Mysticetes baring their teeth: a new fossil whale, *Mammalodon hakataramea*, from the Southwest Pacific

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Abstract
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A small, toothed fossil cetacean from Hakataramea Valley (South Canterbury, New Zealand) represents a new Late Oligocene species, *Mammalodon hakataramea*. The new material is from the Kokoamu Greensand (Duntroonian Stage, about 27 Ma, early to middle Chattian) of the Canterbury Basin, and thus about 2 Ma older than the only other species included in this genus, *Mammalodon colliveri* (Late Oligocene, Victoria, Australia). The anterior pedicle of the tympanic bulla is not fused to the periotic and resembles that of Delphinidae in basic structure. The teeth show extreme attritional and/or abrasive wear, which has obliterated the crowns. Like *Mammalodon colliveri*, *M. hakataramea* was probably raptorial or a benthic suction feeder.

Keywords
systematics, evolution, stratigraphy, anatomy, New Zealand, *Osedax*.

Introduction

New Zealand is a notable source of fossil cetaceans (whales, dolphins) in the Southwest Pacific, with specimens ranging in age from late Middle Eocene to Pleistocene. Rocks of the southern Canterbury Basin (Field et al., 1989), in particular, have produced rare Eocene and more common Late Oligocene to earliest Miocene cetaceans. These mid-Cenozoic fossils include representatives of the archaeocete family Basilosauridae, putative stem neocetes (Kekenodontidae) and diverse odontocetes, such as kentriodontids and other putative delphinoids, waipatiids (e.g. *Otekaikea* Tanaka and Fordyce, 2014, 2015), squalodontids and *Squalodelphis*-like taxa. Mysticetes are represented by a diverse assemblage comprising Eomysticetidae (e.g. *Tohoraata* Boessenecker and Fordyce, 2014a), basal Balaenopteroidea, and enigmatica (e.g. *Horopeta* Tsai and Fordyce, 2015). The key cetacean-bearing units – the Kokoamu Greensand (see below) and the Otekaike Limestone – and the localities in and around the Waitaki Valley that expose them were reviewed in the aforementioned articles.

Here, we name and describe a new species of the toothed mysticete *Mammalodon*, based on specimen OU 22026 from the southern Canterbury Basin. The fossil is distinct from the hitherto monotypic *Mammalodon colliveri* (Late Oligocene, ~23.9-25.7 Ma) of Victoria, Australia (Fitzgerald, 2010), and is probably close to 27 Ma. Of note, the fossil includes a tympanic bulla with a well-preserved anterior pedicle, otherwise poorly described for archaeocetes and archaic Neoceti.

Specimen OU 22026 was listed by Fordyce (1991: 1312) as *Mammalodon* sp. and was later mentioned, but not named, in an abstract (Fordyce and Marx, 2011). Recently, we included OU 22026 in a total-evidence phylogenetic analysis of extant and fossil Mysticeti (Marx and Fordyce 2015: fig. 2; see fig. 4 here), which identified it as sister to *Mammalodon colliveri*, with *Janjucetus hunderi* immediately adjacent (basal). Together, these three species form an expanded Mammalodontidae, which in turn are closely related to a diverse range of aetiocetids described only from the North Pacific. OU 22026 was also sampled for isotopes by Clementz et al. (2014), who reported $\delta^{13}C$ and $\delta^{18}O$ values for structural bone carbonate from the bulla that are inconsistent with (filter-)feeding low in the food chain.
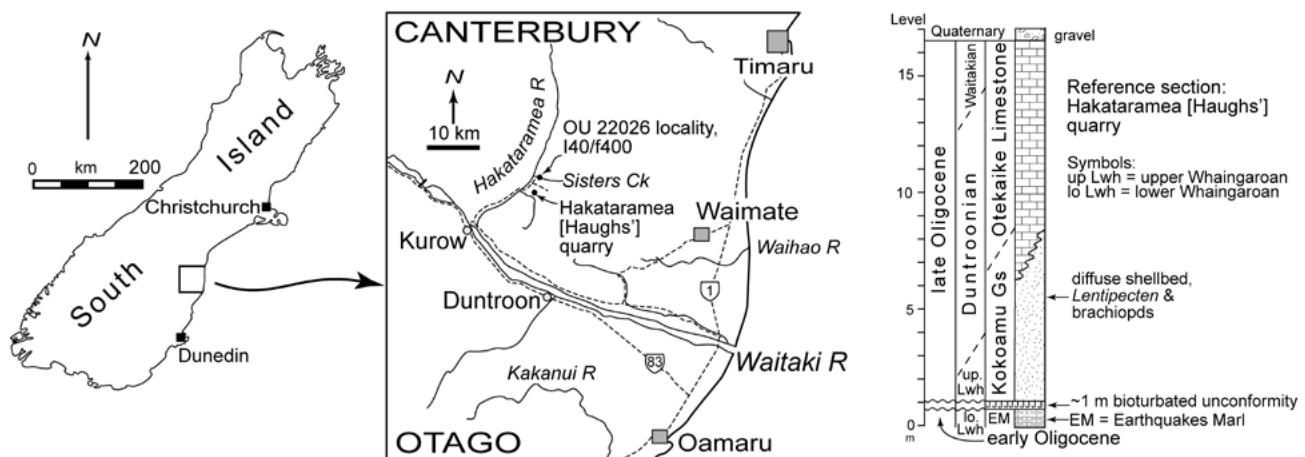
Fig. 1, Locality map and stratigraphy of the Sisters Creek-Homestead Creek area of Hakataramea Valley. The stratigraphic column, right, is modified from that of Tsai and Fordyce (2015) for "Haughs' Quarry", which provides the nearest detailed column to Sisters Creek. *Mammalodon hakataramea* came from about the horizon identified as the diffuse shellbed with *Lentipecten hochstetteri* and brachiopods.

