	Right tympanic bulla	TCWW	
	SAM-PQL46318	Left tympanic bulla	MPPM – G7 1976/2	Early Pliocene
	SAM-PQL69797	Right tympanic bulla	MPPM – Dump 10	Early Pliocene
	SAM-PQL-56477	Two mandibular rami with skull fragments	Uncertain	Uncertain
SAM-PQL50265	Right tympanic bulla	MPPM – bed 3aN	Early Pliocene	
SAM-PQL-69797	Right tympanic bulla	Dump 8 Uncertain	Uncertain	

Table 1. Miocene and Pliocene mysticete specimens from ‘E’ Quarry, Langebaanweg, Varswater Formation, Western Cape Province, South Africa. All the specimens are housed at Iziko South African Museum, Cape Town.

*Locality and unit.* ‘E’ Quarry, Langebaanweg, Western Cape Province, South Africa, Varswater Formation. Konings Vlei Gravel Member (KGM). South end of east area, KGM (bed 1, coarse grit).

*Description and comparisons.* SAM-PQL-20482 includes a seemingly associated left petrosal (Fig. 2A–D) and tympanic bulla (Fig. 3A–D). The relatively long posterior process of the petrosal is transversely narrow (Fig. 2A–C) and flattened ventrally. Anteriorly, the stylomastoid fossa appears as a notch between the anteriormost portion of the posterior process and the promontorium (pars cochlearis). The broken anterior process is short and triangular in both dorsal and ventral views (Fig. 2A). In dorsal view, the border of the anterior process is straight, whereas the medial border is concave. The promontorium (i.e., the eminence that forms the ventromedial part of the petrosal) is markedly elongated along both the anteroposterior and transverse axes (Fig. 2A). The internal acoustic meatus is separated from the endocranial opening of the facial canal by a wide crista transversa (Fig. 2D). The endocranial opening of the facial canal is located lateral to the rim of the internal acoustic meatus and forms a long groove running along the anterior surface of the crista transversa. The groove ends close to the anterior portion of the rim of the internal acoustic meatus (Fig. 2D). A similar groove is present in several mysticete taxa including cetotheriids (e.g., *Piscobalaena*

*nana*) and balaenopterids (e.g., *Plesiobalaenoptera quarantellii*). No groove is evident ventral to the internal acoustic meatus. The aperture for the vestibular aqueduct (endolymphatic foramen) opens on the floor of a wide and elliptical fossa that is located posterior to the internal acoustic meatus. The fenestra cochleae (round window) is not separated from the aperture for the cochlear aqueduct (perilymphatic foramen); this character is present in *Eschrichtius robustus*, some juvenile/foetal balaenopterids (Bisconti 2001) and in fossil balaenopterid taxa, such as ‘*Balaenoptera*’ *sibbaldina* and ‘*Balaenoptera*’ *musculoides*. The dorsal surface of the central portion of the petrosal is dome-shaped and slopes gently anteriorly.

The petrosal of SAM-PQL-20482 (Fig. 2A–D) has two characters that are typical of Balaenopteroidea: (1) a triangular anterior process and (2) an elongated promontorium along both the anteroposterior and transverse axes. A clearly triangular anterior process with pointed apex is typical of Balaenopteridae, whereas in Eschrichtiinae, the anterior process has a more irregular medial border and rounded apex (Ekdale *et al.* 2011, Marx & Fordyce 2015). Therefore, the triangular anterior process with pointed apex suggests a closer balaenopterid affinity. The absence of a groove ventral to the internal acoustic meatus (promontorial groove of Ekdale *et al.* 2011) is a feature typical of extant balaenopterids but not of extinct species of this family, e.g., the promontorial groove is well developed in

