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3 Please check the final publication record for the latest revisions to this article.  
4 [Author's note: one figure, the only known tooth of an eomysticetid, is not present in  
5 this postprint because it was added during final revisions. Consult the formally  
6 published version of record.]

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8 Boessenecker, R.W., and R.E. Fordyce. 2015. A new genus and species of  
9 eomysticetid (Cetacea: Mysticeti) and a reinterpretation of '*Mauicetus*' *lophocephalus*  
10 Marples, 1956: transitional baleen whales from the upper Oligocene of New Zealand.  
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## ABSTRACT

1  
2 The early evolution of toothless baleen whales (Chaemysticeti) remains elusive  
3 despite a robust record of Eocene-Oligocene archaeocetes and toothed mysticetes.  
4 Eomysticetids, a group of archaic longirostrine and putatively toothless baleen whales  
5 fill in a crucial morphological gap between well-known toothed mysticetes and more  
6 crownward Neogene Mysticeti. A historically important but perplexing cetacean is  
7 “*Mauicetus*” *lophocephalus* (upper Oligocene South Island, New Zealand). The  
8 discovery of new skulls and skeletons of eomysticetids from the Oligocene Kokoamu  
9 Greensand and Otekaike Limestone permit a redescription and modern  
10 reinterpretation of “*Mauicetus*” *lophocephalus*, and indicating that this species may  
11 have retained adult teeth. A new genus and species, *Tokarahia kauaeroa*, is erected on  
12 the basis of a well-preserved subadult to adult skull with mandibles, tympanoperiotics,  
13 and cervical and thoracic vertebrae, ribs, sternum, and forelimbs from the Otekaike  
14 Limestone (>25.2 Ma). “*Mauicetus*” *lophocephalus* is relatively similar and  
15 recombined as *Tokarahia lophocephalus*. Phylogenetic analysis supports inclusion of  
16 *Tokarahia* within the Eomysticetidae alongside *Eomysticetus*, *Micromysticetus*,  
17 *Yamatocetus*, and *Tohoraata*, and strongly supports monophyly of Eomysticetidae.  
18 *Tokarahia* lacked extreme rostral kinesis of extant Mysticeti and primitively retained  
19 a delicate archaeocete-like posterior mandible and synovial temporomandibular joint,  
20 suggesting that *Tokarahia* was capable of at most, limited lunge feeding in contrast to  
21 extant Balaenopteridae, and utilized an alternative as-yet unspecified feeding strategy.  
22 Baleen whales-Oligocene-Cetacea-Mysticeti-Eomysticetidae

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## INTRODUCTION

1 Sometime before 1937 an unassuming fragmentary skull was collected from a  
2 limestone quarry near Milton in south Otago, South Island, New Zealand. It was  
3 formally described by University of Otago zoology Professor W.B. Benham (1937) as  
4 *Lophocephalus parki*, and thought to be a new archaeocete; it is now known to have  
5 been collected from the latest Oligocene-earliest Miocene Milburn Limestone (Willett,  
6 1946; Waitakian Stage, 25.2-21.7 Ma, Raine et al., 2012). Subsequent correspondence  
7 led Benham to realize that the genus name was preoccupied and that *Lophocephalus*  
8 *parki* was in fact an archaic baleen whale, which he later renamed *Mauicetus parki*  
9 (Benham, 1942). Additional mysticetes collected by Brian J. Marples from North  
10 Otago from the somewhat older Kokoamu Greensand (Duntroonian stage). In 1956 he  
11 named these *Mauicetus lophocephalus* (based on a partial braincase, mandible,  
12 tympanic bullae, and cervical and thoracic vertebrae), *Mauicetus waitakiensis* (based  
13 on an occipital, tympanic bullae, and cervical vertebrae) and *Mauicetus brevicollis*  
14 (based on a partial vertebral column and scapula). Recently collected material of  
15 *Mauicetus parki* demonstrates that it is Although a reasonable referral at the time  
16 owing to the incomplete knowledge of these Oligo-Miocene mysticetes, new  
17 discoveries of fossil mysticetes from the South Island of New Zealand and other  
18 continents in the past thirty years indicates that at least two of the species of  
19 *Mauicetus* described by Marples (1956) represent fossil mysticetes dramatically  
20 different from anything else known to twentieth century paleocetologists, and are not  
21 closely related to *Mauicetus parki* (Fordyce, 2005; 2006; Boessenecker and Fordyce,  
22 2014a).

23 In 2002, the strange new longirostrine toothless mysticete *Eomysticetus*  
24 *whitmorei* was described from the upper Oligocene of South Carolina, U.S.A.  
25 (Sanders and Barnes 2002b). *Eomysticetus* is characterized by a toothless palate,

1 kinetic rostrum, delicate frontals, a poorly “telescoped” skull, enormous temporal  
2 fossae, elongate and cylindrical zygomatic processes, and basilosaurid-like  
3 tympanoperiotics and postcrania (Sanders and Barnes 2002b). While these authors  
4 recognized that *Mauicetus lophocephalus* was another archaic chaemysticete and  
5 similar in some regards to *Eomysticetus*, albeit not as archaic, they considered it to not  
6 be “[included] within the clade containing *Eomysticetus whitmorei* and [*Yamatocetus*  
7 *canaliculatus*]”. Their assertion that “*Mauicetus*” *lophocephalus* is not an  
8 eomysticetid was not tested by cladistic analysis. Regardless, several features are  
9 shared between “*Mauicetus*” *lophocephalus* and *Eomysticetus*, including enormous  
10 temporal fossae, transversely narrow intertemporal region with a high sagittal crest,  
11 elongate and subcylindrical zygomatic processes, all unique features amongst  
12 Chaemysticeti (although primitively present as well in Basilosauridae and certain  
13 toothed mysticetes). In recognition of these similarities with *Eomysticetus* and  
14 concomitant differences from *Mauicetus parki*, the fragmentary “*Mauicetus*”  
15 *waitakiensis* was transferred to the newly described eomysticetid genus *Tohoraata*  
16 (Boessenecker and Fordyce, 2014a). Unfortunately, the holotype skull and scapulae of  
17 “*Mauicetus*” *lophocephalus* are missing (Fordyce, 1980:20), likely discarded by  
18 university maintenance staff not long before 1962 (J.T. Darby, personal  
19 communication to R.E. Fordyce, May 1978). However, the tympanoperiotics,  
20 mandible, and much of the postcrania remain, permitting limited reassessment of this  
21 critical but poorly understood fossil mysticete.

22       Newly discovered fossil material from the upper Oligocene Otekaike  
23 Limestone of New Zealand (Fig. 1, 2) including a spectacularly preserved and nearly  
24 complete skull with mandibles, tympanoperiotics, and partial postcranial skeleton  
25 (cervical and thoracic vertebrae, ribs, sternum, scapulae, humeri, radius, ulnae) share

1 near identical tympanoperiotic morphology with “*Mauicetus*” *lophocephalus*, and  
2 critically share similar skull morphology with published eomysticetids and  
3 “*Mauicetus*” *lophocephalus*. The skull and skeleton of this new fossil mysticete is  
4 remarkable in its transitional morphology between toothed Mysticeti and Neogene  
5 crown Mysticeti (=Balaenomorpha), serving as an exemplar for comparison between  
6 the two. Another partial skull and skeleton is tentatively referred to “*Mauicetus*”  
7 *lophocephalus*, and notably includes an isolated tooth differing in morphology from  
8 all other cetaceans and indicates that eomysticetids may have primitively retained  
9 non-functional adult teeth (out of convention, “toothed mysticete” hereafter refers to  
10 stem Mysticetes not including eomysticetids). The aim of this study is to report the  
11 new morphological details preserved in this new genus and species of archaic  
12 mysticete and other similar specimens (Fig. 3), provide a new description through  
13 which “*Mauicetus*” *lophocephalus* may be reinterpreted in light of recent advances in  
14 paleocetology, and establish a phylogenetic context for these distinctive fossil  
15 cetaceans through cladistic analysis.

16

## 17 MATERIALS AND METHODS

18 *Preparation, Anatomical Description, and Illustration:* Fossil material in OU  
19 collections was mechanically prepared with pneumatic air scribes. Fine preparation  
20 was performed under a Zeiss binocular microscope. Anatomical terminology follows  
21 Mead and Fordyce (2009), Oishi and Hasegawa (1995) and Ekdale et al. (2011).  
22 Tympanoperiotic orientation follows Mead and Fordyce (2009) using anatomical  
23 structures (e.g. anterior process, posterior process, lateral tuberosity) to dictate  
24 orientation of tympanoperiotics when in isolation from the skull (in contrast to  
25 orientation *in situ*) to facilitate comparisons between taxa.

1 *Osteohistology*: Histologic sections were taken from rib fragments of OU 22235  
2 (*Tokarahia kauaeroa* holotype) and OU 22081 (*Tokarahia* sp., cf. *T. lophocephalus*).  
3 Sections were embedded in epoxy and thin sections were prepared by University of  
4 Otago Petrology Technician B. Pooley. Photomicrographs were captured under non-  
5 polarized light.

6 *Cladistic Methodology*: A cladistic analysis was executed in order to assess the  
7 phylogenetic relationships of *Tokarahia* spp. in addition to the previously described  
8 *Tohoraata raekohao*. This analysis includes 74 terminal taxa (Archaeoceti, n=3;  
9 Odontoceti, n=2, Mysticeti, n=69; 12 extant mysticetes and one extant odontocete)  
10 and a total of 363 morphological characters including cranial (n=251; 104 characters  
11 for the tympanoperiotic complex), mandibular (n=27), dental (n=15), postcranial  
12 (n=46), and soft tissue characters (n=24). Character inclusion began with the matrix  
13 of Marx (2011) and included 101 characters modified from Fitzgerald (2010), 142  
14 characters modified from Fordyce and Marx (2013), and 68 additional newly defined  
15 characters. No character complexes in particular were favoured and an exhaustive  
16 approach towards character selection was taken with an emphasis on identifying  
17 correlated characters and characters applicable toward relationships of stem Mysticeti.  
18 Six nominal eomysticetids were included: *Eomysticetus whitmorei*, *Micromysticetus*  
19 *rothauseni*, *Yamatocetus canaliculatus*, *Tohoraata* spp. (as a single terminal taxon),  
20 *Tokarahia kauaeroa*, and *Tokarahia lophocephalus*. While the two species of  
21 *Tohoraata* were combined into a single terminal taxon in order to permit coding of the  
22 skull morphology of *Tohoraata raekohao* and the vertebral morphology of *Tohoraata*  
23 *waitakiensis*, the two species of *Tokarahia* were considered to be complete enough to  
24 code separately. Although the skull of *Tokarahia lophocephalus* is lost, features  
25 which could be confidently interpreted from published photographs were coded for,

1 and supplementary codings were included from *Tokarahia* sp., cf. *T. lophocephalus*  
2 (OU 22081). Outgroups include basilosaurid archaeocetes (*Dorudon*, *Zygorhiza*;  
3 *Basilosaurus cetoides* and *Basilosaurus isis* were combined into a single terminal  
4 taxon) and extinct odontocetes (*Simocetus*, *Waipatia*). Cladistic analysis was executed  
5 in TNT 1.1 (Goloboff et al., 2008) using the “new technology” search option.  
6 Separate analyses were conducted under equal weights and implied weighting  
7 (constant K=3). Analyses included 10,000 random addition sequences and tree  
8 bisection-reconnection branch swapping saving 10 trees per replicate. Each analysis  
9 (equal weighting and implied weighting) are reported as strict consensus trees with  
10 branch support (reported as GC frequency values) based on symmetric resampling  
11 with 2000 replicates. Synapomorphies listed in the text are confined to nodes  
12 immediately adjacent to Eomysticetidae; a full list of synapomorphies is included in  
13 the appendix.

14 Institutional Abbreviations: **OM**, Otago Museum, Dunedin, New Zealand; **OU**,  
15 Geology Museum, University of Otago, Dunedin, New Zealand.

16

## 17 GEOLOGIC BACKGROUND

18 All eomysticetid material reported herein was collected from the Kokoamu Greensand  
19 (upper Whaingaroan-Duntroonian) or the lower part of the overlying Maerewhenua  
20 Member of the Otekaike Limestone (Duntroonian; Fig. 1). The Kokoamu Greensand  
21 consists of fossiliferous, massively bedded, heavily bioturbated calcareous and  
22 glauconite rich quartz sand, and measures only 3-4 meters thick at Kokoamu Cliffs  
23 (Fig. 1D), but thickens to approximately 8 meters to the north at Hakataramea quarry  
24 (Fig. 1F); it is at least 6-7 meters thick at Island Cliff (Fig. 1E; Gage, 1957; Gottfried  
25 and Fordyce, 2001; Gottfried et al., 2012). At Kokoamu Cliffs and Hakataramea

1 quarry (and many other localities throughout the Waitaki Valley region, e.g. The  
2 Earthquakes) the Kokoamu Greensand overlies the Lower Oligocene (lower  
3 Whaingaroan) Earthquakes Marl (Gage, 1957; Gottfried et al., 2012); the Kokoamu-  
4 Earthquakes contact is an extensively bioturbated disconformity known as the  
5 Marshall Unconformity. Both the Earthquakes Marl and Kokoamu Greensand yield  
6 ostracods and foraminifera indicating transition zone to offshore deposition below 100  
7 m water depth (Ayress 1993). The lower part of the Kokoamu Greensand contains a  
8 sparse macroinvertebrate assemblage; a diffuse shell bed rich in brachiopods and the  
9 bivalve *Lentipecten* is developed further up section and historically marks the base of  
10 the Duntroonian stage (Hornibook, 1966). Above this bed glauconite and quartz  
11 becomes less abundant, grading into the more calcareous Maerewhenua Member of  
12 the Otekaike Limestone. The lower part of the Otekaike is conspicuously more  
13 glauconitic (i.e. with coarser glaucony) than the upper part of the section. These  
14 transitional strata low in the Otekaike Limestone include microfossils indicating  
15 somewhat shallower transition zone deposition (Ayress, 1993). Macroinvertebrates  
16 are mostly sparse, but occasionally occur within thin concentrations within the  
17 Otekaike Limestone, and the lithology grades up into continuously less glauconitic  
18 white-yellow bioclastic calcarenite. Ostracods from the upper parts of the Otekaike  
19 Limestone indicate inner shelf deposition under 50 m water depth (Ayress, 1993),  
20 although the rarity of mm to dm scale bedding suggests infrequent traction currents  
21 and deposition below storm weather wave base.

22         Specimens collected from Kokoamu Bluff include the holotype of *Tokarahia*  
23 *lophocephalus* (fossil record number I40/f0027), and OU 21975 (Fossil record  
24 number J40/f0229). Judging from Marples' field photos, the holotype of *Tokarahia*  
25 *lophocephalus* was collected from a fallen block of Kokoamu Greensand; abundant

1 brachiopods and valves of *Lentipecten hochstetteri* in adhering matrix and in  
2 published photographs of the type specimen during excavation (Marples, 1956: plate  
3 1) indicate it was deposited in the brachiopod-*Lentipecten* rich shell bed that, at the  
4 type section of the Duntroonian at Landon Creek, marks the base of the Duntroonian  
5 stage (Hornibrook, 1966). OU 21975 was collected from a fallen block of Kokoamu  
6 Greensand, also from the brachiopod-*Lentipecten* shell bed. This indicates a basal  
7 Duntroonian age for these two specimens (approximately 27.3-26 Ma). Although  
8 stating that all specimens were collected in the vicinity of Duntroon, Marples (1956)  
9 did not specify an exact locality for OM GL 443 (=OM c.78.2 in old catalog);  
10 adhering glauconitic grains indicate it was likely collected from the Kokoamu  
11 Greensand or lowermost Otekaike Limestone. A lower Duntroonian age for OM GL  
12 443 is probable (27.3-25.2 Ma; Raine et al., 2012), but an upper Whaingaroan age is  
13 possible.

14 OU 22235 was collected from the lower Otekaike Limestone at Island Cliff  
15 (Fig. 1C, 2) from a glauconitic sandy limestone in the transition between the richly  
16 glauconitic Kokoamu Greensand and the glauconite-poor upper parts of the Otekaike  
17 Limestone (Fossil record number I41/f0183). From <100 meters along the outcrop, a  
18 large excavation yielded an associated dentition and vertebral column of the extinct  
19 giant shark *Carcharocles angustidens* (Gottfried and Fordyce, 2001; =*Carcharodon*  
20 of some workers), the large lampriform moon fish *Megalampris keyesi* (Gottfried et  
21 al., 2006), and a dalpiazinid dolphin. From this excavation an  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope ratio  
22 of  $0.708138 \pm 12$  was acquired from a scallop shell from a laterally extensive  
23 *Lentipecten* pavement, reported as 26.0 Ma by Gottfried and Fordyce (2001).  
24 However, updates to the Sr curve include the nearby value of .708139 which  
25 corresponds to an age of 25.2 Ma (McArthur et al., 2012), indicating that the

1 *Lentipecten* pavement locally approximates the Duntroonian-Waitakian boundary  
2 (25.2 Ma; Raine et al., 2012). This *Lentipecten* pavement occurs less than one meter  
3 above the stratum from which OU 22235 was collected, indicating an uppermost  
4 Duntroonian age for OU 22235 (approximately 26-25.2 Ma). Foraminifera and  
5 ostracods reported from the *Carcharocles angustidens* horizon included Duntroonian  
6 indicators and a possible *Globoquadrina dehiscens* (Gottfried and Fordyce, 2001), a  
7 Waitakian indicator, suggesting an uppermost Duntroonian to lowermost Waitakian  
8 age. However, reexamination by R.E. Fordyce indicates this specimen was incorrectly  
9 identified, and thus all existing data are consistent with a Duntroonian age assignment.