Definitions and terminology

Anatomical terminology follows Mead and Fordyce (2009), unless indicated.

Methods

All elements were uncovered by hand scraping from soft matrix. The bulla was recovered fractured but still naturally associated; it was cleaned and consolidated with cyanoacrylate region by region. For photography, the bulla, teeth and skull roof of *M. hakataramea* and the bulla of *Mammalodon colliveri* were coated with sublimed ammonium chloride. Images of the bulla of *M. hakataramea* are composites, stacked (using Adobe Photoshop) from multiple shots at varying foci. Photography used a Nikon 105 mm micro lens with a D700 or D800 (*M. hakataramea*) or D70 (*M. colliveri*) camera body.

Institutional abbreviations

NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia. OU, fossil collection in Geology Museum, University of Otago, Dunedin, New Zealand.

Systematic Palaeontology

Cetacea Brisson, 1762

Neoceti Fordyce and Muizon, 2001

Mysticeti Gray, 1864

Mammalodontidae Mitchell, 1989

Mammalodon Pritchard, 1939

Emended diagnosis of Mammalodon. Small-sized mysticetes differing from chaeomysticetes in having teeth. Differ from all toothed mysticetes except *Janjucetus* in having a foreshortened, dorsoventrally tall rostrum, a linguiform anterior border of the supraorbital process, a triangular wedge of the frontal separating the ascending process of maxilla from the posterolateral margin of the nasal, a roughly horizontal dorsal profile of the braincase (relative to the lateral edge of the rostrum) and posteriorly reclined mandibular cheek teeth; further differ from all other toothed mysticetes except *Janjucetus* and *Chonecetus* in having a distinctly V-shaped fronto-parietal suture in dorsal view; from *Llanocetus* and two previously coded, undescribed archaic mysticetes (ChM PV4745; OU GS10897) in having both relatively and absolutely smaller posterior cheek teeth with proximally fused roots, and an inner posterior prominence of the tympanic bulla that is subequal to the outer prominence in posterior view; from all aetiocetids in having a more elongate intertemporal region and an anteroposteriorly broader coronoid process of the mandible; from *Aetiocetus* and *Fucaia* in lacking a medially expanded lacrimal and a dorsoventrally constricted mandible, and in having more robust cheek teeth with distally separate roots; from *Chonecetus* in having a broader, less anteriorly-thrust supraoccipital bearing a well-developed external occipital crest, and in lacking a parasagittal cleft on the dorsal surface of the parietal; from *Aetiocetus* in having a clearly heterodont dentition and closely-spaced posterior cheek teeth with well-developed enamel ridges on both the labial and lingual sides of the crown; from *Morawanocetus* in having a much more robust postorbital process of the frontal; from *Ashorocetus* in having a less steeply inclined supraoccipital shield and a somewhat more anteromedially oriented basioccipital crest; and from the enigmatic *Willungacetus* in having a clearly marked orbitotemporal crest extending posteriorly on to the intertemporal constriction and a rounded (rather than triangular), less anteriorly-thrust supraoccipital bearing a well-developed external occipital crest. Finally, *Mammalodon* differs from the only other described mammalodontid, *Janjucetus*, in having a rostrum with a bluntly rounded apex and a gently convex lateral profile in dorsal view,

coalesced alveoli for the upper incisors, a gracile, foreshortened and dorsoventrally flattened premaxilla, an anteriorly expanded nasal, a transversely narrow, linguiform ascending process of the maxilla extending posteriorly as far as the nasal, a more anteriorly directed orbit, a more laterally oriented postorbital process, a transversely convex dorsal profile of the parietals with no salient sagittal crest, a more laterally oriented nuchal crest, a broadly rounded apex of the supraoccipital shield in dorsal view, an anterior portion of the tympanic bulla that is squared (rather than obliquely truncated) in ventral view, an inner posterior prominence of the tympanic bulla that is subequal to the outer prominence in posterior view, a straight and comparatively gracile mandible bearing large mental foramina, and three upper and four lower molars, all of which (at least in adult specimens) are affected by heavy occlusal wear.

Remarks. Comparisons of *Mammalodon* with *Ashorocetus eguchii*, *Willungacetus aldingensis* and *Chonecetus sookensis* are currently hampered by the poor state of preservation of the available material; none of the latter, for example, includes the tympanic bulla or teeth. *Ashorocetus* is currently known only from the posterior portion of a braincase preserving little surface detail (Barnes et al. 1995). *Willungacetus* and *Chonecetus sookensis* are based on somewhat more complete, but still highly fragmentary crania having lost their rostra, most or all of the ear bones and much of the (basicranial) surface detail (Pledge, 2005; Russell, 1968). Until the discovery of better material, the comparisons made here are necessarily provisional. The use of occlusal wear as a potential diagnostic character may be queried, as this feature may primarily correlate with age or the foraging environment. Nevertheless, the extreme wear present in the two species of *Mammalodon* is unusual amongst fossil cetaceans as a whole, and highly so in the context of toothed mysticetes in particular. If tooth wear in *Mammalodon* is primarily linked to the manner of occlusion and/or food preferences, it may record a valid character that can be used for diagnostic and cladistic purposes. Without evidence to the contrary, we therefore retain it here as part of the diagnosis.

