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

Erich M.G. Fitzgerald[1,2]

[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.

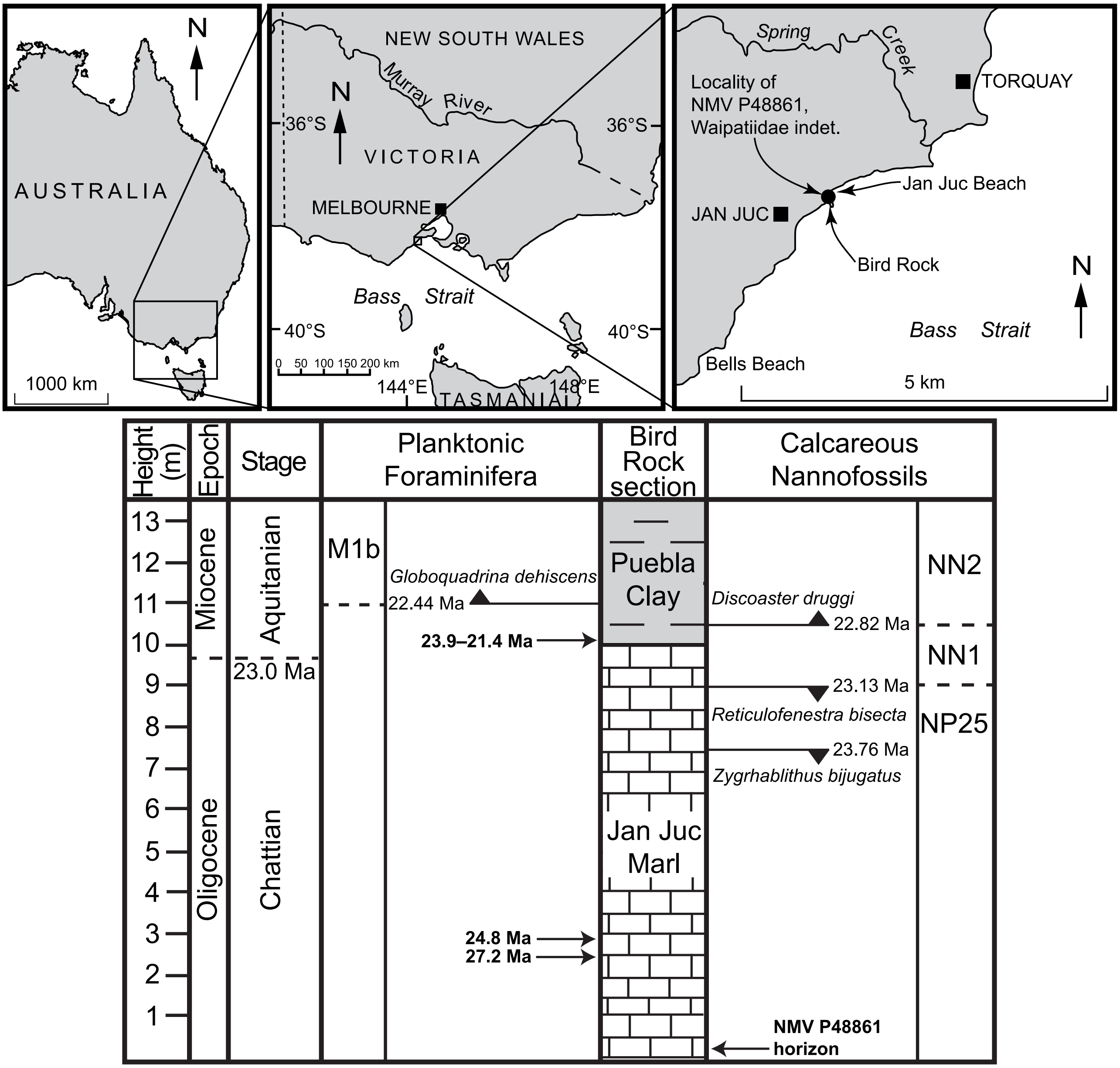

Figure 1. Locality map and stratigraphic section of the locality of NMV P48861, Waipatiidae gen. et sp. indet. Dates in bold text are based on measured $^{87}Sr/^{86}Sr$ ratios in McLaren et al. (2009). Planktonic foraminiferal and calcareous nannofossil stratigraphy, and geochronology are based on Gradstein et al. (2012). Planktonic foraminiferal data from Li et al. (1999), and calcareous nannofossil data from Siesser (1979). The measured section at Bird Rock is based on McLaren et al. (2009).