10 OU 22081 was collected from the active quarry floor at Hakataramea quarry in  
11 South Canterbury within the lower, glauconitic part of the Maerewhenua Member of  
12 the Otekaike Limestone (fossil record number I40/f0392). This specimen was  
13 collected 6-7 meters above the basal Duntroonian brachiopod-*Lentipecten* shellbed  
14 and approximately 6-8 meters below the stratigraphically lowest occurrences of  
15 Waitakian foraminifera, indicating a Duntroonian age. Furthermore, OU 22081 was  
16 collected from 2-3 meters below the holotype specimen of the billfish  
17 *Aglyptorhynchus hakataramea*, which yielded a Duntroonian foraminiferal  
18 assemblage (Gottfried et al., 2012). An upper Duntroonian age is likely for OU 22081  
19 (approximately 26-25 Ma).

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21 SYSTEMATIC PALAEOLOGY

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23 CETACEA Brisson, 1872

24 MYSTICETI Gray, 1864

25 CHAEOMYSTICETI Mitchell, 1989

1 Family EOMYSTICETIDAE Sanders and Barnes 2002b

2 *Emended Diagnosis:* Medium-sized (1-2 meter condylobasal length) archaic  
3 mysticetes differing from all other Mysticeti in possessing extremely elongate nasals  
4 (>65% bizygomatic width), zygomatic processes that are longitudinally twisted with  
5 dorsolaterally facing lateral surface, supramastoid crest that does not extend anterior  
6 to posterior margin of temporal fossa, secondary squamosal fossa, an  
7 anteroposteriorly more elongate and narrow intertemporal region with a well-  
8 developed sagittal crest, and a periotic with a low and discontinuous superior process  
9 with anterior and posterior apices. Eomysticetids differ from toothed mysticetes in  
10 lacking large emergent teeth and possessing a more extremely elongate rostrum and  
11 kinetic maxilla. Eomysticetids differ from all other Chaeomysticeti in retaining  
12 akinetic and rigid nasals and premaxillae, a dorsoventrally shallow palatal keel,  
13 occipital shield far posterior to postorbital process of the frontal, large and  
14 anteroposteriorly elongate temporal fossae, unfused and short posterior processes of  
15 the tympanoperiotic, highest point of skull formed by the nuchal crest and not the  
16 anterior apex of the occipital shield, anteroposteriorly thickened paroccipital  
17 processes, anteroposteriorly oriented zygomatic processes, axis without vertebral  
18 canal, anteroposteriorly elongate cervical series, and an elongate humerus.  
19 Eomysticetids further differ from balaenids and neobalaenids in lacking rostral  
20 arching and primitively retaining unfused cervical vertebrae and an olecranon process  
21 of the ulna, and from Balaenopteridae, Cetotheriidae, Eschrichtiidae, and “cetotheres”  
22 *sensu lato* in primitively retaining a concave glenoid fossa.  
23 *Type species:* *Eomysticetus whitmorei*.  
24 *Included genera:* *Eomysticetus*, *Micromysticetus*, *Tohoraata*, *Tokarahia*, and  
25 *Yamatocetus*.

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*TOKARAHIA* new genus

*Etymology:* After Tokarahi township, located near Island Cliff, North Otago, the type locality of *Tokarahia kauaeroa* n. sp., meaning large (or panoramic) rock, referring to a mesa-like geographic feature. From the Māori toka (rock) plus rahi (large).

*Pronunciation:* To-kah-rah-hi-ah, with *o* as in English “toe”, *a* as in “far”, and *i* as in “we”.

*Type Species:* *Tokarahia kauaeroa* n. sp.

*Included Species:* *Tokarahia kauaeroa* n. sp., *Tokarahia lophocephalus* Marples, 1956

*Diagnosis of Genus:* A large eomysticetid differing from all other eomysticetids in possessing elongate, dorsoventrally tapering zygomatic processes that are medially bowed with a concave lateral margin, an elongate diamond-shaped posterior bullar facet lacking longitudinal striations, and a transverse crest on the dorsal surface of the periotic between the posterodorsal angle and the posterior internal acoustic meatus.

With the exception of *Tohoraata raekohao*, *Tokarahia* differs from all other eomysticetids in exhibiting numerous foramina in the supraorbital process of the frontal, an oval-shaped incisural flange closely appressed to the anteroventral part of the pars cochlearis, a prominent dorsal tubercle between the stylomastoid fossa and apertures for the cochlear and vestibular aqueducts, a triangular anterior process in medial view with a posteriorly placed anterodorsal angle, a concave anterodorsal margin between the anteroventral and anterodorsal angles, an internal acoustic meatus that is anteriorly transversely pinched, a posterodorsal angle that is more acute and approximately 90° or smaller, and lacking a posterior bullar facet that is “folded” into

1 two facets by a hingeline and additionally lacking longitudinal striations on the  
2 posterior bullar facet. *Tokarahia* differs from *Tohoraata* in exhibiting medial and  
3 lateral lobes of the tympanic bulla of equivalent width, possessing a transversely  
4 narrower tympanic bulla, a longer posterior process of the periotic and shorter anterior  
5 process, and a more deeply excavated suprameatal fossa.

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8 *TOKARAHIA KAUAEROA* new species

9 *Etymology*: Kauaeroa, meaning long jaw (referring to the elongate, delicate mandibles  
10 and rostrum of the holotype), from the Māori kauae (jaw) and roa (long).

11 *Pronunciation*: Kau-ae-roa, with *au* as in English “how”, *ae* as in “I”, *o* as in “toe”,  
12 and *a* as in “far”.

13 *Diagnosis of Species*: A species of large eomysticetid differing from all other  
14 eomysticetids except *Eomysticetus whitmorei* in possessing a deeply incised median  
15 furrow of the tympanic bulla in dorsal view, and from all eomysticetids in exhibiting a  
16 pars cochlearis that is anterodorsally excavated and deeper posterodorsally.

17 *Holotype*: OU 22235, partial skeleton including partial cranium, left and right  
18 tympanoperiotics, mandibles, cervical and thoracic vertebrae, ribs, sternum, scapula,  
19 humeri, radii, and ulnae. Specimen recovered from field ventral-up and remaining in  
20 field jacket with dorsal surface completely prepared, with part of postcranial skeleton  
21 removed and prepared in three dimensions. Cast also deposited in Museum of New  
22 Zealand Te Papa Tongarewa.

23 *Type Locality and Stratigraphic Context*: OU 22235 was collected by R.E. Fordyce, A.  
24 Grebneff, B.V.N. Black, G.B. McMurtrie, G. Curline, and C.M. Jenkins, January 10-  
25 February 9 1994, from massive glauconitic limestone facies (grainstone according to

1 the Dunham classification scheme for carbonate rocks) of the lower Maerewhenua  
2 Member of the Otekaike Limestone from a north-facing hill top at Island Cliff,  
3 Awamoko Valley near Tokarahi, 12 km south-southwest of Duntroon, North Otago,  
4 New Zealand (Figs. 1-2). New Zealand Map Series 260 grid reference I41 (1984)  
5 256811, near latitude 44° 58' S, longitude 170° 59' E. Fossil record number I41/f0183  
6 (New Zealand fossil record file, Geological Society of New Zealand). An upper  
7 Duntroonian age is likely for OU 22235 (approximately 26-25.2 Ma; see Geologic  
8 Background).

9 *Tentatively referred specimen:* OU 21975, isolated right periotic, identified as  
10 *Tokarahia* sp., cf. *T. kauaeroa*. OU 21975 was collected by R.E. Fordyce August 12,  
11 1987, from the diffuse brachiopod-*Lentipecten* shell bed in a fallen block of upper  
12 Kokoamu Greensand along the eastern end of Kokoamu Cliffs a few meters north of  
13 the cliff face, 4.5 km southeast of Duntroon, North Otago, New Zealand (Fig. 1). New  
14 Zealand Map Series 260 grid reference J40 (1984) 309(5) 901(5), near latitude 44° 52'  
15 S, longitude 170° 44' E. Fossil record number J40/f0229 (New Zealand fossil record  
16 file, Geological Society of New Zealand). The brachiopod-*Lentipecten* shell bed at the  
17 type Duntroonian locality at Landon Creek marks the base of the Duntroonian Stage  
18 (27.3-25.2 Ma). Therefore, this specimen is lower Duntroonian (approximately 27.3-  
19 26 Ma).

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## 22 **Description**

23 *Premaxilla:* The left premaxilla is nearly complete (Fig. 4, Table 1). The anterior  
24 one-third of the premaxilla is dorsally flattened and slightly transversely wider than  
25 the posterior two-thirds. In the region of the narial fossa, the premaxilla becomes

1 transversely constricted where it is medially excavated by the fossa. Adjacent to the  
2 narial fossa, the premaxilla is raised and forms a transversely rounded crest;  
3 posteriorly it widens and becomes evenly transversely convex. The premaxilla-  
4 maxilla suture is open and unfused along its entire length; the sharp lateral edge of the  
5 premaxilla articulates within a longitudinal groove on the dorsomedial surface of the  
6 maxilla. The elongate, gradually tapering posterior end of the premaxilla articulates  
7 with and is underlain by an anteroposteriorly elongate anteromedial prong of the  
8 frontal. The fronto-premaxillary suture is closed; where the posterior end of the left  
9 premaxilla is missing, parallel longitudinal sutural ridges and grooves are present on  
10 the frontal. The posterior end of the premaxilla terminates 5 cm anterior to the  
11 posterior end of the nasals. Together with the nasals, the premaxillae share a  
12 posteriorly directed V-shaped suture with the frontals.

13 *Maxilla:* The maxillae are incomplete (Fig. 4, Table 1), and the right maxilla is  
14 almost completely missing whereas much of the anterior part of the left maxilla is  
15 present. The shape of the lateral margin of the maxilla is approximated by the dorsal  
16 edge of the left mandible, to which it nearly comes into contact; the mandible  
17 suggests a nearly straight but faintly laterally convex profile of the rostral margin, as  
18 in the more completely preserved eomysticetid *Yamatocetus canaliculatus*. The  
19 visible portion of the maxilla is dorsally flat and smooth; medially it rises towards a  
20 laterally sloping surface adjacent to a longitudinal medial ridge. Medial to this ridge is  
21 the unfused premaxilla-maxilla suture. Anteriorly, the maxilla and premaxilla are  
22 splayed apart slightly, suggesting a greater degree of flexibility than the comparably  
23 tight (and ankylosed) premaxilla-frontal suture. Posteriorly, no obvious articular  
24 surface for the maxilla on the frontal is present. Ventral details are not exposed.

1 *Nasal*: The nasal is very long (90% of postorbital width) and rectangular in dorsal  
2 view (Fig. 4, Table 1); the anterior tip is damaged, but dorsally flat. Posteromedially  
3 opening foramina with longitudinal sulci are present on the posterior half of the nasal.  
4 The posterior third of the nasal is transversely arched, forming the middle portion of a  
5 transverse arching of the median rostral elements (nasal, premaxilla). Each nasal  
6 terminates along a posteriorly-directed V-shaped suture, and extends approximately  
7 7cm behind the posterior tips of the premaxillae. The nasofrontal suture is similar to  
8 the fronto-premaxillary suture, a horizontal planar and ankylosed suture with parallel,  
9 longitudinal ridges and grooves exposed on the frontal where the nasal is missing.

10 *Frontal*: The frontals are incompletely preserved, and the anterior margins of the  
11 supraorbital processes are incomplete (Fig. 4, Table 1). Medially, the supraorbital  
12 process of the frontal is anteroposteriorly narrower than the lateral part; it widens  
13 laterally toward the orbital margin. The posterior margin of the supraorbital process is  
14 concave. An anteroposteriorly elongate anteromedial prong of the frontal is present,  
15 and bears many longitudinal ridges and grooves for the articulation of the nasal and  
16 premaxilla. Medially, the dorsal surface of the frontal bears many anteriorly to  
17 anterolaterally directed radially arranged foramina up to 3 mm in diameter; foramina  
18 close to the midline are vertical and lack sulci. Unlike *Tohoraata raekohao* (OU  
19 22178), OU 22235 exhibits these foramina posterior to the orbitotemporal crest. The  
20 orbitotemporal crest is low, relatively straight, and transversely oriented; laterally the  
21 crest diverges from the posterolaterally directed posterior margin of the frontal. The  
22 orbital margin of the supraorbital process is shallowly dorsally arched in the  
23 anteroposterior plane.

24 The median frontal suture is partially open as a longitudinal median groove;  
25 two bilaterally symmetrical and anteriorly diverging fissures occur on either side of

1 the median frontal suture and extend posteriorly into the frontoparietal suture. The  
2 frontal slopes gradually laterally from the midline; posterior to the orbitotemporal  
3 crest, the frontal is more acutely arched transversely, grading smoothly into the low  
4 sagittal crest of the parietal. The frontoparietal suture is V-shaped, with the suture  
5 originating at the anteromedial edge of the temporal fossa and converging posteriorly.

6 *Parietal:* The parietal is exposed in the posterior interorbital region and the  
7 anterolateral wall of the braincase (Fig. 4, Table 1). The sagittal crest is low but sharp,  
8 and bisected by an unfused median parietal suture; it rises posteriorly to meet the apex  
9 of the occipital shield and dorsally raised above the frontals, giving the dorsal margin  
10 of the intertemporal region a concave profile. The lateral surface of the parietal is  
11 obscured in dorsal view by the laterally overhanging nuchal crest. The anterior part of  
12 the occipital is broken away, exposing the longitudinal ridges and troughs of the  
13 unfused occipital-parietal suture. An interparietal is not evident.

14 *Occipital:* The occipital shield is triangular in dorsal view with a slightly  
15 anterolaterally concave lateral margin (Fig. 4, Table 1). The occipital shield is  
16 transversely concave and deeply concave anteriorly where the subvertical nuchal  
17 crests converge. A high external occipital crest is present and continues posteriorly  
18 almost all the way to the foramen magnum. Most of the supraoccipital is  
19 subhorizontal, in contrast with the more steeply ascending supraoccipital of  
20 *Tohoraata raekohao* and *Tohoraata waitakiensis*. In lateral view, the nuchal crest is  
21 dorsally elevated above the apex of the occipital shield. The exoccipital and  
22 basioccipital are still embedded in matrix and obscured by postcrania.

23 *Squamosal:* Both squamosals are in burial position and disarticulated from the  
24 occipital complex; the left squamosal is close to life position, and the right squamosal  
25 is anteriorly and medially shifted (Fig. 4, Table 1). Ventral surfaces are not exposed.

1 The zygomatic process is elongate and transversely and dorsoventrally tapers towards  
2 its apex. In dorsal view, the zygomatic process is twisted longitudinally so that the  
3 lateral surface faces dorsolaterally, and is also bowed medially so that the medial  
4 margin is convex and the lateral margin is concave. In transverse cross-section, the  
5 zygomatic process is broadly rounded. The medial surface of the zygomatic process  
6 bears a longitudinal groove, as in most other New Zealand Eomysticetidae; it is  
7 unclear whether this feature is anatomically natural or a consequence of bioerosion,  
8 perhaps owing to a naturally weak or porous region of bone. The supramastoid is  
9 posterodorsally directed shelf that does not extend onto the base of the zygomatic  
10 process. The posterior meatal crest is developed as an elongate low ridge that is  
11 obliquely oriented and extends dorsally onto the dorsolateral surface of the squamosal;  
12 it occupies about 75% of the dorsoventral thickness of the zygomatic process. The  
13 anterior meatal crest delineates the ventral margin of the shallow, triangular  
14 sternomastoid fossa.

15 *Periotic*: Both periotics are preserved (Figs. 5-8, Table 2). The periotic is relatively  
16 gracile and similar to *Eomysticetus*, with elongate anterior and posterior processes and  
17 a relatively small hemispherical pars cochlearis that is not dorsally elongated. The  
18 ventral surface of the pars cochlearis is smoothly convex, and lacks a prominent  
19 anteromedial corner in ventral view. Posteriorly the fenestra rotunda opens within a  
20 small fossa; in posterior view it is teardrop-shaped with a dorsally oriented apex  
21 continuous with a minute sulcus extending dorsally to the aperture for the cochlear  
22 aqueduct. The pars cochlearis is dorsoventrally deeper posteriorly at the level of the  
23 fenestra ovalis, and becomes shallower anteriorly; anteriorly the dorsal surface is  
24 obliquely oriented and anterodorsally facing. Shallow, discontinuous, and subparallel  
25 ridges define the indistinct promontorial grooves.

