A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia

Erich M.G. Fitzgerald1,2

1 Geosciences, Museum Victoria, GPO Box 666, Melbourne, Victoria 3001, Australia (efitzgerald@museum.vic.gov.au)
2 Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA

Abstract

Fitzgerald, E.M.G. 2016. A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia. Memoirs of Museum Victoria 74: 117–136.

A partial odontocete skeleton comprising isolated teeth, forelimb elements, ribs, and vertebrae is described from the upper Oligocene (Chattian) Jan Juc Marl of Jan Juc, Victoria, southeast Australia. Its dental and forelimb characters most closely resemble those of the late Oligocene Waipatia and Sulakocetus from New Zealand and the Caucasus, respectively; thus the Jan Juc odontocete is referred to an indeterminate species in the family Waipatiidae (Platanistoidea). This specimen represents the first report of Waipatiidae in Australia, expands the taxonomic diversity of Australian Oligocene Cetacea, and shows that Waipatiidae occurred in the Chattian cetacean assemblages of both Australia and New Zealand.

Keywords

Platanistoidea, Waipatiidae, dolphin, Paleogene, fossil, systematics, taxonomy.

Introduction

The fossil record of Cetacea (whales and dolphins) in Australia is meager: not through lack of Cenozoic marine rock outcrop, which is widespread in southern Australia, but rather a limited history of systematic research (Fitzgerald, 2004; Fordyce, 2006). Yet, the potential for improving this meager record, and gaining broader insights into cetacean evolution, have long been recognized by Thomas H. Rich (Rich, 1976, 1999; Vickers-Rich and Rich, 1993; Rich in Warne et al., 2003). Rich developed an awareness of the potential for research on Australasian fossil Cetacea, first in New Zealand during National Geographic Society-funded fieldwork (Rich, 1975; Rich and Rich, 1982), and then in Australia at the beginning of his career as Curator at the National Museum of Victoria (now Museum Victoria) in 1974. In both instances, this nascent attention paid to fossil Cetacea was encouraged by Dr Frank C. Whitmore, Jr., a United States Geological Survey marine mammal palaeontologist assigned to the National Museum of Natural History (Eshelman and Ward, 1994). By November 1975, Rich had produced a comprehensive inventory of the fossil Cetacea in the Palaeontology Collection of Museum Victoria.

The following year (1976), Rich with the assistance of Ian R. Stewart, collected a partially articulated incomplete fossil cetacean skeleton from the Upper Oligocene Jan Juc Marl at Jan Juc Beach, Victoria (Figs. 1 and 2). This specimen was registered in 1978 as Museum Victoria Palaeontology Collection (NMV P) 48861 and identified as a “squalodontoid?” On 7 October 1987, F. C. Whitmore, Jr. examined some of the homodont anterior teeth of NMV P48861, identifying the specimen as a “delphinoid”. It was not until 2003 that the preparation of NMV P48861 was commenced by the author, resulting in a third (preliminary) attempt at identifying this fossil as “?Eurhinodelphinidae” (Fitzgerald, 2004: 191).

The aims of this paper are to describe the informative parts of the skeleton of NMV P48861, resolve its phylogenetic relationships, and interpret its biogeographic significance. Until now, the described late Oligocene cetacean assemblage from Australia has consisted of a probable kekenodontid archaeocete (‘Squalodon’ gambierensis Glaessner, 1955), two species of toothed mysticete in the family Mammalodontidae (Mammalodon colliveri Pritchard, 1939 and Janjucetus hunderi Fitzgerald, 2006), and isolated teeth referred to the enigmatic odontocete genus Prosqualodon (Fordyce, 1982; Fitzgerald, 2004). In addition, unnamed odontocete remains tentatively attributed to the Eurhinodelphinidae have been described from the fluvio-lacustrine ~Upper Oligocene Namba Formation of northeast South Australia (Fordyce, 1983; Fitzgerald, 2004). The allocation of NMV P48861 to the odontocete clade Waipatiidae marks the first record of this family in Australia, thereby increasing the family-level diversity of cetaceans known locally from the Paleogene, and expanding the record of Australian fossil Cetacea.
Material and Methods

Preparation. Material was prepared at Melbourne Museum primarily using pneumatic engravers and pin vases fitted with tungsten carbide rod. Dilute (10%) acetic acid was used to remove concretionary carbonate surrounding some bones. Limited areas of resistant matrix were removed using an air-abrasive machine. Bone was glued with cyanoacrylate and/or 40% Paraloid B-72 ethyl-methacrylate copolymer dissolved in acetone. A dilute (3%) solution of Paraloid B-72 in acetone was used as a consolidant.

Photography and measurement. Prior to preparation, archival photographs showing the exposed bones in the sediment were made using a 35 mm film Nikon EL SLR. A digital composite of scans of these photographs is depicted in Fig. 2. All other photographs were taken with a Nikon D90 DSLR camera and a 60 mm micro lens. All measurements were made with vernier calipers.
Anatomical terminology. Because all teeth were found isolated their precise position in the tooth row is unknown, therefore each tooth is numbered with Roman numerals (I–IX) in ascending order to indicate its estimated relative position in the tooth row from most anterior (I) to most posterior (IX). Due to uncertain homology with the cusps of other mammals, the term denticle is used instead of cusp for each major projection on the crown. Denticles (d) are coded as main (md), anterior (a, numbered away from the md: ad1, ad2, etc.), or posterior (p, numbered away from the md: pd1, pd2, etc.) following Marx et al. (2015: 16). Postcranial terms follow Flower (1885) and Schaller (2007).

Institutional abbreviations. LACM, Natural History Museum of Los Angeles County, Los Angeles; MLP, Museo de La Plata, La Plata, Argentina; NMV C, Mammalogy Collection, Museum Victoria, Melbourne; NMV P, Palaeontology Collection, Museum Victoria, Melbourne; OU, Geology Museum, University of Otago, Dunedin; USNM, National Museum of Natural History, Washington, DC.

Systematic Palaeontology

Cetacea Brisson, 1762
Odontoceti Flower, 1865, sensu Flower, 1867
Platanistoidea Gray, 1863, sensu Muizon, 1987
Waipatiidae Fordyce, 1994

Gen. et sp. indet.

“...a primitive eurhinodelphinid odontocete.” (Fitzgerald, 2004: 184)

Referred material. NMV P48861, incomplete skeleton consisting of: nine isolated teeth; fragments of one cervical and 12 thoracic vertebrae; parts of 16 ribs; left incomplete scapula, humerus, radius, ulna, two metacarpals, and phalanx; right (fragmentary) scapula, humerus, radius, ulna, metacarpal, and phalanx; and fragments of two presumed carpals plus three phalanges (Figs. 2–11; Tables 1–2). Collected by Thomas H. Rich and Ian Stewart, 1976.

Locality. Shore platform in intertidal zone, immediately north of Bird Rock (a prominent stack), western end of Jan Juc Beach, Jan Juc, Victoria, southeast Australia; near latitude 38° 20' 58" S, longitude 144° 18' 10" E (Fig. 1).

Horizon and age. NMV P48861 was collected as a single large block (dimensions ~850×520×300 mm) of massive light grey friable silty sandy glauconitic marl forming the lowermost ~2 m of the Jan Juc Marl exposed at Bird Rock (Unit BR 1 in Section 4 of Abele, 1979: 23–25) (Fig 1). The sparse associated macrofossils include molluscs (Dosinia, Limopsis chapmani, Notocallista, Ennucula, cf. Tellina, and Turritellidae indet.; T. A. Darragh, pers. comm. 3 July 2015), bryozoans (Otionellina and cf. Lunulites rutella: R. Schmidt, pers. comm. 3 July 2015), and teleost fish bones.