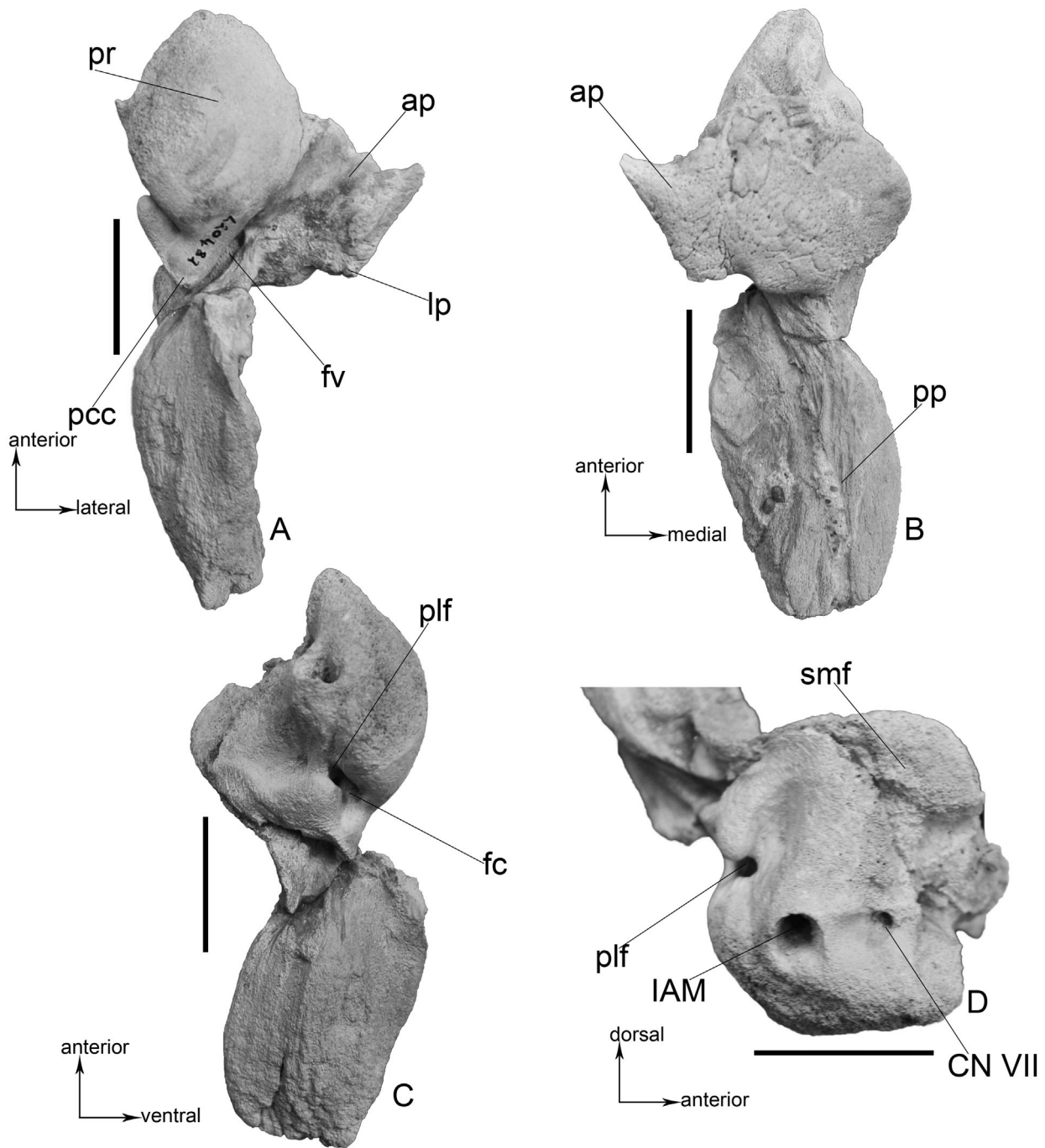


Fig. 2. SAM-PQL-20482. Left petrosal in A, ventral; B, dorsal; C, posterior; and D, dorsomedial views (enlargement). Scale bars = 30 mm. Abbreviations: ap, anterior process; elf, endolymphatic foramen; fv, fenestra vestibuli (oval window); fc, fenestra cochleae (circular window); lp, lateral projection of the anterior process; pr, promontorium; plf, perilymphatic foramen; pp, posterior process; pcc, posterior cochlear crest; smf, suprimeatal fossa; sm, stylomastoid fossa; CN VII, endocranial opening of the facial canal; IAM, internal acoustic meatus.

*Plesiobalaenoptera quarantellii* (Bisconti 2010a). The domed dorsal surface of the central portion of the petrosal is plesiomorphic among Miocene and Pliocene balaenopterids including the holotype of *Plesiobalaenoptera quarantellii* and ‘*Balaenoptera*’ *sibaldina* (RBINS M. 737), as well as ‘*Balaenoptera*’ *musculoides* (RBINS M. 752; see Deméré *et al.* 2005 for a preliminary assessment of the taxonomy of these species). There is no anatomical name for this domed structure provided by Mead & Fordyce (2009). Ekdale

*et al.* (2011) referred to the region as the tegmen tympani. Luo & Gingerich (1999), likewise, defined it as the tegmen tympani (superior process). As documented by Ekdale *et al.* (2011), the tegmen tympani is not present in extant balaenopterids. On the contrary, it is a character typical of some early-diverging thalassotherian mysticetes (*sensu* Bisconti *et al.* 2013), such as *Pelocetus calvertensis*, *Parietobalaena palmeri*, *P. campiniana* and *Isanacetus laticephalus*. In SAM-PQL-20482, the fenestra cochleae is confluent with the aperture of the

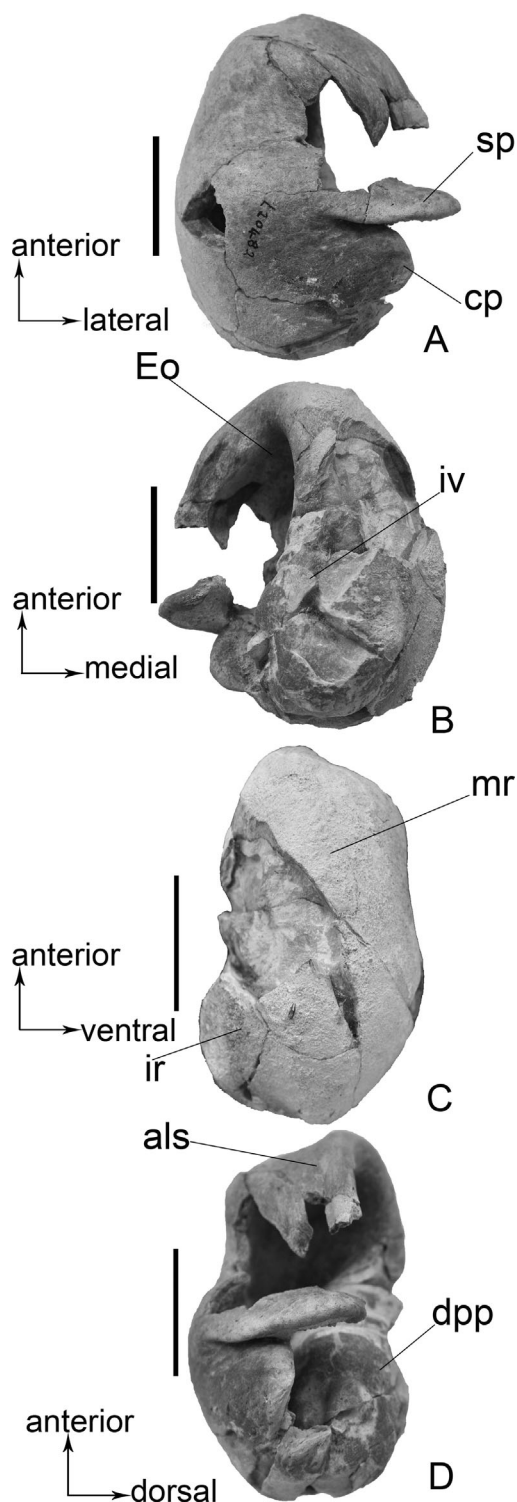


Fig. 3. SAM-PQL-20482. Left tympanic bulla in **A**, ventral; **B**, dorsal; **C**, medial; and **D**, lateral views. Scale bars = 30 mm. Abbreviations: als, anterolateral shelf; cp, conical process; dpp, dorsal posterior prominence; Eo, Eustachian outlet; ir, involucrum ridge; iv, involucrum; mr, main ridge; sp, sigmoid process.

cochlear aqueduct (Fig. 2C); this feature is evident in *Balaenoptera borealis* and taxonomically equivocal specimens of '*Balaenoptera*' *sibbaldina* (RBINS M. 737) and '*Balaenoptera*' *musculoides* (RBINS M. 752).

Unfortunately, the feature can not be determined in the holotype of *Plesiobalaenoptera quarantellii* because matrix obscures this part of the petrosal (see images provided by Bisconti 2010a).