1           The internal acoustic meatus is encircled by a low rim that rises posteriorly,  
2 and is highest posterolaterally so that in medial view, the lateral surface of the internal  
3 wall of the internal acoustic meatus is visible (Fig. 5). This posterolateral prominence  
4 is triangular in medial view, and in anterior view, extends dorsomedially; similarly,  
5 the foramina within the internal acoustic meatus are also dorsomedially oriented so  
6 that they are not visible in dorsal view. The internal acoustic meatus is teardrop-  
7 shaped and transversely narrows anteriorly to a V-shaped slit, while being widest  
8 posteriorly. The spiral cribriform tract and foramen singulare are separated by a low  
9 crest that is about as high as the crista transversa; both crests are recessed  
10 approximately 5 mm into the meatus. The foramen singulare is the smallest foramen  
11 within the meatus; the spiral cribriform tract and dorsal opening of the facial canal are  
12 of similar size, and both are somewhat transversely compressed and oval. The  
13 aperture for the cochlear aqueduct is small, circular, and positioned medially on the  
14 dorsal face of the pars cochlearis, but is not aligned with the spiral cribriform tract and  
15 facial canal as in some Cetotheriidae. The aperture for the vestibular aqueduct is  
16 encircled by a low, sharp ridge of bone; both the peripheral ridge and aperture are  
17 recessed within a common fossa.

18           Anterior to the fenestra ovalis, an oval incisural flange (Boessenecker and  
19 Fordyce, 2014) is closely appressed to the anterolateral base of the pars cochlearis  
20 (Fig. 5a); it is separated from the pars cochlearis by a finely incised, minute sulcus; an  
21 additional sulcus defines the lateral margin of the incisural flange at the base of the  
22 lateral tuberosity and malleolar fossa. The sulcus on the lateral side of this flange  
23 extends anteriorly where it joins the foramen leading to the anterointernal sulcus; the  
24 anterointernal sulcus is anteroposteriorly oriented and extends to the anteroventral  
25 angle. Aside from this sulcus, there is no distinct origin for the tensor tympani

1 insertion; the rest of the medial surface of the anterior process is flat. The anterior  
2 process is transversely compressed and bears a sharp anterior keel; in medial view the  
3 process is nearly triangular except for the triangular anterodorsal angle. The  
4 anteroventral angle is the anteriormost point of the anterior process, while the  
5 anterodorsal angle is positioned midway between the tip of the anterior process and  
6 the pars cochlearis. The anterior margin of the anterior process slopes anteroventrally  
7 from the anterodorsal angle to the anteroventral angle, and is anteriorly concave as in  
8 *Tohoraata raekohao* and *Waharoa ruwhenua*. The ventral margin of the anterior  
9 process is slightly convex, and bears an elongate, triangular anterior bullar facet for  
10 the articulation of the accessory ossicle. In transverse cross-section, the anterior  
11 process is triangular and tapers dorsally. Anterior to the lateral tuberosity, the lateral  
12 surface of the anterior process is somewhat convex.

13         The lateral tuberosity is triangular in ventral view, projects laterally and is  
14 anteroposteriorly compressed and sharp at its apex; posteriorly, a well-defined  
15 rectangular facet for the articulation with the anterior face of the spiny process of the  
16 squamosal is present. The distinct and subtriangular malleolar fossa is situated on the  
17 posteromedial part of the lateral tuberosity, being positioned medial to its apex rather  
18 than posterior to it as in *Basilosauridae*. A shallow pit is present on the lateral surface  
19 of the periotic, adjacent to the lateral tuberosity; a very shallow transversely oriented  
20 anteroexternal sulcus extends dorsally from this pit. However, a more deeply incised  
21 sulcus and fissure is formed within the dorsal half of the shallow furrow, emanating  
22 from a small foramen; this deeply incised sulcus forms a deep notch in the superior  
23 process and terminates at the anterolateral portion of the suprameatal fossa. It is  
24 unclear whether one – or both – of these structures is homologous to the  
25 anteroexternal sulcus. The ventral opening of the facial canal is small with a

1 transversely narrow, V-shaped opening; it opens slightly further anteriorly than the  
2 larger, oval fenestra ovalis. The facial canal opens posteriorly into a shallow facial  
3 sulcus that extends posteriorly to the level of the stapedial muscle fossa, where it  
4 curves ventrally towards the facial crest. The stapedial muscle fossa is deeply concave  
5 and has a somewhat rugose, pitted surface. It is defined medially by the short caudal  
6 tympanic process, which lacks a posterior shelf-like crest. The caudal tympanic  
7 process is oriented posteromedially.

8         The posterior process is relatively long (about 150% of pars cochlearis length).  
9 The posterior bullar facet is large, diamond shaped, and tapers proximally and distally.  
10 With the exception of a few faint longitudinal grooves posterolaterally, the posterior  
11 bullar facet is smooth and transversely convex. The posterior process dorsally  
12 cylindrical and separated from the medial and lateral edges of the posterior bullar  
13 facet by deep longitudinal grooves. The posterodorsal angle is shaped as a blunt  
14 corner, approximately forming a 90° angle between its dorsal and posterior margins.  
15 At the level of the internal acoustic meatus, the dorsal margin of the superior process  
16 is concave and formed as a saddle between the posterior apex of the superior process  
17 (=posterodorsal angle) and the anterior apex (=anterodorsal angle). A deep  
18 suprameatal fossa is developed, and floored by bone with a porous, woven texture.  
19 The posterior part of the lateral face of the periotic is slightly convex and bears  
20 numerous minute pores. The posteroexternal foramen is slit-like and opens into a  
21 dorsoventrally oriented groove positioned posterolateral to the posterodorsal angle.

22         The tentatively referred specimen OU 21975 shares with *Tokarahia kauaeroa*,  
23 *Tokarahia lophocephalus*, and *Tokarahia* sp., cf. *T. lophocephalus* a diamond-shaped  
24 posterior bullar facet and a posterodorsal corner nearly forming a 90\* angle (Fig. 8D,  
25 16, Table 2). OU 21975 shares with *Tokarahia kauaeroa*, to the exclusion of all other

1 eomysticetids, a pars cochlearis that is anterodorsally excavated so that the pars  
2 cochlearis increases in height posteriorly. In general, this periotic is more massive  
3 than the *Tokarahia kauaeroa* holotype (OU 22235) and rugose with a slightly higher  
4 and deeper superior process and suprameatal fossa (respectively). The shorter anterior  
5 process is less acutely pointed in medial view with a less concave anterior margin.  
6 Unlike other *Tokarahia* spp., a large tubercle with vertical striations is developed on  
7 the dorsal margin of the fenestra rotunda; however, a dorsally extending sulcus is  
8 present as in *Tokarahia kauaeroa* and *Tokarahia* sp., cf. *T. lophocephalus* (OU  
9 22081). The prominence on the posterolateral margin of the internal acoustic meatus  
10 is more extremely elevated than in other *Tokarahia* spp., particularly in comparison  
11 with the *Tokarahia lophocephalus* holotype periotic. Although shared with *Tokarahia*  
12 sp., cf. *T. lophocephalus* (OU 22081), a small dorsal tubercle is present between the  
13 apertures for the cochlear and vestibular aqueducts, unlike the *Tokarahia kauaeroa*  
14 holotype (OU 22235). In comparison with the *Tokarahia kauaeroa* holotype (OU  
15 22235), the endocranial opening of the facial canal is more circular and the crista  
16 transversa is less recessed into the internal acoustic meatus, and significantly less  
17 recessed than in *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081). It further differs  
18 from OU 22081 in lacking a superficial bridge of bone that dorsally roofs over the  
19 internal acoustic meatus. Similar to the *Tokarahia kauaeroa* holotype (OU 22235) but  
20 unlike *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081) and the *Tokarahia*  
21 *lophocephalus* holotype, the fenestra rotunda and aperture for the cochlear aqueduct  
22 are very closely positioned. The caudal tympanic process is intermediate in  
23 posteromedial divergence between *Tokarahia kauaeroa* (OU 22235) and *Tokarahia*  
24 sp., cf. *T. lophocephalus* (OU 22081). The pit on the lateral surface immediately  
25 dorsal to the lateral tuberosity is more deeply excavated than in the *Tokarahia*

1 *kauaeroa* holotype (OU 22235), but is similar to *Tokarahia* sp., cf. *T. lophocephalus*  
2 (OU 22081); similarly, a trough-like anteroexternal sulcus is present as in OU 22081  
3 but unlike OU 22235.

4 *Tympanic Bulla*: The tympanic bulla is relatively large and elongate with well-  
5 differentiated medial and lateral lobes; in ventral and dorsal view the bulla has a  
6 cordate outline, tapering anteriorly and widest posteriorly (Fig. 9-11, Table 3). The  
7 involucrum is relatively large, dorsoventrally deepest posteriorly and is shallows  
8 anteriorly. In dorsal aspect, the involucrum abruptly narrows anteriorly where it is  
9 formed as a transversely narrow sharp ridge. At the midpoint of the bulla, faint  
10 transverse creases are present on the involucrum. On the ventromedial surface of the  
11 involucrum, an elongate oval facet with rough surface texture is present; this would  
12 have lain close to the medial edge of the basioccipital crest in life. The dorsomedial  
13 surface of the involucrum is generally smooth but becomes rough ventromedial to the  
14 involucral ridge (Oishi and Hasegawa 1995). The involucral ridge separates smooth  
15 bone inferred to mark the peribullary sinus dorsally from roughened bone embedded  
16 in soft tissues ventrally. The involucral ridge expands posteriorly into the  
17 aforementioned oval facet, and is then posteromedially contiguous with the transverse  
18 crest on the posterior margin of the medial lobe. In medial view, the posterior margin  
19 of the medial lobe bears a slight posteroventral corner formed by the transverse crest,  
20 but it is positioned on an otherwise broadly rounded margin, unlike the angular  
21 margin in Basilosauridae. In posterior view, this transverse crest is ventromedially  
22 oriented. The median furrow forms a well-defined notch in dorsal view. The lateral  
23 lobe extends somewhat further posterior than the medial lobe, and further ventrally, so  
24 that it is visible in medial view below the medial lobe.

1           The inner posterior pedicle is formed as a large tubercle; lateral to the pedicle  
2 is a deeply incised, V-shaped elliptical foramen. The conical process is low and  
3 slightly dorsoventrally thickened. The outer posterior pedicle is a low and  
4 anteroposteriorly short (~7mm long) ridge. The ventral side of the conical process  
5 bears a shallowly incised tympanic sulcus; radiating striae emanate from the sulcus.  
6 The sigmoid process is oval in medial view and separated from the conical process by  
7 a deeply incised sigmoid fissure; the fissure is dorsally vertical and curves  
8 anteroventrally to form a horizontal cleft. The malleolar ridge is low and convex and  
9 separated from the sigmoid process by a shallow furrow. Anterior to the malleus, a  
10 well-developed sulcus for the chorda tympani arises from the anterior process along  
11 and traverses the medial edge of the outer lip. Anteriorly this sulcus passes onto the  
12 dorsal surface, defining a medial lamina of the outer lip that is posteriorly directed  
13 and tongue-like, perhaps articulating with the accessory ossicle as in *Odontoceti*. The  
14 tympanic cavity exhibits a transversely narrow opening that widens anteriorly toward  
15 the oval, anteromedially-oriented musculotubal canal. Internal to the lateral furrow, a  
16 sharp internal ridge is present at about the same position as the low transverse ridge  
17 on the floor of the tympanic cavity; these ridges divide the tympanic cavity into  
18 anterior and posterior compartments.

19           The posterior process of the tympanic bulla is subtriangular in medial view; it  
20 bears an acute anterior apex where it attached to the inner posterior pedicle (Fig. 11).  
21 In medial view, the posterior process is fan-shaped with concave anterodorsal and  
22 anteroventral margins. Posteriorly the process is dorsoventrally expanded and bears a  
23 dorsal spur adjacent to the facet for the periotic. The facet is transversely concave and  
24 bears longitudinal sulci. Anterior to the dorsal spur, a transversely thin crest descends  
25 from the spur to the anterior apex of the posterior process of the tympanic bulla.

1 When articulated, the anterior part of the posterior process extends anteriorly to the  
2 level of the fossa incudis. Furthermore, when the periotic and bulla are placed in  
3 articulation, the orientation of the two elements is distinctly different from that of  
4 archaeocete and toothed mysticetes. When the articulated tympanoperiotic is oriented  
5 with respect to the tympanic bulla, the dorsal surface of the periotic faces  
6 dorsomedially. Because the lateral surface of the periotic articulates along a vertical  
7 butt joint in archaic mysticetes, this configuration implies that the tympanic bulla of  
8 *Tokarahia* is somewhat rotated with respect to archaeocetes and toothed mysticetes,  
9 so that the lateral surface of the outer lip would face ventrolaterally, intermediate  
10 between the non-rotated bulla of archaeocetes (and toothed mysticetes) and the  
11 dorsomedially rotated bulla of crown mysticetes (Bouetel and Muizon, 2006).

12 *Mandible:* Both mandibles are preserved; the left mandible is present in life position  
13 and tightly articulated with the lateral margin of the damaged left maxilla, whereas the  
14 posterior end of the right mandible remains in approximate life position but it is  
15 flipped around 180 degrees (Fig. 4, Table 4). In dorsal view, the mandible is slightly  
16 bowed laterally but not as strongly curved as extant Balaenopteridae; it lacks a  
17 posteriorly recurved section, and is evenly curved along its length. Anteriorly the  
18 mandible is transversely narrow, but at mid-length the body is transversely thick and  
19 nearly cylindrical in cross-section. A sharp ventral crest is present only along the  
20 anterior 30 cm of the mandible, and the rest of the mandible has a broadly rounded  
21 ventral margin in cross section. The dorsal edge of the mandible is sharp along the  
22 entire length of the body but bears a well-developed alveolar groove approximately 1-  
23 1.5 cm in width. Several parallel and anteriorly directed foramina with associated  
24 sulci up to 10 cm long and 3mm wide open within the groove.

1           A longitudinal furrow lies on the dorsolateral margin of the body, laterally  
2 adjacent to the alveolar groove. Within this furrow, 6 mental foramina open into  
3 anteriorly directed sulci up to 5 cm long and 5-8mm wide. The anterior tip of the  
4 mandible lies about  $\frac{3}{4}$  from the ventral margin. The anterior margin of the mandible is  
5 sharply triangular, but not acutely spear-shaped as in OU 22044 and OU 12918. The  
6 anterodorsal part of the anterior tip of the mandible bears a longitudinal groove with  
7 three (possibly four) anteriorly directed foramina. The anteriormost foramen is largest  
8 (approximately 5 mm wide), and positioned ventrally just dorsal to the anterior apex  
9 of the mandible, and each foramen posterior to this is successively smaller and higher  
10 on the anterodorsal margin. Posteriorly, the lateral surface of the mandible becomes  
11 flattened leading toward the region of the coronoid process. The coronoid process has  
12 an anteroposteriorly broad base and is broadly triangular in lateral view; the apex is  
13 damaged so it is unclear whether the apex was triangular or broadly rounded as in  
14 *Yamatocetus*; in *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081), the coronoid  
15 process is broadly rounded. The mandibular condyle and angular process are not  
16 preserved.

17 *Atlas*: The atlas is large, robust, and anteroposteriorly thick; only the posterior side is  
18 exposed (Fig. 4, Table 5). The neural canal is wide dorsally and narrows ventrally, but  
19 is bilobate as in "*Mauicetus*" *lophocephalus*. The neural arch is dorsoventrally  
20 flattened, evenly dorsally convex, and lies far anteriorly with a posterolaterally  
21 directed lamina. Anteriorly the lamina is perforated by a 1 cm wide, transverse  
22 foramen. The transverse processes are damaged, but appear to have been robust and  
23 transversely short and not perforated by a vertebral arterial canal. The ventral margin of  
24 the atlas is truncated as in *Tohoraata waitakiensis*. The vertebral epiphyses of the  
25 atlas are fused.

1 *Axis*: Because the axis is exposed on its side (in lateral view) and obscured by other  
2 bones, few details of its morphology are evident (Fig. 4, Table 6). The neural spine is  
3 high, slightly posterodorsally inclined, and rectangular in lateral view. A small  
4 postzygapophysis extends posteriorly from the neural arch; ventral to this the arch is  
5 posteriorly excavated where the pedicle is anteroposteriorly narrower than the lamina  
6 and spine. The vertebral epiphyses appear to be fused.