Table 1. Measurements in mm of NMV P48861, Waipatiidae gen. et sp. indet.: teeth.

| Tooth | crown height | crown anteroposterior length | crown labiolingual width | maximum root length |
|-------|--------------|------------------------------|--------------------------|---------------------|
| I     | 10.4+        | 6.6                          | 5.8                      | 36.0+               |
| II    | 7.3+         | 5.9                          | 4.7                      | 31.8+               |
| III   | 14.0         | 6.0                          | 5.0                      | 43.0                |
| IV    | 12.0         | 5.7                          | 5.2                      | 27.8+               |
| V     | 8.2+         | 5.9                          | 4.0                      | 22.3+               |
| VI    | 10.1+        | 6.2                          | 4.5                      | 23.9+               |
| VII   | 10.1+        | 9.1                          | 4.7                      | 21.4+               |
| VIII  | 8.5+         | 10.3                         | 6.5                      | 23.2                |
| IX    | 8.4+         | 10.4                         | 6.2                      | 21.0                |

Table 2. Measurements in mm of NMV P48861, Waipatiidae, gen. et sp. indet.: forelimb elements. Dimensions adapted from Uhen (2004). Measurements rounded to nearest 0.5 mm. + symbol denotes measurements of the preserved dimension of an incomplete element.

| Scapula       | left | right |
|---------------|------|-------|
| maximum preserved height | 134.0+ | –     |
| maximum preserved length  | 183.0+ | –     |
| neck of scapula width    | 46.0  | –     |
| depth of glenoid fossa   | 8.0   | –     |

| Humerus       | left | right |
|---------------|------|-------|
| maximum length   | 147.0 | 150.0 |
| maximum width of proximal end | 66.0+ | 65.5+ |
| maximum width of shaft   | 56.0  | 56.0  |
| minimum width of shaft    | 40.0  | 42.0  |
| maximum width of distal end | 38.0 | 37.0  |
| maximum transverse diameter of proximal end | 69.0   | –     |
| transverse diameter of shaft at mid-length | 28.0  | 28.0  |
| transverse diameter of distal end   | 26.0  | 25.0  |

| Ulna         | left | right |
|--------------|------|-------|
| maximum length   | 141.0+ | 172.0+ |
| shaft length    | 99.0+  | 122.5 |
| olecranon length | 68.0+ | 75.0+ |
| maximum width across olecranon | 70.0  | 64.5+ |
| width of shaft at mid-length | 34.0  | 33.0  |
| maximum width of distal end | 41.5+ | 42.5  |

| Radius       | left | right |
|--------------|------|-------|
| maximum length   | 143.0 | –     |
| shaft length    | 118.0 | –     |
| maximum width of proximal end | 28.0+ | 29.0+ |
| width of shaft at mid-length | 35.0  | –     |
| maximum width of distal end | 33.5+ | –     |
Figure 2. The original distribution of elements in matrix prior to preparation, NMV P48861, Waipatidae gen. et sp. indet. **Top**, block of matrix enclosing bones as collected in field, prior to preparation. **Bottom**, tracing of bone outlines in matrix prior to preparation.
Figure 3. Anterior teeth I–III of NMV P48861, Waipatiidae gen. et sp. indet. Tooth I, presumed procumbent incisor in: A, labial; B, anterior; C, posterior; and D, lingual views. Tooth II, anterior tooth in: E, posterior; F, labial; G, anterior; and H, lingual views. Tooth III, right upper anterior tooth in: I, labial; J, posterior; K, anterior; and L, lingual views. Specimens whitened with ammonium chloride.
Figure 4. Right upper anterior/anterior cheek teeth IV–VI of NMV P48861, Waipatiidae gen. et sp. indet., in labial (A, E, I), lingual (B, F, J), anterior (C, G, K), and posterior (D, H, L) views. A–D: tooth IV. E–H: tooth V. I–L: tooth VI. Specimens whitened with ammonium chloride.
Figure 5. Upper cheek teeth VII–IX of NMV P48861, Waipatiidae gen. et sp. indet., in labial (A, E, I), lingual (B, F, J), anterior (C, G, K), and posterior (D, H, L) views. A–D: tooth VII, left upper anterior cheek tooth. E–H: tooth VIII, right upper posterior cheek tooth. I–L: tooth IX, right upper posterior cheek tooth. See Material and Methods for abbreviations. Specimens whitened with ammonium chloride.
Figure 6. Ribs of NMV P48861, Waipatiidae gen. et sp. indet. in anterior view. 1: first right rib. 2: second left rib. 3: third left rib.
A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia

Figure 7. The left forelimb bones of NMV P48861, Waipatiidae gen. et sp. indet. in lateral view. A: scapula. B: humerus. C: radius. D: ulna. Specimens whitened with ammonium chloride.
Figure 8. Scapulae of NMV P48861, Waipatiidae gen. et sp. indet. Left scapula in: A, medial; and B, distal views. C: glenoid region of right scapula in medial view. Specimens whitened with ammonium chloride.
Figure 9. Humeri of NMV P48861, Waipatiidae gen. et sp. indet. Left humerus in: A, medial; B, anterior; C, posterior; and D, proximal views. Right humerus in: E, lateral; and F, medial views. Specimens whitened with ammonium chloride.
Figure 10. Radius and ulnae of NMV P48861, Waipatiidae gen. et sp. indet. A: left radius in anterior view. B: right ulna in anterior view. C: right ulna in medial view. D: left ulna in posterior view. Specimens whitened with ammonium chloride.
A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia

Although planktonic foraminifera are rare in the Jan Juc Marl and rarely age-diagnostic (Li et al., 1999), maximum and minimum age constraints are available. $^{40}$Ar/$^{39}$Ar dating of Angahook Formation basalts underlying the Point Addis Limestone (laterally equivalent to the Jan Juc Marl) at Aireys Inlet gave an age of 28.7 ± 0.2 Ma (McLaren et al., 2009). The oldest age of the Jan Juc Marl based on $^{87}$Sr/$^{86}$Sr ratios measured in brachiopods from the lowest 3 m of the Bird Rock section is 27.2 Ma (McLaren et al., 2009). *Sphenolithus ciperoensis* occurs in the basal beds of the Jan Juc Marl at Bird Rock, marking the base of calcareous nannofossil zone NP24 and therefore an age of <29.62 Ma (Siesser, 1979; Gradstein et al., 2012). Together, these data suggest the Jan Juc Marl in outcrop is no older than the Rupelian–Chattian boundary, 28.1 Ma (McLaren et al., 2009).

The contact between the Jan Juc Marl and conformably overlying Puebla Clay has long been considered to approximate the Oligocene–Miocene boundary (Abele, 1979; Li et al., 1999; McLaren et al., 2009). *Zygrhablithus bijugatus* is absent from the top ~2.5 m of the Jan Juc Marl in the Bird Rock section (Siesser, 1979), its last appearance datum within calcareous nannofossil zone NP25 at 23.76 Ma (Siesser, 1979; Gradstein et al., 2012). Siesser (1979) also reported the last occurrence of *Reticulofenestra bisecta* about 1 m below the Jan Juc Marl/Puebla Clay contact; the last appearance datum of this species marking the top of zone NP25 at 23.13 Ma (Gradstein et al., 2012). The first appearance datum of *Discoaster druggi* marks the boundary between calcareous nannofossil zones NN1 and NN2 (22.82 Ma), and this species is first recorded in the beds above the Jan Juc Marl/Puebla Clay contact (Siesser, 1979; Gradstein et al., 2012) (Fig. 1). The planktonic foram *Globobquadrina dehiscens*, the first occurrence of which marks the base of zone M1b (22.44 Ma) in southern Australia, is first recorded in the basal Puebla Clay (Li et al., 1999; McGowran et al., 2004; Gradstein et al., 2012).