Material and Methods

Preparation. Material was prepared at Melbourne Museum primarily using pneumatic engravers and pin vises 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	36.6+
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+	–

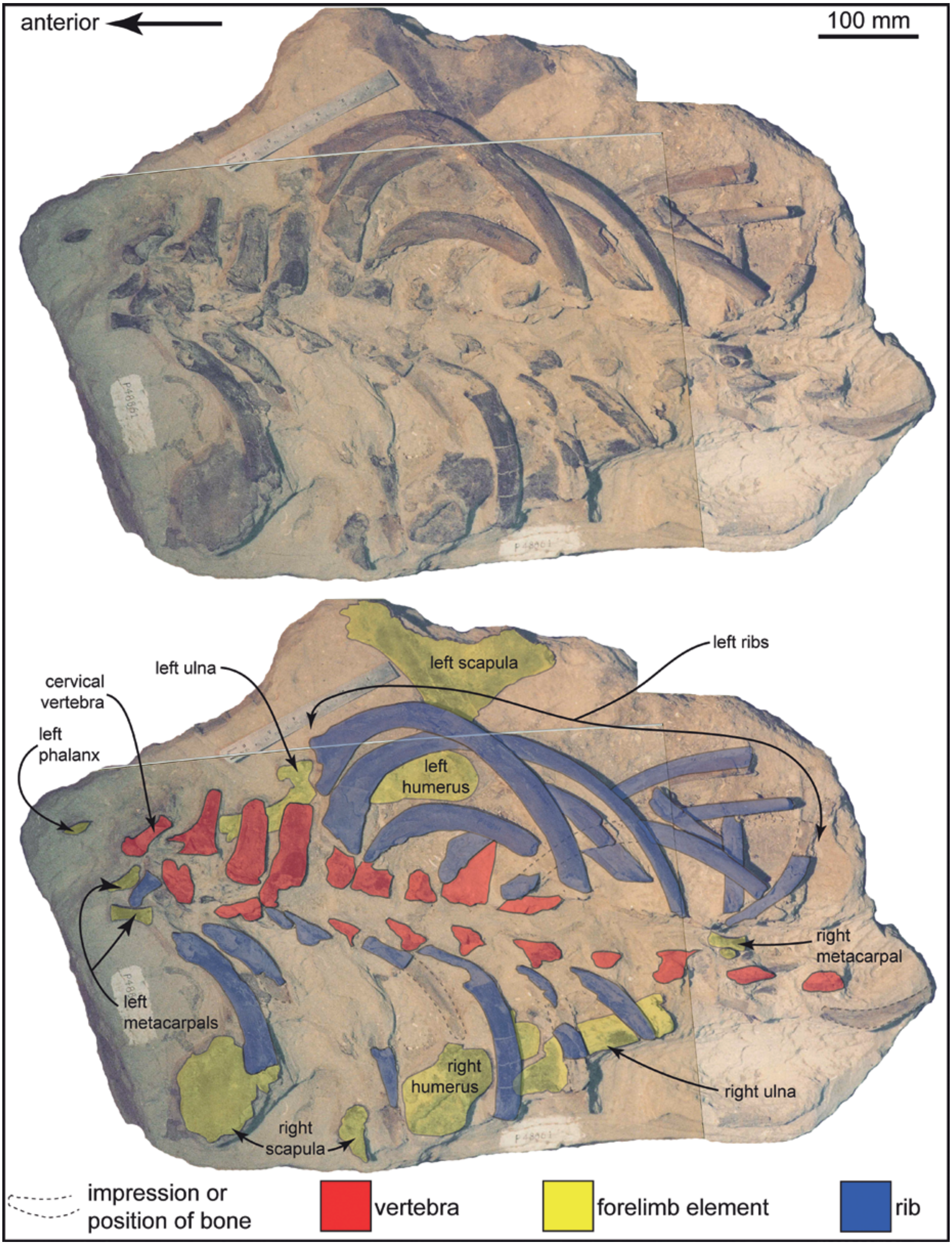

Figure 2. The original distribution of elements in matrix prior to preparation, NMV P48861, Waipatiidae gen. et sp. indet. **Top**, block of matrix enclosing bones as collected in field, prior to preparation. **Bottom**, tracing of bone outlines in matrix prior to preparation.