7 *C3-C7*: All four mid-cervicals are present, but only C3 can be confidently identified  
8 because it remains in articulation with the axis; the others are too incomplete to be  
9 identified to position, but one is identified as ?C4 (Fig. 4). The body of these  
10 vertebrae is round and near circular, and slightly wider than deep. All exhibit a  
11 pointed ventral margin, fused epiphyses which lack notochordal pits, and ventrally  
12 positioned ventrolaterally projecting transverse processes. In ?C4 the transverse  
13 processes are oriented more transversely than ventrolaterally. The pedicles are  
14 subrectangular in lateral view, platelike, dorsolaterally oriented, and exhibit  
15 dorsoventrally compressed postzygopophyses; between the body and the  
16 postzygapophysis, the posterior margin of the pedicle is concave. The neural arch is  
17 triangular, giving the neural canal a wide suboval shape with a triangular dorsal  
18 margin, unlike *Tokarahia lophocephalus*. One cervical vertebra possesses dorsally  
19 positioned and platelike transverse processes contiguous with the pedicles, identifying  
20 it as C7 (Fig. 4, Table 7).

21 *Thoracic Vertebrae*: Nine thoracic vertebrae are preserved (Fig. 4, 12), and the T1  
22 remains in articulation with C7 (Fig. 4). Aside from having an anteroposteriorly  
23 thicker body than the C7, no morphological details are available. Four isolated  
24 thoracic vertebrae are preserved, and four thoracic vertebrae are preserved in  
25 articulation in a block in association with 11 ribs and the radius (Fig. 13A). The

1 thoracic vertebrae exhibit an anteroposteriorly more elongate body, approximately as  
2 long as transversely wide. The pedicles are subvertically oriented, leading toward  
3 anterodorsally positioned knob-like transverse processes. The neural foramen is small  
4 and oval-shaped with a triangular dorsal margin. Tall, transversely narrow,  
5 rectangular, and posterodorsally inclined neural spines are preserved in the articulated  
6 thoracic vertebrae. The vertebral epiphyses of the thoracics are unfused and missing  
7 from the isolated thoracic vertebrae, and present but incompletely fused in the  
8 articulated vertebrae.

9 *Ribs*: Parts of 17 ribs are preserved, both left and right (Fig. 13A, F-G). The  
10 anteriormost ribs have dorsoventrally expanded and anteroposteriorly flattened  
11 proximal portions with dorsally prominent but flattened tubercles. Smaller, posteriorly  
12 inclined secondary tubercles lie slightly distal. The head is missing from these  
13 anterior ribs. The tubercle is elevated far above the broken head. Distally, the anterior  
14 ribs are transversely expanded and anteroposteriorly flattened, with flat (not concave)  
15 posterior surfaces. The posterior ribs have a cylindrical distal portion, and are more  
16 strongly curved in the proximal 1/3 than the anterior ribs. The proximal primary  
17 tubercles are smaller but more closely to the head, whereas the secondary tubercles  
18 are larger than in the anterior ribs. The neck is smaller and the head is indistinct, and  
19 the proximal end is less anteroposteriorly flattened and dorsoventrally expanded than  
20 the anterior ribs.

21 *Sternum*: The sternum is well-preserved and relatively small, and missing its posterior  
22 extremity (Fig. 4, Table 8). It appears to be a single element, as there are no articular  
23 surfaces for other sternal bodies, similar to OU 22044 and OU 22081. The sternum is  
24 approximately triangular and dorsoventrally flattened; it bears a pair of anterolaterally  
25 directed, dorsoventrally flattened semicircular processes for articulation with a single

1 pair of ribs. The anterior and posterolateral margins of the sternum are concave; the  
2 posterior process of the sternum may have been longer, but is broken.

3 *Scapula*: Both left and right scapulae are large and well-preserved (Fig. 14A-B, F,  
4 Table 9). The distal end of the scapula is relatively small in comparison to the  
5 anteroposteriorly broad proximal blade. The vertebral border of the scapula is evenly  
6 curved and dorsally convex. The anterior and posterior ends of the scapula are evenly  
7 curved, without pointed apices. Immediately dorsal to the acromion, the supraspinous  
8 region is not distinctly concave and is developed as a convex region between the spine  
9 and anterior margin, which are nearly contiguous. The acromion is well developed as  
10 a transversely flattened, tongue-shaped, anteriorly directed process that is slightly  
11 longer than dorsoventrally deep. Ventrally, the supraspinous fossa is developed as a  
12 concave trough on the basal, medial surface of the acromion, forming a longitudinal  
13 trough between the acromion and anterior border. The acromion is positioned slightly  
14 dorsal to the glenoid fossa. The glenoid fossa is directed slightly posteroventrally; a  
15 coracoid process is not developed.

16 *Humerus*: The right humerus is missing its proximal end, while the left humerus is  
17 nearly complete and missing the deltopectoral crest; the humeral head is disarticulated  
18 (Fig. 14C-H, Table 9). The humerus has basilosaurid-like proportions, and is  
19 approximately twice as long as the width of the capitulum. The capitulum is  
20 posterodorsally directed, convex, and transversely compressed. The deltopectoral  
21 crest is damaged, but appears to have been transversely compressed and present along  
22 the proximal 2/3 of the humerus. The lateral surface is somewhat flattened, while the  
23 medial surface bears a somewhat rugose prominence near the proximal end of the  
24 diaphysis as in *Yamatocetus*. Distally the medial surface is flat and the lateral surface  
25 is more convex. The distal epiphyseal sutures are closed and nearly obliterated. The

1 distal end bears two distinct fat facets for the radius and ulna that meet at an angle,  
2 unlike *Basilosauridae*. The radial facet is nearly twice as long as the ulnar facet. The  
3 posterior margin of the humerus is straight

4 *Radius*: The left radius is preserved in a large block in association with articulated  
5 thoracic vertebrae and ribs (Fig. 13A, Table 9). The distal epiphyseal suture is closed,  
6 and the proximal end is damaged. The distal half of the radius is anteroposteriorly  
7 broader and transversely flat in comparison to the more cylindrical proximal end. The  
8 radius is slightly bowed anteriorly. In cross section the radius transversely tapers  
9 anteriorly. The distal articular surface is posteroventrally oriented. The interosseus  
10 crest appears to be present and sharp, but damaged.

11 *Ulna*: The right ulna is nearly complete but lacks only the distal epiphysis and the  
12 proximal half of the left ulna is preserved (Fig. 14F, I-N, Table 9). The olecranon is  
13 hatchet-shaped, posterodorsally directed, with a posteroventrally positioned apex. The  
14 articular surface for the humerus is dorsally facing and oval-shaped and  
15 anterodorsally directed; it does not extend onto the olecranon process, but the anterior  
16 surface of the olecranon would have braced the humerus and limited extension of the  
17 humero-antebrachial. The shaft of the ulna narrows just distally to the olecranon  
18 process, and the distal  $\frac{3}{4}$  of the shaft is rectangular and transversely narrows slightly.  
19 No obvious interosseous crest is present. The distal epiphyseal surface bears a  
20 punctate texture.

21 *Rib histology*: The sectioned rib has a lenticular cross-section with a large and narrow  
22 marrow cavity (Fig. 15B, D); the sectioned rib fragment is relatively straight and  
23 similar in dimensions and curvature to the distal  $\frac{2}{3}$  shaft of other preserved ribs. The  
24 marrow cavity is not open but consists of a network of large vascular channels with  
25 trabecular struts that form a cancellous zone. The marrow cavity separates two zones

1 of cortical bone: one on the strongly convex side of the bone, and the second on the  
2 flat side of the bone. The cortex on the convex side is nearly completely remodeled  
3 and composed of dense haversian tissue formed by overlapping secondary osteons  
4 (125-180  $\mu\text{m}$  in diameter) and fragments of secondary osteons (Fig. 15D). Vascular  
5 channels in secondary osteons are generally smaller towards the outer cortex ( $>20 \mu\text{m}$ )  
6 and increase in diameter towards the inner cortex (up to 90  $\mu\text{m}$ ). The cortex-marrow  
7 transition zone consists entirely of former vascular channels deeply infilled by  
8 endosteal lamellae, becoming increasingly remodeled and overprinted by secondary  
9 osteons towards the inner cortex. Thickness of endosteal lamellae decreases toward  
10 the marrow cavity; in the marrow cavity, trabeculae consist of endosteal lamellae  
11 parallel with margins of the vascular channels. In contrast, vascular channels on the  
12 opposite side of the marrow cavity along the flat side of the rib lack thickened  
13 endosteal laminae. The cortex of the flat side of the rib consists of less densely  
14 remodeled bone with numerous secondary osteons that do not often overlap; few  
15 fragments of secondary osteons exist. Non-remodeled lamellar bone parallel with the  
16 flat margin of the rib is present as background tissue. Lamellar bone lacks obvious  
17 primary osteons. Periosteum is absent from the convex margin, and secondary osteons  
18 are truncated at the margin, indicative of resorption; in contrast, ghosts of periosteal  
19 lamellae are visible amongst an opaque diagenetically altered zone (300-400  $\mu\text{m}$ )  
20 along the outer margin of the flat side of the cross section. The altered zone consists  
21 of a densely criss-crossing network of tubular structures under 6  $\mu\text{m}$  in diameter.  
22 Secondary osteons from the flat side generally have larger diameter vascular channels  
23 than the convex side. This pattern is overall suggestive of growth by addition of  
24 lamellae on the flat side with partial remodeling, formation of large vascular channels

1 and then subsequent filling by the addition of endosteal lamellae, intense remodeling,  
2 and eventual resorption along the convex side.

3

4 *TOKARAHIA LOPHOCEPHALUS* comb. nov.

5 *Diagnosis:* A species of *Tokarahia* differing from *Tokarahia kauaeroa* in possessing  
6 zygomatic processes that do not extend anterior to the occipital shield, more  
7 extremely “telescoped” nasal and premaxillae that penetrate the posterior half of the  
8 frontal, a tympanic bulla without a median furrow incised as a notch in the posterior  
9 margin of the tympanic bulla in dorsal view, more widely posteromedially divergent  
10 caudal tympanic process, a more deeply excavated pit on the lateral side of the  
11 anterior process, a fenestra rotunda that is more widely separated from the aperture for  
12 the cochlear aqueduct, lacking a finely sculptured tubercle immediately dorsal to the  
13 fenestra rotunda, and exhibiting a small vertebrarterial canal in the seventh cervical  
14 vertebra.

15 *Holotype:* OM GL 412 (=old catalog number OM c.62.1), partial skeleton including  
16 partial cranium (now lost; Fig. 17), partial right periotic, left and right tympanic bullae,  
17 fragmentary left mandible, seven cervical vertebrae, four thoracic vertebrae, and two  
18 scapulae (both lost). Marples (1956) reported that two scapulae were preserved, and  
19 Fordyce (1979, 1980) mentioned that one scapula was lost alongside the skull, but  
20 that another scapula bearing the old number OM c.62.4 belonged to the holotype  
21 individual. Two scapulae bearing the old number OM c.62.4 exist: one is the right  
22 scapula of “*Mauicetus*” *brevicollis* figured by Marples (1956: figure 6, mistakenly  
23 identified as a left scapula) embedded in a plaster block with the medial surface  
24 exposed, and the other is a less well preserved left scapula prepared in three  
25 dimensions and missing much of the dorsal margin. Matrix adhering to the left

1 scapula is glauconite-poor calcareous limestone matrix similar to the right scapula of  
2 “*Mauicetus*” *brevicollis*, and is otherwise a mirror image of the right scapula,  
3 indicating both belong to “*Mauicetus*” *brevicollis*. Both scapulae bearing the old OM  
4 c.62.4 number, and here interpreted as the holotype scapulae of “*Mauicetus*”  
5 *brevicollis*, bear a well-developed coracoid process, differing from the scapula of  
6 *Tokarahia kauaeroa*.

7 *Referred specimen*: OM GL 443 (=old catalog number OM c.78.2), isolated partial  
8 right tympanic bulla. This specimen formerly bore the old catalog number OM c.62.3,  
9 the same number as the holotype specimen of “*Mauicetus*” *brevicollis*. However,  
10 Fordyce (1980) indicated that Marples (1956) never mentioned this specimen, and re-  
11 labeled the specimen as OM c.78.2; the current catalog number is OM GL 443.

12 Furthermore, the holotype specimen of “*Mauicetus*” *brevicollis* is not an eomysticetid  
13 based on the triangular transverse processes of the atlas, greatly enlarged transverse  
14 processes of the axis with vertebrarterial canals, and anteroposteriorly flattened C3-  
15 C7, differing markedly from *Tohoraata waitakiensis*, *Tokarahia lophocephalus*, and  
16 *Tokarahia kaeuaroa* as well as *Eomysticetus* and *Yamatocetus*. Given the lack of any  
17 connection to “*Mauicetus*” *brevicollis*, this specimen is separated and referred to  
18 *Tokarahia lophocephalus*, from which it is indistinguishable (see below).

19 *Tentatively referred specimen*: OU 22081, partial skeleton including fragmentary  
20 rostrum and braincase, left and right periotics and tympanic bullae, incomplete  
21 mandibles, partial atlas and axis, partial third and fourth cervical vertebrae, and  
22 sternum, identified as *Tokarahia* sp., cf. *T. lophocephalus*. OU 22081 was collected  
23 from about 6-7 meters above the basal Duntroonian brachiopod-*Lentipecten* shellbed  
24 and about 6-8 meters below the lowermost occurrence of Waitakian foraminifera at  
25 Hakataramea Quarry, and approximately 2-3 meters below a horizon yielding

1 Duntroonian foraminifera (= *Aglyptorhynchus hakataramea* type horizon), indicating a  
2 Duntroonian age for OU 22081, probably upper Duntroonian (approximately 26-25.2  
3 *Type Locality and Stratigraphic Context:* The holotype skeleton of *Tokarahia*  
4 *lophocephalus* (OM GL 412) was collected by B.J. Marples in 1942 from massive  
5 glauconitic sandstone of the Kokoamu Greensand, Kokoamu Cliffs, 3 km east  
6 southeast of Duntroon, North Otago, South Island, New Zealand (Fig. 1). Grid  
7 Reference NZMS 260 I40:29890, near latitude 44° 52' S, longitude 170° 42' E. Fossil  
8 record number I40/f0027 (New Zealand fossil record file, Geological Society of New  
9 Zealand). The holotype was probably collected from the diffuse brachiopod-  
10 *Lentipecten* shell bed in the upper part of the unit which at the nearby type  
11 Duntroonian section at Landon Creek marks the base of the Duntroonian stage,  
12 suggesting a lower Duntroonian age (approximately 27.3-26 Ma).

13

#### 14 **Description**

15 *Cranium:* To reduce redundancy with the description of *Tokarahia kauaeroa*, this  
16 description emphasizes features that differ between the two or features of OU 22081  
17 that differ from or are not preserved for OM GL 412. The holotype cranium of  
18 *Tokarahia lophocephalus* (OM GL 412) is lost, but morphological details present in  
19 the low resolution halftone plate published by Marples (1956: Plate 1; reproduced in  
20 Fig. 17) permit a limited redescription. The skull includes a fragmentary proximal  
21 rostrum, complete frontals, squamosals, and braincase. The nasal is elongate with  
22 parallel lateral margins and a squared-off posterior end. The premaxilla appears to  
23 terminate along the lateral side of the nasal as a posteriorly tapering wedge. The  
24 maxilla is almost completely missing. The supraorbital process of the frontal is  
25 transversely wider than anteroposteriorly long. The nasals extend posteriorly to the

1 anteroposterior midpoint of the frontal, nearly to the orbitotemporal crest, further  
2 posterior than in *Tokarahia kauaeroa*. The orbitotemporal crest is positioned near the  
3 posterior margin of the frontal. Medially, the crest is anteriorly retracted from the  
4 posterior margin. An elongate, posteriorly directed postorbital process is present. The  
5 temporal fossa is longer than wide and oval with a concave medial margin. The  
6 intertemporal region is longer than wide and bears a high sagittal crest; the position of  
7 the frontoparietal suture is uncertain. The apex of the supraoccipital shield is  
8 positioned slightly anterior to the posterior margin of the temporal fossa. The  
9 zygomatic process of the squamosal is elongate, cylindrical, anteroposteriorly directed,  
10 and medially bowed so that the lateral and medial margins are concave and convex  
11 (respectively). The supramastoid crest appears to have been absent on the zygomatic  
12 process. The zygomatic process is longitudinally twisted so that the lateral surface  
13 faces dorsolaterally. The occipital shield is triangular with a strongly developed  
14 external occipital crest. The occipital condyles are proportionally small and set out on  
15 a short neck; the exoccipital is anteroposteriorly inflated and club-like as in *Tokarahia*  
16 sp., cf. *T. lophocephalus* (OU 22081). Unlike *Tohoraata*, the exoccipital faces  
17 posteromedially. The parietal-occipital suture is unfused.