The tympanic bulla (Fig. 3A–D) of SAM-PQL-20482 is balaenopterid-like as it shows a circular anterolateral expansion (*sensu* Bisconti 2010a) continuous with the bone's anterior corner (Fig. 3A). The main ridge reaches the anterior border and protrudes slightly onto the posterior border. In dorsal view, the medial border is sinuous and concave along its mid-length (Fig. 3B). The Eustachian outlet is high and the tympanic cavity deep. The sigmoid process is strong and transversely elongated; the conical process is tall but dorsally convex and rounded. The involucrum ridge retracts from the medial edge and, thus, fails to reach the posterior end. In medial view, the main ridge is narrow and parallel to the involucrum.

The tympanic bulla of SAM-PQL-20482 (Fig. 3A–D) resembles that of *Balaenoptera musculus* and *Balaenoptera physalus* in the protruding anteromedial corner. The posterior border of the bulla is morphologically similar to that of *B. physalus*. The involucrum ridge does not reach the posterior end of the tympanic bulla as in *B. musculus*, *B. mysticetus* and *Megaptera* (Ekdale *et al.* 2011). However, the involucrum surface is sinusoidal like those of *B. musculus*, *B. borealis*, *Megaptera* and *Eschrichtius robustus* (Ekdale *et al.* 2011). SAM-PQL-20482 is similar to *Plesiobalaenoptera quarantellii* in that the anterior margin of the tympanic bulla is elongated (Bisconti 2010a). The sigmoidal process of SAM-PQL-20482 is transversely directed, and the conical process is long and triangular. There is a high Eustachian outlet and the anterolateral shelf is similarly well developed as in *Plesiobalaenoptera*.

SAM-PQL-55001 (Figs 4–6)

*Locality and unit.* 'E' Quarry, Langebaanweg, Western Cape Province, South Africa, Varswater Formation. ?LQSM.

*Description and comparisons.* This specimen includes incomplete left and right petrosals (Fig. 4A–F), the right tympanic bulla (Fig. 5A–D) and other poorly preserved skull fragments (Fig. 6A–F).

The posterior process of the petrotympanic is attached to the tympanic bulla (Fig. 5A). It is stocky and short with a flat ventral surface. The anterior process is triangular in dorsal view with externally convex lateral and medial edges (Fig. 4A). The anterior process is convex between the dorsal mid-section of the petrosal (tegmen tympani) and its anterior apex. The promontorium is both transversely and anteroposteriorly elongate (Fig. 4A, E). The outline of the internal acoustic meatus is circular; the endocranial opening of the facial canal is separated from the internal acoustic meatus by a relatively thick crista

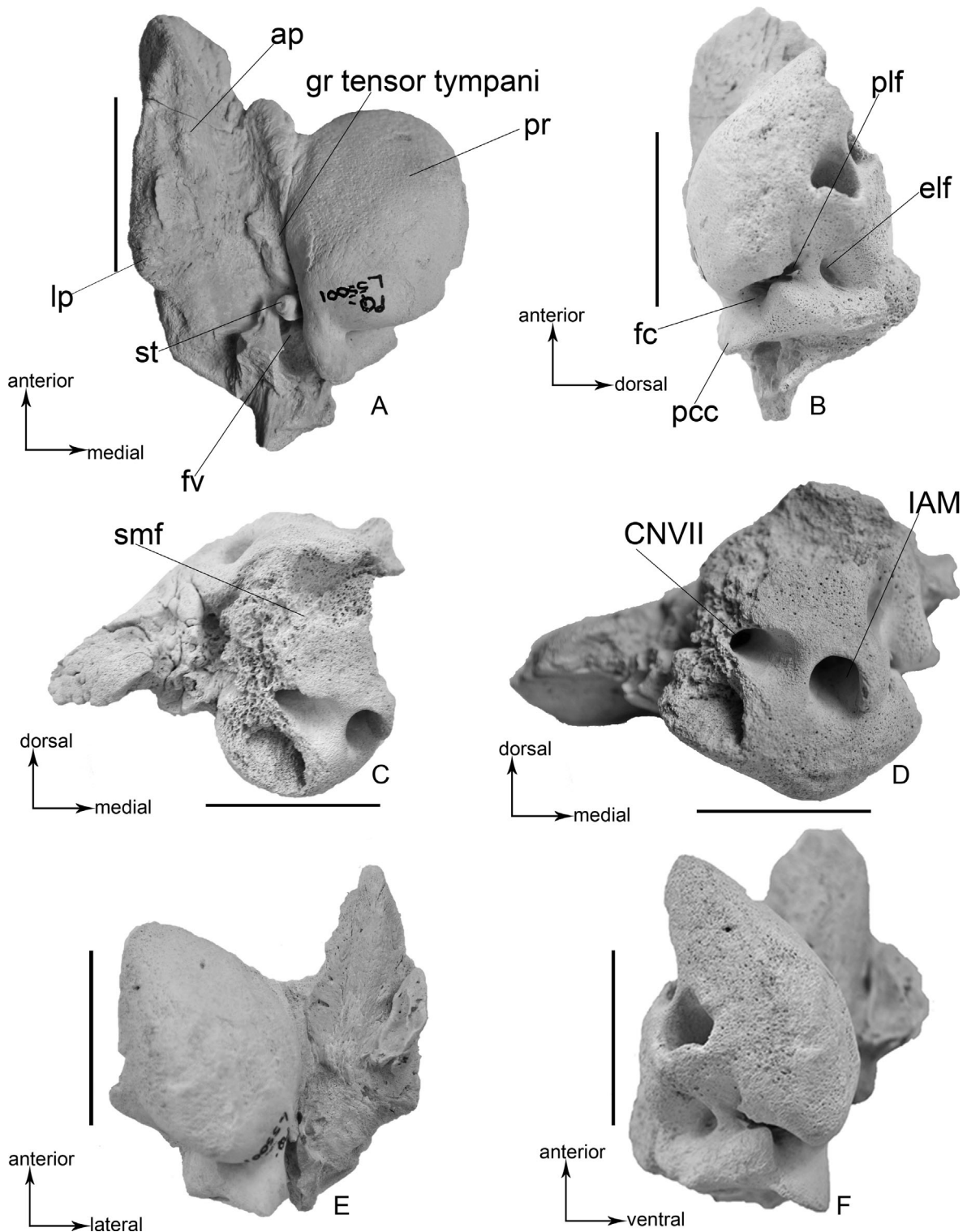


Fig. 4. Petrotympanic region of SAM-PQL-55001. Right petrosal in **A**, ventral; **B**, dorsal; **C**, posterior; **D**, dorsomedial views. Left petrosal in **E** ventral and **F**, dorsal views. Scale bars = 30 mm. Abbreviations: ap, anterior process; elf, endolymphatic foramen; fv, fenestra vestibuli; fc, fenestra cochleae (circular window); lp, lateral projection of the anterior process; pr, promontorium; plf, perilymphatic foramen; pp, posterior process; pcc, posterior cochlear crest; smf, suprameatal fossa; sm, stylomastoid fossa; CN VII, endocranial opening of the facial canal; IAM, internal acoustic meatus.