Mammalodon hakataramea Fordyce and Marx sp. nov.

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Figs. 2, 3

Holotype. OU 22026 – dorsal part of braincase, comprising much of the supraoccipital and parts of the parietals and squamosals, preserved with the original dorsal surface down, and the bioeroded ventral surface upwards; left tympanic bulla lacking the posterior process; five teeth with little or no remnants of the crown. All elements were closely associated, with no other fossil cetacean remains nearby.

Type locality. Open flat bed of Sisters Creek, 70-80 m downstream from a prominent limestone bank directly north of Riverside farmhouse, McHenrys Road, Hakataramea Valley, South Canterbury (Fig. 1). Field number REF 13-10-87-2. Grid reference: latitude 44 deg 38 min 30.5 sec, longitude 170 deg 38 min 45.0 sec, or NZMS260 map I40: 232 158. The Geoscience Society of New Zealand fossil record number is I40/f400. The locality is 2 km NNW of the informally-named "Haughs' Quarry," as shown by Tanaka and Fordyce (2015).

Horizon and age. OU 22026 is from a massive, bioturbated, calcareous section of the Kokoamu Greensand, where it was associated with sparse macrofossils including scattered pectinids (*Lentipecten hochstetteri*) and terebratulid brachiopods. *Lentipecten hochstetteri* and the benthic foraminiferan *Notorotalia spinosa* indicate the Duntroonian Stage. Judging from a comparable section in the Greensand at Haughs' Quarry, about 2 km to the SSE (fig. 1, right; also, see Tsai and Fordyce, 2015), the diffuse shellbed of pectinids and brachiopods is low in the Duntroonian, probably near the base. The Duntroonian is dated as 25.2–27.3 Ma (Raine et al. 2015) and OU 22026 is presumed close to 27 Ma, or early Chattian (Vandenberghe et al., 2012).

Diagnosis. Differs from *M. colliveri* in having smaller teeth, an anteroposteriorly longer supraoccipital and a parabolic nuchal crest that lacks an abrupt anterolateral curve in dorsal view, as well as in having a tympanic bulla with a more distinct interprominential notch, a straight medial margin, an anterolaterally more inflated outer lip, and a deeper involucrum bearing less developed oblique sulci (without adjacent nodules).

Etymology. Hakataramea, a Maori name for the valley where the holotype was collected. Haka, a dance; taramea, a sharp-spined herb, "spear-grass" (Apiaceae: *Aciphylla squarrosa*), with sweet-smelling gum from the flower stalks. The name may commemorate a specific incident (Reed and Dowling, 2010).

Description

Ontogenetic stage. The specimen is probably a mature adult because of the extreme wear that has mostly obliterated the tooth crowns (fig. 1A–E). The parieto-occipital suture is open along parts of the nuchal crest, but this condition is also seen in adult modern baleen whales (e.g. *Balaenoptera acutorostrata*, Miller, 1924: plate 4; *Balaenoptera borealis*, Andrews, 1916: plate 41; *Megaptera novaeangliae*, True 1904: plates 29, 32).

Skull roof. The dorsal roof of the skull (fig. 2 F, G; table 1) is represented by the ventrally eroded, thin parietals, the supraoccipital and, at the posterolateral margins, probably the dorsalmost portions of both squamosals. There is no distinct

Table 1. Measurements of the skull roof of OU 22026, +/- 0.5 mm.