18         The skull of OU 22081 is poorly preserved but includes the anterior half of the  
19 rostrum including left and right maxilla and the left premaxilla and left and right  
20 mandibles exposed in a block in near life position and isolated fragments of maxilla,  
21 premaxilla, and nasals, partial squamosal, basioccipital, exoccipital, and vomer (Figs.  
22 24-25). Bone surfaces are friable but generally pristine and in some cases bioeroded.  
23 *Premaxilla*: The anterior 50 cm of the left premaxilla is exposed and associated with  
24 the palatal portion of the rostrum, and is somewhat disarticulated and shifted laterally  
25 (Fig. 24). The ventral surface of the premaxilla is dorsoventrally shallow laterally and

1 deepens medially; a medial keel is developed anteriorly which gives the premaxilla a  
2 ventrally concave cross-section. This concave trough is evident on the anterior 12 cm  
3 of the premaxilla; two elongate parallel, linear grooves are present anteriorly; these  
4 grooves are parallel with the lateral margin of the premaxilla and are inferred to  
5 articulate with the maxilla.

6 *Maxilla*: The palatal surface of the maxilla of OU 22081 is well preserved but the  
7 lateral margins on both sides are incomplete (Fig. 24). The palatal surface is flat and  
8 lacks palatal foramina with the exception of a single bilateral pair of large anteriorly  
9 opening greater palatine foramina (4-5 mm in diameter) positioned relatively far  
10 anteriorly and medially. They are confluent with deeply entrenched sulci  
11 (approximately 240 mm long) that transversely widen slightly anteriorly and becomes  
12 diffuse 220 mm from the anterior preserved edge of the maxilla. Posterior to the  
13 greater palatine foramen on the left maxilla, two smaller foramina (1.5 mm diameter)  
14 are positioned anteroposteriorly along the medial margin and are contiguous with  
15 anteroposteriorly shorter sulci (15-20 mm in length). The pattern of palatal sulci is  
16 generally reminiscent of *Eubalaena australis* and *Aetiocetus weltoni*. The maxilla  
17 consists of delicate sheet-like dorsal and ventral laminae; no connections between  
18 these laminae are evident anteriorly, but the laminae appear to converge near the  
19 posterior portion of the preserved palate. These laminae define an apparently hollow  
20 wedge-shaped cavity that is dorsoventrally deepest anteriorly (maximum dorsoventral  
21 depth = 23 mm), and presumably forming the canal for the infraorbital maxillary soft  
22 tissues including the maxillary artery and venous sinuses (Walmsley, 1938: 142-143).  
23 This geometry perhaps explains the greater dorsoventral depth of the anterior portion  
24 of the rostrum in *Yamatocetus canaliculatus*.

1 *Nasal*: A fragment of the right nasal of OU 22081 lacks the anterior and posterior  
2 ends. It is rectangular, elongate, transversely narrow, and dorsally flat (Fig. 25B,  
3 Table 1) like the holotype. The dorsolateral surface bears numerous articular grooves  
4 and ridges for the articulation of the medial edge of the premaxilla, which appears to  
5 have dorsally obscured and ankylosed with the lateral portion of the nasal.

6 *Vomer*: The partial vomer of OU 22081 includes most of the ventral portion but lacks  
7 the dorsolateral edges; in dorsal aspect it is elongate and lanceolate (Fig. 25E, Table  
8 1). It exhibits a shallow mesorostral groove, and is transversely convex with a low  
9 ventral crest. Posteriorly the vomer narrows and terminates to a transversely acute,  
10 conical point; approximately 70 mm from the posterior tip there is a slight transverse  
11 swelling. The mesorostral groove ends just anterior to this swelling. Elongate,  
12 dorsolaterally facing facets extend from this swelling to the posterior tip, perhaps  
13 representing the broken bases of the vomerine wings.

14 *Parietal*: OU 22081 includes a fragment of the parietal from the intertemporal region  
15 (Fig. 25A). The parietal is laterally concave and transversely narrow, suggesting a  
16 sharp sagittal crest as in *Tokarahia kauaeroa*. Posteriorly, a pair of matrix-filled  
17 foramina is present with irregular cross sections (approximately 20 mm maximum  
18 diameter), corresponding to the olfactory nerve tract (Godfrey et al. 2013). Anteriorly,  
19 a poorly preserved ethmoid recess is present.

20 *Squamosal*: The right squamosal of OU 22081 is well-preserved and bears an elongate  
21 zygomatic process and a short anteroventrally inclined, anteroposteriorly flattened  
22 postglenoid process (Fig. 25C-D, Table 1). The dorsally arched zygomatic process is  
23 delicate, anterolaterally directed, tapers anteriorly, and curves ventrally at its anterior  
24 apex. Dorsomedially, a deep longitudinal groove is developed along the length of the  
25 zygomatic; it is irregularly excavated in places and appears to be taphonomically

1 enlarged. In cross section the zygomatic process is subcylindrical with an evenly  
2 convex dorsal margin; the supramastoid crest does not extend onto the zygomatic  
3 process or past the posterior margin of the temporal fossa. The zygomatic process is  
4 longitudinally twisted so that the lateral face is dorsolaterally directed; the ventral  
5 surface is flattened. The zygomatic process medially arched so that the lateral and  
6 medial margins are concave and convex (respectively) in dorsal view. Medially within  
7 the shallow squamosal fossa, a minute, subtriangular trough-like secondary squamosal  
8 fossa (*sensu* Sanders and Barnes 2002a, 2002b) is present. The oval glenoid fossa is  
9 concave and bears distinct distinct margins. It is positioned medially on the squamosal,  
10 and laterally the postglenoid process and lateral part of the squamosal descend  
11 ventrally below the level of the glenoid fossa. Medially, the falciform process  
12 descends ventromedially towards the periotic fossa A large pit is present on the  
13 posterolateral margin of the periotic fossa for the articulation of the lateral surface of  
14 the periotic. The subtemporal crest is dorsoventrally thick and anteriorly concave.

15 *Occipital:* The occipital includes the ventral portions of the exoccipitals and  
16 basioccipital (Fig. 25C-D, Table 1). The basioccipital is roughly tabular in ventral  
17 view and damaged anteriorly; it widens posteriorly due to the enlarged and  
18 ventrolaterally flaring basioccipital crests. The ventral surface of the basioccipital is  
19 anteriorly flat and posteriorly concave between the basioccipital crests. A deep  
20 dorsomedially oriented groove is present posterolateral to the basioccipital crest,  
21 which ventrally forms the jugular notch and separates the basioccipital from the  
22 paroccipital process. The hypoglossal foramen opens laterally within the jugular notch.  
23 The paroccipital process of the exoccipital is anteroposteriorly thick and inflated with  
24 a convex posterior margin that faces posterodorsally. The posterior margin of the  
25 exoccipital is posterolaterally oriented. The occipital condyles are large and convex,

1 and distinguished ventrally by a concave pedicle; the condyles are separated  
2 ventromedially by a deep intercondylar notch.

3 *Periotic*: The holotype periotic includes only the pars cochlearis medial to the  
4 fenestra ovalis (Fig. 18, Table 2). The fenestra rotunda is large and oval-shaped, and  
5 not confluent with a dorsally ascending sulcus as in *Tokarahia kauaeroa*. The  
6 posterodorsal margin of the fenestra ovalis is smooth and flat, unlike the convex and  
7 finely sculptured tubercle present in *Tokarahia kauaeroa*, *Tokarahia* sp. (OU 21975),  
8 and *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081). The internal acoustic meatus is  
9 funnel-shaped and anterolaterally directed; the distinction between the spiral  
10 cribriform tract and the foramen singulare is not preserved. Posteriorly, the lateral rim  
11 of the internal acoustic meatus extends slightly more dorsal than the medial rim, so  
12 that the lateral wall of the meatus is visible in medial view. The caudal tympanic  
13 process is damaged but present as a short, low ridge that is posteromedially divergent  
14 from the long axis of the pars cochlearis; it defines the medial margin of the  
15 anteroposteriorly shortened and shallow stapedial muscle fossa. The stapedial muscle  
16 fossa is finely pitted. The stylomastoid fossa is flat and smooth. The posterior edge of  
17 the caudal tympanic process is positioned closely to the fenestra rotunda, forming a  
18 narrow (3-4mm wide) shelf.

19 Both periotics of OU 22081 are well preserved, relatively large and robust,  
20 and bear elongate posterior and anterior processes and well-developed superior  
21 processes (Figs. 9F, 26-27, Table 2); they are very similar to *Tokarahia kauaeroa*  
22 with some exceptions. The caudal tympanic process is damaged but appears to have  
23 been short and posteromedially divergent as in the *Tokarahia lophocephalus* holotype.  
24 Dorsally, the internal acoustic meatus is large and pyriform, and the crista transversa  
25 is deeply recessed; the spiral cribriform tract and foramen singulare are separated by a

1 low crest deeply recessed within the meatus as opposed to the high crest in *Tokarahia*  
2 *kauaeroa* and *Tokarahia* sp., cf. *T. kauaeroa* (OU 21975). The lateral edge of the  
3 meatus is not developed into a robust triangular prominence as in *Tokarahia kauaeroa*,  
4 although a small spur is present. The aperture for the cochlear aqueduct is small and  
5 subcircular, while the aperture for the vestibular aqueduct is transversely wider and  
6 slit-like. The posterior bullar facet is more strongly diamond-shaped in ventral view,  
7 resembling the condition in *Tokarahia* sp., cf. *T. kauaeroa* (OU 21975). The anterior  
8 process is triangular and dorsoventrally deeper than *Tokarahia kauaeroa*, but shares a  
9 concave anterodorsal margin with it and *Tohoraata raekohao*. Anterior to the pars  
10 cochlearis the anterointernal sulcus is anastomosed: a dorsal branch of the sulcus  
11 splits and diverges dorsally, which splits again, and a third anteriorly placed sulcus  
12 descends ventrally and re-joins the ventral branch of the anterointernal sulcus.

13 *Tympanic Bulla*: The tympanic bulla of the holotype, OM GL 443, and OU 22081 are  
14 relatively similar to *Tokarahia kauaeroa*; the left bulla is complete and the sigmoid  
15 region of the right bulla is missing (Figs. 19-20, Table 3). The involucrum lacks an  
16 abrupt bulge on its dorsal margin as in *Tokarahia kauaeroa*. The median furrow does  
17 not form an incised notch as in *Tokarahia kauaeroa* but forms a shallow triangular  
18 furrow between the lobes in dorsal and ventral outline. The conical process is not  
19 connected to the lateral part of the sigmoid process by a horizontal crest as in  
20 *Tokarahia kauaeroa* and *Tohoraata waitakiensis*. The referred bulla OM GL 443  
21 similarly lacks the posteriorly incised median furrow of *Tokarahia kauaeroa* (Fig. 21),  
22 but is slightly anteroposteriorly longer than the holotype bulla. Owing to breakage of  
23 OM GL 443, a few additional details of the tympanic cavity are worth noting. The  
24 floor of the tympanic cavity is pitted, and posteriorly the tympanic cavity forms a  
25 blind end that wraps dorsomedially around the lateral margin of the involucrum,

1 which is developed as a rugose, laterally projecting knob. This knob is ventrally  
2 undercut by the tympanic cavity. Posteriorly, the cavity curves dorsally and narrows  
3 transversely, passing into a furrow that leads to the elliptical foramen. Both tympanic  
4 bullae of OU 22081 are well preserved (Figs. 27-28, Table 3) and nearly identical to  
5 that of the *Tokarahia lophocephalus* holotype (OM GL 412). The tympanic bulla of  
6 OU 22081 principally differs from *T. lophocephalus* in retaining a connection  
7 between the basal sigmoid process and the anterior conical process, although this  
8 horizontal lamina is delicate and raises the possibility that in *T. lophocephalus* it is  
9 damaged. The posterior process of the bulla bears a transversely concave and  
10 anteroposteriorly short facet for the posterior process of the periotic. In medial and  
11 lateral view the posterior process is sharply triangular, bearing a triangular dorsal  
12 apex and a posteroventrally directed spur. The distal surface of the posterior process is  
13 triangular and shallowly concave. As in *Tokarahia kauaeroa* (Fig. 12A, B), the bulla  
14 of OU 22081 is slightly rotated when placed in articulation with the periotic (Fig.  
15 27D), indicating that the outer lip of the bulla would have faced ventrolaterally when  
16 in articulation with the skull.

17 *Dentition.* —A single isolated partial tooth was recovered during preparation of the  
18 palate. The tooth was recovered within 5 cm of the posterior part of the left maxilla;  
19 the crown is missing and may have been damaged during earlier preparation. Despite  
20 being found near the left maxilla, many bone fragments likely representing fragments  
21 of the lateral margins of the maxillae have been separated from the skull and  
22 transposed up to 20 cm away; it is therefore not possible to identify the region in  
23 which the tooth was originally located. Furthermore, it is not possible to identify  
24 which surface is lingual or labial. The more convex margin of the tooth likely  
25 represents the mesial margin as most cetacean teeth are distally recurved. The root is

1 subtriangular in labial/lingual view. The root bears a diamond-shaped, linguo-labially  
2 flattened cross section. On the flatter surface (labial or lingual), a shallow furrow  
3 parallels the distal margin. The root is zoned in cross-section and a dense outer layer  
4 (0.7-1 mm thick) of dentine is visible surrounding a central core of dentine with  
5 parallel fibers and pores; this inner zone may reflect the remnant of a pulp cavity,  
6 which appears to have been completely filled in. This arguably does not represent a  
7 misidentified shark tooth root, because the outer surface of the root lacks pores and  
8 appears to be covered with a smooth layer of cementum. This specimen differs from  
9 all contemporaneous odontocetes in being labiolingually flattened; all  
10 contemporaneous odontocetes (*Otekaikea*, *Waipatia*, Squalodontidae, Tanaka and  
11 Fordyce, 2014; Fordyce, 1994) have tooth roots that are circular or oval in cross-  
12 section, and generally near cylindrical or conical in shape. Southern hemisphere  
13 toothed mysticetes such as mammalodontids also share tooth roots with circular cross-  
14 section and differ from the tooth of OU 22081. Lastly, isolated shark teeth associated  
15 with OU 22081 have well preserved crowns but bioeroded (or completely missing)  
16 roots, and no other odontocete elements were found, strongly suggesting that this  
17 tooth belongs to OU 22081.

18 *Mandible:* A photograph of the holotype specimen of *Tokarahia lophocephalus* in the  
19 field during excavation shows that parts of both mandibles were preserved (Fig. 17B),  
20 but only the fragmentary left mandible survives (Fig. 22). The left mandible is poorly  
21 preserved and includes only the posterior portion. It is badly crushed and  
22 dorsoventrally flattened, and few morphological details are evident. Parts of both  
23 mandibles of OU 22081 are preserved in segments, including nearly the entire  
24 anterior left and right mandibles in life position within a block of matrix, much of the  
25 posterior right mandible and a fragment of the left mandibular condyle and

1 posterodorsal margin (Figs. 24-25, Table 4). The mandible corresponds closely to that  
2 of *Tokarahia kauaeroa*, and better preserves the mandibular terminus, symphyseal  
3 groove, and mandibular foramen. Anteriorly, the dorsal and ventral margins of the  
4 mandible are parallel; the mandibular terminus is positioned at the dorsoventral  
5 midpoint and the anteriormost portion of the mandible (anterior 7.5 cm) is lanceolate  
6 rather than subrectangular. A deeply entrenched and well-preserved symphyseal  
7 groove (16 cm long) is present anteriorly on the medial surface near the ventral  
8 margin. The coronoid process is subtriangular but missing the dorsal tip; it appears to  
9 have been tongue-shaped as in *Eomysticetus* and *Yamatocetus*, with a broadly concave  
10 mandibular notch. The dorsal margin of the mandible rises somewhat gradually  
11 towards the anterior margin of the coronoid process. The mandibular foramen is  
12 greatly enlarged into a large cavity and appears to have an arcuate anterior margin.  
13 The preserved fragment of the mandibular condyle indicates it is transversely narrow  
14 and anteriorly excavated by the enlarged mandibular canal.

15 *Atlas*: The holotype atlas is large and well preserved with an incomplete neural spine  
16 and plate-like transverse processes (Fig. 23A-C, Table 4). The atlas is relatively  
17 anteroposteriorly elongate, similar to *Eomysticetus* and *Yamatocetus*. The condyloid  
18 facets are large, concave, and D-shaped (convex and flat lateral and medial margins,  
19 respectively). The articular surfaces are ventromedially separated at the midline by a  
20 shallow furrow. The neural canal is subrectangular with relatively flat dorsal, ventral,  
21 and lateral margins. The neural canal narrows slightly ventrally. No tubercles for the  
22 transverse ligaments are present between the odontoid portion and neural foramen,  
23 unlike *Tohoraata waitakiensis*. The transverse process is large, robust, rectangular in  
24 anterior view, and anteroposteriorly thick; it is positioned dorsally and measures  
25 approximately half the dorsoventral height of the anterior articular surface. The

1 ventral margin of the atlas is evenly convex (unlike the flattened ventral margin of  
2 *Tohoraata waitakiensis*) and bears a small ventral tubercle posteriorly. The neural  
3 arch is robust and dorsoventrally thick and bears a low but incomplete neural spine;  
4 large (15 mm diameter) lateral vertebral canals are present anteriorly within the  
5 lamina. The posterior articular surface is superficially damaged but flattened and  
6 robust, without sharp margins; ventral to the neural canal it is somewhat concave for  
7 the reception of the odontoid process of the axis. In lateral aspect, the anterior margin  
8 is oblique and faces somewhat anteroventrally while the posterior margin is vertical.  
9 The atlas of OU 22081 is large and robust, and missing the left ventral portion (Fig.  
10 29, Table 5); it does not differ appreciably from the holotype.