The evidence from biostratigraphy shows that the Jan Juc Marl/Puebla Clay contact is between 23.13 and 22.82 Ma, straddling the Oligocene–Miocene boundary at 23.03 Ma (McLaren et al., 2009) (Fig. 1). This is corroborated by $^{87}$Sr/$^{86}$Sr ratios from the basal Puebla Clay, which give a range of possible ages from 23.89–21.39 Ma (McLaren et al., 2009).

The age of the exposed Jan Juc Marl is therefore most rigorously constrained to between about 28.10 and 22.82 Ma, Chattian to earliest Aquitanian. NMV P48861 was collected from the lowest beds in the Bird Rock section of the Jan Juc Marl, stratigraphically below the last occurrence of *Zygrhablithus bijugatus*, which has a last appearance datum of 23.76 Ma (Fig. 1). This constrains the age of NMV P48861 to between about 28.1 and 23.7 Ma, and therefore within the Chattian.

**Diagnosis.** An odontocete with: heterodont dentition including at least one pair of procumbent apical teeth and small double-rooted posterior cheek teeth with triangular crowns bearing two or three posterior denticles; a small rod-like coracoid process of the scapula; an elongated humerus bearing a strongly salient deltoid tuberosity continuous with a distally-elongated crest, and a distal end that is distinctly narrower (anteroposteriorly) than the proximal end of the shaft; a long and anteroposteriorly narrow radius bearing a transversely thin crest on its anterior edge; and a well-developed hatchet-shaped olecranon of the ulna. None of these characters represent unambiguous synapomorphies of Waipatiidae, but this combination of characters is found only in taxa assigned to that clade (see Comparisons below).

**Remarks on Platanistoidea.** The concept of Platanistoidea used here is that of Muizon (1987) with emendations by Fordyce (1994) and Tanaka and Fordyce (2015a); namely that Platanistoidea includes the living family Platanistidae plus the extinct clades.
Squalodelphinidae, Waipatiidae, Oetekaika, and Squalodontidae. This definition and taxonomic content of Platanistoidea has been questioned (Lambert et al., 2014: 988): some recent analyses posit both Squalodontidae and Waipatiidae as stem odontocetes (Geisler et al., 2011, 2014; Lambert et al., 2014, 2015; Sanders and Geisler, 2015); or platanistoids (Murakami et al., 2012; Tanaka and Fordyce, 2015a); or exclude squalodontids from Platanistoidea, but include Waipatiidae in the latter (Tanaka and Fordyce, 2014). The taxonomic content and phylogenetic position of Squalodontidae (and the potentially related Prosqualodon) are enduring problems in cetacean systematics recently reviewed by Tanaka and Fordyce (2014: 27). Their hypothesis for the content of Squalodontidae is followed here. For reviews of the taxonomic content and phylogenetic position of other putative platanistoid clades (i.e. Alldelphinidae, Dalpiazinidae) see Muizon (1988, 1991, 1994), Fordyce (1994), Barnes (2006), Barnes and Reynolds (2009), and Lambert et al. (2014).

Description

Ontogenetic age. The ossified and smooth articular surfaces on the scapula and humerus, twinned with the distal epiphyses of the radius and ulna not being fused, suggests that NMV P48861 represents at least a sexually mature but physically immature adult (Class V) according to the qualitative developmental categories established by Perrin (1975) for the delphinid Stenella attenuata.

Teeth. NMV P48861 is a heterodont odontocete, with evidence of at least one pair of procumbent tusk-like anterior teeth. Six single-rooted teeth (teeth I–VI: Figs. 3–4) and three double-rooted teeth (teeth VII–IX: Fig. 5) are preserved in isolation. The relative position of each tooth is identified with reference to Waipatia maerewhenua (Fordyce, 1994; cast of the holotype OU 22095). All teeth apart from a presumed tasked incisor (tooth I) and conical anterior tooth (tooth II) are interpreted as upper teeth on the basis of their strong lingual curvature. The tasked incisor (tooth I: Figs. 3A–D) has a broken crown exposing dentine and a patent pulp cavity. The enamel-covered crown is subcircular in cross section, lacks keels, and bears enamel with longitudinal ridges on its lingual/posterolingual surface. The anterolingual surface of the crown has a small pyriform wear facet (Fig. 3D). The enamelocementum boundary extends further basally on the lingual/posterolingual side of the crown. The elongate and gently recurved root is missing most of its cementum, exposing dentine.

A conical anterior tooth (tooth II: Figs. 3E–H) has a crown with an oval cross section, and an oblique apical wear facet on its lingual aspect. When complete, the crown was probably relatively short compared to the elongated root. The labial surface of the crown is smooth, with a keeled posterior edge, and fine ridges on its preserved posterolingual surface. Immediately basal to the crown, the single root is slightly waisted, but then becomes inflated in the anteroposterior and labiolingual planes before tapering towards the root apex. The labial surface of the apical one-quarter of the root has a median groove.

Two upper right caniniform anterior teeth (teeth III and IV: Figs. 3I–L and 4A–D, respectively) bear a crown with a single conical denticle and a worn crown apex. The crown is recurved lingually and is somewhat labiolingually inflated at its base. The anterior and posterior edges are strongly keeled, and there are fine longitudinal ridges on the labial side of the crown base. The lingual surface of the crown in tooth III has diffuse longitudinal ridges (Fig. 3L). The single root immediately basal to the crown is waisted such that there is a distinct ‘neck’. Further towards the root apex the root is labiolingually inflated, then tapers towards the root apex.

An upper right anterior tooth (tooth V: Figs. 4E–H) has a crown with a single triangular denticle and a worn crown apex. The relatively small crown is recurved lingually, bears a strongly keeled posterior edge, and has fine ridges on its posterolabial and posterolingual surfaces. The enamelocementum boundary extends further basally at the anterior ends of both labial and lingual sides of the crown. In labial and lingual views there is a distinct ‘neck’ immediately basal to the crown. The single root is strongly labiolingually inflated and bears a median groove on the labial surface of its preserved apex (Fig. 4E).

An upper right anterior tooth (tooth VI: Figs. 4I–L) has a crown with a single triangular denticle and a worn crown apex. The crown is recurved lingually, bears strongly keeled anterior and posterior edges, and fine ridges on its posterolabial and lingual surfaces. The enamelocementum boundary extends further basally at the anterior ends of both labial and lingual sides of the crown. The crown of this tooth closely approximates the morphology of the right upper anterior cheek teeth of Waipatia maerewhenua. The incomplete (presumed) single root is labiolingually inflated.

A double-rooted upper left anterior cheek tooth (tooth VII: Figs. 5A–D) has a crown with a high triangular main denticle (md) bearing keeled anterior and posterior edges, an incipiently papillate anterolingual cingulum, three tiny posterior denticles (pd1–3: Fig. 5B), indistinct ridges along the base of its labial surface, and strong longitudinal ridges along the base of its lingual surface. A distinct ‘neck’ occurs basal to the enamelocementum boundary. The two parallel roots are fused along their entire preserved length, recurved posterodorsally, and labiolingually inflated at approximately mid-length. The anterior root tapers strongly towards its apex such that its preserved apical end is about half the diameter of the posterior root.