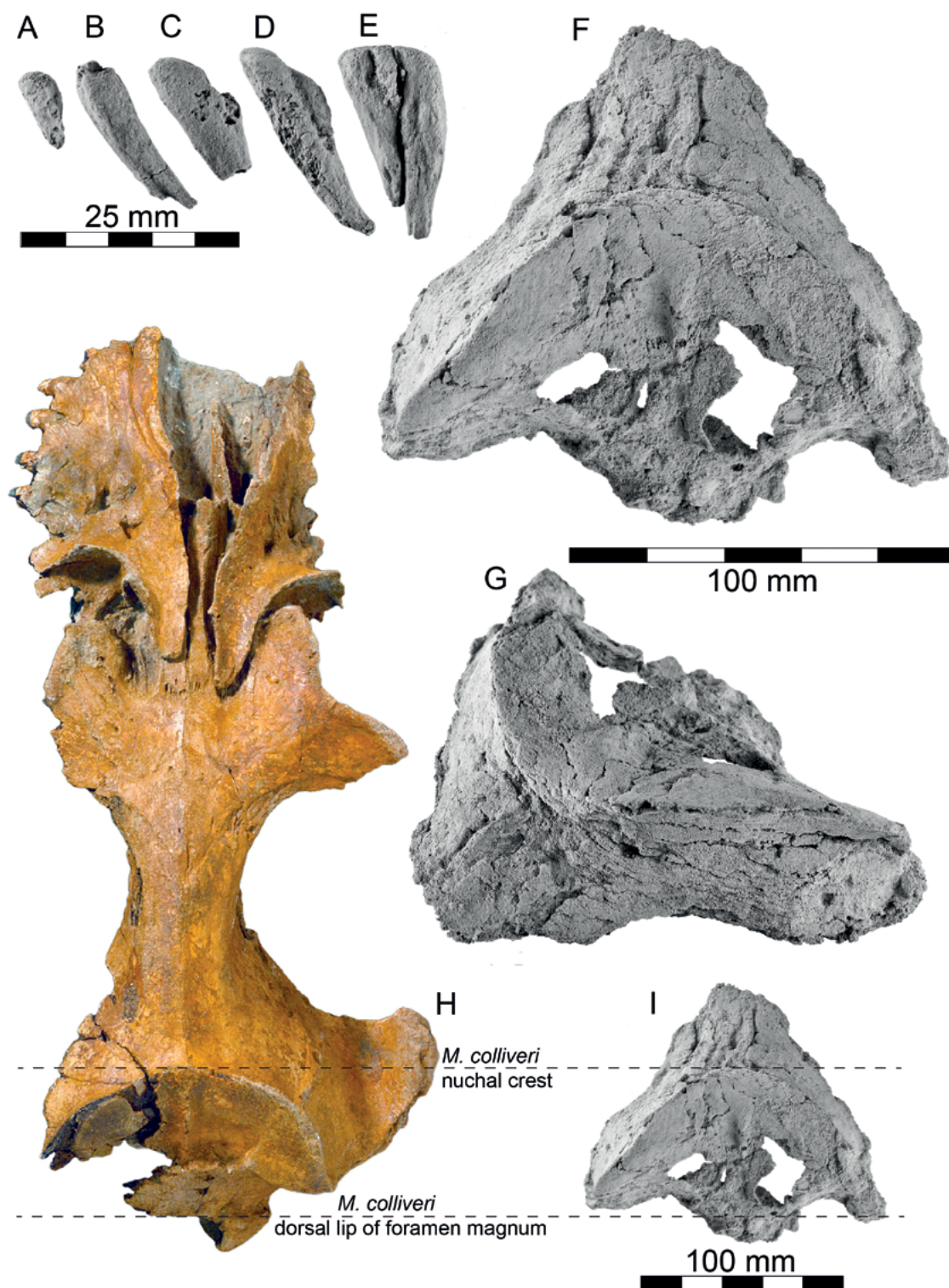|	
Skull roof, anteriormost parietal to posteriormost supraoccipital, midline	+134.5
Length of parietals on vertex	+45.0
Length of supraoccipital, midline	+94.0
Width, outer margins of nuchal crest, posteriormost preserved points (= posterolateral extremities of skull roof)	+154.5