11 *Axis*: The holotype axis is mostly well preserved aside from the damaged pedicles and  
12 transverse process; the body of the axis is similarly anteroposteriorly thickened like  
13 the atlas (Fig. 23D-F, Table 5). The anterior articular surface is broad and figure-8  
14 shaped, but less medially constricted than in *Tohoraata waitakiensis*; the lateral part is  
15 flat on either side of the low odontoid process. The anterodorsal surface of the  
16 odontoid process is flat and contiguous with the dorsal surface of the body within the  
17 neural canal; a slight median ridge is developed on the dorsal surface of the body. The  
18 ventral margin is evenly convex with a well-developed median tubercle, unlike  
19 *Tohoraata waitakiensis*. The neural foramen narrows posteriorly as the posterior  
20 portion of the body – and thus the ventral margin of the neural foramen – is  
21 posteriorly elevated. The convex dorsal margin of the posterior articular surface  
22 bulges into the neural canal, giving it a ventrally concave crescent shape. The  
23 posterior articular surface is transversely narrower than its anterior counterpart, and is  
24 shallowly concave and oval with a centrally positioned slit-like notochordal pit.  
25 Lateral to the posterior articular surface is a flat to slightly concave surface on the

1 posterior surface of the anteroposteriorly flattened, subrectangular transverse process.  
2 The neural arch is robust with a triangular outline, and the anterior spine and neural  
3 spine are missing. The postzygapophyses are developed as a subtriangular sheet with  
4 a small, thickened knob at its posterior apex. The axis of OU 22081 is roughly  
5 triangular and is missing nearly the entire posterior half of the body and  
6 posteroventral part of the neural arch (Fig. 29, Table 6). It differs from the holotype in  
7 having a concave ventral margin without a hypapophysis. Otherwise, the neural spine  
8 is more completely preserved than the holotype and anteriorly exhibits an  
9 anteroventral spine with a small tubercle developed at its extremity.

10 *C3-C7*: The third through seventh cervical vertebrae are all present in the holotype,  
11 but the position of all but *C7* are speculative (Fig. 23I-N, Table 7). These vertebrae  
12 are nearly identical with those of *Tokarahia kauaeroa*. The transverse process bears a  
13 small, incompletely preserved vertebral arterial canal, similar to *Eomysticetus* and  
14 *Yamatocetus* but unlike *Tokarahia kauaeroa*. Two partial mid-cervical vertebrae of  
15 OU 22081 are identified as *C3* (Fig. 29E-F) and *C4* (Fig. 29G-H).

16 *Thoracic Vertebrae*: Parts of four thoracic vertebrae are preserved in the holotype,  
17 two of which remain in articulation (Fig. 23O). These vertebrae have  
18 anteroposteriorly thicker and circular bodies that are as nearly long as transversely  
19 wide, a dorsally positioned pedicle, and large, dorsolaterally positioned transverse  
20 processes developed as subrectangular blocky tubercles with an anterolaterally facing  
21 articular facet for the ribs. The epiphyses are fully closed but unfused with a visible  
22 suture; a notochordal pit is present on each vertebra.

23 *Sternum*: The sternum is preserved in OU 22081 and represented by a single  
24 subtriangular, dorsoventrally flattened element (Fig. 29I-J, Table 8). No distinct  
25 articular facets for any ribs are evident, as the anterolateral portion is dorsoventrally

1 flattened and tapers laterally. The sternum also thins posteriorly, and becomes  
2 transversely narrower posteriorly; the posterior end appears to be broken. The  
3 posterolateral margin of the sternum is concave. The sternum is dorsally flat  
4 longitudinally and slightly transversely concave, and the ventral surface is  
5 transversely convex. On the dorsal surface, a small median groove is present  
6 anteriorly, whereas a small foramen is present anteriorly on the ventral surface.

7 *Rib Histology:* A single rib fragment of OU 22081 was sectioned. In comparison with  
8 OU 22235, no obvious marrow cavity exists (Fig. 14A-B). Although not obvious in  
9 plain light, in crossed-polarized light nearly the entire cross-section is composed of  
10 dense haversian tissue consisting of overlapping secondary osteons (90-216  $\mu\text{m}$  in  
11 diameter) and interstitial fragments of secondary osteons. Large vascular channels are  
12 present, 20-140  $\mu\text{m}$  in diameter. In places, pristine background non-remodeled  
13 lamellar bone is preserved. Where abundant lamellar bone exists, secondary osteons  
14 are rarer and less frequently overlapping. Few obvious primary osteons are visible. No  
15 periosteum is preserved. Along one part of the bone, a fragment of an outer  
16 diagenetically altered zone appearing opaque in thin section adheres to the bone; this  
17 zone is missing from the remainder of the cross-section. This altered zone also  
18 consists of a network of opaque tubular structures under 12  $\mu\text{m}$  in diameter. Although  
19 most structure in this zone is not apparent even as vestiges, secondary osteons are  
20 clearly visible in the innermost part of this opaque zone, demonstrating that as in OU  
21 22235, it is diagenetically altered.

22 *Taphonomy:* Several episkeletozoans are present on OU 22081. Several small coiled  
23 serpulid worm tubes (up to 3 mm in diameter) are present on the parietal fragment,  
24 left mandible fragment, periotic, the posterior process of the left bulla, and on the

1 right bulla. A small (2 mm diameter) patch of bryozoans is present on the right side of  
2 the neural spine of the axis.

3 *Referral of "Mauicetus" lophocephalus and OU 22081 to Tokarahia*: This species is  
4 referable to *Tokarahia* as it shares a relatively elongate bulla with similar proportions  
5 to *Tokarahia kauaeroa*, and has medial and lateral lobes that are equally wide, unlike  
6 *Tohoraata* spp. The periotic also shares a posteromedially divergent caudal tympanic  
7 process with *T. kauaeroa*, absent in *Tohoraata* and other eomysticetids (Fig. 8).

8 Additional shared features unique to *Tokarahia* are also preserved in *Tokarahia* sp., cf.  
9 *T. lophocephalus* (see below). OU 22081 shares a similar tympanic bulla with  
10 *Tokarahia lophocephalus* and *Tokarahia kauaeroa* and aside from aforementioned  
11 minor differences, the bulla of OU 22081 is not separable from *T. lophocephalus*.

12 Furthermore, the periotic of OU 22081 exhibits a posteromedially widely divergent  
13 caudal tympanic process as in *T. lophocephalus*, deviating nearly 45° from the long  
14 axis of the periotic. OU 22081 critically preserves additional skull and periotic  
15 characters not preserved or no longer accessible in the holotype specimen of

16 *Tokarahia lophocephalus*. These additional features link the two species together,  
17 indicating the recognition of a single genus. These additional features uniting the two  
18 species of *Tokarahia* preserved in OU 22081 include a diamond-shaped posterior  
19 bullar facet, a sharp transverse crest on the posterodorsal surface of the periotic  
20 between the posterodorsal angle and the posterior pars cochlearis, and a sharp crest  
21 between the facial sulcus and stapedial muscle fossa.

22

23 PHYLOGENETIC RESULTS AND REMARKS

24

1 Cladistic analysis recovered 37 equally most parsimonious trees under equal  
2 weighting (CI: 0.364; RI: 0.804; 1406 steps; Fig. 30A) and a single most  
3 parsimonious tree under implied weighting (CI: 0.353; RI: 0.751; 120 steps; Fig. 30B).  
4 These results notably show excellently resolved relationships amongst stem Mysticeti,  
5 and represent the highest resolution in these taxa yet published; this possibly reflects  
6 the exhaustive nature of this dataset, which is the largest attempted for mysticetes to  
7 date. Resolution is much lower within crown Mysticeti (Fig. 30), although focus was  
8 placed upon characters directly relevant to stem mysticete relationships. Relationships  
9 amongst stem Mysticeti were nearly identical between the analyses under equal and  
10 implied weighting, with slightly higher bootstrap support in the latter. Most of the  
11 topological differences between the two weighting schemes occurred within crown  
12 Mysticeti, including the intrafamilial topology of the Balaenopteridae, Cetotheriidae,  
13 cetotheres *sensu lato*, and the sister taxon to Balaenopteroidea (cetotheres *sensu lato*  
14 under equal weights, Cetotheriidae under implied weights). Additionally, the early  
15 diverging cetotheriid *Joumocetus* was recovered as the next diverging lineage  
16 crownward of Balaenoidea under equal weighting (Fig. 30). Future discovery and  
17 refinement of characters relevant to crown Mysticeti may improve phylogenetic  
18 resolution in this clade.

19 *Phylogeny of Archaic Mysticeti*: The basal part of the tree including archaeocetes,  
20 Odontoceti, and stem Mysticeti is exceptionally well resolved. Very strong support  
21 for a *Basilosaurus* + *Dorudon* + Neoceti clade (to the exclusion of *Zygorhiza*;  
22 bootstrap support= 100%) and monophyly of Neoceti (bootstrap support=99% in both  
23 analyses), Odontoceti (bootstrap support= 98% under equal weights and 99% under  
24 implied weights), and a monophyletic Charleston toothed mysticete clade (ChM PV  
25 4745 + ChM PV 5720; bootstrap support=99% in both analyses) was recovered.

1 Monophyly of Mysticeti was moderately supported with the Charleston toothed  
2 mysticetes as the earliest diverging mysticete lineage (bootstrap support=58% and  
3 75%); nine synapomorphies common to both analyses supported mysticete  
4 monophyly including a steep face on the antorbital process of the maxilla separating it  
5 from the rostrum (character 18:1), posterior maxilla situated lateral to nasal (20:1), a  
6 firmly sutured premaxilla-maxilla suture with a longitudinal groove (51:1), a  
7 supraorbital process of the frontal that is medially narrow and triangular (74:1),  
8 bulbous basioccipital crest (146:1), inner posterior pedicle of bulla swollen (233:1),  
9 division between cheek tooth roots does not extend past basal edge of enamel (282:1),  
10 and lingual cingulum absent from upper cheek teeth (291:1). A more exclusive  
11 Mammalodontidae + Aetiocetidae + Chaemysticeti clade was recovered under  
12 moderate to strong support (bootstrap support=74% and 83%). Five synapomorphies  
13 common to both analyses supported this clade including premaxilla that widens  
14 anteriorly (4:1), embrasure pits absent on palate (52:1), nuchal crest elevated dorsally  
15 relative to occipital apex (111:1), ventromedial ridge of bulla low or absent (231:1),  
16 and transverse crest on posterior surface of medial lobe of bulla ventromedially  
17 inclined (250:1).

18 Monophyly of Mammalodontidae was strongly supported (bootstrap  
19 support=96% and 98%), but aetiocetid monophyly was only weakly supported;  
20 however, monophyly of *Aetiocetus* was strongly supported (bootstrap support=93%  
21 and 89%) and a more exclusive *Aetiocetus polydentatus* + *Aetiocetus weltoni* clade  
22 was moderately supported under implied weighting only (bootstrap support=53%).  
23 An Aetiocetidae + Chaemysticeti clade was moderately to strongly supported  
24 (bootstrap support =78% and 75%), and supported by six synapomorphies common to  
25 both analyses including palatal sulci and nutrient foramina present (24:1),

1 subtemporal crest well developed and anterolaterally concave in dorsal view (126:1),  
2 mandibular symphysis unsutured (255:1), mandibular body with parallel dorsal and  
3 ventral margins (259:1), symphyseal groove of mandible prominent in adults (278:1),  
4 and concave ventral margin of axis (308:1).

5 *Monophyly of Eomysticetidae*: An important concern of this analysis was to evaluate  
6 whether or not the Eomysticetidae actually constitute a monophyletic group. Previous  
7 analyses have only included two eomysticetids: *Eomysticetus* and *Micromysticetus*  
8 (Geisler and Sanders, 2003), and *Eomysticetus* and *Tokarahia lophocephalus*  
9 (Steeiman, 2007; Marx, 2011). Monophyly of a clade containing *Eomysticetus* and  
10 *Micromysticetus* (Eomysticetoidea; Geisler and Sanders, 2003) or *Eomysticetus* and  
11 *Tokarahia lophocephalus* (Steeiman, 2007; Marx, 2011) was well supported, despite  
12 the absence of the holotype skull of *Tokarahia lophocephalus* and the partial nature of  
13 the holotype skull of *Micromysticetus rothauseni*. The inclusion of six nominal  
14 eomysticetids in this analysis permits evaluation of eomysticetid monophyly. This  
15 study found moderate to strong support for the monophyly of Eomysticetidae  
16 (bootstrap support=58% under equal weighting, 76% under implied weighting; Fig.  
17 30). Seven synapomorphies common to both weighted analyses supported  
18 eomysticetid monophyly, including a frontal with anteromedial projection (77: 1),  
19 subvertical nuchal crest partially obscuring temporal wall of braincase (107:1),  
20 absence of a supramastoid crest along the entire zygomatic process or squamosal  
21 (118:2), zygomatic process of squamosal with parallel medial and lateral margins  
22 (125:1), secondary squamosal fossa developed (127:1), discontinuous superior  
23 process of periotic with anterior (=anterodorsal angle) and posterior (=posterodorsal  
24 angle) apices (161:1), and distinct ventromedial ridge developed on bulla (231:0,

1 reversal). Other synapomorphies were unique to the results from equal or implied  
2 weighting.

3 Strong to moderate support was found for more inclusive clades within  
4 Eomysticetidae including a *Tokarahia* + *Tohoraata* clade to the exclusion of Northern  
5 Hemisphere eomysticetids (bootstrap support=80% and 70%; Fig. 30). Five  
6 synapomorphies common to both weighting schemes supporting a New Zealand  
7 eomysticetid clade include an incisural flange closely appressed to the anteroventral  
8 margin of the pars cochlearis of the periotic (Character 168:1), dorsal and posterior  
9 margins of posterodorsal angle of periotic meeting at  $\leq 90^\circ$  (178:1), concave  
10 anterodorsal margin of anterior process of the periotic (179:1), anterior portion of  
11 internal acoustic meatus of the periotic pinched or roofed over by projections of the  
12 meatal rim (205:1), and a crista transversa deeply recessed into the internal acoustic  
13 meatus of the periotic (219:1).

14 Strong to moderate support was also recovered for *Tokarahia* monophyly  
15 (bootstrap support=78% and 95%; Fig. 30). *Tokarahia* monophyly was supported by  
16 three synapomorphies common to both weighting schemes: smooth posterior bullar  
17 facet of the periotic (173:0, reversal), clear separation of the stapedial muscle fossa  
18 stylomastoid fossa (198:1), and presence of a sharp transverse crest on the dorsal  
19 surface of the periotic between the posterodorsal angle and the internal acoustic  
20 meatus and separating the suprimeatal and stylomastoid fossae (206:1). A  
21 monophyletic clade of northern hemisphere Eomysticetidae (*Eomysticetus*,  
22 *Micromysticetus*, and *Yamatocetus*) was weakly supported under implied weighting  
23 only.

24 Critically, this study follows Geisler and Sanders (2003) in recognizing a clade  
25 including *Eomysticetus* and *Micromysticetus rothauseni* (Fig. 30). Earlier,

1 *Micromysticetus* had been placed in the subfamily Cetotheriopsinae by Sanders and  
2 Barnes (2002a), which they considered a subfamily of the “Cetotheriidae” (*sensu lato*,  
3 e.g. Bouetel and Muizon, 2006). The Cetotheriopsinae was subsequently erected to  
4 familial status by Geisler and Sanders (2003), who erected the new clade  
5 Eomysticetoidea to contain both the Eomysticetidae and Cetotheriopsidae. These  
6 actions overemphasized family level diversity and underemphasized the close  
7 similarity between *Eomysticetus* and *Micromysticetus*. Furthermore, Sanders and  
8 Barnes (2002a; 2002b) did not differentiate between Eomysticetidae and  
9 Cetotheriopsinae, nor did they provide any synapomorphies to diagnose the  
10 Cetotheriopsinae. Geisler and Sanders (2003) listed two potential features in their  
11 diagnosis to differentiate the Cetotheriopsidae from Eomysticetidae, including an  
12 anteroposteriorly shorter intertemporal region and zygomatic processes that do not  
13 extend anteriorly beyond the apex of the occipital shield. However, the intertemporal  
14 region is relatively short in *Tokarahia*, and when the squamosal is placed into  
15 approximate articulation with the braincase, the occipital shield extends far anteriorly,  
16 as in *Cetotheriopsis* and implied for *Micromysticetus rothauseni* (Geisler and Sanders,  
17 2003: 71). However, in *Micromysticetus rothauseni*, the zygomatic processes clearly  
18 extend somewhat anterior to the occipital shield (Sanders and Barnes, 2002a; fig. 7,  
19 10), and therefore does not differ from the condition in *Eomysticetus* and other  
20 eomysticetids. Here, *Micromysticetus* is recognized as an eomysticetid, and  
21 Cetotheriopsidae restricted to the poorly known *Cetotheriopsis lintianus*. While it is  
22 possible that *Cetotheriopsis* is also a member of this clade – which would make  
23 Eomysticetidae a junior synonym of Cetotheriopsidae – the fragmentary nature of the  
24 skull and absence of a rostrum, tympanoperiotic, and postcrania make *Cetotheriopsis*  
25 *lintianus* a poor hypodigm for a family. Furthermore, the lack of eomysticetid

1 synapomorphies precludes recognition of an eomysticetid-cetotheriopsid clade, and  
2 precludes ready diagnosis of the Cetotheriopsidae. Discovery of more-complete  
3 diagnostic cranial material of *Cetotheriopsis lintianus* would be required to declare  
4 Eomysticetidae as a junior synonym of Cetotheriopsidae.