A double-rooted upper right posterior cheek tooth (tooth VIII: Figs. 5E–H) has a crown with a relatively low triangular md and two small posterior denticles (pd1–2: Fig. 5E). The md is heavily worn on its anterior edge and apex. The posterior denticles are worn on their apices. The posterior edges of all denticles bear strong keels. The labial surface of the crown bears indistinct fluted ornament, whereas enamel on the lingual surface is heavily ornamented with longitudinal ridges and wrinkles arising from a basal papillate cingulum. A distinct ‘neck’ basal to the enamelocementum boundary can be seen in labial and lingual views. The two parallel roots are fused for about three-quarters of their length, recurved posterodorsally (at an angle of ~60° to the axis of the crown), and strongly labiolingually inflated in their basal half. Both roots taper towards their apex, although the apical end of the anterior root is less than half the diameter of the posterior root. A prominent elongate swelling on the lingual aspect of the posterior root probably represents a vestigial fused third root (Fig. 5F).
A double-rooted upper right posterior cheek tooth (tooth IX: Figs. 5I–L) has a crown with a low triangular md and three posterior denticles (Fig. 5I). The posterior denticles decrease in size away from the md (anteroposterior diameter = 5.4 mm): pd1 anteroposterior diameter = 2.2 mm; pd3 anteroposterior diameter = 1.3 mm. The main denticle plus pd1 and pd2 have heavily worn apices. Additionally, the anterior edge of the md is worn (Fig. 5K). A distinct shear wear facet occurs on the lingual surface of the crown at the level (anteroposteriorly) of the notch between the md and pd1 (Fig. 5J). The posterior edges of all denticles are keeled. The labial surface of the crown bears distinct ridged and fluted ornament. The enamel on the lingual surface of the crown is more heavily ornamented with longitudinal ridges and wrinkles arising from a strongly papillate basal cingulum. This cingulum wraps around the anterior and posterior edges of the crown base and on to the antero- and posterolabial corners of the basal crown. The crown of this tooth resembles the morphology of the third-to-last upper cheek teeth of *Waipatia maerewhenua*. A clear ‘neck’ occurs basal to the enameloementum boundary. The two parallel roots are fused for about two-thirds of their length, recurved posterosdorsally (at an angle of ~50° to the axis of the crown), and strongly labiolingually inflated in their basal half. There is a prominent anterior bulge at the base of the anterior root, and both roots are strongly tapered towards their apices.

**Vertebrae.** The fragmentary spinous processes, right halves of the vertebral arch, and transverse processes of one cervical (probably the seventh), and twelve thoracic vertebrae (first to twelfth) are preserved (Fig. 2). Thoracic vertebrae 1–3 have high and transversely flat spinous processes, with the spinous process of thoracic vertebra 1 being approximately half the width of those of thoracic vertebrae 2 and 3. The rest of the preserved parts of the vertebrae are uninformative.

**Ribs.** Parts of 16 ribs, five right, eight left (five of which are double-headed), and three indeterminate, are preserved (Fig. 6). A partial right rib 1 has a wide and flat shaft (29 mm maximum and 10 mm minimum diameter proximally), which increases in width distally (34 mm maximum diameter at preserved distal end). Three left double-headed ribs (damaged ventrally) are interpreted as ribs 2, 3, and a mid-series rib (based on position in the sediment relative to the vertebral column and comparisons with modern odontocetes, e.g., *Platanista gangetica* NMV C27417 and *Delphinus delphis* NMV C24964), and are 262+, 322+, and 284+ mm in chord length, respectively. Left ribs 2 and 3 are anteroposteriorly flat and wide along their length (rib 2, 25 mm maximum and 11 mm minimum diameter at mid-shaft; rib 3, 19 mm maximum and 9 mm minimum diameter at mid-shaft). The left mid-series rib is narrower and more ovoid in cross-section (18 mm maximum and 11.5 mm minimum diameter at mid-shaft).

**Scapula.** Both left and right scapulae are incomplete: the left scapula lacks the dorsal margin (Figs. 7, 8A), and the right scapula is represented by an uninformative fragment of dorsal margin (Fig. 2) plus the coracoid process and approximately half of the glenoid (Fig. 8C). Orientation of the scapula follows Tanaka and Fordyce (2015a: 32) whereby the glenoid fossa is ventral. The scapula is: fan-shaped, its anterior and posterior edges forming an angle of about 100°; transversely thin (especially in the middle of the infraspinous fossa); and, by analogy with other odontocete scapulae (e.g., Benke, 1993; Muizon, 1994), probably longer than high. Anteriorly, there are two projections: the acromion and coracoid process.

Viewed laterally (Fig. 7), the long (80+ mm) acromion projects anteroventrally, has a dorsoventrally high base, and does not expand distally. In distal view (Fig. 8B), the acromion curves gently laterally at its base, but more distally curves anteromedially. The rod-like coracoid process arises from a robust base (8.5 mm width, 12 mm height) ventromedial to the acromion. The coracoid process is strongly recurved ventromedially, and long relative to its transverse diameter (32 mm long; minimum and maximum diameters of 5.7 mm and 7.6 mm, respectively, at mid-length). Viewed distally, the angle between the coracoid process and acromion is about 40°. The coracoid process is distinctly waisted about 10 mm from its distal apex, which is slightly globular (Fig. 8C). The scapular neck is constricted. Distally, the glenoid fossa has an oval outline, longer than wide (47 mm length, 35 mm width).

In lateral view (Fig. 7), the base of the acromion is continuous posterosdorsally with the scapular spine, which curves anterodorsally. Anteriorly, the preserved supraspinous fossa is anteroposteriorly narrow. It is separated from the anteroposteriorly broad infraspinous fossa by a ridge with a tabular lateral surface (anteroposterior diameter 19 mm). The infraspinous fossa has a smoothly undulating surface. Its posterior edge is formed by a subtle convexity for the border between the infraspinous and teres major fossae. The posterior edge of the scapula has a gently concave profile in lateral view (angle between posterior edge of the scapula and neck of the scapula is ~140°). The medial surface of the scapular blade is dominated by the broad V-shaped subscapularis fossa (Fig. 8A).

**Humerus.** The left humerus is nearly complete (Figs. 7, 9A–D), but the head of the right humerus is eroded (Fig. 9E). Surface detail on both humeri is generally well preserved. The humerus is relatively elongated (length ≥250% of maximum width), and has a slightly transversely flattened shaft (minimum width of shaft ~140% of its transverse diameter) (Table 2). The distal end of the humerus is significantly narrower than the proximal end (width of distal end of humerus ~57% of its proximal end).

The locations of some muscle attachments on the humerus differ between odontocete families, and in some cases depart from their homologues in terrestrial mammals. Notable here is the insertion for *M. deltoideus*, which in terrestrial mammals is a distinct deltoideus tuberosity and/or crest (Flower, 1885; Schaller, 2007). However, in odontocetes the deltoideus tuberosity varies in its relative size and position, and indeed may not be present at all, hence *M. deltoideus* inserts on: a distinct deltoid tuberosity and/or crest (Flower, 1885; Schulte and Smith, 1918); lateral surface of the distal end of the humerus in *Inia* (Klima et al., 1980), *Pontoporia* (Strickler, 1978), *Neophocaena* (Howell, 1927), and *Phocoena* (Smith et al., 1976); anterior edge and lateral surface of the humerus in *Monodon* (Howell, 1930); and the...
anteroventral edge and adjacent lateral surface of the humerus in *Tursiops* and *Stenella* (Benke, 1993). For this study, muscle attachments are identified using a combination of the aforementioned literature on odontocete myology, plus artiodactyls (Nickel et al., 1986; Schaller, 2007).