Fig. 2. A-G, I, holotype of *Mammalodon hakataramea*, OU 22026; all material coated with sublimed ammonium chloride and lit from upper left. A-E, individual isolated teeth in labial or lingual view. F, G, I, holotype skull roof of *Mammalodon hakataramea*. F, I, dorsal view, anterior towards the top; G, oblique dorsolateral view from the left, anterior towards the lower left. H, holotype skull of *Mammalodon colliveri* Pritchard, NMV P199986, dorsal view, not coated with sublimed ammonium chloride. H and I are shown at the same scale to compare the differences in size and profile between the two *Mammalodon* species. The two dashed lines show the position of the apex of the nuchal crest and the dorsal lip of the foramen magnum in *M. colliveri*; *M. hakataramea* is aligned with the upper line.
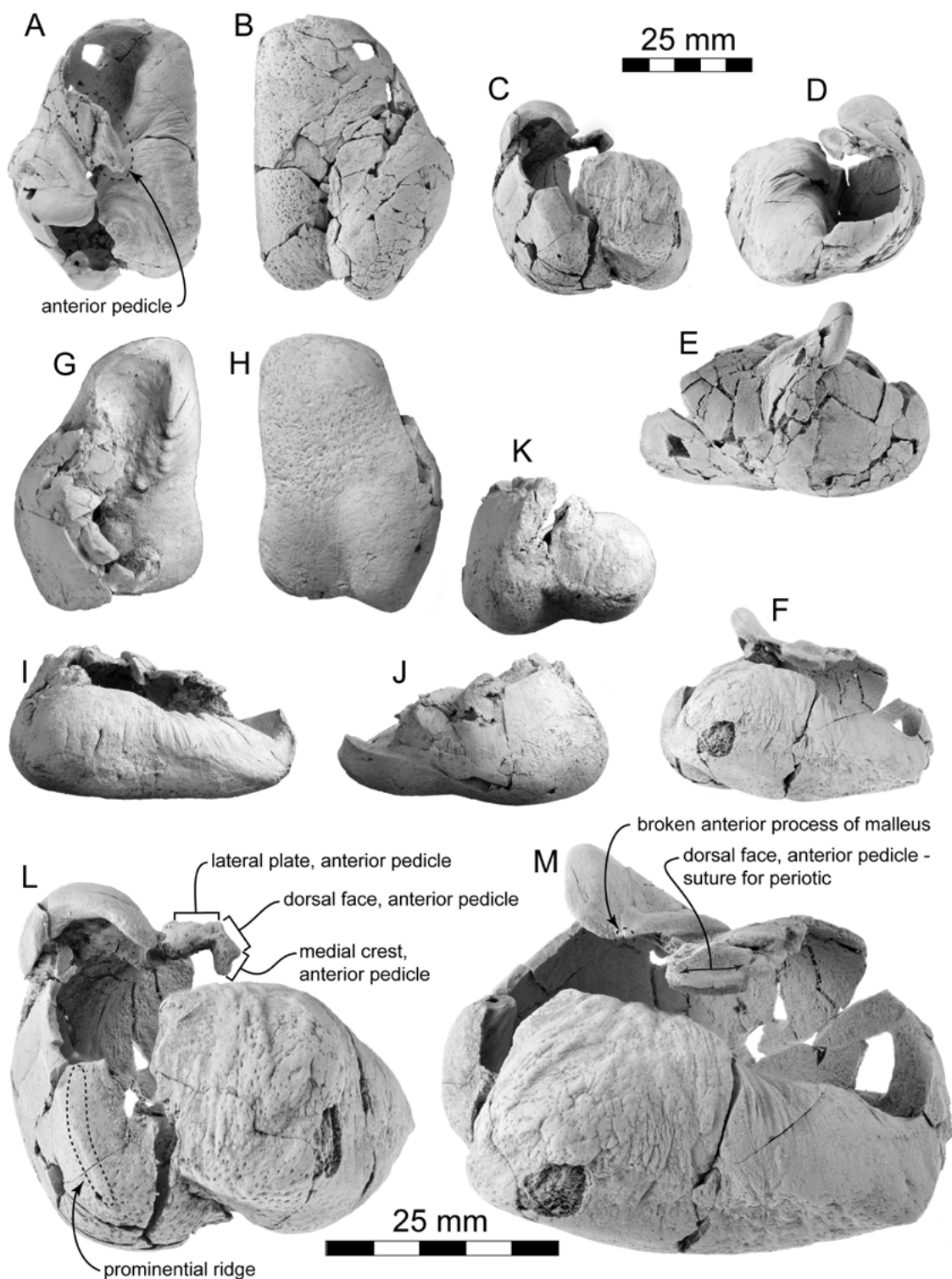
Fig. 3. A-F, L, M, holotype left tympanic bulla of *Mammalodon hakataramea*, OU 22026; all views show the bulla coated with sublimed ammonium chloride and lit from upper left. A, dorsal. B, ventral. C, posterior. D, anterior. E, lateral. F, medial. G-K, holotype right tympanic bulla of *Mammalodon colliveri* Pritchard, NMV P199986, with views mirrored for ease of comparison with *M. hakataramea*; bulla is coated with sublimed ammonium chloride and mirrored views show lighting from upper right. G, dorsal. H, ventral. I, medial. J, lateral. K, posterior. L, M, enlarged views of left tympanic bulla of *Mammalodon hakatarame*a to show anterior pedicle. L, slightly dorsomedial posterior view. M, slightly posterior dorsomedial view.

interparietal. The dorsal periosteal surfaces are damaged by patchy bioerosion, which in two places has also led to the perforation of the supraoccipital. Enough remains to see that the supraoccipital is longer, from its apex to the margin of foramen magnum, than in *M. colliveri* (fig. 2H, I). The gently concave supraoccipital is raised little (~ 3 mm) above the parietals, and forms a thin-edged nuchal crest with a parabolic profile and a smoothly rounded apex in dorsal view (fig. 2F, G). By contrast, the crest in *M. colliveri* is more robust, with abruptly curved anterolateral corners that markedly overhang the parietals (fig. 2H). A lateral or oblique view (fig. 2G) shows the nuchal crest gently convex anteriorly but markedly steepening posteriorly, as if descending toward the posterior margin of the temporal fossa. Anteriorly, the supraoccipital has a small, flattened dorsal apex, passing backwards into a short but well-developed external occipital crest. Posteriorly, the supraoccipital is raised and thickened in the midline, with the adjacent surfaces steepening bilaterally; in *M. colliveri*, such features are developed near the foramen magnum.

What remains of the parietals suggests that the fused bones form a wide and smoothly rounded intertemporal region without any salient sagittal or parasagittal crests, contrasting with the narrower, dorsally tabular, condition in *M. colliveri*. Irregular parasagittal grooves could result from bioerosion, but are more likely to be sulci associated with parietal foramina. Poorly-preserved irregularities in the bone surface posteriorly (fig. 2G) may represent the parieto-squamosal sutures.

Tympanic bulla (fig. 3A–F, L–M; table 2). The left bulla is slightly crushed, with the outer lip a little compressed ventrally. The anterior pedicle has been distorted post-mortem and rotated ventromedially, so that the suture for the anterior bullar facet of the periotic is steeply dipping, rather than sub-horizontal. The posterior process, conical process and the anterolateral crest of the outer lip are lost.

