Pliocene marine mammals from the Whalers Bluff Formation of Portland, Victoria, Australia

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Abstract

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The most diverse and locally abundant Australian fossil marine mammal assemblages are those from late Neogene (Late Miocene through Late Pliocene) sediments in Victoria and Flinders Island, Tasmania. However, none of these assemblages have hitherto been described. The Pliocene (>2.5–4.8 Ma) Whalers Bluff Formation, exposed in beach cliff sections and offshore reefs, at Portland, western Victoria (38°19'S, 141°38'E) has yielded a small but moderately diverse assemblage of marine mammals represented by fragmentary material. Taxa present include: right whales (Balaenidae); rorqual whales (Balaenopteridae); a physeterid similar to the extant sperm whale (cf. *Physeter* sp.); the first Australian fossil record of pygmy sperm whales (Kogiidae); at least three genera of dolphins (Delphinidae: cf. *Tursiops* sp., *Delphinus* sp. or *Stenella* sp., and an undetermined genus and species); and probable earless or true seals (Phocidae). This small assemblage represents the first Australian fossil marine mammal assemblage to be described in detail. The taxonomic composition of this Pliocene marine mammal assemblage is generally similar to the present day marine mammal assemblage in north-west Bass Strait. The occurrence of extant cetacean genera in the Portland Pliocene and Flinders Island Cameron Inlet Formation assemblages indicates that the marine mammal fauna off south-east Australia had acquired an essentially modern aspect by the Late Pliocene. Several of the cetacean genera recorded in the Portland Pliocene assemblage also occur in similar-aged assemblages in other ocean basins. This corroborates the hypothesis that many cetacean taxa that are widely distributed in the world's oceans today were equally widespread during the Pliocene.

Keywords

Cetacea, Carnivora, Pinnipedia, Phocidae, Mysticeti, Odontoceti, Australia, Victoria, Portland, Whalers Bluff Formation, Pliocene

Introduction

The Pliocene epoch (1.8–5.3 Ma) is generally considered to be the time during which the modern marine mammal fauna evolved, with the extinction of archaic taxa (as well as some taxa with novel adaptations), and widespread geographic distribution of extant families and genera (Barnes, 1977; Fordyce, 1989; Fordyce and Barnes, 1994; Fordyce and Muizon, 2001; Fordyce et al., 2002; Deméré et al., 2003). Although the Pliocene marine mammals of the North Pacific (e.g. Barnes, 1973a, 1977, 1998) and eastern tropical Pacific (e.g. Muizon, 1981, 1984; Muizon and DeVries, 1985; Muizon and Domning, 1985, 2002) have been described and discussed in some detail, the Pliocene marine mammals of the Southwest Pacific (Australia and New Zealand) remain poorly known (Fordyce et al., 2002: 53). This is despite the fact that Australian late Neogene marine mammals (mostly cetaceans) are relatively abundant in museum collections, especially the Palaeontology Collections of Museum Victoria, Melbourne.

The majority of Pliocene marine mammal fossils in these collections are rather fragmentary with one partially complete skull and associated skeleton known (NMV P179005, cf. *Megaptera* sp.). Despite this general lack of diagnostic skull material, some details of the SW Pacific Pliocene marine mammal fauna may be filled in by the study of certain isolated skeletal elements such as periotics. As noted by Barnes (1977: 322), study of these isolated elements may provide data on the taxonomic diversity within an assemblage and wider fauna. Pliocene marine mammal assemblages have hitherto not been described from Australia, so descriptions of even fragmentary material provide an initial basis for understanding marine mammal evolution off southern Australia during the Pliocene. This description of marine mammals from the Pliocene Whalers Bluff Formation assemblage comprises a preliminary basis for the late Neogene fossil record of marine mammals in Australia.
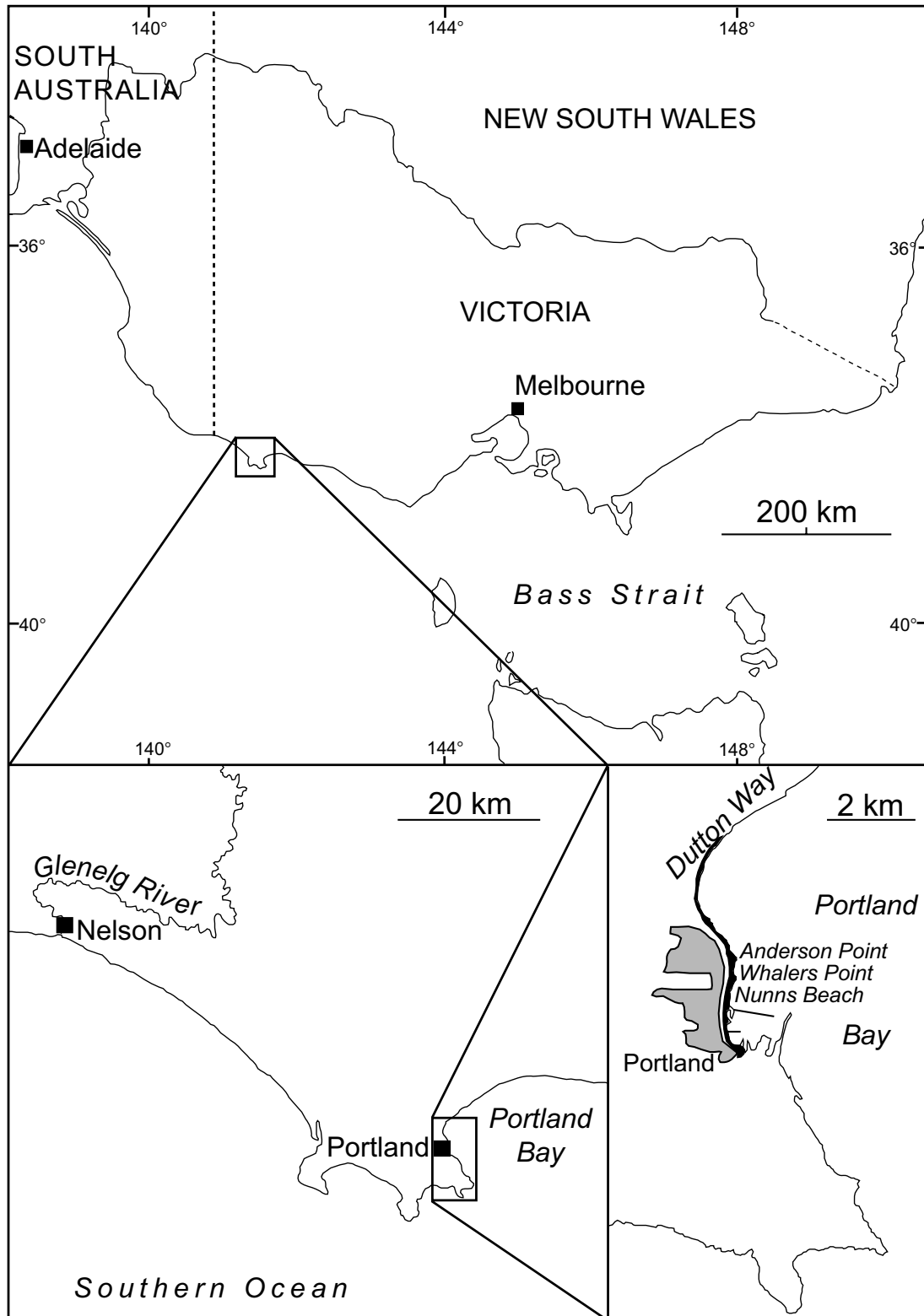
Figure 1. Locality of Portland in Victoria, south-east Australia, and the Portland fossil marine vertebrate localities. Fossils have been collected as float along the beach and from adjacent cliffs between Dutton Way and Portland Harbour. Black shading indicates areas of cliff outcrop of the Whalers Bluff Formation.

All fossils were collected from coastal exposures of the Whalers Bluff Formation lining Portland Bay in western coastal Victoria, southeast Australia (38°19'S, 141°38'E) (Fig. 1). Unfortunately, details of the geological context of virtually all fossils are unknown apart from whether the fossils were collected from the Whalers Bluff Formation or underlying limestone. Fitzgerald (2004a, 2004b) mentioned the Portland fossil marine mammals in previous publications. Bearlin (1987: 177) briefly noted the occurrence of cf. *Balaena* sp., and cf. *Balaenoptera* sp. in private collections in an unpublished Ph.D. thesis. The vertebrate faunal list for Portland given by Fitzgerald (2004b: 186) was completed prior to the recognition of two distinct, stratigraphically/temporally disjunct marine vertebrate assemblages at Portland. The majority of the vertebrates listed by Fitzgerald (2004b) were derived from the Pliocene Whalers Bluff Formation although some vertebrates from the Portland Late Miocene assemblage were listed under the Whalers Bluff Formation assemblage. The Portland Late Miocene marine vertebrate assemblage, from the Port Campbell Limestone, is considerably more diverse than the Pliocene Whalers Bluff Formation assemblage, and is to be described in a subsequent publication. Below is an emended list of the vertebrates recorded in the assemblage from the Whalers Bluff Formation at Portland.

Chondrichthyes
        Isurus sp.
        Carcharodon carcharias Linnaeus, 1758
        Carcharodon megalodon Agassiz, 1835
        Myliobatis sp.
        Ischyodus dolloi Leriche, 1902

Mammalia
    Marsupialia
        ?Dasyuromorphia incertae sedis
        Diprotodontoidea gen. et sp. undet.
        Diprotodontoidea gen. et sp. undet. C
        Diprotodontidae gen. et sp. undet. A
        Zygomaturinae gen. et sp. undet. T
        Palorchestes sp.
        Vombatidae gen. et sp. undet.
        Sthenurus sp.
        Protemnodon sp.
        Macropus sp.
        Macropodidae gen. et sp. undet. C
        Ektopodontidae gen. et sp. undet.
    Rodentia
        Rodentia incertae sedis
    Carnivora
        ?Phocidae gen. et sp. indet.
    Cetacea
        Balaenidae gen. et sp. indet.
        Balaenopteridae gen. et sp. indet.
        cf. *Physeter* sp.
        Kogiidae gen. et sp. indet.
        Delphinoidea incertae sedis
        cf. *Tursiops* sp.
        Delphinus sp. or *Stenella* sp.
        Delphinidae gen. et sp. undet. A

Materials and methods

All fossil specimens were collected by Mr Sean Wright of Portland and are in the Palaeontology Collections of Museum Victoria. Anatomical terminology for periotics and tympanics follows Evans (1993), Fordyce (1994), Fordyce and others (2002) and Kasuya (1973) with minor modifications. All periotic and tympanic measurements follow the methods and dimensions outlined by Kasuya (1973) and were made using vernier callipers. Photographs were taken using a 35 mm Nikon Nikkormat EL SLR with a 105 mm macro-lens, and a Nikon D70 digital SLR with a 60 mm macro-lens. Where indicated, specimens were coated with a sublimate of ammonium chloride to enhance contrast in black and white (denoted by AC in figure captions). Where necessary, fragile specimens were consolidated with a hardener consisting of 3% solution of Paraloid B72 (ethyl methacrylate/methyl acrylate copolymer) in acetone.

Institutional abbreviations. NMV C, Museum Victoria Comparative Anatomy Collection, Melbourne; NMV P, Museum Victoria Palaeontology Collection, Melbourne; CD, Phylum Chordata catalogue, New Zealand Geological Survey, Lower Hutt; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, DC. For a complete list of specimens referred to in this study, see table 1.

Geology and age of the Whalers Bluff Formation

For about 4 km along cliffs north of Portland Harbour the Pliocene Whalers Bluff Formation is exposed (Singleton et al., 1976). This formation is about 7.6 m thick, being comprised of horizontally bedded fossiliferous clay, oyster-rich beds and sandy limestones (Abele et al., 1988). These sediments unconformably overlie the Upper Miocene Port Campbell Limestone and infill a karst topography developed in the top of the Miocene limestone (Boutakoff and Sprigg, 1953; Dickinson et al., 2002). The Whalers Bluff Formation is unconformably capped by basalts.

The age of the Whalers Bluff Formation is well constrained relative to some other Neogene marine mammal-bearing units in the SW Pacific (Fig. 2). However, the determination of the younger age limit of the Whalers Bluff Formation has proved problematic. The Port Campbell Limestone which underlies the Whalers Bluff Formation is Late Miocene (indicated by presence of *Globorotalia miotumida*; planktonic foraminiferal zones N16-basal N17; Tortonian; 8–10.8 Ma) (Dickinson et al., 2002). Deposition of the Whalers Bluff Formation began during planktonic foraminiferal zone N19 (indicated by the presence of *Globorotalia puncticulata* at the base of the formation) and ensued into the base of planktonic foraminiferal zone N21 (Fig. 2) (Singleton et al., 1976; Dickinson et al., 2002). K-Ar dates of 2.51 Ma from basalts that cap the Whalers Bluff Formation have been reported (Singleton et al., 1976).

Beu and Darragh (2001) have suggested that the Whalers Bluff Formation is latest Pliocene to earliest Pleistocene (>1.5–2.0 Ma) based on the presence of the pectinid bivalve *Pecten fumatus* Reeve, 1852 in a section along the Glenelg River. However, *Pecten fumatus* does not occur in the Whalers Bluff Formation at Portland (Darragh in Singleton et al., 1976; T.A. Darragh, pers. comm.). *Zenatiopsis ultima* Darragh and Kendrick, 1971 occurs in the Whalers Bluff Formation at Portland but is a Pliocene species and never occurs with

Table 1. Specimens referred to in this study. For more detailed locality/stratigraphic data see Fitzgerald (2004b). Abbreviations: e=Early; m=Middle; l=Late; M=Miocene; P=Pliocene; Pt=Pleistocene; R=Recent; Vic. = Victoria; Tas. = Tasmania; NZ = New Zealand.