transversa (Fig. 4D). As in SAM-PQL-20482, the endocranial opening of the facial canal is located more laterally than the entire rim of the internal acoustic meatus; a groove runs along the anterior face of the crista transversa from the endocranial opening of the facial

canal to the anterior portion of the rim of the internal acoustic meatus (Fig. 4D). In the right petrosal, there is an excavation ventral to the internal acoustic meatus that corresponds to the promontorial groove in non-balaenopterid mysticetes (Ekdale *et al.* 2011). A similar



structure is evident in the left petrosal of the *Plesiobalaenoptera quarantellii* holotype specimen (Bisconti 2010a). The dorsal surface of the petrosal (tegmen tympani and superior process: Luo & Gingerich 1999) is domed. The fenestra cochleae (round window: *sensu* Geisler & Luo 1996) equating to the fenestra rotunda (cochlear window/round window: Mead & Fordyce 2009) is not separated from the aperture for the cochlear aqueduct (Fig. 4B, F). The endolymphatic duct opens in a shallow fossa (Fig. 4B, F). The stapes is preserved in articulation with the fenestra vestibuli (oval window) thus obscuring much of its morphology. A tensor tympani groove is present at the anterior end of the promontorium, ventral to the base of the anterior process (Fig. 4A).

The petrosal SAM-PQL-55001 is clearly balaenopterid-like in its triangular anterior process and elongate promontorium, which extends along both the anterior and posterior transverse axes (Fig. 4A). A raised dorsal portion of the petrosal is also present in basal thalassotherians (i.e., *Pelocetus* and *Isanacetus*) and in Balaenidae (Ekdale *et al.* 2011). Separation of the internal acoustic meatus from the endocranial opening of the facial canal is otherwise not typical of extant adult balaenopterids, but is known in juvenile *Balaenoptera physalus* (Bisconti 2001), and some early balaenopterids including *Plesiobalaenoptera quarantellii* and *Diunatans luctoretemergo* (Bisconti 2010a, Bosselaers & Post 2010). Continuation of the fenestra cochleae with the perilymphatic duct is characteristic of early balaenopterids, such as '*Balaenoptera*' *musculoides* (RBINS M. 752) and '*Balaenoptera*' *sibbaldina* (RBINS M. 737).

The tympanic bulla (Fig. 5A–D) closely resembles that of SAM-PQL-20482. It has an expanded anterolateral lobe, anteriorly projecting anteromedial corner, transversely elongated sigmoid process and a convex posterior border. However, the posterior border is transversely narrower than that of SAM-PQL-20482, and the medial border of the involucrum is planar like those of *B. edeni*, *B. omurai* and *B. physalus* (Ekdale *et al.* 2011). Key balaenopterid characters (Ekdale *et al.* 2011, Bisconti 2010a) of the specimen are the expansion of the anterolateral lobe, the high Eustachian outlet with deep tympanic cavity, and the presence of a prominent main ridge. The conical process of SAM-PQL-55001 is tall and triangular, and similar to that of *Megaptera novaeangliae* (Ekdale *et al.* 2011).

The tympanic bulla is similar to *Plesiobalaenoptera quarantellii* in the uniformly round medial border (Bisconti 2010a). The anterolateral border is similarly expanded in SAM-PQL-55001 and the anterolateral shelf is also well developed. The sigmoid process is orientated transversely; the conical process is low and triangular in SAM-PQL-55001 when compared with *Plesiobalaenoptera* (Bisconti 2010a).

There are several cranial fragments associated with SAM-PQL-55001 (Fig. 6A–F). Laterally, the zygomatic process of the squamosal is incomplete (Fig. 6B). The

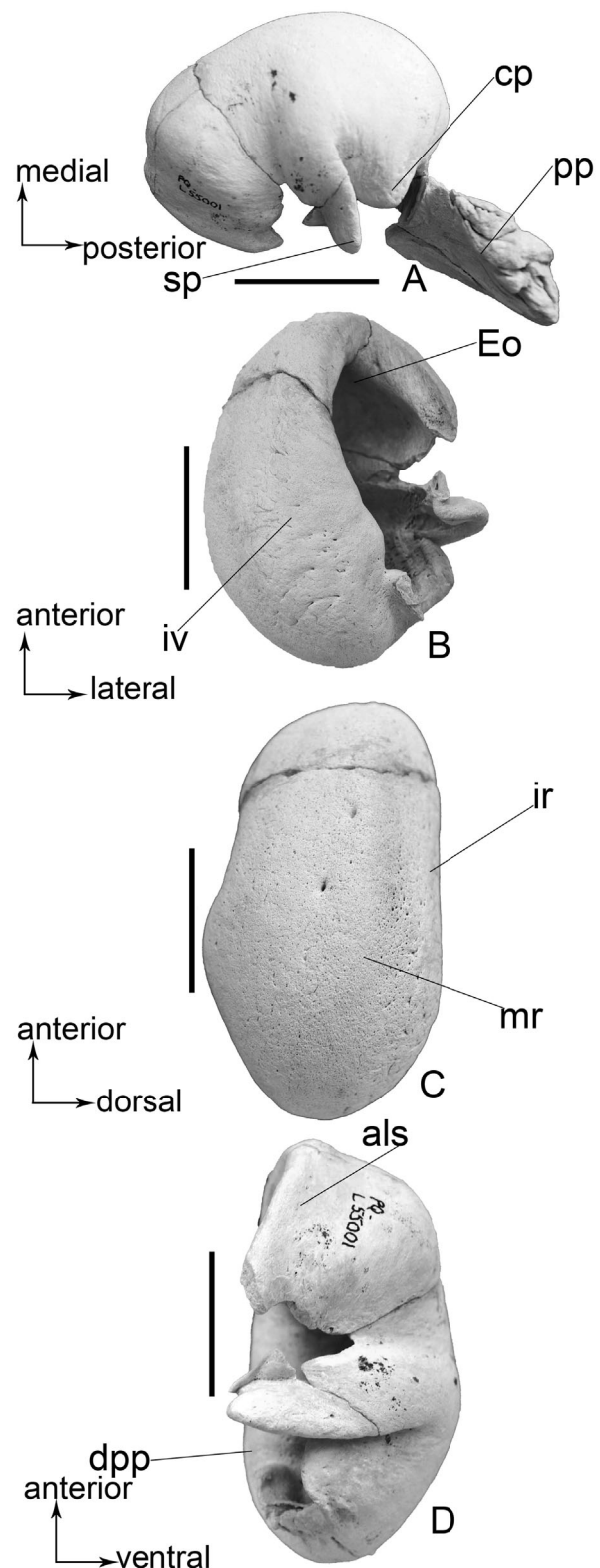


Fig. 5. SAM-PQL-55001. Right tympanic bulla in **A**, ventral; **B**, dorsal; **C**, medial; **D**, lateral views. Scale bars = 30 mm. Abbreviations: als, anterolateral shelf; cp, conical process; dpp, dorsal posterior prominence; Eo, Eustachian outlet; ir, involucrum ridge; iv, involucrum; mr, main ridge; sp, sigmoid process.