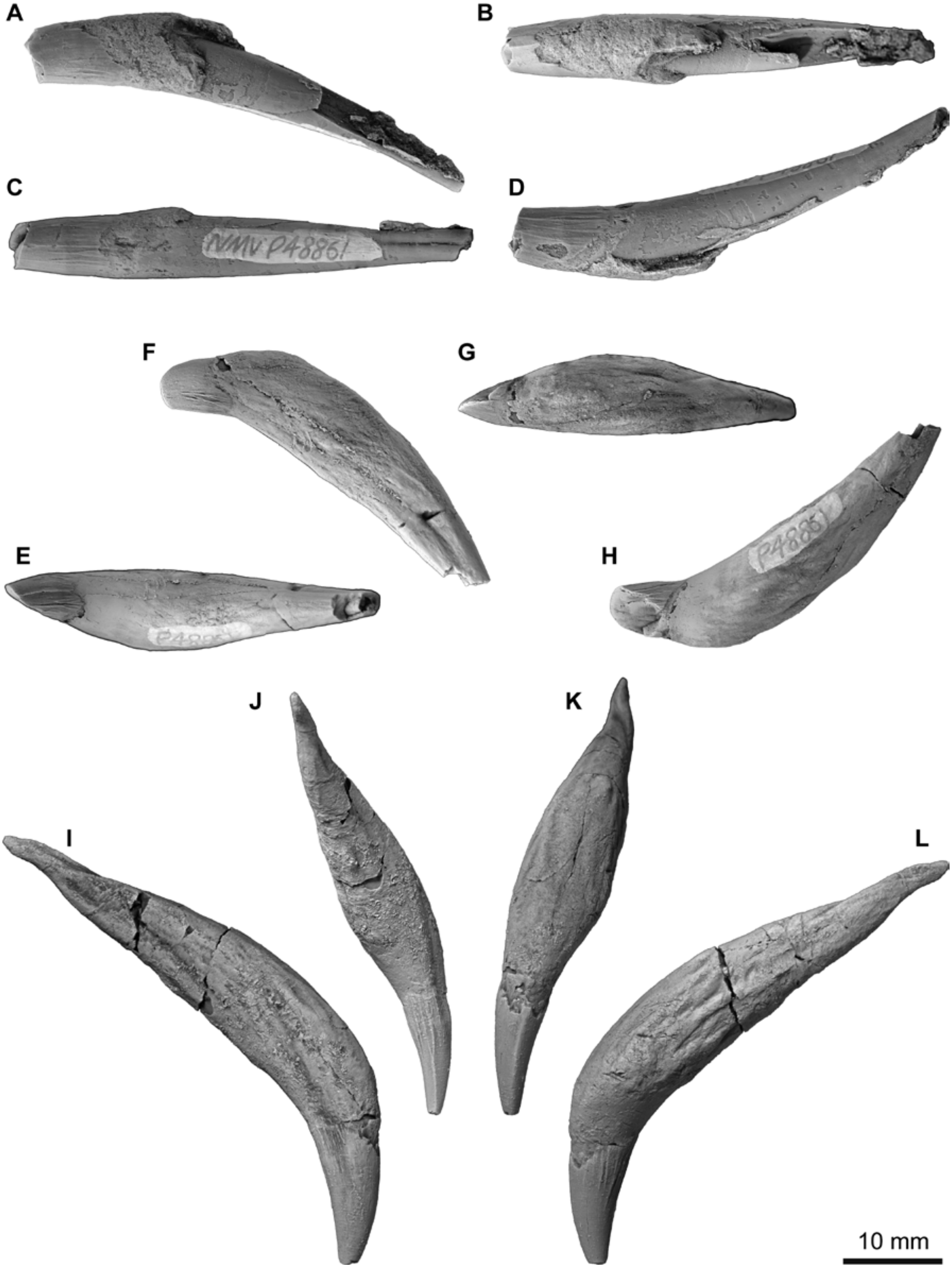

Figure 3. Anterior teeth I–III of NMV P48861, Waipatiidae gen. et sp. indet. Tooth I, presumed procumbent incisor in: **A**, labial; **B**, anterior; **C**, posterior; and **D**, lingual views. Tooth II, anterior tooth in: **E**, posterior; **F**, labial; **G**, anterior; and **H**, lingual views. Tooth 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.