The proximal end of the humerus is dominated by a smooth, rounded, head that has a semi-elliptical outline in lateral view (Fig. 7), and represents about 30% of the length of the humerus. Viewed proximally, the head of the humerus is approximately the same size as the tubercles, from which it is separated by a deep sulcus (Fig. 9D). In anterior and posterior views the proximal edges of the head and lesser tubercle are at approximately the same level, and a distinct neck separates the head from the body of the humerus (Figs. 9B–C). Medial to the head, the proximal surface of the lesser tubercle has a distinct flattened region for insertion of the M. subscapularis. A distinct intertubercular sulcus separates the lesser tubercle from the anteriorly adjacent and relatively small greater tubercle, which has a flattened area on its proximomedial aspect for insertion of M. supraspinatus that marks a steep step between the proximal surfaces of the two tubercles. The insertion of the M. supraspinatus continues posterolaterally into a deep pit and ventrolaterally angled flattened area. Further distally, on the lateral surface of the humerus and below the anterior edge of the head, is a proximodistally long fossa for the insertion of M. infraspinatus, which terminates in a deep pit (but not a patent foramen) at the level of the proximal one-third of shaft length (Fig. 9E). The anterior edge of the humerus is transversely thin and sigmoidal in lateral/medial view. A strongly developed and proximodistally long (~40 mm length) deltoid tuberosity occupies about half of the length and the maximum width of the shaft. The apex of the deltoid tuberosity is located within the proximal 65% of the humerus. The deltoid crest of the humerus runs distally from the deltoid tuberosity, becoming indistinct proximal to the radial angle (Figs. 9E–F). Distally, the radial and ulnar facets have gently undulating surfaces, are separated by a sharp distal crest, and form an obtuse angle in lateral view (Fig. 7). A low ulnar crest marks the transition from the distal part of the ulnar facet to its pentagonal part on the posterior aspect of the humerus (Fig. 9C). Proximomedial to the latter feature is a small, flattened olecranon facet for attachment of the olecranon ligament.

**Radius.** The left and right radii are nearly complete, but somewhat crushed mediolaterally; and the right radius is corroded and lacks some of its external surface (Figs. 7, 10A). The shaft is narrow and elongated, in lateral view having a gently convex anterior edge and slightly concave posterior edge (Fig. 7). The distal epiphysis is incompletely fused to the shaft. Proximally, the fovea of the head of the radius has a quadrangular outline with a distinct concavity at its anteromedial corner. The surface of the fovea (articular face for the radial facet of the humerus) is posteromedially-tilted (Fig. 10A). Anteriorly, the shaft bears a thin crest that extends from the head of the radius distally to the shaft’s mid-length (Fig. 10A). The distal half of the radius widens gradually towards the distal epiphysis, which is wider than the proximal end. The carpal facet has an angular distal profile in lateral view (Fig. 7).

**Ulna.** The left ulna is nearly complete, lacking the anteroproximal region of the olecranon and part of the distal end (including epiphysis) (Figs. 7, 10D). The right ulna lacks the posterior edge of the olecranon, but is otherwise virtually complete (Figs. 10B–C). The proximal and distal ends of the ulna are robust (23 mm and 19 mm transverse diameter, respectively) with the shaft being transversely thin at its mid-length (~11 mm); giving the shaft of the ulna a subtly hourglass-shaped outline in anterior and posterior views (Figs. 10B, D). The olecranon projects proximally and posteriorly as a transversely thin blade. Anteriorly, the olecranon bears a rugose and proximodistally elongated facet for the olecranon ligament, located proximal to the hourglass-shaped trochlear notch (Fig. 10B). Posteriorly, the outer edge of the olecranon has a rugose surface (Fig. 10D). In lateral view, the trochlear notch forms a nearly 90° angle, with its vertical part being transversely narrower (18 mm maximum transverse diameter) than the horizontal part (22 mm maximum transverse diameter) (Figs. 7, 10C). Anterodistal to the trochlear notch is a small tuberosity that fits a notch in the postero proximal edge of the radius (Fig. 7). The distal half of the lateral surface of the shaft bears numerous nutrient foramina of uncertain homology (Fig. 7). The interosseous and posterior borders of the shaft gradually diverge towards the distal end, to which the ellipsoid epiphysis is not fused.

**Carpals.** Two bone fragments (presumed carpals) are uninformative and are not described.

**Metacarpals.** Three metacarpals were found in the sediment during preparation of NMV P48861: two close to the distal end of the left antebrachium (hence identified as left metacarpals), and one close to the distal end of the right antebrachium (hence identified as a right metacarpal) (Figs. 2, 11A–C). Each metacarpal has: an approximately rhomboid outline, with concave anterior and posterior edges; transversely convex lateral surface; and a transversely flattened palmar surface. The shorter left metacarpal (Fig. 11A) is relatively wide (20.5 mm maximum width, 36 mm length) and ellipsoid in cross section (6 mm transverse diameter, 16 mm wide at mid-length). The longer left metacarpal (Fig. 11B) is elongated (18 mm maximum width, 39 mm length) and more ovoid in cross section (8 mm transverse diameter, 12 mm wide at mid-length). The right metacarpal (Fig. 11C) is nearly identical in size and shape to the longer left metacarpal. It is not possible to accurately identify which position each metacarpal occupied in the manus.

**Phalanges.** Four phalanges were found in the sediment during preparation of NMV P48861, although only one phalanx is complete enough to merit description (Fig. 11D). It was found close to the distal end of the left antebrachium (Fig. 2), and is hence identified as a left phalanx. It is flattened transversely (5 mm transverse diameter, 12 mm wide at mid-length), and relatively long (28.5 mm long, 18 mm width at proximal end). This elongated form, and possession of a wider proximal than distal (16 mm) end, suggests that this is a proximal phalanx. It is hourglass-shaped in lateral/plantar views, with flat proximal and distal ends.
A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia

**Discussion**

**Comparisons.** NMV P48861 differs from archaeocetes by having relatively tiny heterodont cheek teeth and a humerus that lacks a trocheated distal end, instead possessing distinct radial and ulnar facets. NMV P48861 differs from mysticetes (including toothed stem taxa) (e.g., *Fucana gaedertorum* (Barnes and Furusawa in Barnes et al., 1995), LACM 131146; Kellogg, 1965; Benke, 1993; Boessenecker and Fordyce, 2015a) by having an elongated and narrow rod-like coracid process of the scapula, and a humerus that is longer than the antebraichium. NMV P48861 can be further differentiated from the toothed mysticete clades: Llanocetidae and Mammalodontidae by having smaller and lower-crowned cheek teeth lacking strongly developed ridges on both labial and lingual surfaces of the crown; and Aetiocetidae by having posterior cheek teeth with more strongly developed ornament on the labial surface of the crown. NMV P48861 is not a xenorophid, simocetid, mirocetid, or agorophiid odontocete, differing by having smaller posterior cheek teeth. In addition, the humerus of NMV P48861 is more specialized than that of *Mirocetus riabinini* Mchedlidze, 1970 (Sanders and Geisler, 2015) by having: a less laterally-projecting head; a less prominent deltid crest distal to the deltid tuberosity; and distinct radial and ulnar facets on the distal end. NMV P48861 differs from *Prosqualodon* by having: relatively small posterior cheek teeth that lack strong nodular crown ornament; an elongated coracid process on the scapula; a humerus with a straight posterior edge (viewed laterally) and a strongly developed deltid tuberosity; and a more elongated antebraichium. NMV P48861 differs from crown odontocetes other than Platanistoidea in lacking: homodont conical posterior teeth. NMV P48861 possesses a combination of dental and forelimb characters of Platanistoidea (i.e. *Squalodelphinidae* + *Platanistidae*) and/or evolved independently in *Prosqualodon* and *Squalodon*. NMV P48861 shares tusk-like anterior teeth and a rod-like morphology of the coracid process with *Otekaikea*, but differs from that genus by having: more strongly heterodont cheek teeth with lower, less conical crowns bearing salient posterior denticles; a scapula with a posteroventral border forming a 45° angle with the horizontal in lateral view (cf. ~15° in *Otekaikea*); a more elongated humerus (minimum anteroposterior width of shaft is <30% humerus length); the dorsal edge of the head of the humerus approximately level with the dorsal edge of the lesser tubercle; an infraspinous fossa that does not terminate distally in a distinct ovoid pit on the lateral surface of the humeral shaft; and a longer antebraichium (length of radius is nearly equal to humerus length).