Specimen	Taxon	Locality	Formation	Age
NMV P221242	*Isurus* sp.	Portland, Vic.	Whalers Bluff	P
NMV P218415	*Carcharodon megalodon*	Portland, Vic.	Whalers Bluff	P
NMV P218418	*Carcharodon carcharias*	Portland, Vic.	Whalers Bluff	P
NMV P218470	*Myliobatis* sp.	Portland, Vic.	Whalers Bluff	P
NMV P218296	*Ischyodus dolloi*	Portland, Vic.	Whalers Bluff	P
NMV P221241	?Dasyuromorphia gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P218500	Diprotodontoidea gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P218498	Diprotodontoidea gen. et sp. undet. C	Portland, Vic.	Whalers Bluff	P
NMV P218499	Diprotodontidae gen. et sp. undet. A	Portland, Vic.	Whalers Bluff	P
NMV P221230	Zygomaturinae gen. et sp. undet. T	Portland, Vic.	Whalers Bluff	P
NMV P221231	*Palorchestes* sp.	Portland, Vic.	Whalers Bluff	P
NMV P221238	Vombatidae gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P221232	*Protemnodon* sp.	Portland, Vic.	Whalers Bluff	P
NMV P221235	*Macropus* sp.	Portland, Vic.	Whalers Bluff	P
NMV P221227	?*Macropus* sp.	Portland, Vic.	Whalers Bluff	P
NMV P221237	*Sthenurus* sp.	Portland, Vic.	Whalers Bluff	P
NMV P221229	Macropodidae gen. et sp. undet. C	Portland, Vic.	Whalers Bluff	P
NMV P197795	Ektopodontidae gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P221240	Rodentia indet.	Portland, Vic.	Whalers Bluff	P
NMV P218273	?Phocidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218465	?Phocidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218269	Balaenidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218268	Balaenopteridae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218298	cf. *Physeter* sp.	Portland, Vic.	Whalers Bluff	P
NMV P218407	Kogiidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218283	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218284	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218286	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218266	cf. *Tursiops* sp.	Portland, Vic.	Whalers Bluff	P
NMV P218265	*Delphinus* or *Stenella* sp.	Portland, Vic.	Whalers Bluff	P
NMV P218264	Delphinidae gen. et sp. undet. A	Portland, Vic.	Whalers Bluff	P
NMV P16198	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P41759	Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P42523	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160399	Phocidae gen. et sp. undet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160433	Phocidae gen. et sp. undet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160441	Phocidae gen. et sp. undet.	Grange Burn, Vic.	Grange Burn	eP
NMV P215759	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P16195	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P48865	Balaenidae gen. et sp. indet.	Grange Burn, Vic.	Grange Burn	eP
NMV P160438	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P197824	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P171503	*Balaenoptera edeni* or *B. brydei*	Tidal River, Vic.	N/A	R
NMV P179005	*Megaptera* sp.	Lakes Entrance, Vic.	Jemmys Point	eP
NMV P23961	?*Mesoplodon* sp.	Cameron Inlet, Tas.	Cameron Inlet	P
NMV P13033	"*Steno*" *cudmorei*	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P204352	Delphinidae gen. et sp. undet. A	Henley, England	Red Crag	P-Pt
NMV P218481	Delphinidae gen. et sp. undet. A	Henley, England	Red Crag	P-Pt
NMV C24972	*Kogia breviceps*	Cape Conran, Vic.	N/A	R
NMV C24976	*Kogia breviceps*	Shelley Beach, Vic.	N/A	R
NMV C27879	*Eubalaena australis*	Altona Bay, Vic.	N/A	R
NMV C28892	*Megaptera novaeangliae*	Venus Bay, Vic.	N/A	R
CD 53	Delphinidae gen. et sp. undet. A	Chatham Island, NZ	Unnamed	?P
USNM 22953	*Orycterocetus crocodilinus*	Calvert County, USA	Calvert	mM
USNM 183007	Physeteridae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP
USNM 452993	*Scaphokogia cochlearis*	Aguada de Lomas, Peru	Pisco	lM
USNM 183008	Kogiidae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP
USNM 251118	Kogiidae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP

Figure 2. Stratigraphic correlation of the Portland fossil marine mammal-bearing formations with selected major late Neogene marine mammal-bearing units. Stratigraphy and geochronology are from Barnes (1973, 1977, 1984, 1998), Muizon and DeVries (1985), Muizon and Bellon (1986), Gottfried et al. (1994), Whitmore (1994), Prothero (1998), Fordyce (2002a), Fordyce et al. (2002), Fitzgerald (2004b), Muizon et al. (2004), Barnes et al. (2005) and Gradstein et al. (2004). Abbreviations: **AGL**, Pisco Formation, Aguada de Lomas level; **BL**, Batesford Limestone; **BRS**, Black Rock Sandstone; **CLB**, Pisco Formation, Cerro la Bruja; **ELJ**, Pisco Formation, El Jahuay level; **GBF**, Grange Burn Formation; **LAF**, Lower Member, Almejas Formation; **MTM**, Pisco Formation, Montemar level; **SAO**, Pisco Formation, Sacaco level; **SAS**, Pisco Formation, Sud-Sacaco level; **SDF**, San Diego Formation; **UAF**, Upper Member, Almejas Formation; **WBF**, Whalers Bluff Formation.

P. fumatus, the latter first appearing at the base of the Pleistocene (T.A. Darragh, pers. comm.).

These data indicate that the Whalers Bluff Formation at Portland is Early to Late Pliocene (Zanclean to Piacenzian; >2.5–4.8 Ma). Further study of terrestrial mammals from the Whalers Bluff Formation may help refine the geological age of this unit. Unfortunately, the exact bed from which fossil vertebrates were collected within the Whalers Bluff Formation is unknown. Thus, a finer age resolution than that given above for the assemblage is currently unavailable. The age range of the Whalers Bluff Formation presented herein is considered to be the best estimate based on available data and the reader must be cautioned that future work may yield a younger limit on the minimum age.

The Whalers Bluff Formation (as well as, in part, laterally equivalent Victorian marine mammal-bearing units such as the Grange Burn Formation, Black Rock Sandstone and Jemmys Point Formation) has been interpreted as representing a prograding quartz-carbonate barrier system with the clastic-dominated units listed above representing an initial marine incursion (Dickinson et al., 2002: 290).

Systematics of marine mammals

Order **Cetacea** Brisson, 1762

Suborder **Mysticeti** Flower, 1864

Family **Balaenidae** Gray, 1821

Genus and species indeterminate

Referred specimen. NMV P218269, incomplete right periotic; anterior and superior processes virtually complete, but pars cochlearis almost entirely worn off, and only anteriormost base of posterior process preserved (Fig. 3A).

Description. P218269 is highly polished and abraded. The anterior process is blunt and globose, being indistinct from the superior process. There is marked lateral exostosis of the superior process lateral to the epitympanic recess. The lateral aspect of the anterior process is rugose and pitted. Posteriorly, this pitting decreases in density. Only the lateralmost region of the pars cochlearis is preserved. In medial view, the most notable feature is the sulcus for the facial nerve (cr. VII), the course of cr. VII being preserved from its entry into the body of the periotic at the aperure of the internal facial foramen, to its ventral exit into the epitympanic cavity via the ventral facial foramen. All other features of the pars cochlearis and epitympanic recess have been obliterated. Posterior to the broad and shallow hiatus epitympanicus is a remnant of the base of the posterior process (which is directed posterolaterally and somewhat ventrally).

Discussion. Miller (1924: 8–9) listed the following features that distinguish the periotics of Balaenidae from those of Balaenopteridae (and other baleen-bearing Mysticeti): (1) axis of anterior process of periotic parallel with axis of internal acoustic meatus; (2) [longitudinal] axes of anterior and posterior processes converge at an acute angle; and (3) pars cochlearis small relative to rest of periotic. In addition to the preceding features, the possession of massive lateral exostosis of the anterior process and anterolateral superior process, such that the anterior process appears swollen (as noted by Fordyce, 1982: 48), seems to be a feature shared by all extant and late Neogene balaenid periotics. It is largely on the basis of the latter character and the phenetic similarity of P218269 to a periotic (P16195) from the Lower Pliocene Black Rock Sandstone of Beaumaris identified as belonging to cf. *“Balaena”* (Gill, 1957) that P218269 is referred to Balaenidae, genus and species indeterminate.

The fossil record of Balaenidae begins in the Late Oligocene (c. 28 Ma: Fordyce, 2002b), although the record only becomes reasonably well known from the Mio-Pliocene boundary onwards (McLeod et al., 1993; Bisconti, 2003). *Morenocetus parvus* Cabrera, 1926 is the geologically oldest named balaenid, from the early Early Miocene (Aquitanian) of Patagonia. From the end Aquitanian to early Tortonian of the Miocene the evolutionary history of Balaenidae is virtually unknown. The extant balaenids include *Balaena mysticetus* Linnaeus, 1758, *Eubalaena australis* Desmoulins, 1822, *E. glacialis* Müller, 1776, and *E. japonica* Lacépède, 1818 (e.g., Cummings, 1985; Reeves and Leatherwood, 1985; Bannister, 2002). Note that Rice (1998) included all extant balaenids in the genus *Balaena* and recognised only two species, *B. mysticetus* and *B. glacialis*. The taxonomic scheme of Bannister (2002) is used herein. *Balaena* is known from the Early Pliocene of the North Atlantic (McLeod et al., 1993; Westgate and Whitmore, 2002). There are very few confirmed pre-Quaternary fossil records of *Eubalaena*. Bisconti (2003, 2005) referred the Pliocene *Balaena belgica* Abel, 1941 to *Eubalaena belgica*. McLeod and others (1993: 63) suggested that a balaenid periotic from the Early Pliocene of South Australia (originally recorded by Howchin: 1919) could represent *Eubalaena* (as opposed to its original referral to *Balaena*). Dixon (1990) described an incomplete Recent *Eubalaena australis* skeleton from Altona Bay, near Melbourne, Victoria. The latter specimen (C27879) includes tympanics and periotics. The extinct genera *Balaenula* and *Balaenotus* have been recorded from the Late Miocene through Pliocene of the N Pacific (Barnes, 1977; McLeod et al., 1993) and N Atlantic (McLeod et al., 1993; Bisconti, 2003 and references therein). Recently, Bisconti (2005) described a new genus and species of relatively small balaenid, *Balaenella brachyrhynus*, from the Early Pliocene of Belgium.

The incompleteness of P218269 and lack of information on the extent of intraspecific and ontogenetic variation in balaenid periotics, hampers comparisons with described extant and fossil balaenid taxa. Furthermore, there are as yet no published criteria for discriminating between the periotics of *Balaena* and *Eubalaena*. Despite these problems, it may be noted that P218269 is similar in overall size to several isolated balaenid periotics from the uppermost Miocene to Lower Pliocene Black Rock Sandstone and Grange Burn Formation of Victoria (e.g. P16195, P48865, P160438, and P197824). The discovery of a more complete periotic (including the pars cochlearis) is necessary before any further comparisons between the Portland Pliocene balaenid and the other Victorian specimens listed above can be made.

Family **Balaenopteridae** Gray, 1864

Genus and species indeterminate

Referred specimen. NMV P218268, incomplete right periotic; lacking medial three-quarters of pars cochlearis and posterior process (Fig. 3B).

Description. P218268 is polished, rolled and may be secondarily phosphatised. The anterior process is elongated and some-what attenuated anteriorly. The dorsal surface of the anterior process is smooth, with only slight rugosity, as seen in the periotics of extant Balaenopteridae. An oblique groove on the dorsolateral surface of the anterior process near its preserved apex is interpreted as a trace of a vascular sulcus. The latter feature has previously been considered a sulcus for the capsuloparietal emissary vein (Geisler and Luo, 1998; Geisler and Sanders, 2003) or as a sulcus marking the path of an artery, specifically part of the middle meningeal artery (Fordyce, 1994). Fordyce (1994) and Watson and Fordyce (1994) described this feature as the anteroexternal sulcus whereas Geisler and Sanders (2003) treated the anteroexternal sulcus and sulcus for the capsuloparietal emissary vein as separate features. Further work is required to better establish the venous/arterial correlate of this osteological feature which in this study is referred to as the sulcus for the capsuloparietal emissary vein. In extant balaenopterids, this sulcus usually courses posteriorly to a point level with the position of the mallear fossa. However, in P218268 any more posterior continuation of the sulcus for the capsuloparietal emissary vein, if formerly present, no longer occurs due to abrasion.

The ventral presentation of the periotic exhibits several features. As occurs in extant *Balaenoptera* and *Megaptera*, the lateralmost eminence of the ventrolateral ridge of the superior process (sensu Geisler and Luo, 1996) is situated at the same level as the anterior margin of the pars cochlearis. The mallear fossa is poorly differentiated from the rest of the epitympanic recess.

The preserved posterolateral margin of the periotic is formed by the hiatus epitympanicus. The course of the facial nerve on the ventral surface of the periotic is marked by the facial sulcus which is bounded anteriorly by the aperture of the ventral facial foramen. In ventral view, a distinct bridge of bone at the anterolateral corner of the preserved pars cochlearis represents the ventral roof of the ventral facial foramen. The endocranial aspect of the pars cochlearis preserves the aperture of the internal facial foramen. Anterior to this aperture is a deep excavation in the medial surface of the periotic at the base of the anterior process. This region (composed of cancellous bone in extant balaenopterids) marks the site of ankylosis between the anterior process and the body of the periotic. As in other Balaenopteridae, the pars cochlearis appears to have been elongated towards the cranial cavity.