5 *Chaeomysticete Phylogeny:* This study found strong support (bootstrap support=98%  
6 under both weighting schemes) for a clade including Eomysticetidae and all other  
7 Chaeomysticeti (Fig. 30). Chaeomysticete monophyly was supported by 19  
8 synapomorphies common to both weighting schemes including an ascending process  
9 of the maxilla wider than long or indistinct (39:1), frontal-maxilla contact loose and  
10 sutured only along ascending maxilla (44:1), premaxilla-maxilla contact unsutured  
11 (51:2), lacrimal not sutured to adjacent elements (57:1), orbit low and in line with  
12 rostrum edge or slightly above (70:1), supraorbital process of frontal similar in  
13 anteroposterior length medially and laterally (74:0, reversal), supraorbital process of  
14 frontal that is transversely wider than anteroposteriorly long (75:1), optic groove  
15 positioned in posterior 1/3 of supraorbital process of frontal (85:1),  
16 tympanosquamosal recess and pit for sigmoid process absent from squamosal (137:1),  
17 stylomastoid fossa of periotic large and occupying much of posterolateral part of pars  
18 cochlearis (217:1), dorsal margin of involucrem of bulla smooth in medial view  
19 (243:1), conical process of bulla reduced to a low ridge or absent (249:1), gingival  
20 foramina present in mandible (268:1), hypophysis absent from atlas and axis (297:1),  
21 neural canal of atlas circular or rectangular and transverse width >2/3 of dorsoventral  
22 height of canal (299:1), sternum composed of single element (317:1), deltopectoral  
23 crest positioned on proximal 1/2 of humerus (328:1), lesser tuberosity of humerus  
24 absent (329:1), distal humerus with flattened oval facets for ulna and radius (330:1).

1 A clade including all “cetotheres” *sensu lato*, Cetotheriidae, and all extant  
2 Mysticeti was very strongly supported (bootstrap support=100% in both analyses; Fig.  
3 30), equivalent in taxonomic inclusion to the Balaenomorpha of Geisler and Sanders  
4 (2003), if differing in topology. Balaenomorph monophyly was strongly supported by  
5 34 synapomorphies; examples include loss of dentition and alveolar groove (35:2), a  
6 temporal fossa wider than long (character 88:1), paroccipital process extends further  
7 posterior to occipital condyles (106:1), loss of dorsal condyloid fossae (112:1),  
8 anterior pedicle of tympanoperiotic fused (150:1), elliptical foramen of the tympanic  
9 bulla absent (223:1), and flattened medial margin of mandible (254:1); see Geisler  
10 and Sanders (2003) for a discussion of character support for this clade. New  
11 synapomorphies supporting this clade include examples such as the loss of the  
12 subtemporal crest (126:2), dorsal flattening of the nasals and premaxillae (62:1), and  
13 glenoid fossa developed as a convex surface (128:1). With a few exceptions,  
14 resolution within this clade is poor. Monophyly of several well-established family-  
15 level clades was strongly or moderately supported, including Balaenidae (bootstrap  
16 support= 98% and 93%), Balaenopteridae (bootstrap support= 69% and 79%);  
17 however, support for the monophyly of the Cetotheriidae was strongly supported  
18 under implied weighting only (bootstrap support= 71%) and support for  
19 Eschrichtiidae monophyly was weak. An Eschrichtiidae + Balaenopteridae clade  
20 (Balaenopteroidea) was also moderate to well supported (bootstrap support= 72% and  
21 88%). Resolution within Balaenopteridae was generally poor, with moderate support  
22 recovered for a *Balaenoptera musculus* + *Balaenoptera physalus* clade (bootstrap  
23 support = 50%, equal weighting only) and a *Balaenoptera acutorostrata* +  
24 *Balaenoptera bonaerensis* clade (bootstrap support= 67%, implied weighting only).

1           This study also found very strong support for monophyletic Balaenoidea under  
2 equal weighting (bootstrap support=97%), although this relationship was only weakly  
3 supported under implied weighting (Fig. 30); neobalaenid monophyly was strongly to  
4 moderately supported (bootstrap support=79% and 62%). Within Balaenidae,  
5 *Balaenella brachyrhynchus* was weakly recovered as sister to all other balaenids. Strong  
6 support under implied weighting was found for monophyly of *Balaena* (bootstrap  
7 support=80%) and a *Eubalaena* + *Balaenula* clade (bootstrap support=74%).  
8 Resolution within Cetotheriidae was higher under implied weighting, with moderate  
9 support for monophyletic *Cetotherium* (bootstrap support=50%) positioned in a  
10 poorly supported clade also including *Metopocetus*, *Vampalus*, and *Kurdalagonus*  
11 positioned sister to all herpetocetines. An exclusive herpetocetine clade including  
12 *Piscobalaena*, *Nannocetus*, and *Herpetocetus* was moderately supported under  
13 implied weights only (bootstrap support=59%). Moderate support was found for  
14 monophyly of *Herpetocetus* (bootstrap support=61% and 70%); furthermore,  
15 *Herpetocetus transatlanticus* was resolved as sister to a moderately supported clade  
16 under implied weights containing the remaining species from the North Pacific  
17 (*Herpetocetus bramblei*, *Herpetocetus morrowi*, and *Herpetocetus sendaicus*;  
18 bootstrap support=61%). A full list of synapomorphies can be seen in the Electronic  
19 Supporting Information.

20

21

## DISCUSSION

### 22 **Stratigraphic Distribution of *Tokarahia***

23 Fossils of *Tokarahia* spp. are known from the Kokoamu Greensand and the lower  
24 glauconitic part of the overlying Otekaike Limestone (Fig. 1D-F). The holotype  
25 specimen of *Tokarahia kauaeroa* was collected from a stratum higher than that of

1 *Tokarahia lophocephalus*, but the two cannot be interpreted as sharing an ancestor-  
2 descendent relationship. The referred periotic identified as *Tokarahia* sp., cf. *T.*  
3 *kauaeroa* (OU 21975) was collected from the type Duntroonian brachiopod-  
4 *Lentipecten* shell bed at Kokoamu Cliffs, as was the holotype of *T. lophocephalus*.  
5 Similarly, the tentatively referred fragmentary skull and partial skeleton of OU  
6 222081 (*Tokarahia* sp., cf. *T. lophocephalus*) was collected from a higher  
7 stratigraphic level within the lower Otekaike Limestone, from a level roughly  
8 equivalent to the type horizon of *Tokarahia kauaeroa*. The distribution of these  
9 specimens indicate that both species were preserved in the Kokoamu Greensand  
10 (lower Duntroonian) in addition to the lower Otekaike Limestone (upper  
11 Duntroonian), demonstrating that both species likely inhabited the western South  
12 Pacific during the early Late Oligocene (~27.3-25.2 Ma).

13

#### 14 **Ontogeny**

15 The ontogenetic age of *Tokarahia* specimens is difficult to ascertain. Few studies  
16 describing stem mysticetes have addressed their ontogenetic status in detail (notable  
17 exceptions being Fitzgerald 2006:2957, Fitzgerald 2020:374, and Deméré and Berta  
18 2008:313). Designating juveniles as type specimens should be avoided if possible  
19 (International Commission on Zoological Nomenclature, 1999: 73, article 69.A.4)  
20 because juveniles are known to lack the derived features attained during later  
21 ontogeny. This can lead to incorrect phylogenetic placement even when the species is  
22 known (Campione et al., 2013; Tsai and Fordyce, 2014). Ontogenetic status therefore  
23 dictates the diagnosability and phylogenetic position of fossil mysticetes. In the case  
24 of many archaic mysticetes for which ontogeny has not been investigated (e.g.  
25 *Aetiocetus cotylalveus*, *Aetiocetus polydentatus*, *Aetiocetus tomitai*, *Ashorocetus*,

1 *Chonecetus goedertorum*, *Chonecetus sookensis*, *Eomysticetus carolinensis*,  
2 *Eomysticetus whitmorei*, *Morawanacetus*, *Yamatocetus*), it is unclear whether certain  
3 key features are truly archaic or derived (e.g. large orbits, inflated braincase in  
4 Mammalodontidae and Aetiocetidae) or are plesiomorphic features exhibited by  
5 juveniles. Determining ontogenetic status from gross morphology in fossil Cetacea  
6 may be attempted by examining closure of cranial and vertebral sutures (Uhen, 2004;  
7 Walsh and Berta, 2010) in addition to tooth wear and tooth eruption (non-  
8 chaeomysticetes only), as well as the surface texture of articular surfaces (Sanders and  
9 Barnes, 2002a; Aguirre-Fernández and Fordyce, 2014). Tooth histology has also been  
10 used to determine ontogenetic age in fossil Cetacea (Uhen 2004), but this is not  
11 applicable in Chaeomysticeti.

12         Few cranial sutures of the skull are closed or obliterated. The premaxilla-nasal,  
13 nasofrontal, frontoparietal, median frontal, parietosquamosal, and parieto-occipital  
14 sutures are all closed but visible, and certain postcranial sutures remain unfused  
15 (proximal humeral epiphysis, some vertebral epiphyses) while others are closed  
16 (distal humeral and ulnar epiphyses, some vertebral epiphyses). The retention of an  
17 open, kinetic suture in most of the rostral elements in adult Chaeomysticeti (or,  
18 maxilla-premaxilla and fronto-maxilla sutures in *Tokarahia*) reduces the number of  
19 potentially useful macroscopic features for determining ontogenetic status in this  
20 group. One feature, a fully fused occipital, is not possible to assess in the holotypes of  
21 *Tokarahia kauaeroa* or *Tokarahia lophocephalus*, but is fully fused in *Tokarahia* sp.,  
22 cf. *T. lophocephalus* (OU 22081), suggesting that this specimen does not represent a  
23 very young individual as this element fuses within the first year of growth in extant  
24 balaenopterids and gray whales (Walsh and Berta, 2010).

1           Microscopic study of bone histology offers an additional tool to assess relative  
2 ontogenetic age in fossil cetaceans. Although not preserving periodic growth marks  
3 such as lines of arrested growth which permit accurate determination of absolute  
4 ontogenetic age (Woodward et al., 2013), the style of bone microstructure permits  
5 assessment of ontogenetic age at a gross level. For example, the cortices of juvenile  
6 mammal bones are typically composed of fast-growing, well-vascularized,  
7 disorganized woven bone, while old adults typically possess heavily remodeled bone  
8 consisting primarily of overlapping secondary osteons, and individuals of  
9 intermediate age will possess a partially remodeled cortex (Kerley, 1965;  
10 Huttonlocker et al., 2013; Woodward et al., 2013). These patterns, and the density of  
11 secondary osteons in a cross section can reliably determine ontogenetic age in human  
12 cadavers (Kerley, 1965). The rib section from *Tokarahia kauaeroa* (OU 22235)  
13 included some partially remodeled lamellar bone, but was dominated by remodeled  
14 haversian bone (Fig. 14D), suggestive of maturity. The retention of some partially-  
15 remodeled lamellar bone suggests that perhaps this individual was near skeletal  
16 maturity but not an old adult, mirroring the partial fusion of postcranial epiphyses.  
17 Similarly, nearly the entire sectioned rib of OU 22081 (*Tokarahia* sp., cf. *T.*  
18 *lophocephalus*) is composed of dense haversian tissue consisting of overlapping  
19 secondary osteons and interstitial fragments of secondary osteons (Fig. 14B),  
20 indicative of adult status. The absence of a marrow cavity in OU 22081 is noteworthy  
21 as it could signify osteosclerosis of ribs in *Tokarahia*; however, rib number and  
22 proximodistal position of the fragment that the thin section was taken from is  
23 unknown, and because the histology of archaeocete ribs change along the length of  
24 the bone (Buffrenil et al., 1990), a medullary cavity may have been present elsewhere  
25 in the rib of OU 22081. No ribs of the *Tokarahia lophocephalus* holotype were

1 available for histologic study, but its slightly larger size than the *Tokarahia kauaeroa*  
2 holotype suggests a somewhat older ontogenetic age.

3

#### 4 **Body Size and Skeletal Reconstruction**

5       The body size of different specimens of *Tokarahia* was initially estimated  
6 based upon skull size using both the equations provided by Lambert et al. (2010) and  
7 by Pyenson and Sponberg (2011) for stem Mysticeti. These equations utilize  
8 bizygomatic width and explain the relationship between this skull metric and skeletal  
9 length. Bizygomatic width of *Tokarahia lophocephalus* was measured from Marples  
10 (1956: Plate 1) using ImageJ and the known width of the frontals published by  
11 Marples. Body length estimated by Pyenson and Sponberg (2011) was consistently  
12 slightly lower than Lambert et al. (2010). Body length of OU 22235 was estimated at  
13 5.61 and 5.78 meters, and OU 22081 was estimated at 5.81 and 5.98 meters.  
14 *Tokarahia lophocephalus* was somewhat larger and estimated at 6.32 and 6.49 meters.  
15 In sum, these estimates suggest an approximate body length of 6 meters for adult  
16 *Tokarahia*.

17       Despite possessing an incomplete postcranial skeleton, enough postcranial  
18 features are preserved to evaluate these estimations (Fig. 3). The postcranial skeleton  
19 of *Tokarahia kauaeroa* is perhaps the most complete and well-preserved for any  
20 described archaic mysticete, despite lacking much of the vertebral column. Other  
21 described archaic mysticetes such as some Aetiocetidae and Eomysticetidae include  
22 postcrania, either possessing a nearly complete vertebral column but lacking forelimb  
23 elements (e.g. *Aetiocetus cotylalveus*, Emlong 1966), preserving incomplete  
24 postcranial skeletons that remain unpublished (e.g. *Chonecetus goedertorum* and  
25 *Aetiocetus polydentatus*, Barnes et al., 1995), or possessing postcranial skeletons of

1 similar completeness to *Tokarahia* but of fragmentary nature (e.g. *Eomysticetus*  
2 *whitmorei*, Sanders and Barnes, 2002b). The *Yamatocetus canaliculatus* holotype is  
3 notable for its well-preserved postcrania. Using this well-preserved postcranial  
4 material of OU 22235, a skeletal reconstruction of *Tokarahia* was completed, using a  
5 rib and thoracic vertebral count from *Eomysticetus whitmorei* since the total number  
6 of ribs in *Tokarahia kauaeroa* is unknown.

7         During the process of producing a skeletal reconstruction of *Tokarahia*  
8 *kauaeroa*, it became clear that both the equations of Lambert et al. (2010) and  
9 Pyenson and Sponberg (2011) likely underestimated body length. Utilizing the rib and  
10 thoracic vertebra count for *Eomysticetus whitmorei* and constraining body length to  
11 5.6-5.8 meters would result in a body with a proportionally shorter lumbocaudal  
12 section of the vertebral column than any extant mysticete. Our reconstruction favors a  
13 slightly longer body length, perhaps 6-7 meters in length for the *Tokarahia kauaeroa*  
14 type specimen, and a slightly larger size (7-8 meters) for the holotype (OM GL 412)  
15 and tentatively referred skeleton (OU 22081) of *Tokarahia lophocephalus* (Fig. 3).  
16 This range of body size is comparable to the extant dwarf minke whale of the  
17 southern hemisphere (Perrin and Brownell, 2009), although the skull is slightly  
18 absolutely longer (approximately 2.0 m in OU 22235) and much transversely  
19 narrower (0.47 m) than dwarf minke whale specimens (1.6 m condylobasal length, 0.9  
20 m bizygomatic width) of similar body length (7 meters; Arnold et al., 1987).

21

## 22 **Comparisons**

23 *Comparisons with Toothed Mysticeti:* *Tokarahia* differs from toothed mysticetes in its  
24 much larger size (except *Llanocetus*), elongate temporal fossae and intertemporal  
25 region with a concave medial margin and high sagittal crest, development of a palatal

1 keel (preserved in OU 22081), anteroposteriorly shorter supraorbital processes of the  
2 frontal, paroccipital process that extends further posterior than occipital condyles, an  
3 occipital shield that extends further anteriorly than the zygomatic processes  
4 (*Tokarahia kauaeroa* only), zygomatic processes of squamosal that lack supramastoid  
5 crests and are medially bowed, mandible with parallel dorsal and ventral margins  
6 pointed anterior margin of the bulla in ventral view, a periotic with a longer posterior  
7 process (except *Llanocetus*), and with an oval incisural flange closely appressed to the  
8 anteroventral part of the pars cochlearis.