flared squamosal is angled to the zygomatic process and narrows medially towards its contact with the pterygoid. Its edges are incomplete; the grooved surface forms part

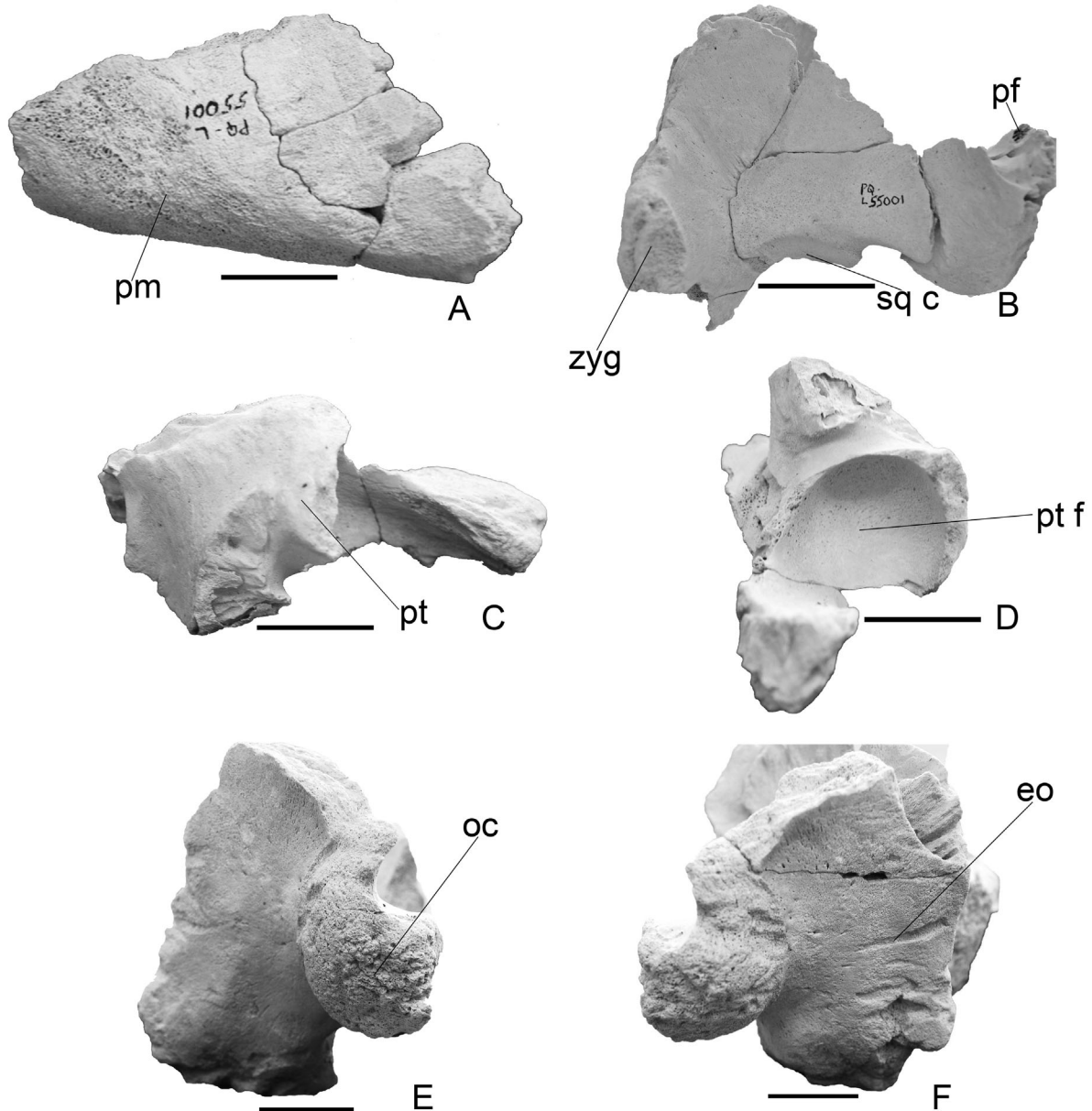


Fig. 6. Cranial fragments of SAM-PQL-55001. A, Maxilla fragment. B, Zygomatic process. C, Pterygoid. D, Pterygoid fossa. E, Left occipital condyle. F, Right occipital condyle. Scale bars = 30 mm. Abbreviations: eo, exoccipital; oc, occipital condyle; pm, premaxilla; pf, pseudovalve foramen; pt, pterygoid; pt f, pterygoid fossa; sq c, squamosal crest; zyg, zygomatic process of the squamosal.

of the highly complex and interdigitating squamosal-parietal suture. The squamosal itself is caudoventrally curved. The incomplete left squamosal is poorly preserved. In the left squamosal, the zygomatic process has an anterior facet that is moderately wide and very rugose (Fig. 6B). The incomplete pterygoid is attached to the right squamosal. It has a deeply concave surface with an almost circular outline (Fig. 6B, 6C).

The left exoccipital (Fig. 6E) is more complete than the right (Fig. 6F), which has suffered taphonomic damage dorsally and laterally. The irregular-shaped exoccipital flares dorsoventrally and widens ventrally. Ventrolaterally, there is a broad paroccipital process. The occipital condyles are moderately well developed and have a rugose, porous surface indicating

cartilaginous attachment (Fig. 6E, F). The sutures, where traceable, are raised and not fully fused, suggesting osteological immaturity (see Walsh & Berta 2011). There is no intercondylar notch.

#### SAM-PQL-21230 (Figs 7–9)

*Locality and unit.* 'E' Quarry, Langebaanweg, Western Cape Province, South Africa. Either KGM (Bed 1) or LQSM (Bed 2) of the Varswater Formation.