Discussion. That P218268 is a balaenopterid periotic is evident by the possession of: (1) elongated, triangular and anteriorly attenuated anterior process; (2) a triangular lateral eminence of the ventrolateral ridge; and (3) a relatively large pars cochlearis elongated towards the cranial cavity. Because P218268 is represented only by an incomplete periotic, it is not possible for it to be identified below family level. The size of P218268 is comparable to that of periotics of subadult *Balaenoptera edeni* Anderson, 1879 or *B. brydei* Olsen, 1913 (P171503) and juvenile *Megaptera novaeangliae* Borowski, 1781 (C28892). However, the periotics of extant *Megaptera novaeangliae* and an undescribed species of *Megaptera* from the Early Pliocene of Victoria (P179005) possess the following features which differentiate them from P218268: (1) the anterior process is

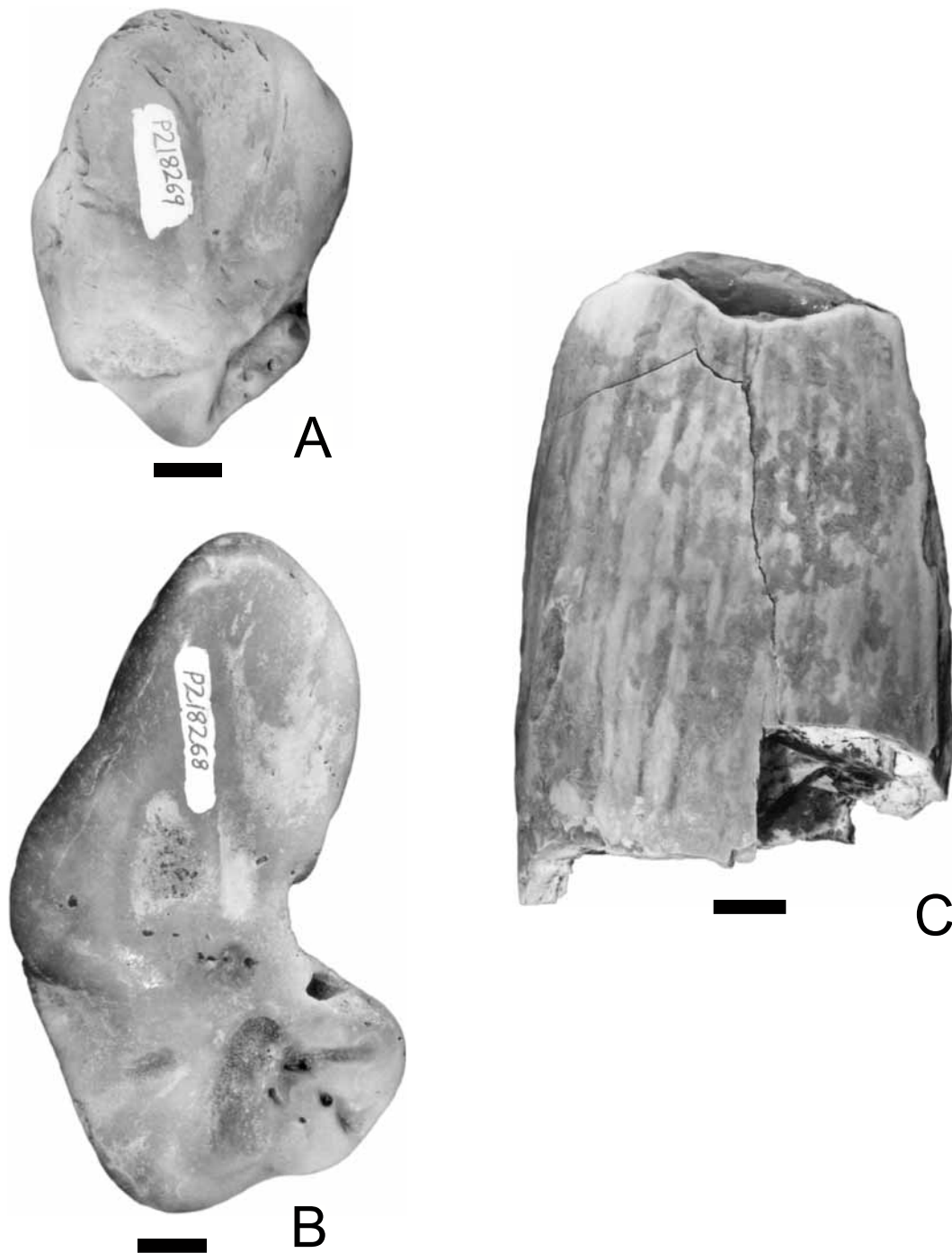Figure 3. Mysticeti and Physeteridae from the Pliocene Whalers Bluff Formation, Portland. **A**, Balaenidae gen. et sp. indet., incomplete right periotic, NMV P218269, in ventrolateral view (**AC**); **B**, Balaenopteridae gen. et sp. indet., incomplete right periotic, NMV P218268, in ventral view (**AC**); **C**, cf. *Physeter* sp., apical crown of tooth, NMV P218298, in side view (**AC**). Scale bars equal 10 mm.

relatively shorter; (2) anterior process is more dorsoventrally compressed; (3) in endocranial view, there is an anteroposteriorly thickened region of cancellous bone in the pars cochlearis anterior to the internal facial foramen; and (4) no deep excavation in the endocranial surface of the periotic anterior to the pars cochlearis. Many of these features may be related to ontogenetic variation. At least, the lack of these four features in P218268 may indicate that this periotic is not referrable to *Megaptera* and may belong to an indeterminate species in the genus *Balaenoptera*.

Suborder **Odontoceti** Flower, 1867

Family **Physeteridae** Gray, 1821

cf. *Physeter* sp. Linnaeus, 1758

Referred specimen. NMV P218298, isolated, worn-down apical region of tooth crown (Fig. 3C).

Description. P218298 has an ovoid cross-section at its base which becomes more ellipsoid towards the preserved apex of the crown. In occlusal view, the apex of the tooth crown is incised by a deep anteroposterior cleft which is attributed to tooth wear. Shallow longitudinal grooves in the surface occur on all faces of the crown. The basal end of the tooth is broken to reveal a cross-section through the crown. The only notable feature of this aspect of the tooth is the presence of thick layers of cementum.

Discussion. The large size of this tooth and the thick layers of cementum suggest that P218298 represents a physeterid. Little more can be said about the systematics of this specimen although its size and similarity to teeth of large adult *Physeter macrocephalus* suggest affinities with the extant sperm whale.

Family **Kogiidae** Gill, 1871

Genus and species indeterminate

Referred specimen. NMV P218407, incomplete left tympanic bulla (Fig. 4A-B).

Description. The most striking aspect of the morphology of P218407 is its small size. The tympanic is polished with rolled edges being rounded off. The preserved portion includes only the medial half of the bulla with very little of the outer lip present. The base of the posterior process of the tympanic has been worn off. In dorsal and ventral view, there is a distinct furrow in the medial edge of the involucrum between the inner posterior prominence and the inner anterior prominence. In ventral view, the furrow between the prominences of the involucrum forms an obtuse angle. There is no preserved ventral keel and the median furrow is very shallow such that it is poorly differentiated from the surrounding ventral surface of the tympanic. The interprominential notch is relatively broad. The anterior edge of the involucrum and outer lip is squared-off. In dorsal view, the involucrum has a consistent width along its length, but is expanded at the level of the inner posterior prominence.

Discussion. P218407 is referred to the Kogiidae on the basis of the following features shared with extant and fossil kogiids: (1) small overall size [as Kasuya (1973: 25) noted among extant Odontoceti only *Pontoporia blainvillei* Gervais and d'Orbigny, 1844 has a smaller tympanic, and P218407 does not resemble the tympanic of that taxon]; (2) distinct embayment in the medial edge of the involucrum between the inner anterior and posterior prominences; and (3) squared-off anterior edge of the involucrum and outer lip. It should be noted that the second feature is also seen in the tympanic bullae of *Physeter macrocephalus* Linnaeus, 1758, *Orycterocetus crocodilinus* Cope, 1868 (USNM 22953) (Kellogg, 1965) (Fig. 5C–D), and an Early Pliocene physeterid (USNM 183007) (Fig. 5A, B). Despite this similarity between P218407 and the tympanics of Physeteridae, the relatively large size of physeterid tympanics precludes P218407 from being considered as a physeterid. Furthermore, the inner posterior prominence in physeterid tympanics is generally more pointed in outline than the rounded outer posterior prominences in kogiid tympanics.

Among fossil Kogiidae, the tympanics of *Praekogia cedrosensis* (Barnes, 1973b) have not been described. A skull of *Scaphokogia cochlearis* Muizon, 1988 (USNM 452993) includes an associated incomplete left tympanic (Fig. 4E, F). The tympanic of *S. cochlearis* is similar to the tympanics of extant *Kogia* in its relatively small size and possession of a distinct embayment in the medial side of the involucrum between the inner anterior and posterior prominences. The most notable difference between the tympanic of *S. cochlearis* and the Portland kogiid tympanic lies in the more marked inflation of the inner posterior prominence of P218407. *S. cochlearis* possesses a less expanded inner posterior prominence, such that the embayment in the medial face of the involucrum is not as deep as in P218407. In this respect, *Scaphokogia cochlearis* is similar to two undescribed Early Pliocene kogiids from the Lee Creek Mine, North Carolina (USNM 183008, Fig. 4G–H; USNM 251118, Fig. 4C, D) and the extant *Kogia breviceps* Blainville, 1838 (Fig. 4I, J).

The features which Kasuya (1973) used to differentiate between Recent *Kogia breviceps* and *K. sima* Owen, 1866 are not preserved in P218407. However, comparison between figures of the tympanic of *K. sima* (Kasuya, 1973: plate VIII), and actual specimens of *K. breviceps* (C24972, C24976), indicate that P218407 differs from both extant *Kogia* species in: (1) embayment in medial edge of involucrum between the inner prominences is markedly deeper; and (2) the involucrum is less dorsoventrally and mediolaterally inflated. Despite these differences, P218407 is almost identical in size to the tympanics of *Kogia breviceps*. Given that the currently available evidence is meagre, P218407 is not identified below family level. Table 2 compares some dimensions of the tympanics of kogiids and physeterids discussed above.

P218407 is the first fossil record of Kogiidae from Australia. Fossil kogiids have previously been reported in the SW Pacific region, from the ?Late Miocene of the Chatham Rise, east of New Zealand (Fordyce, 1984a) but that record has a poorly constrained age (Fordyce, 1989, 1991b).

Table 2. Measurements of tympanics of Physeteridae and Kogiidae. Measurements follow methodology of Kasuya (1973). All measurements are in mm.

	NMV C24972	NMV P218407	USNM 22953	USNM 183007	USNM 452993	USNM 183008	USNM 251118
Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence	26.0	–	31.0	42	–	29.0	31
Distance from anterior tip to posterior end of inner posterior prominence	19.9	21.6	27.0	38	28	31.0	28
Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process	21.28	–	–	–	–	–	–
Distance from posteroventral tip of outer posterior prominence to tip of conical process	15.3	–	–	–	–	–	–
Width of tympanic bulla at the level of the sigmoid process	26.0	–	–	–	–	–	–
Height of tympanic bulla, from tip of sigmoid process to ventral keel	26.5	–	–	–	–	–	–
Width across inner and outer posterior prominences	19.0	–	20.2	24	–	22.5	20+

Superfamily **Delphinoidea** Gray, 1821

Incertae sedis

Referred specimens. NMV P218283, P218284 and P218286, all isolated teeth (not figured).

Description. P21283, P218284 and P218286 all represent small odontocete teeth possessing conical enamel-covered crowns that bear fine wrinkling ornamentation, and curve lingually towards the crown apex. As in kentriodontids, there is a lingual bulge at the base of the crown but this feature is not as prominent in the teeth from Portland. None possesses an open pulp cavity suggesting that all were derived from adult individuals.

P218283 is an incomplete tooth, its preserved maximum length and maximum width of the crown being 16 mm and 6 mm respectively. Due to the incomplete nature of this tooth it does not warrant further description.

P218284 is the most highly polished and the most complete. It differs from the others in having a mediolaterally compressed root with a more prominent mesial-distal bulge at its midpoint. The preserved apex of the root curves posteriorly.

The most notable feature of P218286 distinguishing it from the other teeth is its bulbous root, which contrasts with the transversely flattened morphology of P218284.

Discussion. Only one delphinoid odontocete has previously been described from the Tertiary of Australia, the latest Miocene-earliest Pliocene "*Steno*" *cudmorei* Chapman (1917) from the Black Rock Sandstone of Beaumaris, Victoria (Fitzgerald, 2004b). Fordyce (1982) questioned the taxonomic identity of "*S.*" *cudmorei* (the holotype, P13033, being an isolated tooth) and Fitzgerald (2004b) referred "*S.*" *cudmorei* to Delphinidae, genus and species indeterminate. Chapman (1917) assigned P13033 to *Steno* on the basis of the resemblance of its crown ornamentation to that seen in the teeth of the extant *Steno bredanensis* Cuvier in Lesson, 1828 (e.g., Miyazaki and Perrin, 1994). Given that *Steno* is probably in a basal position in the phylogeny of Delphinidae (Miyazaki and

Perrin, 1994; LeDuc et al., 1999) and that some of the presumed ancestors of Delphinidae, the Kentriodontidae (Barnes, 1978, 2002; LeDuc, 2002), possessed *Steno-like* crown ornamentation (e.g., Kellogg, 1966), the anastomosing striae on the crown of P13033 (and P218283, P218284, P218286) are of dubious use in assessing the phylogenetic affinities of isolated teeth. Furthermore, non-delphinid small odontocetes such as *Lipotes vexillifer* Miller, 1918 possess anastomosing wrinkling on tooth crown enamel (Miller, 1918; Brownell and Herald, 1972; Barnes, 1985) which casts doubt on any perceived taxonomic or phylogenetic signal present in these teeth.

The isolated teeth from Portland are assigned to Delphinoidea incertae sedis. None of the Portland Pliocene teeth share demonstrably close affinities with the holotype tooth of "*Steno*" *cudmorei*.

Family **Delphinidae** Gray, 1821

cf. ***Tursiops*** sp. Gervais, 1855 sp.

Referred specimen. NMV P218266, virtually complete right periotic (Fig. 6).