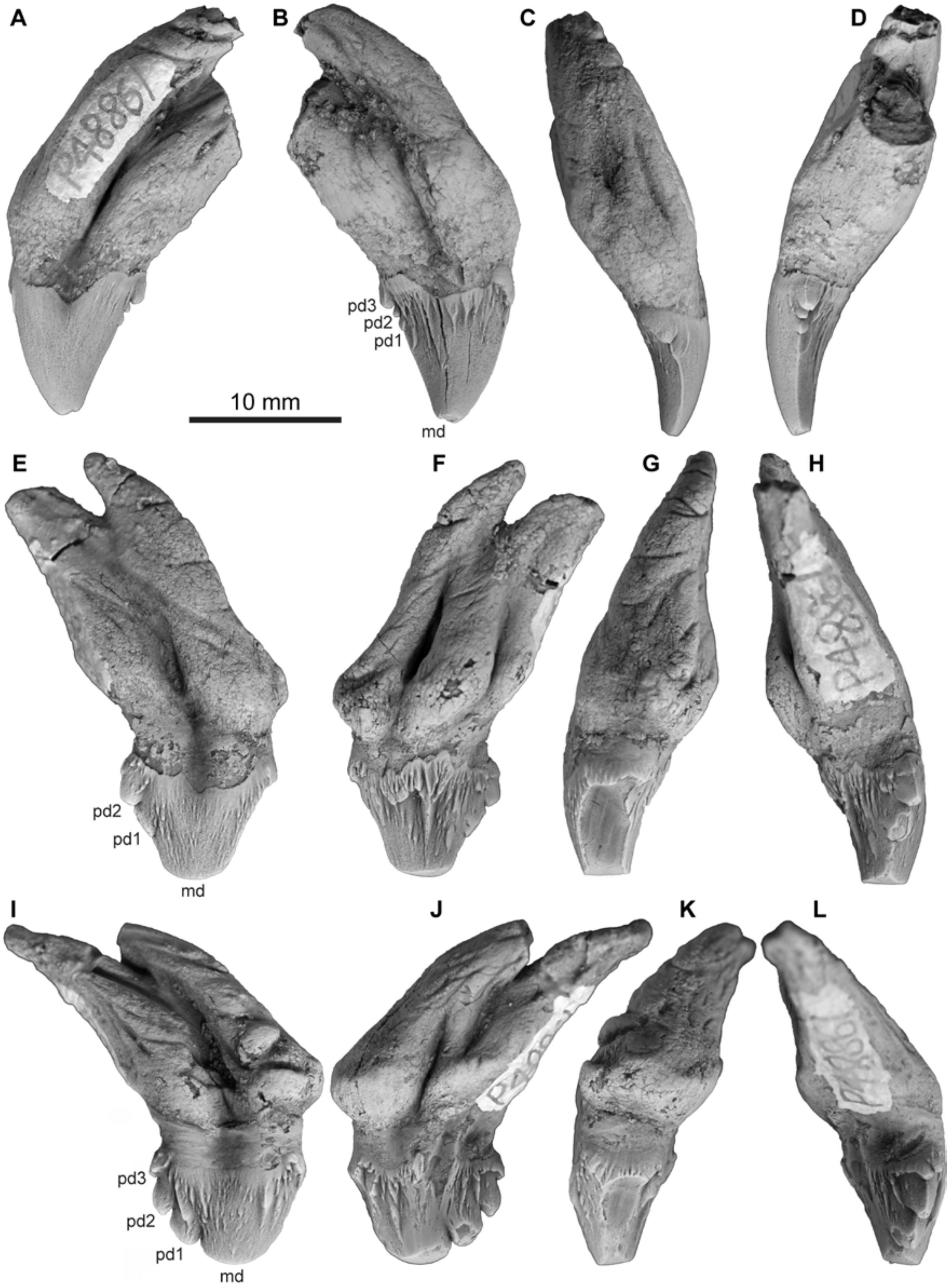

Figure 5. Upper cheek teeth VII–IX of NMV P48861, Waipatiidae gen. et sp. indet., in labial (A, E, I), lingual (B, F, J), anterior (C, G, K), and posterior (D, H, L) views. **A–D**: tooth VII, left upper anterior cheek tooth. **E–H**: tooth VIII, right upper posterior cheek tooth. **I–L**: tooth IX, 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.