Amongst described platanistoids, NMV P48861 is most similar to *Waipatia* in having heterodont dentition including: tusk-like anterior teeth; and double-rooted posterior upper cheek teeth with small (<12 mm length) triangular crowns bearing two or three posterior denticles. NMV P48861 differs from *Waipatia maerewhenua* in its posterior upper cheek teeth having finer and more diffuse ridges on the labial surface of the crown. NMV P48861 differs from *W. hectori* (Benham, 1935) by having larger and less labiologically inflated cheek teeth with shorter and more shallowly notched denticles. Neither described species of *Waipatia* are known from appendicular elements (Fordyce, 1994; Tanaka and Fordyce, 2015b), so it is unclear whether *Waipatia* possessed forelimb morphology similar to that of *Otekaikea* and NMV P48861. However, the holotype of *Sulakocetus dagestanicus*, which is probably a waipatid (Fordyce, 1994, 2003; Fordyce and Muizon, 2001), includes much of the forelimb skeleton (Mchedlidze, 1984; Pilleri, 1986). NMV P48861 shares with *Sulakocetus*: small heterodont cheek teeth; coracid process of the scapula present and apparently long and rod-like (Mchedlidze, 1984:43, Plate XVI); elongated humerus (minimum anteroposterior width of shaft is <30% humerus length); dorsal edge of the head of the humerus approximately level with the dorsal edge of the lesser tubercle; distinct intertubercular sulcus on humerus (Mchedlidze, 1984:43, Plate XII); strongly salient deltid tuberosity with adjacent crest developed distally; a distal end of the humeral shaft with an anteroposterior width less than that of the proximal end of the shaft; and a radius with a transversely narrow crest on its anterior edge. NMV P48861 differs from *Sulakocetus* by having: somewhat larger humerus, radius and ulna; a head of the humerus subequal in size to the lesser tubercle; and a relatively longer and narrower radius. Because NMV P48861 possesses a combination of dental and forelimb characters only recorded in *Waipatia* or *Sulakocetus*, and lacks any synapomorphies that link this specimen with other odontocete clades, it is referred to an indeterminate species in the family Waipatiidae. A modern redescription and phylogenetic analysis of *Sulakocetus* (to test its relationship with *Waipatia*), plus discovery of forelimb bones referable to *Waipatia*, are required to test the relationships of NMV P48861 hypothesized here.
Biogeography. NMV P48861 represents the first evidence of Waipatiidae from Australia. Previously reported records of waipatiids include Waipatia maerewhenua and W. hectori from the late Chattian of New Zealand (Fordyce, 1994; Tanaka and Fordyce, 2015b), plus the potential waipatiids Sulakocetus dagestanicus from the late Chattian of Caucasus (Mchedlidze, 1976, 1984) and Sachalinocetus chelomicus Dubrovo in Siryk and Dubrovo, 1970 from the early Miocene of Sakhalin. In addition, rostral and mandibular fragments with teeth, as well as isolated periostics, referred to Waipatiidae were described from the early Miocene of Malta (Bianucci et al., 2011). Given this geographic and stratigraphic distribution, the occurrence of Waipatiidae in late Oligocene strata of southeast Australia is not surprising and indeed was anticipated by Fordyce (2006: 766).

Nevertheless, the waipatiid from the Jan Juc Marl is only the second odontocete taxon recognized from the Oligocene of Australia, the first, and hitherto only, recorded odontocete being Prosqualodon (represented by isolated teeth: Hall, 1911; Fordyce, 1982; Fitzgerald, 2004). Other cetaceans in this assemblage include a probable kekenodontid archaeocete (‘Squalodon’ gambierensis; Fordyce, 2004; Fitzgerald, 2004), and several small-bodied toothed mysticetes in the family Mammalodontidae (Fitzgerald, 2006, 2010, 2012). Each of these families also occurs in the late Oligocene of New Zealand (Fordyce, 1984, 1991, 2003; Fordyce and Marx, this volume), suggesting a generally similar cetacean fauna throughout the southwest Pacific that lacks confirmed records of taxa typical of Oligocene assemblages elsewhere, e.g., Aetiocetidae (North Pacific) and Xenorophidae (North Atlantic) (Fordyce, 2003). Despite the family-level taxonomic similarities between the late Oligocene cetacean assemblages of Australia and New Zealand, a notable disparity lies in the numerical dominance (and taxonomic richness) of toothed mysticete fossils in Australia versus the rarity of their remains in New Zealand (Fordyce and Marx, this volume). Furthermore, whereas fossils of Eomysticetidae and other Chaeomysticeti are relatively abundant and diverse in the late Oligocene of New Zealand (Boessenecker and Fordyce, 2015a–c; Tsai and Fordyce, 2015), they have not yet been recognized from southeast Australia. However, with continuing research, the absence in Australia of cetacean families recorded in the New Zealand Oligocene will likely become more apparent than real—as exemplified by the waipatiid described here.

Acknowledgements

T. Park, D. Pickering, A. Werner, and T. Ziegler are thanked for finishing preparation of NMV P48861. R. E. Fordyce and A. Grebneff (University of Otago) provided casts of OU 22095, the type specimen of Waipatia maerewhenua. L. Barnes and S. McLeod (Natural History Museum of Los Angeles County), D. Bohaska (National Museum of Natural History, Smithsonian Institution), I. von Lichtan (University of Tasmania), and M. Reguero (Museo de La Plata) are thanked for providing access to specimens in their care. Part of this research was carried out during a Smithsonian Postdoctoral Fellowship at the National Museum of Natural History. R. E. Fordyce and O. Lambert carefully and constructively reviewed the manuscript. Tom Rich encouraged the author’s interest in Australian fossil Cetacea, for which he is thanked.