Description. P218266 is typically delphinid in possessing: (1) posterior process of the periotic projects laterally and postero-laterally; (2) longitudinal grooves on the articular facet of the posterior process of the tympanic (this feature also occurs in Monodontidae); (3) relatively low crista transversa; (4) internal facial foramen opens at the same level as the tractus spiralis foraminosus in the internal acoustic meatus; (5) a short, blunt, rectangular anterior process of the periotic which in anterior, dorsal and ventral views appears laterally compressed; (6) a large fovea epitubaria for the accessory ossicle eliminates the anterior bullar facet on the anterior process; (7) prominent parabullary ridge; (8) inflated pars cochlearis; and (9) relatively shallow internal acoustic meatus (Kasuya, 1973; Fordyce et al., 2002). The first character is usually only seen in Delphinidae but several taxa in the extinct delphinoid grade-
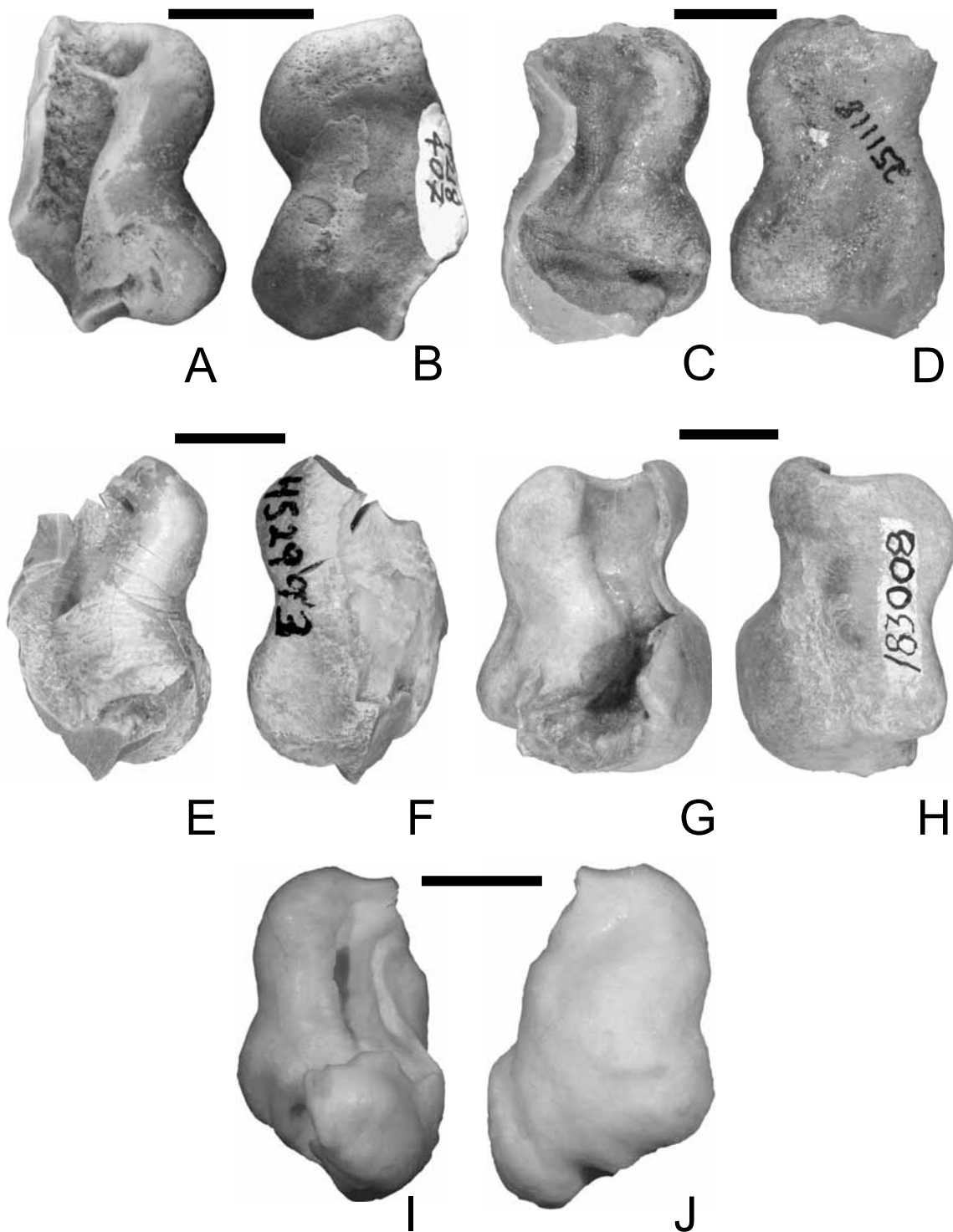
Figure 4. Miocene to Recent Kogiidae tympanics. **A-B**, Kogiidae gen. et sp. indet. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), incomplete left tympanic, NMV P218407 (**AC**). **C-D**, Kogiidae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), incomplete left tympanic, USNM 251118. **E-F**, *Scaphokogia cochlearis* (Upper Miocene Pisco Formation, Aguada de Lomas level, Arequipa Department, Peru), incomplete left tympanic, USNM 452993. **G-H**, Kogiidae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), incomplete right tympanic, USNM 183008. **I-J**, *Kogia breviceps* (Recent, Shelley Beach, Victoria, Australia), incomplete left tympanic, NMV C24976. **A**, **C, E**, **G**, **I**, all in dorsal view. **B**, **D**, **F**, **H**, **J**, all in ventral view. Scale bars equal 10 mm.
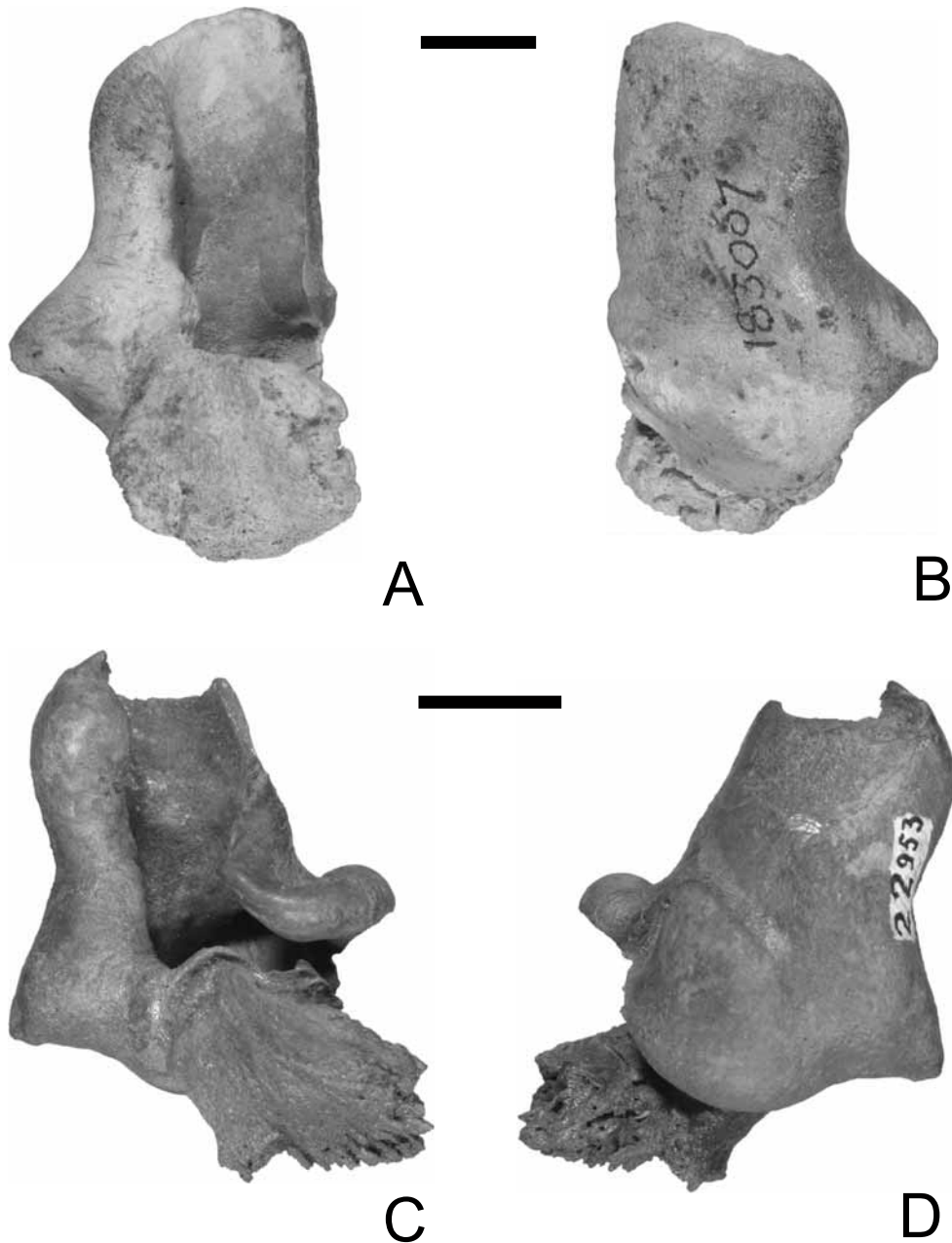
Figure 5. Miocene to Pliocene Physeteridae tympanics. **A-B**, Physeteridae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), right tympanic, USNM 183007. **C-D**, *Orycterocetus crocodilinus* (Middle Miocene Calvert Formation, Zone 14, south of Randle Cliff Beach, Calvert County, Maryland, U.S.A.), right tympanic, USNM 22953. **A** and **C** in dorsal view. **B** and **D** in ventral view. Scale bars equal 10 mm.

taxon Kentriodontidae possess a posterolaterally projecting posterior process of the periotic (eg., Barnes and Mitchell, 1984; Dawson, 1996) as does *Albireo whistleri* (Albireonidae) (Barnes, 1984). P218266 and the other odontocete periotics described below possess all of the characters listed above, justifying their assignment to Delphinidae. Table 3 presents comparative measurements of selected dimensions for all delphinid periotics described herein.

Discussion. Within Delphinidae, P218266 is most similar to *Tursiops* and *Lissodelphis*. P218266 is similar to the periotics of *Tursiops* in: (1) its overall size; (2) having the aperture of the internal acoustic meatus opening at the same level as the endocranial surface of the body of the periotic; (3) having a deep internal facial foramen; and (4) having an aquaeductus vestibuli located at the same level as the foramen for the vestibular branch of the vestibulocochlear nerve. P218266

Table 3. Measurements of delphinid periotics from the Whalers Bluff Formation and delphinid periotics from the Red Crag, England. Measurements follow methodology of Kasuya (1973). All measurements are in mm.

	NMV P218264	NMV P218265	NMV P218266	NMV P204352	NMV P218481
Standard length of periotic, from tip of anterior process to posterior end of posterior process, measured on a straight line parallel with cerebral border	28.00	26.66	32.50	29.94	29.40
Thickness of superior process at the level of upper tympanic aperture	11.00	10.00	11.90	12.14	11.58
Width of periotic across pars cochlearis and superior process, at the level of upper tympanic aperture	20.00	17.76	23.00	20.00	19.58
Least distance between the margins of fundus of internal acoustic meatus and of aperture of aquaeductus vestibuli	2.56	2.16	1.58	3.00	2.50
Least distance between the margins of fundus of internal acoustic meatus and of aperture of aquaeductus cochleae	3.00	3.00	3.14	1.50	2.20
Length of the posterior bullar facet	11.00	11.00	11.00	12.46	12.62
Antero-posterior diameter of pars cochlearis	17.00	16.00	17.80	14.66	16.16

differs from *Tursiops* in: (1) the possession of a more acute angle between the anterior process and pars cochlearis; (2) having an aquaeductus cochleae positioned further from the fenestra cochleae, and further dorsally on the endocranial side of the pars cochlearis; (3) having a lower crista transversa; (4) having a poorly developed septum between the tractus spiralis foraminosus and the foramen for the vestibular branch of the vestibulocochlear nerve; and (5) having a less rounded pars cochlearis.

P218266 shares with the periotic of *Lissodelphis*: (1) endocranial surface of the periotic bordering the posterior margin of the internal acoustic meatus, aperture of aquaeductus vestibuli, and aquaeductus cochleae, is uniformly flat; and (2) aperture of the aquaeductus cochleae opens on the same plane as the aperture of the internal acoustic meatus (note that this condition is also seen in *Steno*). P218266 differs from the periotic of *Lissodelphis* by: (1) being markedly larger in overall size; and (2) having a mediolaterally broader aperture of the internal acoustic meatus.

The balance of features noted above indicates that P218266 is a delphinid with close affinities to *Tursiops*. This periotic is not identified as undoubtedly as such due to the subtle differences between P218266 and the periotic of extant *Tursiops* spp. Barnes (1990) provided a thorough review of the fossil record of *Tursiops*. He recognised four fossil species of *Tursiops*: *T. cortesii* Sacco, 1891 (Italy; Late Pliocene, c. 1.75–3.5 Ma, and possibly Early Pliocene, c. 5 Ma); *T. astensis* Sacco, 1891(Italy; early Late Pliocene, c. 3-3.5 Ma); *T. capellinii* del Prato, 1898 (Italy; middle Pliocene, c. 3.5 Ma); *T. ossenae* Simonelli, 1911 (Italy; middle Pleistocene or late Pleistocene, c. 0.5–0.8 Ma). Other unnamed pre-Pleistocene records of *Tursiops* include: aff. *Tursiops* from the Purisima Formation, California (Late Pliocene, 1.8–3 Ma) (Barnes, 1977); and *Tursiops* sp. from the Yorktown Formation, North Carolina (Early Pliocene, 3.5–4.5 Ma) (Whitmore, 1994).

The record from the Pliocene of Victoria is the first probable pre-Pleistocene fossil record of *Tursiops* from the Southwest Pacific. Furthermore, this fossil occurrence provides corroboration for Barnes' (1990: 18) hypothesis that *Tursiops* has been as geographically widespread during the last six million years as it is at the present time.

Delphinus sp. Linnaeus, 1758 or **Stenella** sp. Gray, 1866

Referred specimen. NMV P218265, virtually complete left periotic (Fig. 7).

Description. P218265 is smaller than P218266 (cf. *Tursiops* sp.) (Fig. 6), closely matching the periotics of both *Delphinus* and *Stenella* in overall proportions. Morphological similarities between P218265 and *Delphinus* include: (1) relatively large diameter of the aperture of the fenestra cochleae; and (2) aperture of the aquaeductus vestibuli is ellipsoid to slit-like in outline and opens posteriorly. However, P218265 differs from *Delphinus* in: (1) the suprameatal area of the periotic, lateral to the aperture of the internal acoustic meatus, is less planar and more convex; (2) the lateral wall of the internal acoustic meatus lacks an elevated platform which obscures the vestibular foramen in endocranial view; (3) the crista transversa is lower; and (4) the aperture of the internal facial foramen is narrower.

Discussion. Whitmore (1994) noted that it is very difficult to distinguish between *Delphinus* and *Stenella* on the basis of periotic morphology. Confounding generic identification of P21265 is the fact that the periotics of *Stenella* show wide individual variation (Kasuya, 1973). In both *Delphinus* and *Stenella*, the aquaeductus cochleae opens at a similar position on the posterior wall of the pars cochlearis. Most preserved features indicate closer affinities with *Stenella* than *Delphinus*. However, all of the identified differences between P218265 and *Delphinus* are subtle, representing differences in degree rather than kind. I do not advocate the definitive placement of P218265 within either *Delphinus* or *Stenella*. In any event, the somewhat intermediate morphology of P218265 between the periotics of *Delphinus* and *Stenella* may indicate that P218265 is from an extinct genus closely related to both of the extant genera in question. In either case, P218265 is the first record of a periotic of the *Delphinus-Stenella* type recorded from the Neogene of Australia.