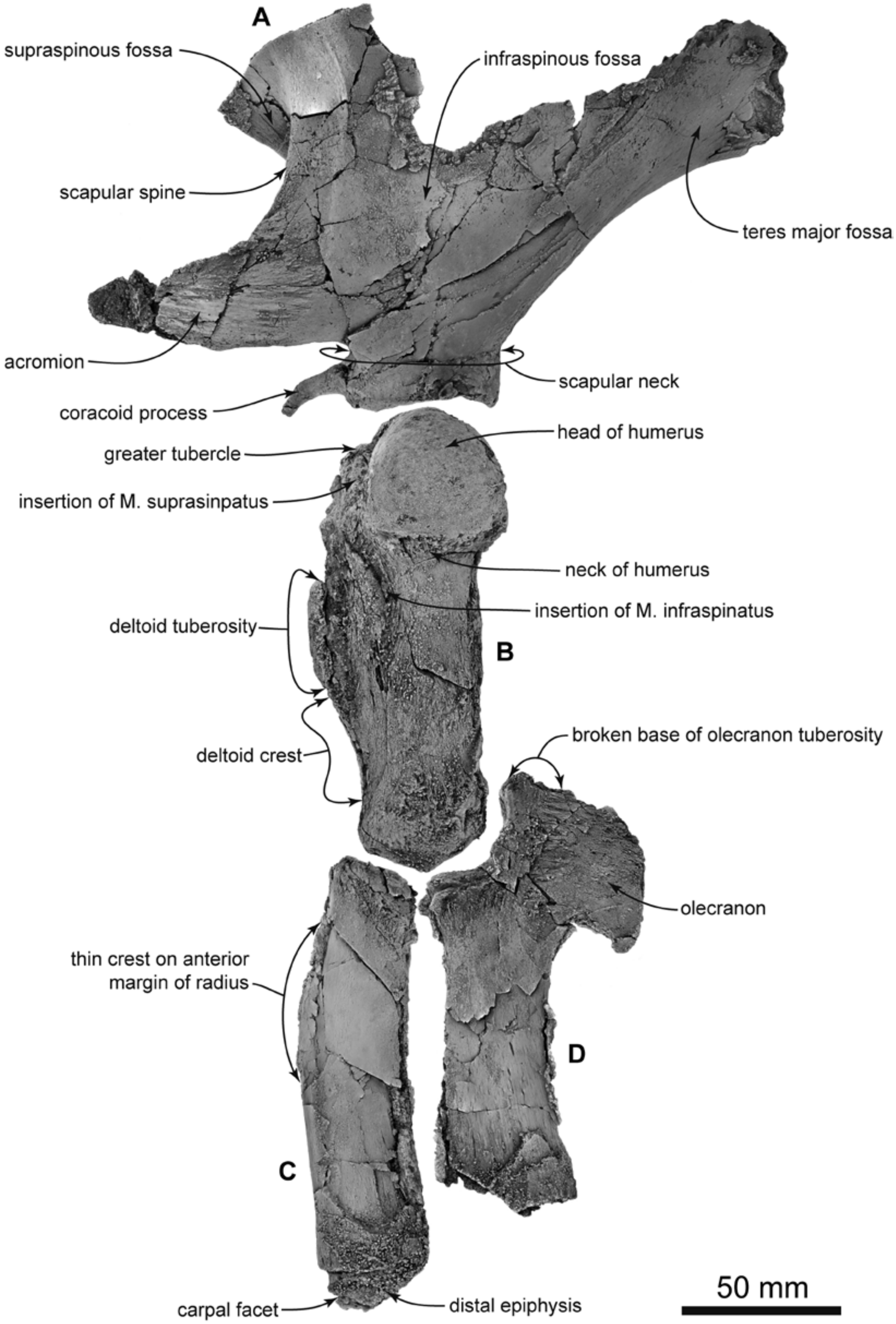

Figure 7. The left forelimb bones of NMV P48861, Waipatiidae gen. et sp. indet. in lateral view. **A**: scapula. **B**: humerus. **C**: radius. **D**: ulna. Specimens whitened with ammonium chloride.

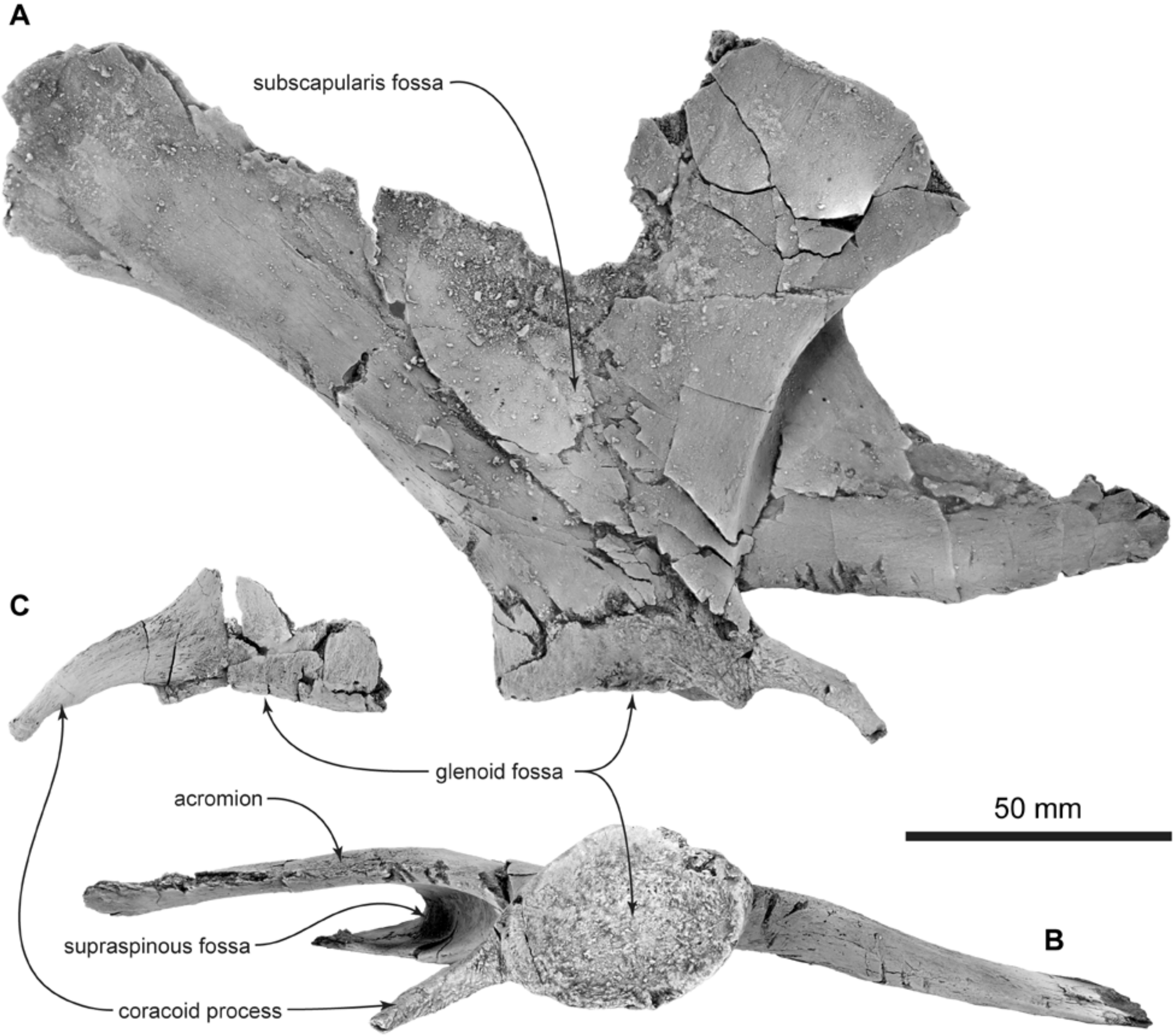

Figure 8. Scapulae of NMV P48861, Waipatiidae gen. et sp. indet. Left scapula in: **A**, medial; and **B**, distal views. **C**: glenoid region of right scapula in medial view. Specimens whitened with ammonium chloride.