In dorsal view (fig. 3A), the bulla has a straight medial profile, a bluntly rounded, slightly squared apex and an inflated outer lip, with the bone attaining its greatest width at the level of the sigmoid process. The two posterior prominences or lobes are separated by the conspicuous, near-perpendicular interprominential notch (fig. 3A, B). In dorsal or ventral view, the outer prominence is sharp, passing dorsally into a marked

prominential ridge (*sensu* Tsai and Fordyce, 2015). The inner prominence is more smoothly rounded and does not extend as far posteriorly, which may indicate an anteromedial *in situ* orientation of the long axis of the bulla as seen, for example, in *Janjucetus hunderi*. In posterior view (fig. 3C, L) a strong, slightly oblique ridge crosses the inner prominence to reach the interprominential notch; there is no ridge on the outer prominence. Ventrally (fig. 3B), the interprominential notch passes into a median furrow 22–23 mm long, about half the length of the bulla.

The Eustachian outlet forms a shallow, anteromedially oriented notch (fig. 3A, M). The adjacent portion of the involucrum is obliquely flat medially and excavated laterally. Posteriorly, the involucrum rises and widens via an abrupt, obliquely oriented step at mid-length. Oblique striae that cross the involucrum are finer than in *M. colliveri* (fig. 3F) and not separated by tubercles laterally. The otherwise smooth dorsal surface anteriorly on the involucrum was probably covered by a lobe of the peribullary sinus; this smooth bone extends posteriorly 20+ mm, at least to the oblique "step" in the dorsal profile, and possibly to the level of the prominent sub-vertical postmortem crack (fig. 3M). Further posteriorly, the elevated involucral surface is considerably rougher, suggesting that the peribullary sinus may not have extended over the involucrum here. In medial view, the involucrum has a horizontal zone of irregular fine creases, probably marking tendinous connections to the basioccipital crest (fig. 3F, M). A large irregular depression on the posteriormost portion of the involucrum (fig. 3M) is probably a collapsed cluster of galleries formed by the osteophagous siboglinid worm *Osedax* (see Boessenecker and Fordyce, 2014b for similar occurrences in other New Zealand Oligocene Cetacea). In posterior view, the involucrum is more prolonged in a dorsolateral-ventromedial plane than the sub-cylindrical involucrum of *M. colliveri* (compare figs. 3C, D and 3K). An oblique (slightly lateral) dorsal view, not figured here, shows a slight concavity in the medial profile of the involucrum – much less than in *M. colliveri*, in which this concavity is pronounced.

The outer lip preserves a sharp crest at the Eustachian outlet and becomes anterolaterally inflated as it passes back towards the anterior pedicle. The anterolateral corner of the tympanic bulla formed by this inflated portion is more rounded than in *M. colliveri* (compare fig. 3B, H). The crest of the outer lip is broken to reveal the tympanic cavity in dorsal view. The floor of the latter is smooth and has a marked transverse saddle about level with the anterior pedicle, behind which the tympanic cavity deepens markedly, and narrows. The cavity both undercuts the involucrum and, at its posterior limit, rises dorsally to excavate it below the inner posterior pedicle.

The anterior pedicle has a narrow, anteroposteriorly long junction with the outer lip (fig. 3A, M). The junction is cracked, and it is uncertain if a groove for the chorda tympani nerve was present. In dorsal or dorsomedial view (fig. 3A, M), the anterior pedicle has three elongate faces roughly perpendicular to each other. The original structure and orientations are interpreted thus: a lateral plate that descends to the outer lip; an elongate sub-oval dorsal face with a shallow grooved suture for the periotic; and a descending medial crest, with a groove that presumably contributes to the origin of the tensor tympani

Table 2. Measurements of left bulla of OU 22026, +/- 0.5 mm

Length, apex adjacent to Eustachian outlet to apex of outer posterior prominence	56.5
Length, parallel with medial face	55.5
Width, maximum, immediately below sigmoid cleft	38.0
Depth of involucrum, maximum, at anterior margin of broken base of inner posterior pedicle	25.5
Depth, tip of sigmoid process to ventral surface with bulla sitting in stable position	38.0
Length, apex adjacent to Eustachian outlet to apex of sigmoid process	38.5

muscle (following Tsai and Fordyce 2015). A posterior view (fig. 3L) shows the silhouetted cross section of the pedicle, with the three surfaces bounding an elongate V- to U-shaped ventral groove. On the dorsal face, the suture for the anterior bullar facet of the periotic is a long, shallow groove (fig. 3L, M); accordingly, the fovea epitubaria was probably shallow and flat, rather than saddle-shaped. The dorsal face of the pedicle does not show any clear region of fusion with the anterior margin of the mallear fossa, although the lateral edge of the posterior apex has lost a sub-mm area of surface bone which might indicate fusion.

Adjacent to the anterior pedicle, the outer lip bears a shallow vertical groove, but no obvious lateral furrow (fig. 3E). The mallear ridge is prominent, oriented obliquely and most raised at its mid-length. Posteriorly, at the inner margin of the sigmoid process, the ridge passes into a tiny projection representing the broken anterior process of the malleus (fig. 3M). In anterior or posterior view (fig. 3D, L), the dorsal profile of the sigmoid process has three indistinctly separate faces: a medial one, probably marking the proximity of the malleus; a dorsal one, possibly apposing the sigmoid fossa of the squamosal; and a lateral one. The enrolled posterior lip of the sigmoid process overhangs a sigmoidal cavity (*sensu* Tsai and Fordyce, 2015) delimited by a low oblique ridge presumably for the tympanic sulcus (fig. 3L). In lateral view (fig. 3E), the sigmoid process is bounded ventrally by a damaged, anteroventrally oblique sigmoid cleft. The conical process is lost. A strong prominential ridge (*sensu* Tsai and Fordyce, 2015) lateral to the elliptical foramen is matched by a thickened ridge within the tympanic cavity. Judging from well-preserved thin flanges, the elliptical foramen was patent as a narrow opening about 5 mm deep.