Fossils representing *Delphinus* or *Stenella* have been recorded from: Upper Member Almejas Formation, Baja California Sur (latest Miocene to Early Pliocene, 3.5–6 Ma) (Barnes, 1998); San Mateo Formation, California (Late

Figure 6. cf. *Tursiops* sp. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), right periotic, NMV P218266 (**A**C). **A**, ventral view. **B**, cranial view. **C**, medial view. **D**, lateral view. Scale bar equals 10 mm.

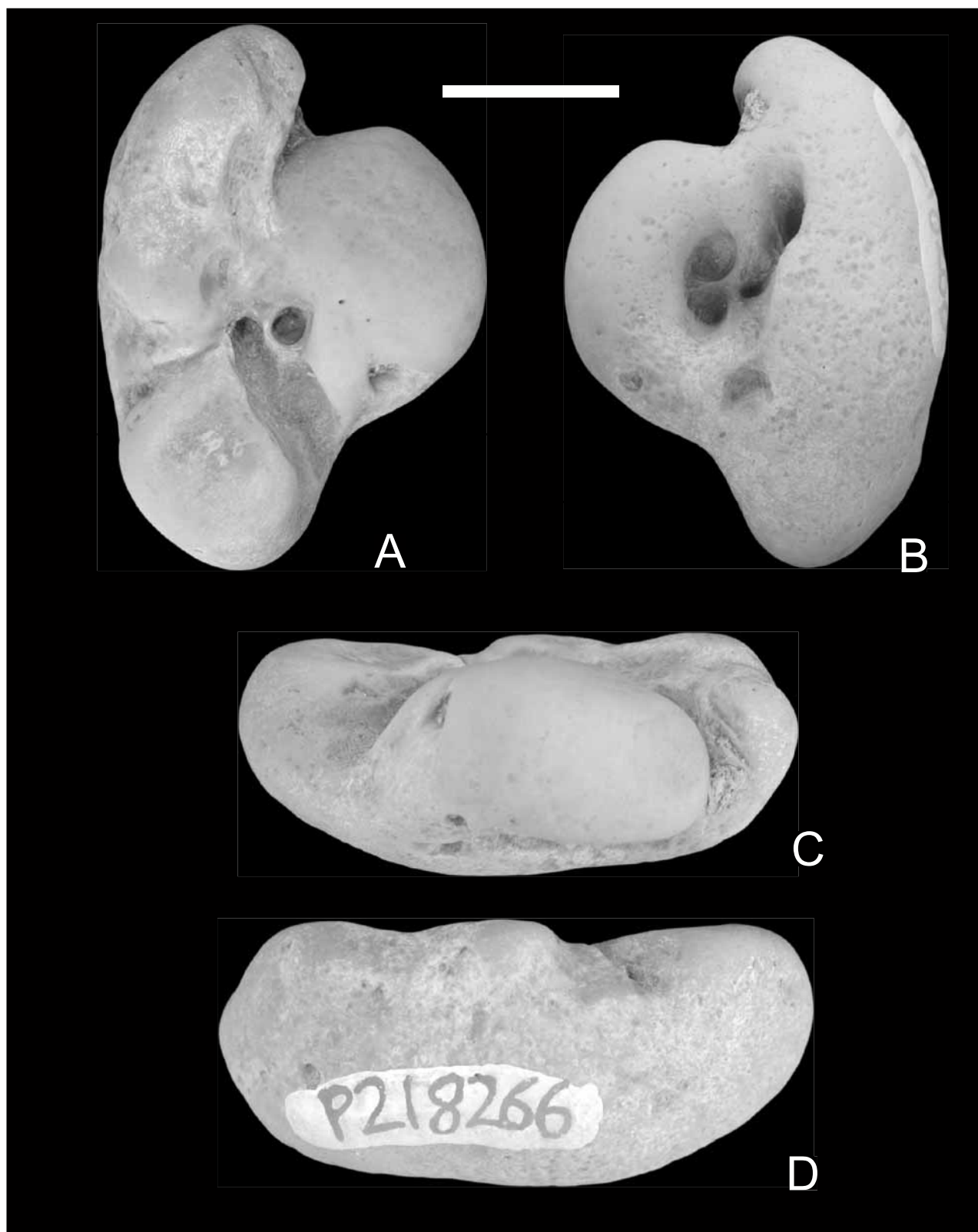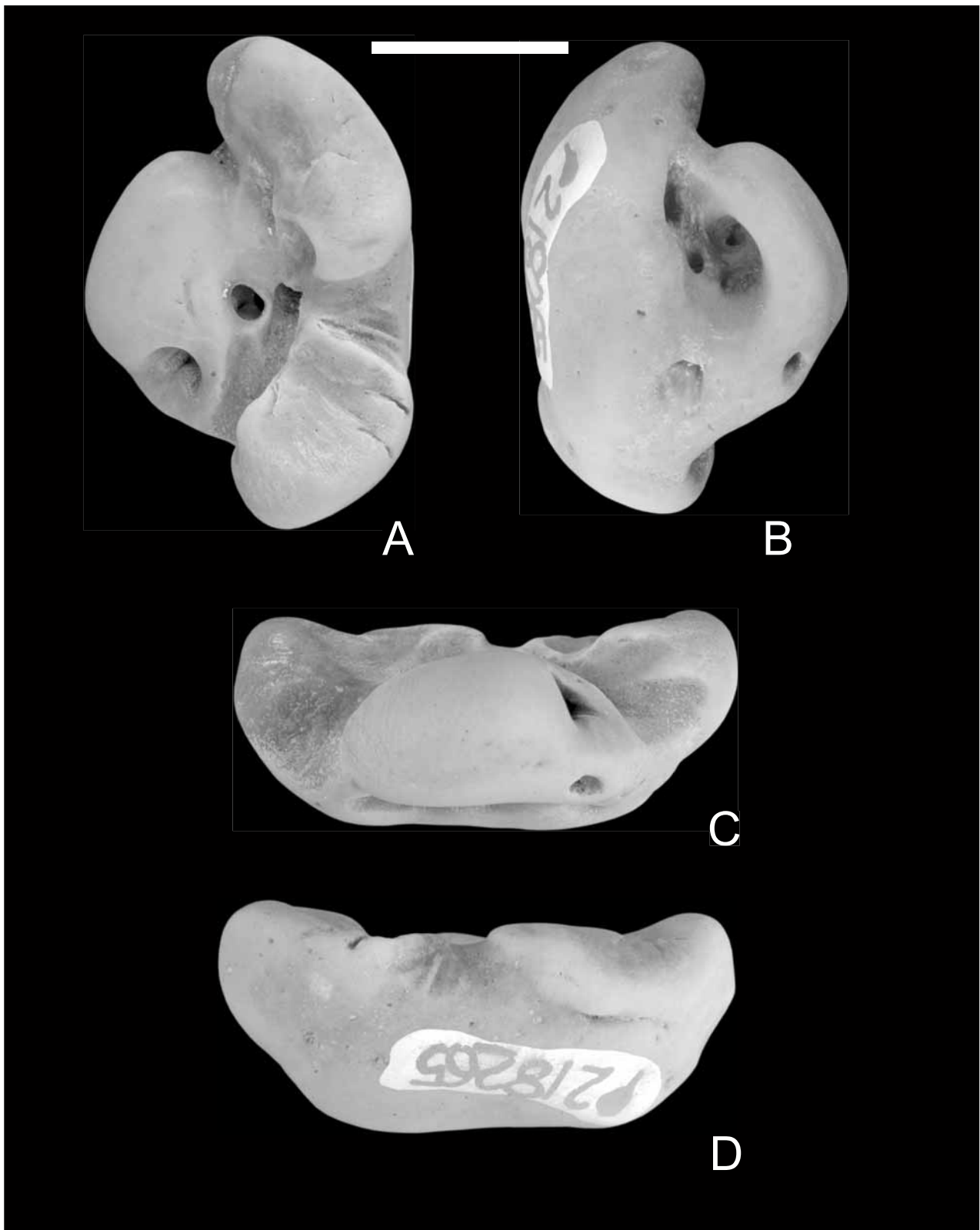Figure 7. *Delphinus* sp. or *Stenella* sp. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), left periotic, NMV P218265 (**A**C). **A**, ventral view. **B**, cranial view. **C,** medial view. **D**, lateral view. Scale bar equals 10 mm.

Miocene to Early Pliocene, 5–9 Ma) (Barnes et al., 1981); unnamed blue clays at Waihi Beach, Hawera, New Zealand (Early Pliocene, 3–3.6 Ma; Beu, 1995) (McKee and Fordyce, 1987; Fordyce, 1991a: 1262); Yorktown Formation, North Carolina (Early Pliocene, 4.5 Ma) (Whitmore, 1994); Salada Formation, Baja California Sur (Early to Late Pliocene, 3–5 Ma) (Barnes, 1998); Tirabuzón Formation, Baja California Sur (middle Pliocene, 3–4 Ma) (Barnes, 1998); SAO Level of the Pisco Formation, Peru (late Early to early Late Pliocene, 3.0–4.0 Ma) (Muizon and DeVries, 1985; Muizon and Domning, 2002); and San Diego Formation, California (Late Pliocene, 1.8–3.4 Ma) (Barnes, 1973, 1977, 1998).

Genus and species undetermined A

Referred specimen. NMV P218264, virtually complete right periotic (Fig. 8).

Description. P218264 differs from all previously described delphinid periotics from the Pliocene of Portland in its relatively good state of preservation, indicating less post-mortem transport and abrasion, with fine surface details intact. P218264 is distinct from P218265 and P218266 but intermediate in overall size. Notable differences between P218264 and P218265 and P218266 include: (1) a mediolaterally thickened periotic body lateral to the pars cochlearis; (2) apex of anterior process with distinct tubercle; (3) possession of two deep creases in the anteromedial face of the anterior process; (4) aperture of the internal acoustic meatus is mediolaterally compressed, such that in endocranial view the meatus is more ellipsoidal and slit-like in outline than that of either or the others; (5) the aperture of the internal facial foramen is narrow; and (6) the aperture of the aquaeductus vestibuli is so narrow that it appears closed.

Discussion. P218264 does not closely resemble the periotics of any Recent delphinids in the Museum Victoria collections, nor any of the Recent delphinid periotics figured by Kasuya (1973). However, P218264 (Fig. 8) closely resembles two fossil delphinid periotics from the Plio-Pleistocene Red Crag of England (P204352, P218481: Fig. 9). Both periotics were originally identified as *Globicephalus uncidens* Lankester, 1864 (sensu Lydekker, 1887) by persons unknown. The *Globicephalus uncidens* periotic figured by Lydekker (1887: plate II fig. 11) probably represents a *Globicephala* periotic, *Globicephalus* being a junior synonym of *Globicephala*. However, P204352 and P218481 (Fig. 9) do not represent *Globicephala* periotics.

An incomplete delphinid periotic (CD 53) has been described from late Neogene sediments of uncertain age on Chatham Island, east of New Zealand (Fordyce and Campbell, 1990). The following features of CD 53 are shared with P218264: well-developed, laterally expanded, parabullary ridge with a globose, tubercle-like anterior apex; anteroventral angle is rounded off; creases in ventrolateral parabullary ridge; and short, broad, fan-like posterior process with heavily fissured posterior bullar facet. Based on these similarities, it is hypothesised that CD 53 is in the same genus, at least, as P218264. Given the Pliocene age of P218264, and Plio-Pleistocene age of P204352 and P218481, this taxonomic assignment of CD 53 suggests a lowest Opoitian (Early Pliocene) or younger age for the Chatham Island delphinid

periotic and its host sediments. Fordyce and Campbell (1990: 62–63) suggested a Late Miocene or younger age for CD 53. Pending the discovery of more complete cranial material including periotics of this type, P218264 is referred to an undetermined genus and species of Delphinidae (as are P204352, P218481 and provisionally CD 53).

Order **Carnivora** Bowdich, 1821

Suborder **Pinnipedia** Illiger, 1811

Family ?**Phocidae** Gray, 1821

Genus and species indeterminate

Referred specimens. NMV P218465, incomplete left horizontal ramus of mandible (Fig. 10). NMV P218273, isolated upper incisor or canine tooth (not figured).

Description. P218465 is an incomplete left horizontal ramus with a preserved length of 69 mm, depth at level of dorsal concavity of 21 mm, and mediolateral thickness at level of posterior alveolus for m1 of 10 mm. The surface detail of P218465 is well preserved relative to most of the other marine vertebrate fossils recovered from the Whalers Bluff Formation. P218465 lacks all of the horizontal ramus anterior to the anterior alveolus for p4 and all of the ascending and horizontal rami posterior to the anteriormost corner of the fossa for *m. masseter pars profundus*. No teeth are preserved in situ in the mandible. In overall proportions, the ramus is lightly built. In posterior and dorsal view, slight medial inflection of the ramus is visible. In lateral aspect, there is a small mental foramen located ventral to the position of the interalveolar septum between the anterior and posterior alveoli of p4 (Fig. 10B). This position is almost identical to that of the posteriormost mental foramen on a mandible referred to *Piscophoca* sp. by Walsh and Naish (2002). Such small mental foramina are also present on the mandibles of *Zalophus californianus* Lesson, 1828 (Howell, 1929; pers. obs.). Immediately posterior to the posterior alveolus of m1 is a prominent dorsal concavity 25 mm long (measured from the m1 alveolus to the anterior margin of the fossa for *m. masseter pars profundus*). This dorsal concavity resembles that of *Piscophoca*. The preserved anterior region of the fossa for *m. masseter pars profundus* differs from that of *Piscophoca* in being dorsoventrally broader with a more rounded outline.

P218273 represents an isolated incisor or canine tooth, 28 mm long; its mesiodistal width at a level just below the base of the crown is 8 mm while its buccolingual width at the same level is 6 mm. The crown has smooth enamel and is recurved towards the apex. The root has a consistent thickness and is buccolingually compressed.