References

Abele, C. 1979. Geology of the Anglesea area, central coastal Victoria. Memoir of the Geological Survey of Victoria 31: 1–71.
Barnes, L.G. 2006. A phylogenetic analysis of the superfamily Platanistoidea (Mammalia, Cetacea, Odontoceti). Beiträge zur Paläontologie 30: 25–58.
Barnes, L.G., and Reynolds, R.E. 2009. A new species of early Miocene alodelphinid dolphin (Cetacea, Odontoceti, Platanistoidea) from Cajon Pass, southern California, U.S.A. Museum of Northern Arizona Bulletin 65: 483–507.
Barnes, L.G., Kimura, M., Furusawa, H., and Sawamura, H. 1995. Classification and distribution of Oligocene Aetiocetiidae (Mammalia; Cetacea; Mysticeti) from western North America and Japan. The Island Arc 3: 392–431. [For 1994.]
Benham, W.B. 1935. The teeth of an extinct whale, Microcetus hectorii n. sp. Transactions of the Royal Society of New Zealand 65: 239–243.
Benke, H. 1993. Investigations on the osteology and the functional morphology of the flipper of whales and dolphins (Cetacea). Investigations on Cetacea 24: 9–252.
Berzin, A.A. 1972. The Sperm Whale (Kashalot). Israel Program for Scientific Translations, Jerusalem. 394 pp. [Translated from Russian.]
Bianucci, G., Gatt, M., Catanzariti, R., Sorbi, S., Bonavia, C.G., Curmi, R., and Varola, A. 2011. Systematics, biostratigraphy and evolutionary pattern of the Oligo-Miocene marine mammals from the Maltese Islands. Geobios 44: 549–585.
Boessenecker, R.W., and Fordyce, R.E. 2015a. A new genus and species of eomysticeti (Cetacea: Mysticeti) and a reinterpretation of ‘Mauicetus’ lophocephalus Marples, 1956: Transitional baleen whales from the upper Oligocene of New Zealand. Zoological Journal of the Linnean Society 175: 607–660.
Boessenecker, R.W., and Fordyce, R.E. 2015b. A new eomysticetid (Mammalia: Cetacea) from the late Oligocene of New Zealand and a re-evaluation of ‘Mauicetus’ waitakiensis’. Papers in Palaeontology 1: 107–140.
Boessenecker, R.W., and Fordyce, R.E. 2015c. Anatomy, feeding ecology, and ontogeny of a transitional baleen whale: a new genus and species of Eomysticetiidae (Mammalia: Cetacea) from the Oligocene of New Zealand. PeerJ 3:e1129. DOI 10.7717/peerj.1129
Cabrera, A. 1926. Cetáceos fósiles del Museo de La Plata. Boletín del Museo Nacional de La Plata 29: 363–411.
Cozzuol, M.A. 1996. The record of the aquatic mammals in southern South America. Pp. 321–342 in: Arratia, G. (ed.), Contributions of Southern South America to Vertebrate Paleontology. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paliontologie, 30.
Cozzuol, M.A., and Humbert-Lan, G. 1989. On the systematic position of the genus Prosqualodon Lydekker, 1893, and some comments on the odontocete family Squalodontidae. Abstracts of Papers and Posters, Fifth International Theriological Congress, Rome, 22–29 August 1989, 1: 483–484.
Eshelman, R.E., and Ward, L.M. 1994. Tribute to Frank Clifford Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29: 3–10.
Fitzgerald, E.M.G. 2004. A review of the Tertiary fossil Cetacea (Mammalia) localities in Australia. Memoirs of Museum Victoria 61: 183–208.
A late Oligocene waipatiid dolphin (Odontoceti: Waipatiidae) from Victoria, Australia

Fitzgerald, E.M.G. 2006. A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. Proceedings of the Royal Society B: Biological Sciences 273: 2955–2963.

Fitzgerald, E.M.G. 2010. The morphology and systematics of Mammalodon colliveri (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. Zoological Journal of the Linnean Society 158: 367–476.

Fitzgerald, E.M.G. 2012. Archaeocete-like jaws in a baleen whale. Biology Letters 8: 94–96.

Flower, W.H. 1885. An Introduction to the Osteology of the Mammalia. Third Edition. Macmillan and Co., London [reprinted by A. Asher and Co., Amsterdam (1966)]. 382 pp.

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

Fordyce, R.E. 1983. Rhabdosteid dolphins (Mammalia: Cetacea) from the Middle Miocene, Lake Frome area, South Australia. Alcheringa 7: 27–40.

Fordyce, R.E. 1984. 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. 1203 pp.

Fordyce, R.E. 1991. 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. 1437.

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. Proceedings of the San Diego Society of Natural History 29: 147–176.

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. 541 pp.

Fordyce, R.E. 2004. The transition from Archaeoceti to Neoceti: Oligocene archaeocetes in the southwest Pacific. Journal of Vertebrate Paleontology 24 (Supplement to 3): 59A.

Fordyce, R.E. 2006. A southern perspective on cetacean evolution and zoogeography. Pp. 755–778 in: Merrick, J.R., Archer, M., Hickey, G.M., and Lee, M.S.Y. (eds), Evolution and Biogeography of Australasian Vertebrates. Auscipub: Oatlands. 942 pp.

Fordyce, R.E., and Marx, F.G. 2016. Mysticetes barring their teeth: a new fossil whale, Mammalodon hakatarae, from the southwest Pacific. Memoirs of Museum Victoria 74: 112.

Fordyce, R.E., and Muizon, C. de. 2001. Evolutionary history of cetaceans: a review. Pp. 169–233 in: Mazin, J.-M. and Buffrénil, V. (eds), Vertebrate Zoogeography and Evolution in Australasia. Cambridge University Press: Cambridge. 712 pp.

Geisler, J.H., McGowen, M.R., Yang, G., and Gatesy, J. 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11: 112.

Geisler, J.H., Colbert, M.W., and Carew, J.L. 2014. A new fossil species supports an early origin for toothed whale echolocation. Nature 508: 383–386.

Glaessner, M.F. 1955. Pelagic fossils (Aturia, penguins, whales) from the Tertiary of South Australia. Records of the South Australian Museum 11: 353–372.

Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G. 2012. The Geologic Time Scale 2012. Elsevier, Oxford. 1144 pp.

Hall, T.S. 1911. On the systematic position of the species Squalodon and Zeuglodon described from Australia and New Zealand. Proceedings of the Royal Society of Victoria 23: 257–265.

Howell, A.B. 1927. Contribution to the anatomy of the Chinese finless porpoise, Neomiris phocaenoides. Proceedings of the United States National Museum 70: 1–43.

Howell, A.B. 1930. Myology of the narwhal (Monodon monoceros). The American Journal of Anatomy 46: 187–215.

Kellogg, A.R. 1925. On the occurrence of remains of fossil porpoises of the genus Eurhinodelphis in North America. Proceedings of the United States National Museum 66: 1–40.

Kellogg, A.R. 1965. Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia: Part 1. A new whalebone whale from the Miocene Calvert Formation. United States National Museum Bulletin 247: 1–45.

Klima, M., Oelschläger, H.A., and Wünsch, D. 1980. Morphology of the pectoral girdle in the Amazon dolphin Inia geoffrensis with special reference to the shoulder joint and the movement of the flippers. Zeitschrift für Säugetierkunde 45: 288–309.

Lambert, O., Bianucci, G., and Urbina, M. 2014. Huaridelphis raimondii, a new early Miocene Squalodelphinidae (Cetacea, Odontoceti) from the Chilicatay Formation, Peru. Journal of Vertebrate Paleontology 34: 987–1004.

Lambert, O., Muizon, C. de, and Bianucci, G. 2015. A new archaic homodont toothed cetacean (Mammalia, Cetacea, Odontoceti) from the Early Miocene of Peru. Geodiversitas 37: 79–108.

Li, Q., Davies, P.J., and McGowran, B. 1999. Foraminiferal sequence biostratigraphy of the Oligo-Miocene Janjukian strata from Torquay, southeastern Australia. Australian Journal of Earth Sciences 46: 261–273.

Marin, G.O., Tsai, C.-H., and Fordyce, R.E. 2015. A new Early Oligocene toothed ‘baleen’ whale (Mysticeti: Aetiocetiidae) from western North America: one of the oldest and the smallest. Royal Society Open Science 2: 150476. http://dx.doi.org/10.1098/rsos.150476

McGowran, B., Holdgate, G.R., Li, Q., and Gallagher, S.J. 2004. Cenozoic stratigraphic succession in southeastern Australia. Australian Journal of Earth Sciences 51: 459–496.