*Description and comparisons.* SAM-PQL-21230 includes an incomplete petrosal (Fig. 7A–E) and left tympanic bulla (Fig. 8A–D), together with cranial fragments including the occipital condyles (Fig. 9A–D).

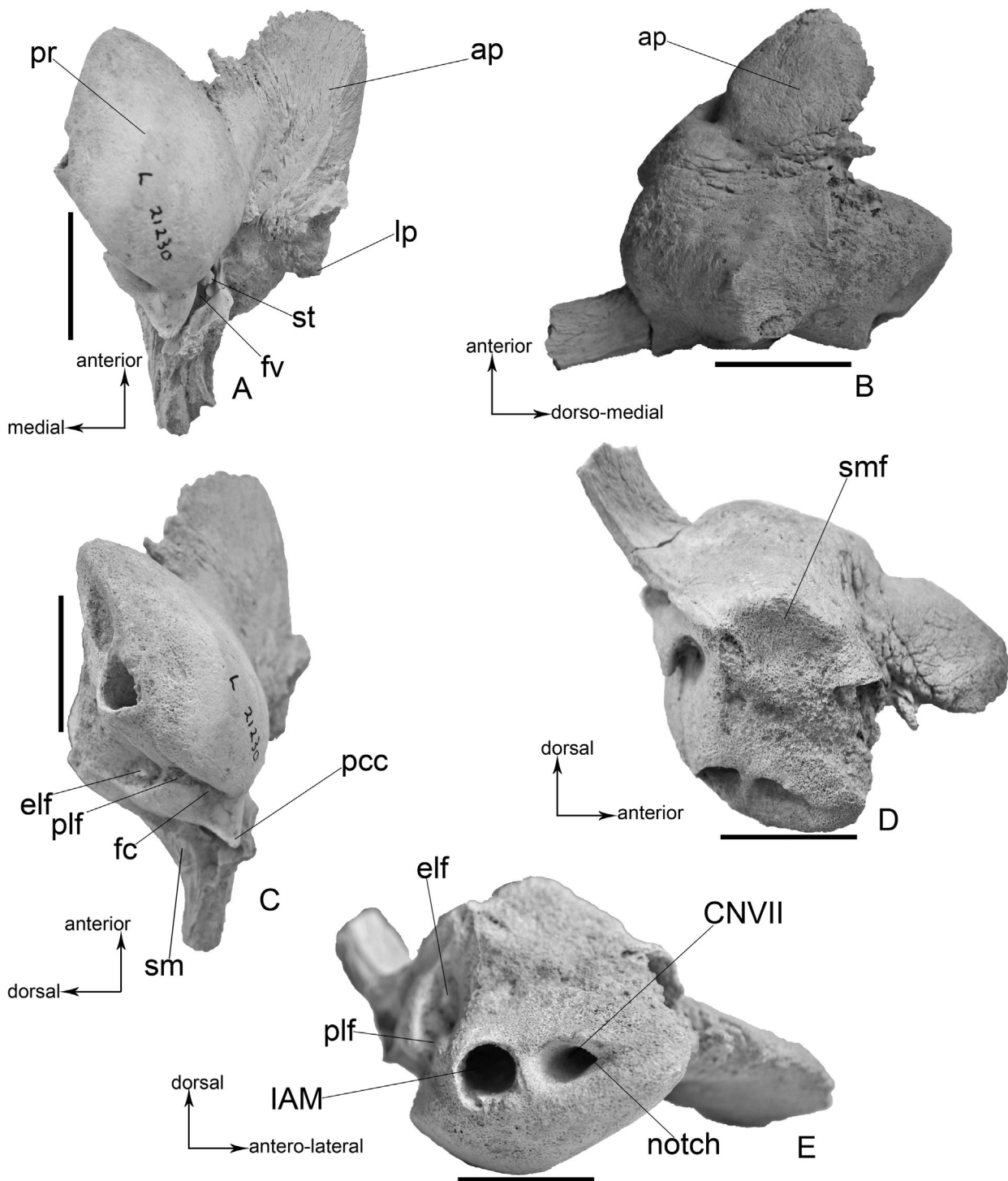


Fig. 7. Petiotic region of SAM-PQL-21230. Left petrosal in A, ventral; B, dorsal; C, posterior; D, posterodorsal; E, dorsomedial views. Scale bars = 30 mm. Abbreviations: ap, anterior process; elf, endolymphatic foramen; fv, fenestra vestibuli; fc, fenestra cochleae (circular window); lp, lateral projection of the anterior process; pr, promontorium; plf, perilymphatic foramen; pp, posterior process; pcc, posterior cochlear crest; smf, suprameatal fossa; sm, stylomastoid fossa; CN VII, endocranial opening of the facial canal; IAM, internal acoustic meatus.

The posterior process of the petrosal has not been preserved (Fig. 7A). Its more anterior portion includes the stylomastoid fossa. The promontorium is elongated along the anteroposterior and transverse axes. There is no promontorial groove. The internal acoustic meatus is circular (Fig. 7E), and close to the endocranial opening

of the facial canal (Fig. 7E); the latter being elliptical with an anterior notch similar to those of some juvenile thalassotherians (*Herpetocetus* sp.: Geisler & Luo 1996) and balaenopterids (*Balaenoptera physalus*: see Bisconti 2001). The endocranial opening of the facial canal opens on the same plane as the internal acoustic