Teeth (fig. 2A–E; table 3). Five teeth are represented by roots, with one tooth (fig. 2B) retaining a tiny possible dentine remnant of the crown. The other four teeth are worn, exposing sections through the infilled pulp cavity. The worn, sub-ovate surfaces curve down both labiolingually and mesiodistally. Wear exposes lines of arrested growth (growth-layer groups, as commonly used for Cetacea), marked by alternating lighter and darker coloured bands in the outer biomineral, which is presumed to be cementum. Occlusal surfaces were examined under high magnification, but no wear patterns (grooves, striations) were apparent. Tooth A of Figure 2 is laterally compressed and conical. Tooth B is conical, with a double distal tip, perhaps representing two fused roots. Tooth C is laterally compressed. Tooth D is grooved on the labial and lingual faces, perhaps representing two fused roots. Tooth E has two closely approximated large roots that taper and converge distally, with a small third root between the two larger adjacent to the occlusal surface. Tooth E is the only one that can reasonably be identified to position, as a posterior premolar or molar.

Discussion

Mammalodon hakataramea is one of relatively few toothed mysticetes to be formally described, and only the third member of the highly unusual and seemingly rather localised mammalodontids (fig. 4). Bianucci et al. (2011), however,

mentioned a potential record of this family from the Mediterranean. *Mammalodon hakataramea* is also the first new species of archaic toothed mysticete from the New Zealand region to be formally named as such. Other New Zealand Oligocene Cetacea likely also represent archaic Mysticeti, but have either been misidentified or remain undescribed. One example of such material is "*Squalodon*" *serratus* Davis, 1888, an isolated cheek tooth that may have belonged to an aetiocetid (Fordyce, 2008). Another is an Early Oligocene specimen described by Keyes (1973) as a "proto-squalodont", but identified as a basal mysticete by Marx and Fordyce (2015) based on as-yet undescribed portions of the skull (OU GS10897). Nevertheless, toothed mysticetes from New Zealand are rare, and only a handful of potential candidates have been recovered during Fordyce's field programme of 30 years.

The holotype of *Mammalodon hakataramea* shows two features that are noteworthy in terms of structure and/or function. First, the anterior pedicle of the bulla reveals details rarely preserved in basal mysticetes: the long, thin lateral plate merging with the outer lip, the dorsal face with the suture for the anterior bullar facet of the periotic and the medial crest, all of which bound a ventral groove. These structures are readily homologised with the anterior pedicle, or accessory ossicle, in extant Delphinidae, e.g. *Tursiops truncatus* and *Globicephala melas*. In the delphinids, the lateral plate descends to the groove for the chorda tympani. The dorsal face (with a faintly grooved suture for the periotic) is short and arched anteroposteriorly to match the saddle-shaped fovea epitubaria. The medial plate is inflated and nodular (thus partly closing the ventral groove), and contributes to the origin for the tensor tympani (see Mead and Fordyce, 2009: fig. 25W). A ventrally-grooved anterior pedicle and unfused bulla/periotic contact also occur in at least one kekenodontid and one eomysticetid at OU, albeit in pedicles broken from the bulla. In the putative gulp-feeding Late Oligocene mysticetes *Mauicetus parki* and *Horopeta umarere* (both Chaeomysticeti), the dorsal face of the anterior pedicle is partly fused posteriorly to the periotic. In addition, the medial ridge is not developed in these taxa, but extends dorsally up the medial face of the periotic. Accordingly, there is no ventral groove.