Discussion. The pinniped fossils recovered from the Whalers Bluff Formation do not include elements preserving unequivocal synapomorphies of suprageneric pinniped taxa. Berta (1991) and Berta and Wyss (1994) listed the possession of a bony flange below the angular process of the mandible as an unequivocal synapomorphy of Superfamily Phocoidea (sensu Wyss and Flynn, 1993) but the posterior region of the mandible is not preserved in P218465. However, P218465 is tentatively
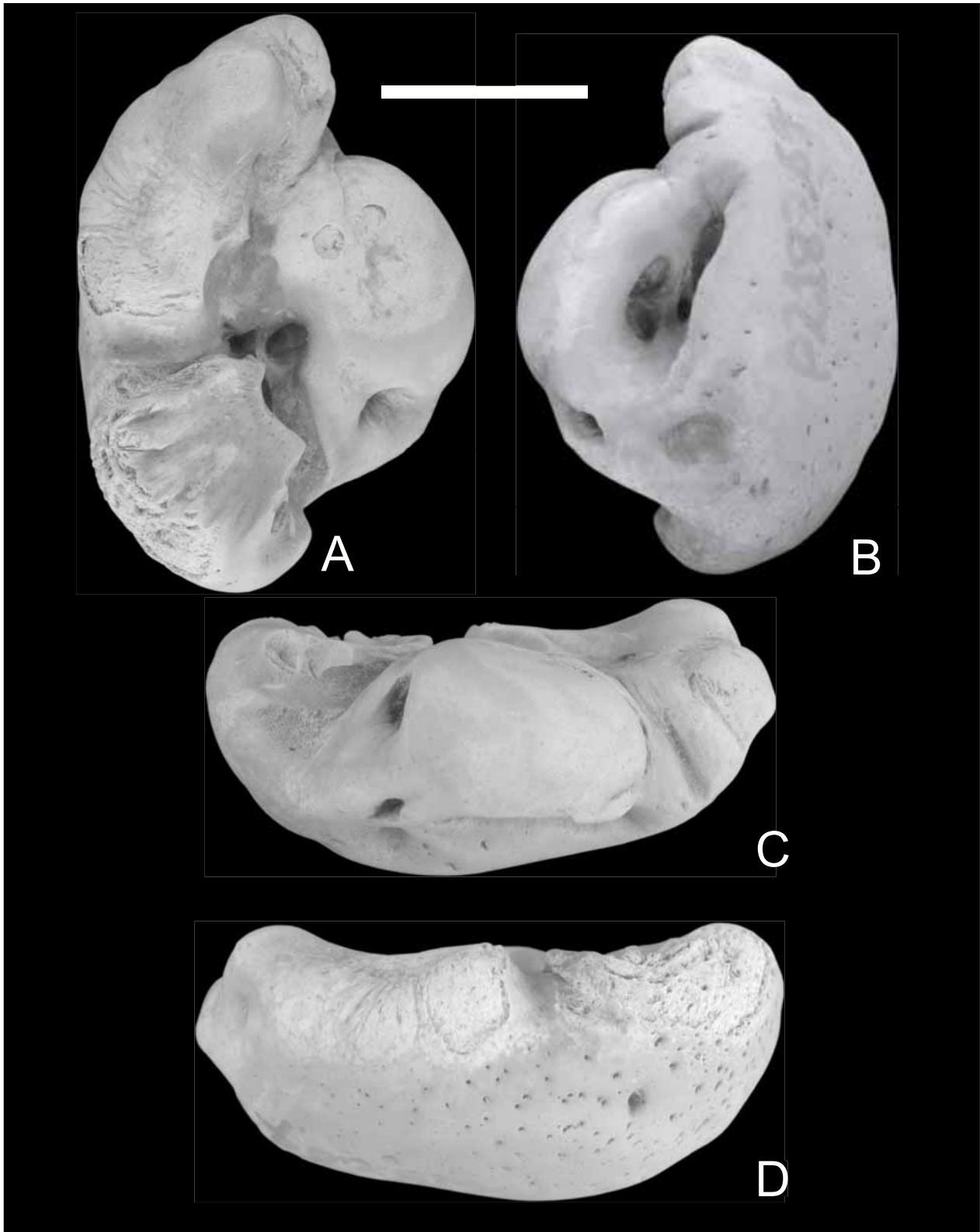
Figure 8. Delphinidae gen. et sp. undet. A (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), right periotic, NMV P218264 (**AC**). **A**, ventral view. **B**, cranial view. **C**, medial view. **D**, lateral view. Scale bar equals 10 mm.

Figure 9. Delphinidae gen. et sp. undet. A (Pleistocene-Pliocene Red Crag, Henley, England), right periotic, NMV P218481 (**AC**). **A**, ventral view. **B**, cranial view. **C**, medial view. **D**, lateral view. Scale bar equals 10 mm.
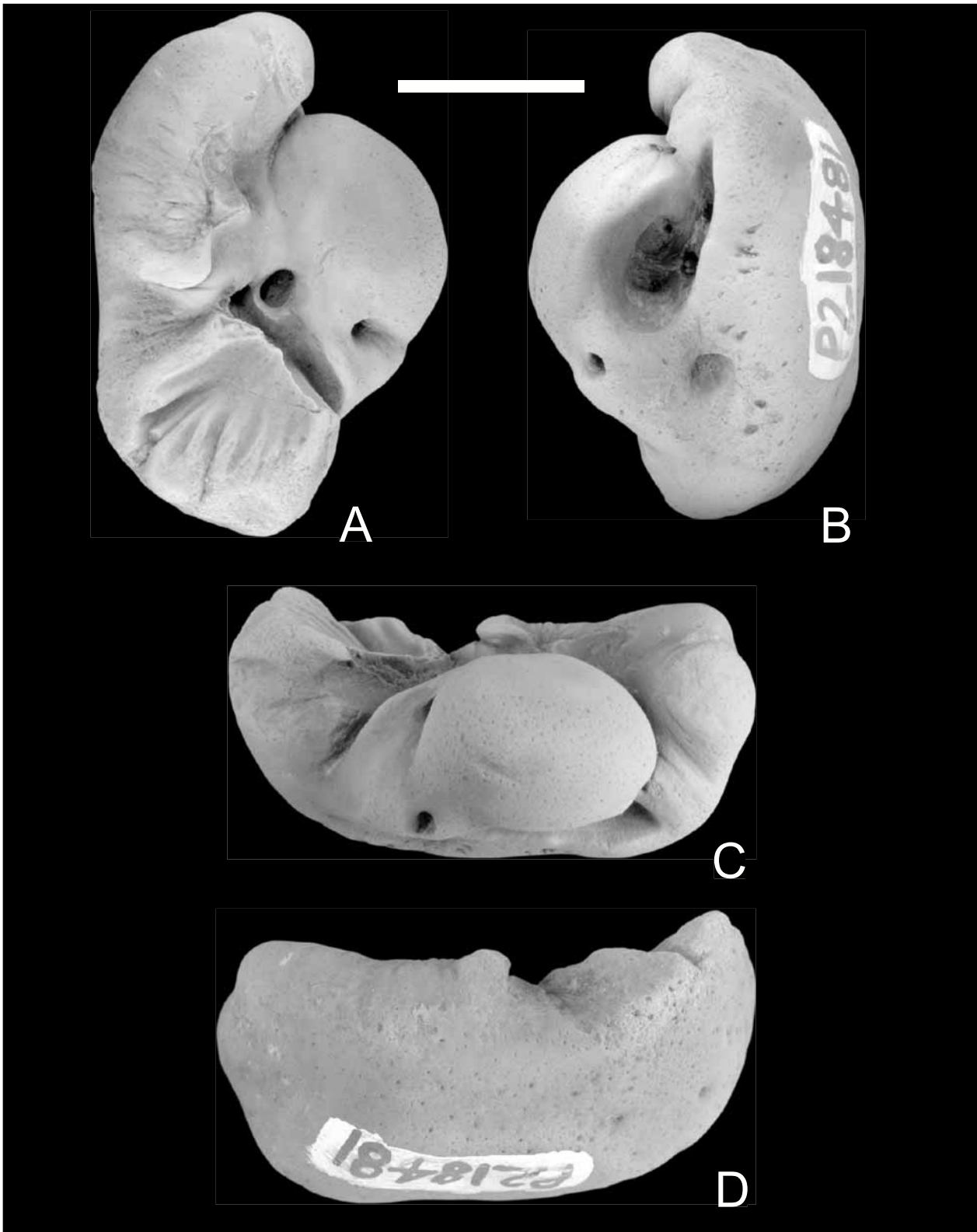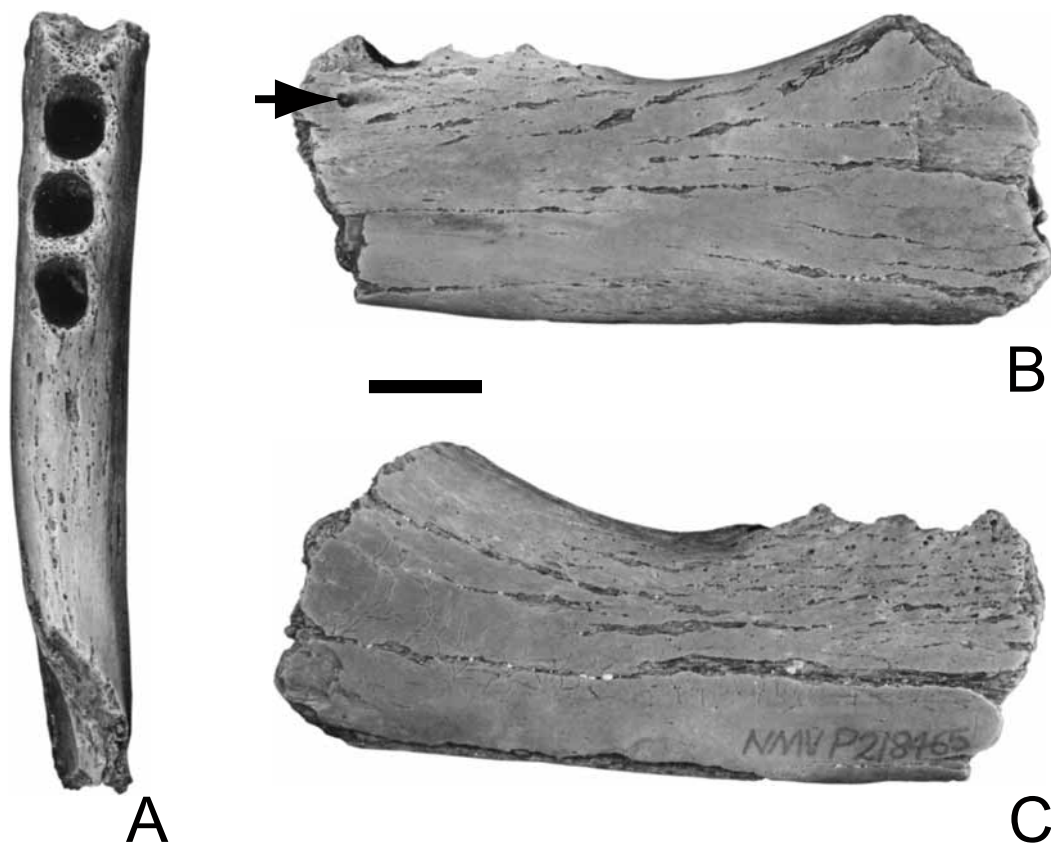
Figure 10. ?Phocidae gen. et sp. indet. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), incomplete left mandible, NMV P218465 (**AC**). **A**, dorsal view. **B**, lateral view. **C**, medial view. Black arrow in **B** points to mental foramen. Scale bar equals 10 mm

referred to the Phocidae on the basis of its morphology and proportions being most similar to the mandibles of phocid seals, as opposed to otariids and odobenids. It remains possible that P218465 represents an otariid mandible. If this were the case, then a major rethinking of otariid evolutionary biogeography would be necessary, as current estimates place the otariid dispersal into the Southern Hemisphere at around the Pliocene/Pleistocene boundary (Deméré et al., 2003; contra Repenning and Tedford, 1977, who indicated a latest Miocene dispersal event at the earliest), and the age of P218465 (and P218273) probably predates that horizon.

Given that P218465 is not similar in morphology to Otariidae but shares certain features with some phocids (see description and discussion below), there is no firm evidence to suggest that the Portland mandible represents an otariid. The fact that phocid seal fossils have previously been reported from Pliocene-aged sediments in Victoria (Fordyce and Flannery, 1983) whereas otariids have not lends further support to the assignment of P218465 to the Phocidae. However, P218465 and P218273 are not referred unquestionably to Phocidae because the late Neogene fossil record of marine mammals in the SW Pacific remains too poorly documented to provide any absolute idea of the composition of the marine mammal fauna during the Pliocene.

Among extant and fossil phocid mandibles, P218465 is most similar to those of the Pliocene taxa *Acrophoca longirostris* Muizon, 1981, *Homiphoca capensis* Hendey and Repenning, 1972, and *Piscophoca pacifica* Muizon, 1981. P218465 may be clearly distinguished from *Acrophoca*, as it lacks the wide diastema between cheek teeth characteristic of *Acrophoca* (Muizon, 1981). The Portland mandible can be further distinguished from *Homiphoca* (Hendey and Repenning, 1972; Muizon and Hendey, 1980) by the possession of a well-developed dorsal concavity posterior to m1. P218465 is generally very similar to the mandible of *Piscophoca* (Muizon, 1981) in its overall proportions, relative length of the dorsal concavity posterior to m1, subequal diameters of the alveoli and relatively closely spaced alveoli along the tooth row. However, it is not possible at this stage to determine whether the Portland mandible belongs to a species of *Piscophoca* or not.

The Australian fossil record of pinnipeds is currently poor. Fordyce (1991b) summarised the state of knowledge at the beginning of the 1990s, and virtually nothing has been added since that time. The oldest fossil pinnipeds from the SW Pacific are latest Miocene (c. 6 Ma) at the earliest and are from Australia (Fitzgerald, 2004b). Fordyce and Flannery (1983) provided a preliminary assessment of these fragmentary fossils suggesting that they represented monachine phocids. The fossils represent one ?incisor tooth (P16198), two right temporals

(P160399 and P160441), two fused sacral vertebrae (P41759) and an articulated series of eight thoracic vertebrae with five ribs (P160433). None of these specimens has yet been described and only one of the temporals (P160399) has been figured (Fordyce and Flannery, 1983: 99). Recently, two other pre-Pleistocene ?phocid fossils have been discovered: P42523, isolated right metatarsal V; and P215759, isolated left metatarsal V. Both P42523 and P215759 were derived from beds immediately overlying a phosphatic nodule horizon at the base of the Black Rock Sandstone (Beaumaris, Victoria), and are thus early Early Pliocene in age. The exact relationships of the phocids represented by temporals to extant Monachinae and their fossil sister-taxa (*Acrophoca*, *Homiphoca* and *Piscophoca*) have yet to be determined. The report herein of two probable phocid pinniped fossils from Portland brings the number of known Australian pre-Pleistocene pinniped specimens to nine.