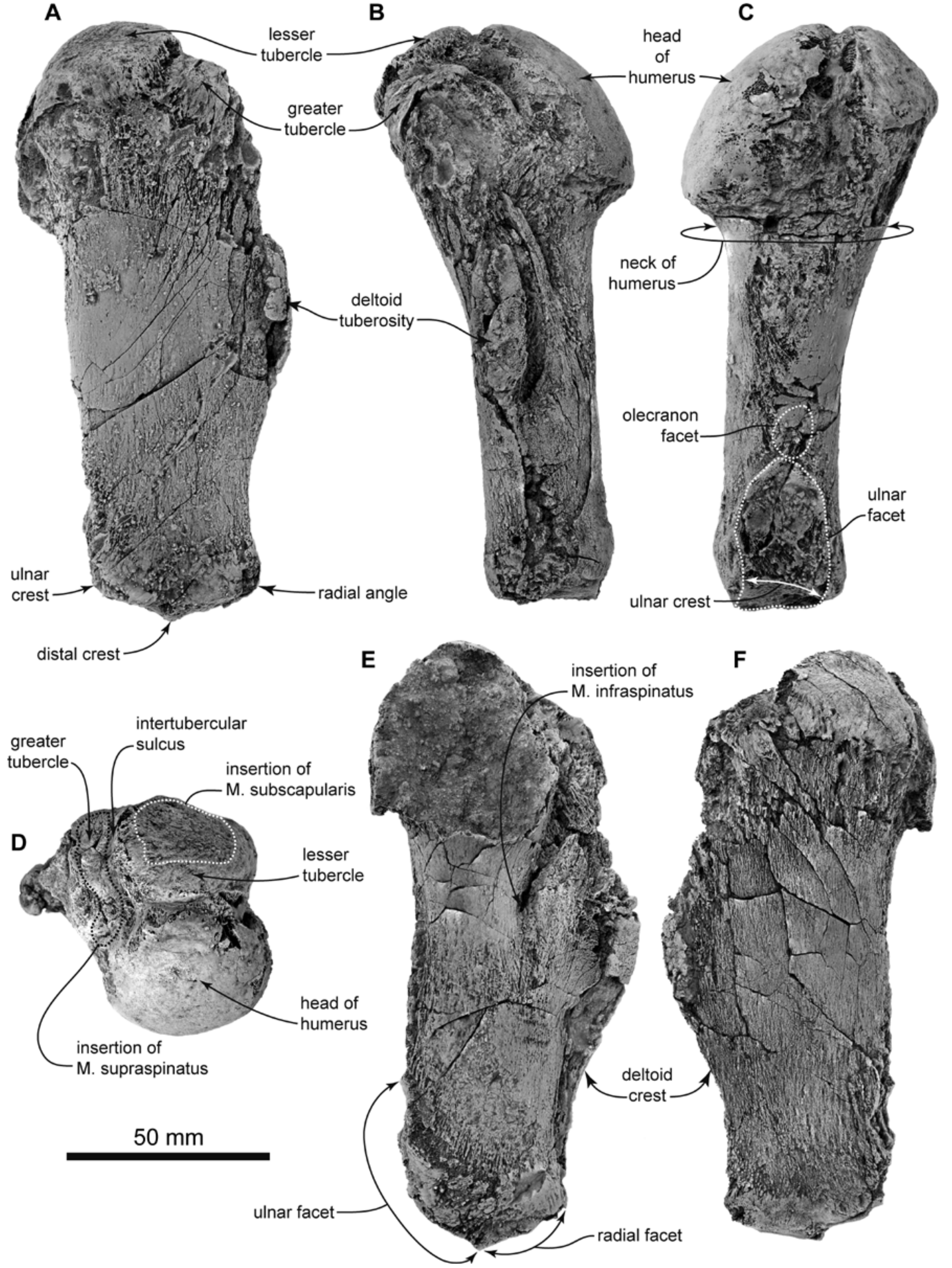

Figure 9. Humeri of NMV P48861, Waipatiidae gen. et sp. indet. Left humerus in: **A**, medial; **B**, anterior; **C**, posterior; and **D**, proximal views. Right humerus in: **E**, lateral; and **F**, medial views. Specimens whitened with ammonium chloride.