Table 3. Measurements of teeth of OU 22026, +/- 0.5 mm

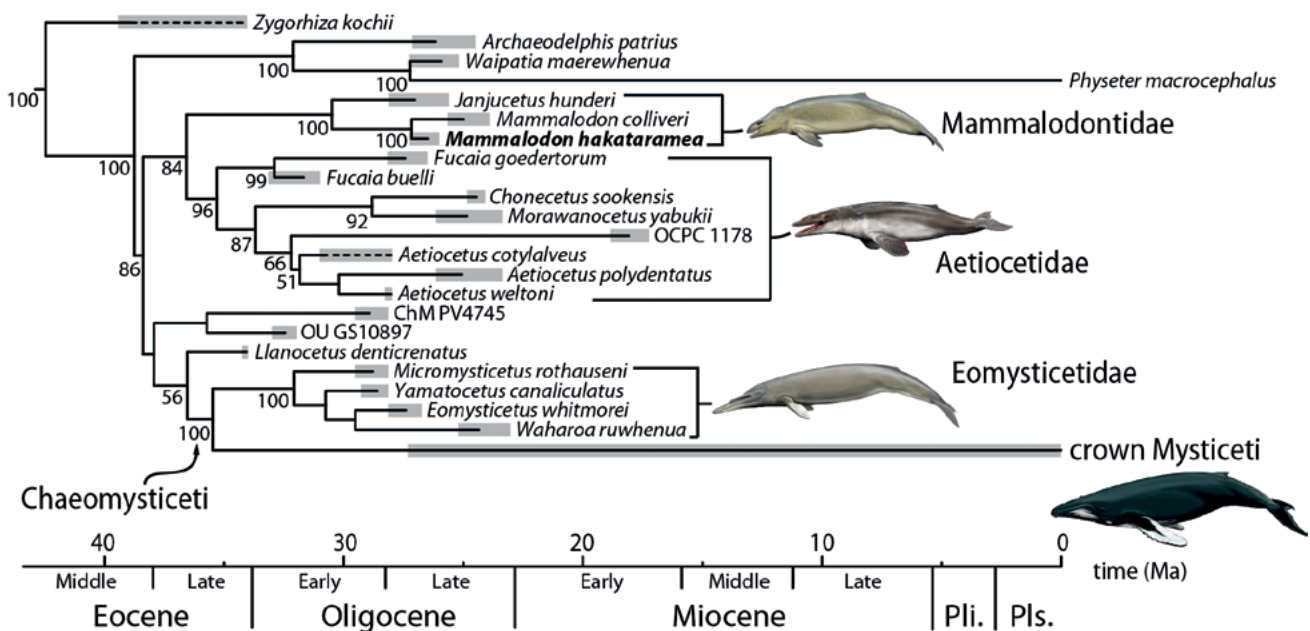|	
Tooth of Fig. 2A, maximum length of root	9.5
Tooth of Fig. 2A, maximum diameter	4.0
Tooth of Fig. 2B, maximum length of root	21.0
Tooth of Fig. 2B, maximum diameter	5.5
Tooth of Fig. 2C, maximum length of root	16.5
Tooth of Fig. 2C, maximum diameter	7.0
Tooth of Fig. 2D, maximum length of root	26.0
Tooth of Fig. 2D, maximum diameter	7.0
Tooth of Fig. 2E, maximum length of root	23.5
Tooth of Fig. 2E, maximum diameter, mesiodistal	11.0

Fig. 4. Relevant detail of phylogeny from Marx and Fordyce (2015: Fig. 2), showing relationships of *Mammalodon hakataramea* and other Mysticeti basal to the crown group. Pli., Pliocene; Pls., Pleistocene.

Secondly, the worn occlusal surfaces of the teeth curve down on to the mesiodistal and labiolingual faces of the roots. The similar shape and surface detail amongst the teeth suggest that the wear is not post-mortem bioerosion, but was likely caused by abrasion. Phylogenetic bracketing (fig. 4) implies that *M. hakataramea* actually had functional tooth crowns on robust teeth in a short rostrum, like its sister taxon *M. colliveri*. The rounded worn surfaces in *M. hakataramea* contrast with the more clearly planar wear characterising the cheek tooth crowns in the holotype of *M. colliveri* (see Fitzgerald, 2010). Nevertheless, planar attrition cannot be ruled out as a factor earlier in the ontogeny of OU 22026, and it is possible that the rounded wear surfaces reflect old age. Extensive attritional wear might have removed much of the tooth crown, as in *M. colliveri*, until proper occlusion, and thus further attrition, became impossible. Abrasive wear, conversely, could have continued through on-going contact of the teeth with food or ingested sediment.

That OU 22026 survived despite having lost functional tooth crowns argues against tooth-assisted filter feeding, as was also argued by Fitzgerald (2010). This conclusion is consistent with the isotopic values reported by Clementz et al. (2014), which indicate that *M. hakataramea* fed higher in the food chain than typical filter feeding mysticetes. We agree with Fitzgerald (2010) that the extensive wear in *Mammalodon* is more easily reconciled with suction feeding than with raptorial feeding, which depends on functional teeth for grasping and/or processing large prey; nevertheless, facultative durophagy or raptorial sarcophagy cannot be ruled out.

Cetacean ecology during the Oligocene was rather different from today. Modern seas are dominated by one clade of mysticetes – the gulp-feeding rorquals (Balaenopteridae) – and two clades of echolocating odontocetes: the deep-diving, suction-feeding beaked whales (Ziphiidae) and the ecologically rather plastic dolphins (Delphinidae). Like the modern species, some of New Zealand's Late Oligocene baleen whales (e.g. *Mauicetus parki, Horopeta umarere*), probably filter-fed by skimming or gulping. The long- and narrow-jawed eomysticetids, with no modern equivalents, could have been skimmers or suction feeders, but probably not gulp feeders. The small-toothed mysticetes from the wider Australasian region were rather disparate, and probably included both raptorial and (benthic) suction feeders, such as *Mammalodon colliveri*. Given their overall similarity and shared extreme tooth wear, *M. colliveri* and *M. hakataramea* were perhaps suction feeders. Late Oligocene odontocetes were all echolocators, with assemblages dominated by platanistoid dolphins in contrast to the dominant delphinids of modern seas. These platanistoids included both clearly heterodont taxa, such as shark-toothed dolphins with a robust dentition suitable for crushing food, and near-homodont forms that – like modern dolphins – probably swallowed with minimal processing. Remarkably, kekenodontid archaeocetes coexisted, until about 26 Ma, with cetaceans of "modern" feeding habit, presumably snap-feeding raptorially and without the benefit of echolocation.

Acknowledgements

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