Mechedlidze, G.A. 1970. Nekotorye Obshchie Cherty Istorii Kitoobraznykh. Chast' 1. Akademia Nauk Gruzinskoi S.S.R., Institut Paleobiologii, Metsniereba, Tbilisi. 112 pp. [In Russian.]

Mechedlidze, G.A. 1976. Osnovnuye Cherty Paleobiologicheskoi Istorii Kitoobraznykh. Akademia Nauk Gruzinskoi S.S.R., Institut Paleobiologii, Metsniereba, Tbilisi. 136 pp. [In Russian.]

Mechedlidze, G.A. 1984. General Features of the Paleobiological Evolution of Cetacea. Amerind Publishing Co. Pvt. Ltd., New Delhi. 139 pp. [English translation from Russian.]

McLaren, S., Wallace, M.W., Gallagher, S.J., Dickinson, J.A., and McAllister, A. 2009. Age constraints on Oligocene sedimentation in the Torquay Basin, southeastern Australia. Australian Journal of Earth Sciences 56: 595–604.

Muizon, C. de. 1987. The affinities of Notocetus vanbenedeni, an Early Miocene platanistoid (Cetacea, Mammalia) from Patagonia, southern Argentina. American Museum Novitates 2904: 1–27.

Muizon, C. de. 1988. Le polyphylétisme des Acrodélphidés, odontocètes longirostrés du Miocène européen. Bulletin du Muséum National d’Histoire Naturelle (Paris) (4)1, Sect. C 10: 31–88.

Muizon, C. de. 1991. A new Ziphiid (Cetacea) from the Early Miocene of Washington State (USA) and phylogenetic analysis of the major groups of odontocetes. Bulletin du Muséum National d’Histoire Naturelle (Paris) (4)3-4, Sect. C 12: 279–326. [For 1990.]
Muizon, C. de. 1994. Are the squalodonts related to the platanistoids? *Proceedings of the San Diego Society of Natural History* 29: 135–146.

Murakami, M., Shimada, C., Hikida, Y., and Hirano, H. 2012. A new basal porpoise, *Pterophocaena nishinoi* (Cetacea, Odontoceti, Delphinoidea), from the upper Miocene of Japan and its phylogenetic relationships. *Journal of Vertebrate Paleontology* 32: 1157–1171.

Nickel, R., Schummer, A., Seiferle, E., Frewein, J., Wilkens, H., and Wille, K.-H. 1986. *The Anatomy of the Domestic Animals. Volume 1. The Locomotor System of the Domestic Mammals.* Verlag Paul Parey, Berlin. 499 pp.

Perrin, W.F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography of the University of California* 21: 1–206.

Pilleri, G. 1986. *Beobachtungen an den Fossilen Cetaceen des Kaukasus.* Hirnanatomisches Institut, Ostermundigen, Switzerland. 40 pp.

Pritchard, G.B. 1939. On the discovery of a fossil whale in the older Tertiaries of Torquay, Victoria. *The Victorian Naturalist* 55: 151–159.

Rich, T.H.V. 1975. Potential pre-Pleistocene fossil tetrapod sites in New Zealand. *Mauri Ora* 3: 45–54.

Rich, T.H. 1976. Recent fossil discoveries in Victoria. *Victorian Naturalist* 93: 198–206.

Rich, T.H. 1999. Australia: vertebrate paleontology. Pp. 140–149 in: Singer, R. (ed), *Encyclopedia of Paleontology. Volume 1: A–L.* Fitzroy Dearborn Publishers: Chicago. 687 pp.

Rich, T.H., and Rich, P.V. 1982. Search for fossils in New Zealand and Australia. *National Geographic Society Research Reports* 14: 557–568.

Sanders, A.E., and Geisler, J.H. 2015. A new basal odontocete from the upper Rupelian of South Carolina, U.S.A., with contributions to the systematics of *Xenorophus* and *Mirocetus* (Mammalia, Cetacea). *Journal of Vertebrate Paleontology* 35:1, e890107.

Schaller, O. 2007. *Illustrated Veterinary Anatomical Nomenclature. Second Edition.* Enke Verlag, Stuttgart. 614 pp.

Schulte, H. von W., and Smith, M. de Forest. 1918. The external characters, skeletal muscles, and peripheral nerves of *Kogia breviceps* (Blainville). *Bulletin of the American Museum of Natural History* 38: 7–72.

Siesser, W.G. 1979. Oligocene–Miocene calcareous nannofossils from the Torquay Basin, Victoria, Australia. *Alcheringa* 3: 159–170.

Siryk, I.M., and Dubrovo, I.A. 1970. Iskopayemyy Zubatyy Kit V Miotsenovikh Otlozheniyakh Yuzhnogo Sakhalina [Fossil toothed whale from the Miocene deposits of the south Sakhalin Island.]. *Geologija i geofigiaka, Novosibirsk* 1970 (9): 123–129. [In Russian.]

Smith, G.J.D., Browne, K.W., and Gaskin, D.E. 1976. Functional morphology of the harbour porpoise, *Phocoena phocoena* (L.). *Canadian Journal of Zoology* 54: 716–729.

Strickler, T.L. 1978. Myology of the shoulder of *Pontoporia blainvillei*, including a review of the literature on shoulder morphology in the Cetacea. *American Journal of Anatomy* 152: 419–431.

Tanaka, Y., and Fordyce, R.E. 2014. Fossil dolphin *Otekaikea marplesi* (latest Oligocene, New Zealand) expands the morphological and taxonomic diversity of Oligocene cetaceans. *PLoS ONE* 9(9): e107972.

Tanaka, Y., and Fordyce, R.E. 2015a. A new Oligo-Miocene dolphin from New Zealand: *Otekaikea huata* expands diversity of the early Platanistoidea. *Palaeontologia Electronica* 18.2.23A: 1–71.

Tanaka, Y., and Fordyce, R.E. 2015b. Historically significant late Oligocene dolphin *Microcetus hectori* Benham 1935: a new species of *Waipatia* (Platanistoidea). *Journal of the Royal Society of New Zealand* DOI: 10.1080/03036758.2015.1016046.

Tsai, C.-H., and Fordyce, R.E. 2015. The earliest gulp-feeding mysticete (*Cetacea: Mysticeti*) from the Oligocene of New Zealand. *Journal of Mammalian Evolution* 22: 535–560.

Uhen, M.D. 2004. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an archaeocete from the Middle to Late Eocene of Egypt. *University of Michigan Papers on Paleontology* 34: 1–222.

Vickers-Rich, P., and Rich, T.H. 1993. *Wildlife of Gondwana.* Reed, Chatswood. 276 pp.

Warne, M.T., Archbold, N.W., Bock, P.E., Darragh, T.A., Detmann, M.E., Douglas, J.G., Gratsianova, R.T., Grover, M., Holloway, D.J., Holmes, F.C., Irwin, R.P., Jell, P.A., Long, J.A., Mawson, R., Partridge, A.D., Pickett, J.W., Rich, T.H., Richardson, J.R., Simpson, A.J., Talent, J.A., and VandenBerg, A.H.M. 2003. Palaeontology: the biogeohistory of Victoria. Pp. 605–652 in: Birch, W.D. (ed), *Geology of Victoria. Geological Society of Australia Special Publication* 23, Geological Society of Australia (Victoria Division): Melbourne. 842 pp.