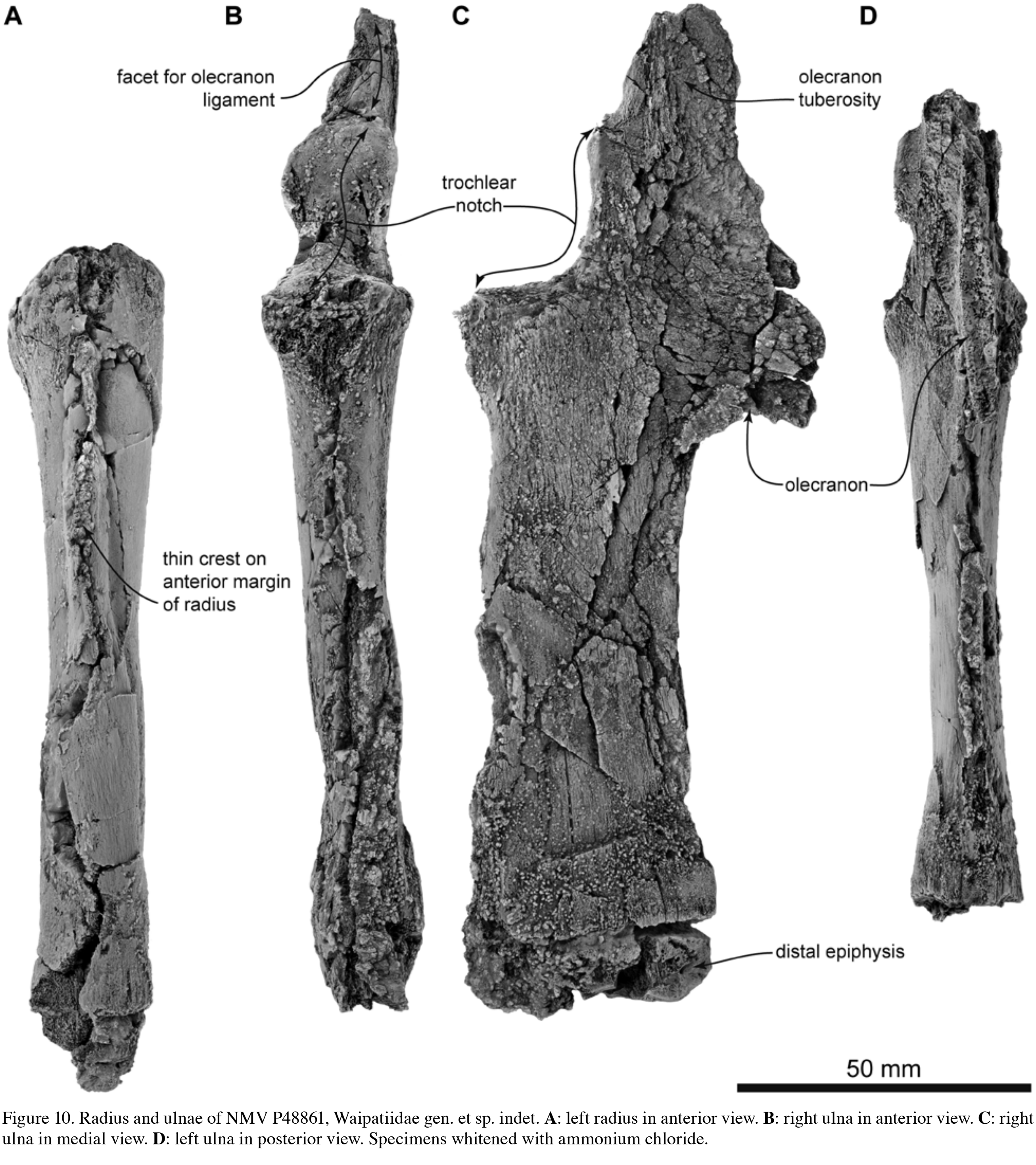

Figure 10. Radius and ulnae of NMV P48861, Waipatiidae gen. et sp. indet. **A**: left radius in anterior view. **B**: right ulna in anterior view. **C**: right ulna in medial view. **D**: left ulna in posterior view. Specimens whitened with ammonium chloride.