Conclusions

The fossil marine mammal assemblage from the Pliocene-aged Whalers Bluff Formation is the first to be described in detail from Australia. All marine mammal taxa represent members of extant families and for the most part extant genera: *Physeter*, *Tursiops*, and *Delphinus* or *Stenella*. Other taxa, of uncertain affinities below family level, include a balaenid, balaenopterid, a third undetermined genus of delphinid and a phocid pinniped. The diversity of marine mammals in the Portland Pliocene assemblage is impoverished relative to extant faunas, with at least 18 marine mammal species regularly occurring in northwest Bass Strait (Warneke in Menkhorst, 1995; pers. obs.).

Published details of other SW Pacific Pliocene marine mammal assemblages are scanty (Fordyce, 1991a, 1991b; Fitzgerald, 2004b). Only three Australian assemblages provide a reasonable basis for comparison with the Portland Pliocene assemblage; the Beaumaris Local Fauna (Victoria), Grange Burn assemblage (Victoria) and Cameron Inlet assemblage (Flinders Island, Bass Strait). However, only the Cameron Inlet assemblage is approximately contemporaneous with the Portland Pliocene assemblage (about 2.5–4.8 Ma), the Cameron Inlet Formation being late Early to Late Pliocene (about 2.0–4.0 Ma; Fitzgerald, 2004b and references therein). The Beaumaris Local Fauna spans the Miocene–Pliocene boundary, with an age range for the Black Rock Sandstone of about 4.5–5.8 Ma (Dickinson et al., 2002; Wallace et al., 2005). The Grange Burn assemblage is perhaps slightly younger than the Beaumaris Local Fauna, with the Grange Burn Formation being Early Pliocene (>4.35–5.3 Ma) (Dickinson et al., 2002; Fitzgerald, 2004; Wallace et al., 2005). Both the Beaumaris Local Fauna and the Grange Burn assemblage are (at least in part) phosphatic nodule bed deposits.

A significant problem in making meaningful comparisons between the Portland Pliocene assemblage and the other assemblages listed above lies in the great disparity in numbers of specimens collected. Whereas the Portland Pliocene and Cameron Inlet assemblages are known from 30–40 specimens, the Beaumaris Local Fauna and Grange Burn assemblage are known from hundreds of fossils. Nevertheless, with this bias in mind some preliminary comparisons can be made.

In all four assemblages almost all marine mammal families present are extant. The sole exception to this is the occurrence of the paraphyletic family 'Cetotheriidae' (Fordyce and Barnes, 1994; Fordyce, 2003; Geisler and Luo, 1996; Geisler and Sanders, 2003; Kimura and Ozawa, 2002) in the Beaumaris Local Fauna and Grange Burn assemblage (Fitzgerald, 2004b). At the generic level, there appear to be some differences between the known diversity of marine mammals in the Portland Pliocene assemblage/Cameron Inlet assemblage and the Beaumaris Local Fauna/Grange Burn assemblage. In the latter two, extant genera include cf. *Eubalaena*, *Balaenoptera*, *Megaptera*, *Physeter* and cf. *Mesoplodon*. The delphinids from the phosphatic nodule bed assemblages do not appear to be closely related to extant genera, contrary to earlier assessments (e.g., Chapman, 1917). Rather, delphinid periotics and middle ear ossicles from the Beaumaris Local Fauna possess a relatively high number of primitive characters with respect to extant Delphinidae. This is markedly different from the Portland Pliocene assemblage in which most described delphinid periotics seem to represent extant genera. Other apparently archaic aspects of the Beaumaris Local Fauna/Grange Burn assemblage include the high diversity of physeterid taxa (three genera, including a small form similar to the form genus *Scaldicetus* and another similar to *Physeterula dubusii* Van Beneden, 1877) relative to the present (one genus).

The Cameron Inlet assemblage appears to be essentially modern in aspect based on fossils recovered to date. Fordyce (1991b:1183) listed ziphiids (including *Mesoplodon* sp., based on isolated periotics), physeterids (cf. *Physeter macrocephalus*) and balaenopterids in this assemblage. Fitzgerald (2004: 198) included cf. *Balaenoptera*, cf. *Megaptera* and a possible delphinid. Sutherland and Kershaw (1971) reported an incomplete skull (NMV P23961) as *Ziphius* sp. but Fordyce (1984b: 939) later questioned this assignment and re-identified NMV P23961 as ?*Mesoplodon* sp. The Cameron Inlet assemblage is generally similar to the Portland Pliocene assemblage which is perhaps not unexpected given their similar geological age and geographic proximity.

It has previously been noted that latest Miocene through Pliocene marine mammal assemblages across the globe include extinct, often aberrant, genera and families and formerly wider (in some cases unexpected) geographic ranges for extant taxa that today have restricted geographic distributions (Fordyce et al., 2002 and references therein). Indeed, the apparently recent evolution of marine mammal faunas of modern aspect led Fordyce and colleagues (2002) to suggest that among cetaceans at least a major ecological change occurred about 3–4 million years ago. This change is marked by the last appearance in the fossil record of genus and family-level taxa displaying relatively primitive grades of evolution (e.g., Albireonidae, *Herpetocetus*: Barnes, 1984; Whitmore, 1994; Oishi and Hasegawa, 1995; Barnes and Furusawa, 2001; Fordyce and Muizon, 2001) as well as novel morphological adaptations and inferred palaeoecology (e.g., Odobenocetopsidae, *Australodelphis*: Fordyce et al., 2002; Muizon and Domning, 2002).

The early Pliocene is marked by a global warming trend beginning at c. 4.5–5.5 Ma with the rapid development of full-scale Northern Hemisphere and Antarctic glaciation occurring

in the late Pliocene at approximately 2.75–3.2 Ma (Zachos et al., 2001; Ravelo et al., 2004; Wara et al., 2005). Gallagher and colleagues (2003) presented data indicating that the earlier Pliocene (3.1–5.3 Ma) was a time of generally stable marine temperatures in Bass Strait with surface temperatures perhaps as much as 3°C warmer than today (Ravelo et al., 2004). The Late Pliocene in Bass Strait was characterised by a fluctuating, overall cooler climate than the preceding Early Pliocene (Gallagher et al., 2003). As Fordyce and colleagues (2002) have indicated, climatic and oceanic changes associated with rapid global cooling at c. 3.2 Ma were likely major influences on the evolution of the modern marine mammal fauna. A larger sample of marine mammal fossils from Pliocene-aged assemblages in south-east Australia with finer resolution of stratigraphic distribution of marine mammal taxa during the Pliocene is required for more detailed correlations between Pliocene marine mammal and climatic evolution.

The description of the Pliocene marine mammal assemblage from Portland alleviates the dearth of information on SW Pacific marine mammal assemblages during the late Neogene. The occurrence of extant cetacean taxa (*Balaenoptera, Physeter, Delphinus/Stenella* and *Tursiops*) in the Whalers Bluff Formation (>2.5–4.8 Ma) (and Cameron Inlet Formation) indicates that the marine mammal fauna off south-east Australia had begun to take on a modern aspect by at the earliest 4.8 Ma and latest around 2.5 Ma. Indeed, most of the cetacean species still exist in the seas off Portland (Warneke in Menkhorst, 1995; pers. obs.). That the latter cetacean taxa occur in Early-Late Pliocene deposits in the SW, SE and NE Pacific, and NW Atlantic, suggests that several extant cetacean genera were widespread in the world's ocean basins prior to about 2.5 Ma.

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References

Abele, C., Gloe, C.S., Hocking, J.B., Holdgate, G., Kenley, P.R., Lawrence, C.R., Ripper, D., Threlfall, W.F., and Bolger, P.F. 1988. Tertiary. Pp. 251–350 in: Douglas, J.G. and Ferguson, J.A. (eds), *Geology of Victoria.* Victorian Division, Geological Society of Australia Incorporated: Melbourne.

Bannister, J.L. 2002. Baleen whales: mysticetes. Pp. 62–72 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals.* Academic Press: San Diego.

Barnes, L.G. 1973a. Pliocene cetaceans of the San Diego Formation, San Diego, California. Pp. 37–42 in: Ross, A. and Dowlen, R.J. (eds), *Studies on the Geology and Geologic Hazards of the Greater San Diego Area, California.* San Diego Association of Geologists: San Diego.

Barnes, L.G. 1973b. *Praekogia cedrosensis*, a new genus and species of fossil pygmy sperm whale from Isla Cedros, Baja California, Mexico. *Contributions in Science, Natural History Museum of Los Angeles County* 247: 1–20.

Barnes, L.G. 1977. Outline of eastern North Pacific fossil cetacean assemblages. *Systematic Zoology* 25: 321–343.

Barnes, L.G. 1978. A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odontoceti). *Bulletin of the Natural History Museum of Los Angeles County* 28: 1–35.

Barnes, L.G. 1984. Fossil odontocetes (Mammalia: Cetacea) from the Almejas Formation, Isla Cedros, Mexico. *PaleoBios* 42: 1–46.

Barnes, L.G. 1985. Fossil pontoporiid dolphins (Mammalia: Cetacea) from the Pacific coast of North America. *Contributions in Science, Natural History Museum of Los Angeles County* 363: 1–34.

Barnes, L.G. 1990. The fossil record and evolutionary relationships of the genus *Tursiops.* Pp. 3–26 in: Leatherwood, S. and Reeves, R.R. (eds), *The Bottlenose Dolphin.* Academic Press: San Diego.

Barnes, L.G. 1998. The sequence of fossil marine mammal assemblages in México. *Avances En Investigación. Publicación Especial 1 (Paleontología de Vertebrados)*: 26–79.

Barnes, L.G. 2002. Delphinoids, evolution of the modern families. Pp. 314–316 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals.* Academic Press: San Diego.

Barnes, L.G., and Furusawa, H. 2001. A primitive albireonid dolphin (Cetacea, Odontoceti, Delphinoidea) from Hokkaido, Japan. *Journal of Vertebrate Paleontology* 21 (Supplement to No. 3): 31A.

Barnes, L.G., and Mitchell, E.D. 1984. *Kentriodon obscurus* (Kellogg, 1931), a fossil dolphin (Mammalia: Kentriodontidae) from the Miocene Sharktooth Hill Bonebed in California. *Contributions in Science, Natural History Museum of Los Angeles County* 353: 1–23.

Barnes, L.G., Howard, H., Hutchison, J.H., and Welton, B.J. 1981. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. Pp. 53–70 in: Abbott, P.L. and O'Dunn, S. (eds), *Geologic Investigations of the San Diego Coastal Plain.* San Diego Association of Geologists: San Diego.

Barnes, L.G., Pyenson, N.D., and McLeod, S.A. 2005. Middle Miocene marine ecosystems and cetacean diversity as exemplified by the Sharktooth Hill Bonebed, California, USA. Pp. 6–7 in: Uhen, M.D. (ed), *Evolution of Aquatic Tetrapods: Fourth Triannual Convention Abstracts.* Cranbrook Institute of Science Miscellaneous Publications 1.

Bearlin, R.K. 1987. The morphology and systematics of Neogene Mysticeti from Australia and New Zealand. Ph.D. Thesis, University of Otago: Dunedin. 212 pp.

Berta, A. 1991. New *Enaliarctos** (Pinnipedimorpha) from the Oligocene and Miocene of Oregon and the role of "enaliarctids" in pinniped phylogeny. *Smithsonian Contributions to Paleobiology* 69: 1–33.

Berta, A., and Wyss, A.R. 1994. Pinniped phylogeny. Pp. 33–56 in: Berta, A. and Deméré, T.A. (eds), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History 29.

Beu, A.G. 1995. Pliocene limestones and their scallops: lithostratigraphy, pectinid biostratigraphy and paleogeography of eastern North Island late Neogene limestone. *Institute of Geological and Nuclear Sciences Monograph* 10: 1–243.

Beu, A.G., and Darragh, T.A. 2001. Revision of southern Australian Cenozoic fossil Pectinidae (Mollusca: Bivalvia). *Proceedings of the Royal Society of Victoria* 113: 1–205.

Bisconti, M. 2003. Evolutionary history of Balaenidae. *Cranium* 20: 9–50.

Bisconti, M. 2005. Skull morphology and phylogenetic relationships of a new diminutive balaenid from the Lower Pliocene of Belgium. *Palaeontology* 48: 793–816.

Boutakoff, N., and Sprigg, R.C. 1953. Summary report on the petroleum possibilities of the Mount Gambier sunklands. *Mining and Geological Journal, Department of Mines, Victoria* 5: 28–42.

Brownell, R.L., Jr., and Herald, E.S. 1972. *Lipotes vexillifer*. *Mammalian Species* 10: 1–4.

Chapman, F. 1917. New or little-known Victorian fossils in the National Museum. Part XXI. Some Tertiary cetacean remains. *Proceedings of the Royal Society of Victoria* 30: 32–43.

Cummings, W.C. 1985. Right Whales, *Eubalaena glacialis* (Müller, 1776) and *Eubalaena australis* (Desmoulins, 1822). Pp. 275–304 in: Ridgway, S.H. and Harrison, R. (eds), *Handbook of Marine Mammals. Volume 3: The Sirenians and Baleen Whales*. Academic Press: London.

Dawson, S.D. 1996. A description of the skull and postcrania of *Hadrodelphis calvertense* Kellogg 1966, and its position within the Kentriodontidae (Cetacea; Delphinoidea). *Journal of Vertebrate Paleontology* 16: 125–134.

Deméré, T.A., Berta, A., and Adam, P.J. 2003. Pinnipedimorph evolutionary biogeography. *Bulletin of the American Museum of Natural History* 279: 32–76.

Dickinson, J.A., Wallace, M.W., Holdgate, G.R., Gallagher, S.J., and Thomas, L. 2002. Origin and timing of the Miocene-Pliocene unconformity in southeast Australia. *Journal of Sedimentary Research* 72: 288–303.