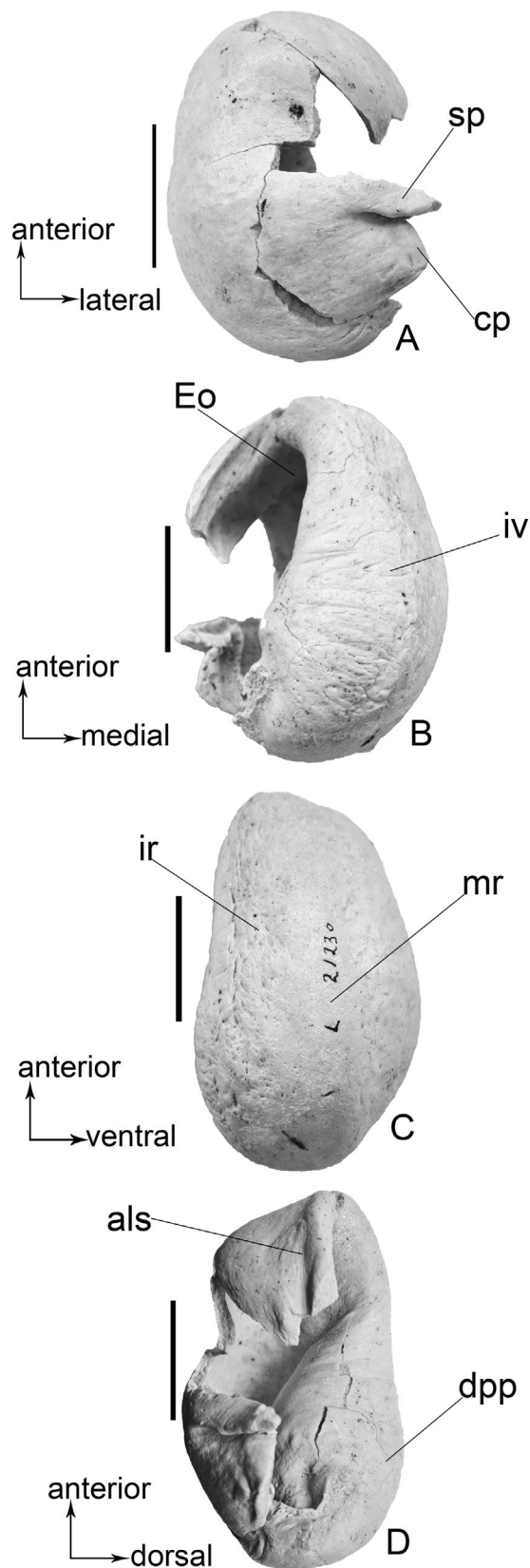


Fig. 8. Left tympanic bulla of SAM-PQL-21230 in **A**, ventral; **B**, dorsal; **C**, medial; **D**, lateral views. Scale bars = 30 mm. Abbreviations: als, anterolateral shelf; cp, conical process; dpp, dorsal posterior prominence; Eo, Eustachian outlet; ir, involucrem ridge; iv, involucrem; mr, main ridge; sp, sigmoid process.

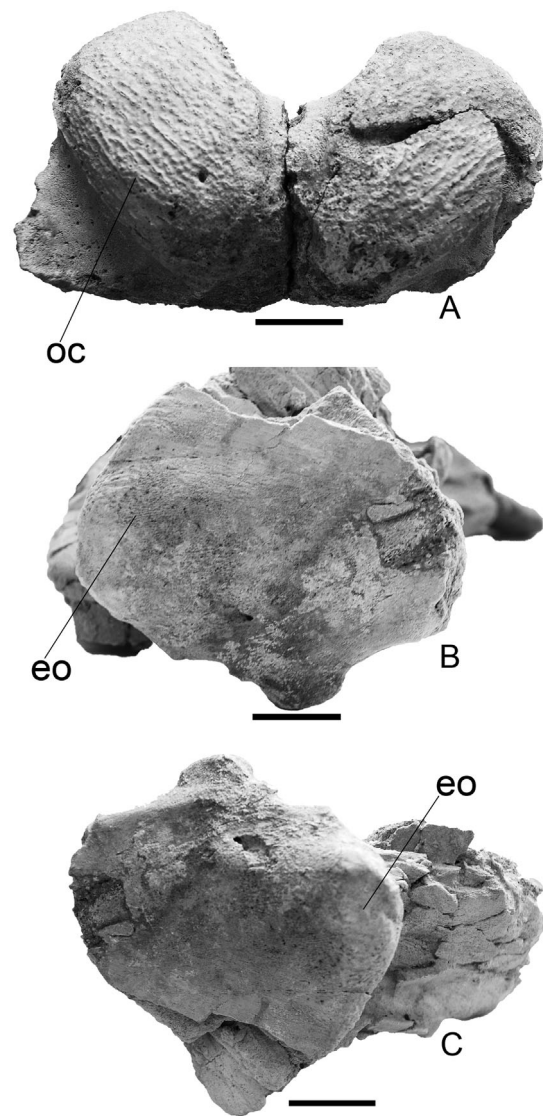


Fig. 9. SAM-PQL-21230. Skull fragments. **A**, Occipital condyles. **B**, Left exoccipital. **C**, Right exoccipital. Scale bars = 30 mm. Abbreviations: eo, exoccipital; oc, occipital condyle.

meatus; there is no groove anterior to the thin crista transversa (Fig. 7E). The suprimeatal area is flattened and the tegmen tympani area raised (Fig. 7D). The suprimeatal area bears anterior and posterior tubercles. The anterior process is short and rectangular (Fig. 7A). In medial view, its dorsoventral diameter is high relative to other examples from 'E' Quarry. Endolymphatic and perilymphatic foramina open in a deep recess posterior and medial to the internal acoustic meatus (Fig. 7C, E); the perilymphatic foramen is not separated from the fenestra cochleae (Fig. 7C).

The anterior process of SAM-PQL-21230 resembles that of *Megaptera novaeangliae* (Ekdale *et al.* 2011) in its broadly rectangular outline with externally convex medial and lateral borders. However, the promontorium differs from those of both *M. novaeangliae* and '*M. miocaena* in

lacking a projected anterior border, and widely separated internal acoustic meatus and endocranial opening of the facial canal respectively. The complex shape of the supra-meatal area and domed tegmen tympani are not recognisable in extant balaenopterid species (Bisconti 2001, Ekdale *et al.* 2011). A raised tegmen tympani is otherwise known in *Plesiobalaenoptera quarantellii*, the ‘E’ Quarry specimens, and in early thalassotherians and balaenids (see above). The close proximity of the internal acoustic meatus and the endocranial opening of the facial canal suggest affinity with extant balaenopterids; however, the presence of an anterior notch in the endocranial opening of CNVII (Fig. 7E) indicates osteological immaturity (Bisconti 2001), as does the continuous fenestra cochleae and cochlear aqueduct aperture (Fig. 7C), which occurs in juveniles of *B. borealis* (based on USNM 504699: Bisconti pers. obs.).

The tympanic bulla (Fig. 8A–D) has a prominent ridge running along the ventral surface from the anteromedial to posterolateral extremities. The Eustachian outlet is high and the tympanic cavity is deep (Fig. 8B, D). The anterolateral lobe is expanded but to a lesser extent than in other ‘E’ Quarry specimens (Fig. 8A). The anteromedial extremity does not protrude anteriorly and is continuous with the anterolateral expansion. In dorsal view, the medial border of the involucrum is slightly concave (Fig. 8B). The sigmoid process has been broken off. The conical process is dorsally convex and tall. The prominent conical process is similar to that of *Balaenoptera bonaerensis* but more triangular like *Megaptera* (Ekdale *et al.* 2011). In medial view, the involucrum surface is slightly sinusoidal, whereas the ventral surface is convex posteriorly, thus resembling *B. musculus*, *B. borealis* and *Megaptera novaeangliae* (Ekdale *et al.* 2011).