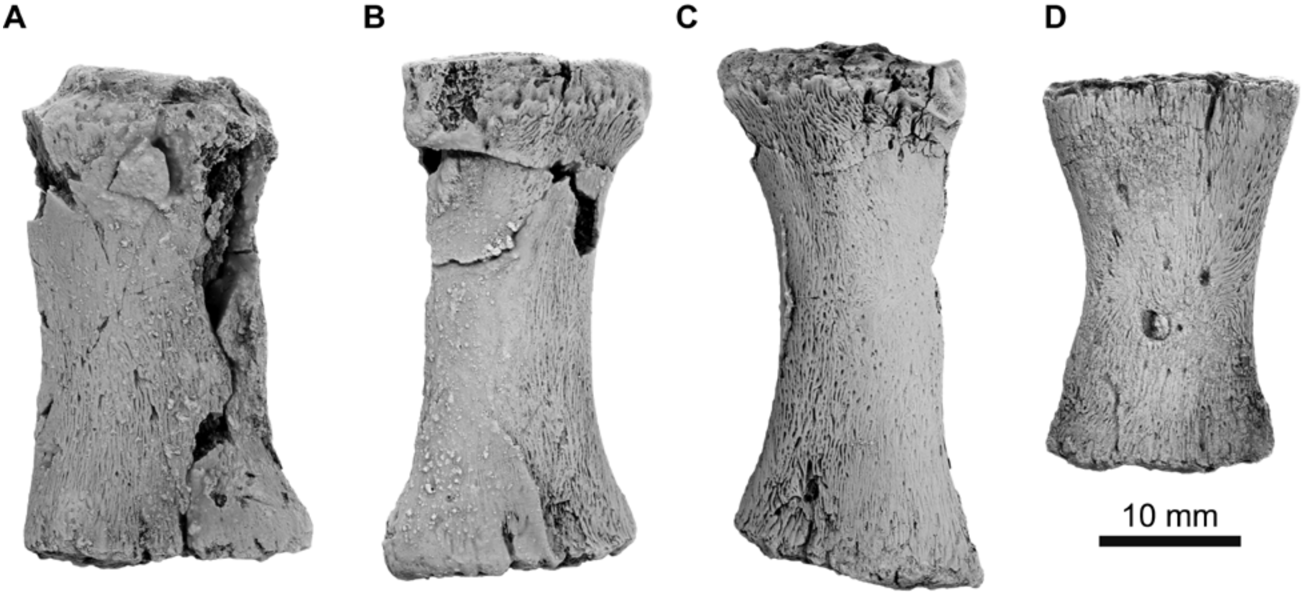

Figure 11. Metacarpals and phalanx of NMV P48861, Waipatiidae gen. et sp. indet. **A**: left metacarpal. **B**: left metacarpal. **C**: right metacarpal. **D**: left phalanx in lateral view. Specimens whitened with ammonium chloride.

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 Jan Juc Marl in the Bird Rock section (Siesser, 1979), its last appearance datum within calcareous nannofossil zone NP25 at 23.76 Ma (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 *Globoquadrina 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 emendments by Fordyce (1994) and Tanaka and Fordyce (2015a); namely that Platanistoidea includes the living family Platanistidae plus the extinct clades

Squalodelphinidae, Waipatiidae, *Otekaikea*, 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. Allodelphinidae, 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 tusked incisor (tooth I) and conical anterior tooth (tooth II) are interpreted as upper teeth on the basis of their strong lingual recurvature. The tusked 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 posterior 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 enamelocementum boundary. The two parallel roots are fused for about two-thirds of their length, recurved posterodorsally (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 posterodorsally 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 deltoid tuberosity and/or crest (Flower, 1885; Schaller, 2007). However, in odontocetes the deltoid 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 adjacent crest of humerus in *Physeter* (Berzin, 1972) and *Kogia* (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 hemi-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 posteroproximal 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.

Discussion

Comparisons. NMV P48861 differs from archaeocetes by having relatively tiny heterodont cheek teeth and a humerus that lacks a trochleated distal end, instead possessing distinct radial and ulnar facets. NMV P48861 differs from mysticetes (including toothed stem taxa) (e.g., *Fucaia goedertorum* (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 coracoid process of the scapula, and a humerus that is longer than the antebrachium. 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 deltoid crest distal to the deltoid 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 coracoid process on the scapula; a humerus with a straight posterior edge (viewed laterally) and a strongly developed deltoid tuberosity; and a more elongated antebrachium. NMV P48861 differs from crown odontocetes other than Platanistoidea in lacking: homodont conical posterior teeth, a distal end of the humeral shaft with an anteroposterior width ≥ to that of the proximal end of the shaft, and a strongly developed coracoid process that enlarges distally. Although the coracoid process of the scapula is reduced in eurhinodelphinids to a rod-like form (*Xiphiacetus bossi* Kellogg, 1925, USNM 11867, Muizon, 1994), NMV P48861 further differs from this family by lacking a distinct crest between the infraspinatus fossa and teres major fossa on the scapula.

Based on these comparisons and the character combinations described above, NMV P48861 is assigned to the Platanistoidea. Within Platanistoidea, NMV P48861 differs from all taxa other than Squalodontidae and Waipatiidae in having heterodont dentition and double-rooted posterior cheek teeth. However, it differs from Squalodontidae by lacking large robust teeth. NMV P48861 lacks the two scapular characters proposed as synapomorphies of Platanistoidea: the acromion positioned on the leading (anterior) edge of the scapula, resulting in loss of the supraspinous fossa; and absence of the coracoid process (e.g., Muizon, 1987, 1994). However, several taxa hypothesized to be platanistoids possess both a supraspinous fossa and a distinct coracoid process on the scapula: the squalodontid *Phoberodon arctirostris* Cabrera, 1926 (Cozzuol and Humbert-Lan, 1989; Cozzuol, 1996; MLP 5-4); *Otekaikea* spp. (Tanaka and Fordyce, 2014, 2015a); and *Sulakocetus dagestanicus* Mchedlidze, 1976 (Mchedlidze, 1984; Muizon, 1987). Hence, the scapular characters of Muizon (1987) may be synapomorphies of a more exclusive clade within 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 coracoid 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 antebrachium (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 labiolingually 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 waipatiid (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; coracoid 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 deltoid 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 cholmicus* Dubrovo in Siryk and Dubrovo, 1970 from the early Miocene of Sakhalin. In addition, rostral and mandibular fragments with teeth, as well as isolated periotics, 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.

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