Dixon, J.M. 1990. Record of a southern right whale (*Eubalaena australis*) skeleton from Altona Bay, Victoria, Australia. T*he Victorian Naturalist* 107: 159–162.

Evans, H.E. 1993. *Miller's Anatomy of the Dog. Third Edition*. W. B. Saunders Company: Philadelphia. 1113 pp.

Fitzgerald, E.M.G. 2004a. The fossil record of cetaceans (Mammalia) on the Australian continent. *Fossil Collector Bulletin* 72: 5–32.

Fitzgerald, E.M.G. 2004b. A review of the Tertiary fossil Cetacea (Mammalia) localities in Australia. *Memoirs of Museum Victoria* 61: 183–208.

Fordyce, R.E. 1982. A review of Australian fossil Cetacea. *Memoirs of the National Museum of Victoria* 43: 43–58.

Fordyce, R.E. 1984a. Preliminary report on cetacean bones from Chatham Rise (New Zealand). *Geologisches Jahrbuch, Reihe* D Heft 65: 117–120.

Fordyce, R.E. 1984b. Evolution and zoogeography of cetaceans in Australia. Pp. 929–948 in: Archer, M. and Clayton, G. (eds), *Vertebrate Zoogeography and Evolution in Australasia*. Hesperian Press: Perth.

Fordyce, R.E. 1989. Origin and evolution of Antarctic marine mammals. Pp. 269–281 in: Crame, J.A. (ed), *Origins and Evolution of the Antarctic Biota*. Geological Society Special Publication No. 47.

Fordyce, R.E. 1991a. A new look at the fossil vertebrate record of New Zealand. Pp. 1191–1316 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.

Fordyce, R.E. 1991b. The Australasian marine vertebrate record and its climatic and geographic implications. Pp. 1165–1190 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.

Fordyce, R.E. 1994. *Waipatia maerewhenua*, new genus and new species (Waipatiidae, new family), an archaic Late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. Pp. 147–176 in: Berta, A., and Deméré, T.A. (eds), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History 29.

Fordyce, R.E. 2002a. Fossil sites. Pp. 471–482 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals*. Academic Press: San Diego.

Fordyce, R.E. 2002b. Oligocene origins of skim-feeding right whales: a small archaic balaenid from New Zealand. *Journal of Vertebrate Paleontology* 22 (Supplement to No. 3): 54A.

Fordyce, R.E. 2003. Cetacean evolution and Eocene-Oligocene oceans revisited. Pp. 154–170 in: Prothero, D.R., Ivany, L.C., and Nesbitt, E.A. (eds), *From Greenhouse to Icehouse: the Marine Eocene-Oligocene Transition*. Columbia University Press: New York.

Fordyce, R.E., and Barnes, L.G. 1994. The evolutionary history of whales and dolphins. *Annual Review of Earth and Planetary Sciences* 22: 419–455.

Fordyce, R.E., and Campbell, H.J. 1990. Fossil dolphin bones from the Chatham Islands, New Zealand. *New Zealand Natural Sciences* 17: 61–65.

Fordyce, R.E., and Flannery, T.F. 1983. Fossil phocid seals from the late Tertiary of Victoria. *Proceedings of the Royal Society of Victoria* 95: 99–100.

Fordyce, R.E., and Muizon, C. de. 2001. Evolutionary history of cetaceans: a review. Pp. 169–233 in: Mazin, J.–M. and Buffrénil, V. de (eds), *Secondary Adaptation of Tetrapods to Life in Water*. Verlag Dr. Friedrich Pfeil: München.

Fordyce, R.E., Quilty, P.G., and Daniels, J. 2002. *Australodelphis mirus*, a bizarre new toothless ziphiid-like fossil dolphin (Cetacea: Delphinidae) from the Pliocene of Vestfold Hills, East Antarctica. *Antarctic Science* 14: 37–54.

Gallagher, S.J., Greenwood, D.R., Taylor, D., Smith, A.J., Wallace, M.W., and Holdgate, G.R. 2003. The Pliocene climatic and environmental evolution of southeastern Australia: evidence from the marine and terrestrial realm. *Palaeogeography, Palaeoclimatology, Palaeoecology* 193: 349–382.

Geisler, J.H., and Luo, Z. 1996. The petrosal and inner ear of *Herpetocetus* sp. (Mammalia: Cetacea) and their implications for the phylogeny and hearing of archaic mysticetes. *Journal of Paleontology* 70: 1045–1066.

Geisler, J.H., and Luo, Z. 1998. Relationships of Cetacea to terrestrial ungulates and the evolution of cranial vasculature in Cete. Pp. 163–212 in: Thewissen, J.G.M (ed), *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea*. Plenum Press: New York.

Geisler, J.H., and Sanders, A.E. 2003. Morphological evidence for the phylogeny of Cetacea. *Journal of Mammalian Evolution* 10: 23–129.

Gill, E.D. 1957. The stratigraphical occurrence and palaeoecology of some Australian Tertiary marsupials. *Memoirs of the National Museum of Victoria* 21: 135–203.

Gottfried, M.D., Bohaska, D.J., and Whitmore, F.C., Jr. 1994. Miocene cetaceans of the Chesapeake Group. Pp. 229–238 in: Berta, A. and Deméré, T.A. (eds), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History 29.

Gradstein, F.M., Ogg, J.G., Smith, A.G., Agterberg, F.P., Bleeker, W., Cooper, R.A., Davydov, V., Gibbard, P., Hinnov, L., House, M.R., Lourens, L., Luterbacher, H.-P., McArthur, J., Melchin, M.J., Robb, L.J., Shergold, J., Villeneuve, M., Wardlaw, B.R., Ali, J., Brinkhuis, H., Hilgen, F.J., Hooker, J., Howarth, R.J., Knoll, A.H., Laskar, J., Monechi, S., Powell, J., Plumb, K.A., Raffi, I., Röhl, U., Sadler, P., Sanfilippo, A., Schmitz, B., Shackleton, N.J., Shields, G.A., Strauss, H., Van Dam, J., Veizer, J., van Kolfschoten, T., and Wilson, D. 2004. *A Geologic Time Scale 2004.* Cambridge University Press: Cambridge. 500 pp.

Hendey, Q.B., and Repenning, C.A. 1972. A Pliocene phocid from South Africa. *Annals of the South African Museum* 59: 71–98.

Howchin, W. 1919. [Tympanic bone of *Balaena* from the Pliocene of South Australia]. *Transactions and Proceedings of the Royal Society of South Australia* 43: 430.

Howell, A.B. 1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). P*roceedings of the United States National Museum* 73: 1–142.

Kasuya, T. 1973. Systematic consideration of Recent toothed whales based on the morphology of tympano-periotic bone. T*he Scientific Reports of the Whales Research Institute* 25: 1–103.

Kellogg, R. 1965. Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia. Part 2. The Miocene Calvert sperm whale *Orycterocetus*. *United States National Museum Bulletin* 247: 47–63.

Kellogg, R. 1966. Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia. Part 4. A new odontocete from the Calvert Miocene of Maryland. *United States National Museum Bulletin* 247: 99–101.

Kimura, T., and Ozawa, T. 2002. A new cetothere (Cetacea: Mysticeti) from the Early Miocene of Japan. *Journal of Vertebrate Paleontology* 22: 684–702.

LeDuc, R.G., Perrin, W.F., and Dizon, A.E. 1999. Phylogenetic relationships among the delphinoid cetaceans based on full cytochrome b sequences. *Marine Mammal Science* 15: 619–648.

LeDuc, R.G. 2002. Delphinids, overview. Pp. 310–314 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals*. Academic Press: San Diego.

Lydekker, R. 1887. The Cetacea of the Suffolk Crag. *Quarterly Journal of the Geological Society* 43: 7–18.

McKee, J.W.A., and Fordyce, R.E. 1987. Dolphin mandible (Delphinidae) from the Waipipian Stage (Pliocene), Waihi Beach, Taranaki, New Zealand. *New Zealand Journal of Geology and Geophysics* 30: 321–323.

McLeod, S.A., Whitmore, F.C., Jr., and Barnes, L.G. 1993. Evolutionary relationships and classification. Pp. 45–70 in: Burns, J.J., Montague, J.J., and Cowles, C.J. (eds), *The Bowhead Whale.* The Society for Marine Mammalogy Special Publication Number 2.

Menkhorst, P.W. 1995. *Mammals of Victoria: Distribution, ecology and conservation.* Oxford University Press: Melbourne. 359 pp.

Miller, G.S., Jr. 1918. A new river-dolphin from China. *Smithsonian Miscellaneous Collections* 68(2486): 1–12.

Miller, G.S., Jr. 1924. A Pollack whale from Florida presented to the National Museum by the Miami Aquarium Association. *Proceedings of the United States National Museum* 66 (Article 9): 1–15.

Miyazaki, N., and Perrin, W.F. 1994. Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). Pp. 1–21 in: Ridgway, S.H., and Harrison, R. (eds), *Handbook of Marine Mammals, Volume 5: The First Book of Dolphins.* Academic Press: London.

Muizon, C. de. 1981. Les vertébrés fossiles de la formation Pisco (Pérou). Première partie: Deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène de Sud-Sacaco. *Travaux de l'Institut Français d'Etudes Andines* 22: 1–161.

Muizon, C. de. 1984. Les vertébrés fossiles de la Formation Pisco (Pérou). Deuxième partie: Les odontocètes (Cetacea, Mammalia) du Pliocène inférieur de Sud-Sacaco. *Travaux de l'Institut Français d'Etudes Andines* 27: 1–188.

Muizon, C. de. 1988. Les vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les odontocètes (Cetacea, Mammalia) miocènes. *Travaux de l'Institut Français d'Etudes Andines* 42: 1–244.

Muizon, C. de, and Bellon, H. 1986. Nouvelles données sur l' âge de la Formation Pisco (Pérou). *Comptes-Rendus de l'Académie des Sciences Paris. Série II. Mécanique-Physique-Chimie, Sciences de l'Univers, Sciences de la Terre* 303: 1401–1404.

Muizon, C. de, and DeVries, T.J. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74: 547–563.

Muizon, C. de. and Domning, D.P. 1985. The first records of fossil sirenians in the southeastern Pacific Ocean. *Bulletin du Muséum Nationale d'Histoire Naturelle (Paris)* (4)7, Sect. C, 3: 189–213.

Muizon, C. de, and Domning, D.P. 2002. The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications. *Zoological Journal of the Linnean Society* 134: 423–452.

Muizon, C. de, and Hendey, Q.B. 1980. Late Tertiary seals of the South Atlantic Ocean. *Annals of the South African Museum* 82: 91–128.

Muizon, C. de, McDonald, H.G., Salas, R., and Urbina, M. 2004. The youngest species of the aquatic sloth *Thalassocnus* and a reassessment of the relationships of the nothrothere sloths (Mammalia: Xenarthra). *Journal of Vertebrate Paleontology* 24: 387–397.

Oishi, M., and Hasegawa, Y. 1994 (1995). Diversity of Pliocene mysticetes from eastern Japan. *The Island Arc* 3: 436–452.

Prothero, D.R. 1998. The chronological, climatic, and paleogeographic background to North American mammalian evolution. Pp. 9–36 in: Janis, C.M., Scott, K.M., and Jacobs, L.J. (eds), *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals.* Cambridge University Press: Cambridge.

Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O., and Wara, M.W. 2004. Regional climate shifts caused by gradual cooling in the Pliocene epoch. *Nature* 429: 263–267.

Reeves, R.R., and Leatherwood, S. 1985. Bowhead Whale, *Balaena mysticetus* Linnaeus, 1758. Pp. 305–344 in: Ridgway, S.H. and Harrison, R. (eds), *Handbook of Marine Mammals. Volume 3: The Sirenians and Baleen Whales.* Academic Press: London.

Repenning, C.A., and Tedford, R.H. 1977. Otarioid seals of the Neogene. *United States Geological Survey Professional Paper* 992: 1–93.

Rice, D.W. 1998. *Marine Mammals of the World: Systematics and Distribution.* The Society for Marine Mammalogy Special Publication Number 4. 231 pp.

Singleton, O.P., McDougall, I., and Mallett, C.W. 1976. The Pliocene-Pleistocene boundary in southeastern Australia. *Journal of the Geological Society of Australia* 23: 299–311.

Sutherland, F.L., and Kershaw, R.C. 1971. The Cainozoic geology of Flinders Island, Bass Strait. *Papers and Proceedings of the Royal Society of Tasmania* 105: 151–175.

Wallace, M.W., Dickinson, J.A., Moore, D.H., and Sandiford, M. 2005. Late Neogene strandlines of southern Victoria: a unique record of eustasy and tectonics in southeast Australia. *Australian Journal of Earth Sciences* 52: 279–297.

Walsh, S., and Naish, D. 2002. Fossil seals from late Neogene deposits in South America: a new pinniped (Carnivora, Mammalia) assemblage from Chile. *Palaeontology* 45: 821–842.

Wara, M.W., Ravelo, A.C., and Delaney, M.L. 2005. Permanent El Niño-like conditions during the Pliocene warm period. *Science* 309: 758–761.

Watson, A.G., and Fordyce, R.E. 1994. Skeleton of two minke whales, *Balaenoptera acutorostrata*, stranded on the south-east coast of New Zealand. *New Zealand Natural Sciences* 20: 1–14.

Westgate, J.W., and Whitmore, F.C., Jr. 2002. *Balaena ricei*, a new species of bowhead whale from the Yorktown Formation (Pliocene) of Hampton, Virginia. Pp. 295–312 in: Emry, R.J. (ed), *Cenozoic Mammals of Land and Sea: Tributes to the Career of Clayton E. Ray*. Smithsonian Contributions to Paleobiology 93.

Whitmore, F.C., Jr. 1994. Neogene climatic change and the emergence of the modern whale fauna of the North Atlantic Ocean. Pp. 223–227 in: Berta, A. and Deméré, T.A. (eds), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr*. Proceedings of the San Diego Society of Natural History 29.

Wyss, A.R., and Flynn, J.J. 1993. A phylogenetic analysis and definition of the Carnivora. Pp. 32–52 in: Szalay, F.S., Novacek, M.J. and McKenna, M.C. (eds), *Mammal Phylogeny*. Springer-Verlag: Berlin.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.