The rectangular occipital condyles are convex (Fig. 9A), similar to that figured by Nagasawa & Mitani (2004, fig. 5C) with rugose surfaces indicative of a cartilage covering. Laterally, the exoccipital forms a moderately wide expansion that is incomplete dorsally and medially (Fig. 9B, C). In the middle of the lateral border, the exoccipital is wide, thick and has a rugose surface. The lateral border of the exoccipital thins dorsally and ventrally. In posterior view, the exoccipital midline is raised. There are two notches along the ventral border of the exoccipital: the first is deeper and separated from the adjacent notch by a low tubercle. Another tubercle is present on the ventrolateral surface; this is anteroposteriorly narrow, elongated and projects below the thicker ventral border of the exoccipital.

## Discussion

The Langebaanweg mysticetes share numerous characteristics with balaenopterids: the anterior process of the petrosal is triangular with a pointed apex; the posterior process is flattened (combination of that of the tympanic bulla and periotic); the promontorium is elongated along the transverse axis; the tympanic bulla has

a reniform shape and rounded anterolateral extremity; the Eustachian outlet is elevated in the tympanic bulla; and an anterolateral shelf is present (Bisconti 2010a). In SAM-PQL-20482 the tympanic bulla is morphologically similar to *B. musculus* and *B. physalus* (Ekdale *et al.* 2011), whereas the petrosal has a mosaic of primitive and derived traits. Of particular significance is the domed dorsal surface of the tegmen tympani, which is indicative of early balaenopterids (e.g., *Plesiobalaenoptera quarantellii*; Bisconti 2010a) and basal thalassotherians (e.g., *Pelocetus*, *Parietobalaena* and *Isanacetus*; Kellogg 1965, 1968, Kimura & Ozawa 2002). The continuous fenestra cochleae and aperture for the cochlear aqueduct are also plesiomorphic among early balaenopterids, *Eschrichtius robustus* and the extant *Balaenoptera borealis* (Ekdale *et al.* 2011); however, this feature is ontogenetically variable (see Bisconti 2001).

In comparison with the tympanic bullae of extant balaenopterids, SAM-PQL-55001 has an elongate anterolateral lobe that is similar to that of *Balaenoptera edeni* and *B. borealis* (Ekdale *et al.* 2011). The straight medial border of the involucrum is also preserved in fossil taxa including *Plesiobalaenoptera quarantellii* and *Diunatans luctoretmergo*, and the extant balaenopterids *B. edeni*, *B. omurai* and *B. physalus* (Bisconti 2010a, Bosselaers & Post 2010, Ekdale *et al.* 2011).

The bulla of SAM-PQL-21230 resembles that of *Balaenoptera musculus* as described by Ekdale *et al.* (2011). It lacks both the protrusion in the anteromedial extremity and slightly concave medial border on the involucrum (elsewhere observable in *B. edeni*, *B. omurai* and *B. physalus*: Ekdale *et al.* 2011). Bisconti (2008 and literature therein) alternatively found these states to be highly variable, thus limiting their taxonomic utility; a factor further compounded here by incomplete preservation. Nevertheless, morphological compatibility of the various ear bones suggests that the South African balaenopterids were potentially related to *Plesiobalaenoptera quarantellii*. If confirmed by future discoveries, this placement will lend support to the hypothesis that antitropical distributions among balaenopterids had evolved by the late Miocene, thus setting the pattern for later geographical radiations that are still evident today (Bisconti 2010b).

The generally poor condition of the ‘E’ Quarry cetacean fossils might be a product of the prevailing palaeoenvironment off South Africa’s west coast during the late Miocene to early Pliocene. This time frame witnessed a marine transgression over high relief topography around Langebaanweg, which formed an archipelago by linking Saldanha and St Helena Bays (Hendey 1981, Hendey & Dingle 1989, Erasmus 2005, Roberts *et al.* 2011). The Cape Flats were likewise inundated linking Table and False Bays and forming islands of Table Mountain and other peaks around the Cape Peninsula (Olson, 1983). Accompanying depositional settings were thus lagoonal to estuarine with segregation

from the open ocean via sand bars and beaches (Roberts *et al.* 2011). Because SAM-PQL-20482, SAM-PQL-55001 and SAM-PQL-21230 appear to be juveniles, they might evidence stranding along these tidal beaches during coastal migrations, as occurs in extant whales and dolphins (Schäfer 1972). Young or sick animals might have also been caught in currents or misdirected into shallower water.

The palaeobiogeographic history of mysticetes remains poorly resolved. Although Bisconti (2015) provided palaeobiogeographic inferences for mysticetes based on a phylogenetic analysis focussed on Northern Hemisphere cetotheriids, Southern Hemisphere representatives and distributions have been largely overlooked. The new material emerging from 'E' Quarry and recent discoveries elsewhere in the austral continents should advance our understanding of cetacean evolution in the Southern Hemisphere. The current sample of Miocene–Pliocene mysticete fossils from Langebaanweg represents balaenopterids, although unidentifiable odontocetes are also present. This association is consistent with coeval assemblages from New Zealand and Peru, perhaps suggesting that balaenopterids were dominant throughout the Southern Hemisphere during the Neogene (Dathe 1983, Bearlin 1988, Pilleri 1989, Brand *et al.* 2004, Amiot *et al.* 2008, Bisconti 2011).

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Acknowledgements

The work was done in part during RG's postdoctoral fellowship at UCT funded by Claude Leon Foundation (2010–August 2011). RG thanks the Cenozoic Collections staff at Iziko South African Museum for their assistance. We thank Dr O. Lambert from the Royal Belgian Institute of Natural Sciences in Bruxelles for photographs of the plates of *Megaptera affinis* from Van Beneden (1882). RG thanks Dr P.B. Best for his help during the initial stages of this project and Dr D. Thomas for his advice. RG thanks Mr D. Ohland and Mr N. Fouten for their assistance with the extant cetacean taxa house at Iziko South African Museum, Cape Town. We thank Erich Fitzgerald and Oliver Hampe for their constructive comments; Stephen McLoughlin (*Alcheringa* Editor in Chief) and Ben Kear (Assistant Editor) provided comments on the manuscript helping to improve its quality and clarity. The authors contributed equally to this work.

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