9 *Comparisons with other Eomysticetidae: Tokarahia kauaeroa* differs from  
10 *Eomysticetus whitmorei* in exhibiting frontals with numerous dorsal foramina  
11 (equivocal in *Tokarahia lophocephalus*), having a more anteriorly thrust occipital  
12 shield (past the level of the zygomatic processes) and concomitantly shorter  
13 intertemporal region (Fig. 31), and a mandible with a dorsolateral longitudinal furrow,  
14 and seventh cervical vertebra that lacks a lateral foramen. *Tokarahia lophocephalus*  
15 differs from *Eomysticetus whitmorei* in possessing a transversely wider occipital  
16 shield (Fig. 31). Both species differ in lacking a transverse expansion at the zygomatic  
17 apex and having medially bowed zygomatics, larger and more elongate tympanic  
18 bullae with a further posteriorly extending lateral lobe, more robust and fan-like  
19 posterior processes of the bullae, and periotics with a triangular anterior process with  
20 a concave anterodorsal margin and longer and diamond-shaped posterior bullar facet  
21 that lacks striations and is not divided into two facets by a longitudinal crest (Fig. 8).  
22 The periotics of *Tokarahia* spp. further differ in lacking a subtriangular ventral outline  
23 of the pars cochlearis (Fig. 8).

24 *Tokarahia* spp. differ from *Micromysticetus rothauseni*, here recognized as an  
25 eomysticetid for the first time (cf. Sanders and Barnes, 2002a; Geisler and Sanders,

1 2003), by lacking an anterolaterally convex occipital shield, squamosal prominences,  
2 a smaller secondary squamosal fossa (Fig. 31), and a coracoid process of the scapula,  
3 and possessing medially bowed zygomatic processes, a subtriangular ventral outline  
4 of the pars cochlearis, a triangular anterior process of the periotic, and an elongate and  
5 smooth posterior bullar facet that is not divided into two facets by a longitudinal  
6 hinge-line.

7 *Tokarahia* spp. differ from *Yamatocetus canaliculatus* in their much larger  
8 size, triangular, transversely wider and more anteriorly thrust occipital shield,  
9 anteroposteriorly narrower and more delicate frontals with several supraorbital  
10 foramina, less elongate nasals (Fig. 31), and a distal humerus that is of similar width  
11 to the humeral shaft. *Tokarahia kauaeroa* also differs from *Yamatocetus* in having a  
12 narrower and straight-sided rostrum and lacking a vertebrarterial foramen in the  
13 seventh cervical vertebra.

14 *Tokarahia* spp. differ from *Tohoraata raekohao* in possessing paroccipital  
15 processes that extend posterior to the occipital condyles (Fig. 31), a periotic with a  
16 longer and diamond-shaped posterior process, a shorter and less bladelike anterior  
17 process, lacking an accessory tubercle on the lateral side of the anterior process (Fig.  
18 8), and medial and lateral lobes of the tympanic bulla of equivalent transverse width.

19 *Tokarahia kauaeroa* differs from *Tokarahia lophocephalus* in exhibiting a  
20 slightly different pattern of cranial “telescoping” (Figs. 4, 17, 31). The occipital shield  
21 is thrust further anteriorly in *T. kauaeroa*, and the nasal and premaxilla do not extend  
22 as far posteriorly as in *T. lophocephalus* where they reach the level of the posterior  
23 half of the frontal. *Tokarahia kauaeroa* bears a pars cochlearis that is dorsoventrally  
24 shallow anteriorly, a more strongly developed dorsal projection posterior to the  
25 internal acoustic meatus, a shallower pit adjacent to the lateral tuberosity, a median

1 furrow of the tympanic bulla that is deeply incised into the posterior margin in dorsal  
2 view, and a seventh cervical vertebra that appears to lack a vertebralarterial canal.  
3 *Comparisons with crown Chaemysticeti*: A myriad of archaic features differentiates  
4 *Tokarahia* from more crownward Neogene chaemysticetes. These include firmly  
5 sutured premaxilla-nasal, nasofrontal, and fronto-premaxilla sutures; extremely  
6 elongate nasal; prominent sagittal crest and narrow intertemporal region; supraorbital  
7 processes of frontal dorsally elevated and horizontal; a poorly “telescoped” braincase  
8 with wide anteroposterior separation of the occipital shield and nasal bones; large  
9 temporal fossae longer than wide; elongate, anteroposteriorly directed and medially  
10 bowed zygomatic processes lacking supramastoid crests; anteroposteriorly thick  
11 paroccipital crest; short and unfused posterior processes of the tympanoperiotic;  
12 mandible with large tongue-shaped coronoid process and enlarged mandibular  
13 foramen; elongate cervical series; axis not significantly wider than atlas; and an  
14 elongate humerus with elongate deltopectoral crest and similar in length to radius and  
15 ulna. *Tokarahia* further differs from balaenopterids, eschrichtiids, and *Caperea* in  
16 lacking a cranially elongate pars cochlearis. *Tokarahia* differs from balaenids,  
17 *Caperea*, and *Eschrichtius* in lacking an arched rostrum and possessing a large  
18 coronoid process, and further differs from balaenids and *Caperea* in retaining unfused  
19 cervical vertebrae, and further yet from balaenids in lacking an anteroposteriorly  
20 narrow and transversely elongate and sub-cylindrical supraorbital process of the  
21 frontal.

22

### 23 **Dentition in Eomysticetidae**

24 *Eomysticetus* was initially proposed as the earliest diverging toothless  
25 mysticete (Sanders and Barnes, 2002b), but Meredith et al. (2010) speculated that it

1 (and other stem edentulous mysticetes, and even archaic crown mysticetes) may have  
2 retained vestigial teeth. Indeed, the lateral edge of the maxilla and dorsal edge of the  
3 mandible of *Eomysticetus whitmorei* are missing and damaged (respectively). The  
4 *Yamatocetus canaliculatus* holotype is more complete and preserves a series of oval  
5 to flattened alveoli within an alveolar groove, but no teeth were recovered during  
6 preparation; regardless, Okazaki (2012) inferred these alveoli to have housed teeth at  
7 some point during ontogeny. The discovery of a possible tooth consisting of a root  
8 (but missing the crown) with OU 22081 (*Tokarahia* sp., cf. *T. lophocephalus*) lends  
9 substantial support to the hypothesis that eomysticetids retained adult teeth. The tooth  
10 bears a linguolabially flattened root, which matches the flattened oval-shaped alveoli  
11 of *Yamatocetus canaliculatus* and other New Zealand eomysticetids (OU 22044); the  
12 alveolar morphology of *Tokarahia* cannot be confirmed because specimens either  
13 have a fragmented lateral maxilla (OU 22081) or are incompletely prepared (OU  
14 22235; *Tokarahia kauaeroa*). Because *Tokarahia* is a stem mysticete, the retention of  
15 teeth does not preclude a single loss of enameled teeth within mysticetes; at present  
16 no extinct crown mysticetes have been recovered with alveoli or associated teeth. The  
17 tiny size and peg-like shape of the tooth, restriction of alveoli to the anterior oral  
18 cavity in other eomysticetids (OU 22044, *Yamatocetus*), and host of bulk filter  
19 feeding adaptations in *Tokarahia* and other eomysticetids (baleen, unfused  
20 mandibular symphysis, lengthened palate, incipient rostral kinesis; see below)  
21 suggests that the dentition was non-functional. Because Mitchell (1989) defined the  
22 Chaemysticeti as a clade uniting all mysticetes with baleen and lacking a functional  
23 dentition, eomysticetids are provisionally retained as the earliest diverging members  
24 therein.  
25

1 **Functional Anatomy, Feeding Ecology, Locomotion, and Oligocene Mysticete**  
2 **Diversity**

3 Sanders and Barnes (2002b) concluded that *Eomysticetus* was a filter feeder,  
4 but did not discuss its feeding behavior further. Extant mysticetes employ three  
5 general styles of feeding behavior: lunge or engulfment feeding in Balaenopteridae,  
6 benthic suction feeding in Eschrichtiidae, and skim or continuous ram feeding in  
7 Balaenidae (Pivorunas, 1979). These behaviors are not mutually exclusive, as  
8 *Eschrichtius* is capable of lunge feeding (Werth, 2000) and *Balaenoptera borealis* has  
9 been reported employing skim feeding; similarly, this species has the finest baleen  
10 amongst balaenopterids and has an incipiently arched rostrum (Miller, 1924;  
11 Kawamura, 1974).

12 *Tokarahia* appears to be superficially similar to balaenopterids in sharing a  
13 narrow and triangular but non-arched rostrum and mandibles with a well-developed  
14 coronoid process. However, the posterior mandible of *Tokarahia* differs from all  
15 extant Mysticeti in its relatively delicate construction with an enlarged mandibular  
16 canal and “pan bone” (Fig. 25F), essentially similar to the mandible of archaeocetes  
17 and odontocetes; additionally, the coronoid process is greatly enlarged relative to  
18 balaenopterids, where it is distinct but small, and balaenids, *Caperea*, and  
19 *Eschrichtius*, where it is completely absent or reduced to a small tubercle. Additional  
20 differences are noted on the squamosal – unlike *Eschrichtius* and balaenopterids, a  
21 distinct glenoid fossa is present (Fig. 25D) – indicating that unlike the fibrocartilage  
22 temporomandibular joint in extant rorquals and gray whales (Schulte, 1916; Johnston  
23 et al., 2009), a synovial temporomandibular joint was present in *Tokarahia* and other  
24 eomysticetids, similar to extant Balaenidae (Lambertsen et al., 2005) and juvenile  
25 *Caperea* (R.E. Fordyce, pers. obs.). The delicate morphology of the mandible and

1 absence of a fibrocartilaginous temporomandibular joint strongly suggests that  
2 *Tokarahia* was incapable of lunge feeding. Perhaps more obvious are the extremely  
3 narrow cranial proportions of *Tokarahia* (and other eomysticetids); the rostrum of  
4 *Tokarahia* constitutes 70.2% of the skull length and bizygomatic width constitutes  
5 only 23.6% of skull length. In contrast, the rostrum in *Balaenoptera acutorostrata* is  
6 equivalent to 57-68% of condylobasal skull length and bizygomatic width is much  
7 wider, approximately 50-57% of condylobasal length (Arnold et al., 1987).

8         Other cranial structures implicate an uncertain feeding behavior in *Tokarahia*.  
9 *Tokarahia* is the most basal mysticete with incipient rostral kinesis. Kinesis was  
10 proposed for the toothed mysticete *Aetiocetus weltoni* (see Deméré and Berta, 2008)  
11 as the premaxilla-maxilla suture is developed as a groove. However, in all aetiocetids  
12 examined during this study, the maxilla still appears to be tightly ankylosed to the  
13 premaxilla and frontal. Unfortunately, all described aetiocetids have been recovered  
14 from concretions or highly indurated mudrocks from Japan and the Pacific coast of  
15 North America where it is not possible to separate loosely articulated elements, and  
16 until adult aetiocetid specimens with clearly disarticulated rostra are recovered,  
17 recognition of rostral kinesis in this group is equivocal. Regardless, the postmortem  
18 separation of the maxilla and premaxilla in *Tokarahia* is clear (Figs. 4, 24),  
19 demonstrating the lack of an ankylosed suture, and well-developed kinesis at the  
20 premaxilla-maxilla suture, and probably the fronto-maxillary suture as well. The  
21 nature of vomerine articulations are unclear owing to incompleteness of the vomer.  
22 However, the damaged posterior left premaxilla has uncovered an extensive and  
23 presumably firm suture between the premaxilla and nasal, with the premaxilla  
24 overriding the dorsolateral margin of the nasal (Fig. 4). Although often missing in  
25 fossils, both nasals are firmly in place along with the premaxillae, both pairs of which

1 share an ankylosed suture with the frontal. In the closely related *Tohoraata raekohao*,  
2 an elongate anteromedial spur of frontal extends anteriorly with sutural surfaces for  
3 the premaxilla and nasal. This suggests a relatively robust connection between the  
4 premaxilla-nasal, nasofrontal, and fronto-premaxillary sutures, and that while the  
5 maxilla was kinetic, the median rostral elements were rigid. The unique condition in  
6 *Tokarahia* illuminates the manner in which the rigid rostrum of toothed mysticetes  
7 was transformed into the highly kinetic rostrum of extant mysticetes.

8 *Tokarahia* is somewhat basilosaurid-like in skull form as it includes a poorly  
9 telescoped skull with delicate frontals, a high sagittal crest, and cavernous,  
10 anteroposteriorly elongate temporal fossae (Fig. 4). The long intertemporal region  
11 indicates that *Tokarahia* lacked the anteriorly placed insertions for epaxial  
12 musculature on the occipital shield as in extant Mysticeti (Godfrey et al., 2013),  
13 additionally suggesting an inability to lunge feed. The enlarged temporal fossae and  
14 prominent sagittal and nuchal crests indicate that the temporalis origin must have been  
15 enormous in *Tokarahia*; indeed, the cross-sectional area of the temporal fossa (lateral  
16 surfaces of the braincase and squamosal fossa included) in Eomysticetidae (Fig. 31)  
17 are the largest amongst all Mysticeti. In total, these features indicate that *Tokarahia*  
18 was not a lunge feeder; however, distinguishing between the remaining two types of  
19 feeding behavior in Eomysticetidae – skim feeding and benthic suction feeding – will  
20 await description of more complete eomysticetid remains that demonstrate  
21 ontogenetic changes in feeding morphology (Boessenecker and Fordyce, 2013).

22 Filter feeding upon zooplankton by *Tokarahia* is supported by earlier stable  
23 isotopic studies. One specimen, OU 22081 (*Tokarahia* sp., cf. *T. lophocephalus*)  
24 yielded relatively low  $\delta^{13}\text{C}$  values in the range of extant balaenids and some  
25 balaenopterids (Clementz et al., 2013). Notably,  $\delta^{13}\text{C}$  values for *Tokarahia* and other

1 New Zealand fossil Eomysticetidae were amongst the lowest recorded values amongst  
2 analyzed cetacean specimens, with the single exception of the Oligocene archaeocete  
3 *Kekenodon* (Clementz et al., 2013). Low  $\delta^{13}\text{C}$  may also suggest foraging at higher  
4 latitudes and thus may imply that *Tokarahia* performed seasonal migrations.

5         The postcranial skeleton of *Tokarahia kauaeroa* is one of the most completely  
6 known for an Oligocene mysticete (Fig. 3). The postcranial skeleton is a mosaic of  
7 derived and archaic features, and includes an elongate series of cervical vertebrae  
8 similar to basilosaurids, a remarkably derived and large scapula that is  
9 anteroposteriorly longer than deep and lacks a coracoid process, a humerus with  
10 basilosaurid and derived mysticete features, and a radius and ulna that are  
11 longitudinally straight (Fig. 32). Most extant balaenopterids, *Eschrichtius*, and  
12 *Caperea* retain a coracoid process, whereas it is lost in balaenids and *Megaptera*.  
13 Although it suggests decreased importance of the coracobrachialis and possible  
14 absence of the biceps brachii (absent in extant cetaceans; Uhen, 2004), the functional  
15 implications remain ambiguous. The reduction in size of the supraspinous fossa and  
16 anterior placement of the scapular spine is widespread in extant cetaceans and Neoceti  
17 as a whole, suggesting a decreased supraspinatus. The humerus of *Tokarahia*  
18 *kauaeroa* is relatively elongate and approximately the length of the radius and ulna, in  
19 contrast to basilosaurids where the humerus is often longer and extant Mysticeti  
20 where it is much shorter. However, the shaft is of near uniform thickness, as in extant  
21 Mysticeti, and exhibits flattened, plate-like articular facets for the radius and ulna  
22 unlike the smoothly convex trochlea of Archaeoceti (Uhen, 2004). Unlike extant  
23 Mysticeti, the deltopectoral crest is elongate and occupies nearly  $\frac{3}{4}$  of the length of  
24 the humerus. The olecranon process of the ulna is robust and extends further  
25 proximally than the humeral articular facet. This combination of features suggests that

1 the forelimb of *Tokarahia* had an inflexible non-synovial elbow joint as in extant  
2 mysticetes, but did not yet possess proximally positioned insertions for the deltoideus,  
3 and primitively retained robust attachments for the triceps brachii and flexor carpi  
4 ulnaris on the ulna.

5 To date four named eomysticetid species in two genera are known from the  
6 upper Oligocene of New Zealand, including *Tokarahia kauaeroa* and *Tokarahia*  
7 *lophocephalus*. At least two additional undescribed eomysticetids are present  
8 (Fordyce, 2006; Boessenecker and Fordyce, 2013). Several additional mysticetes  
9 including putative early balaenids with an arched rostrum (Fordyce, 2002), the  
10 “cetother”-like *Mauicetus parki* (Benham, 1937; Fordyce, 2005), additional  
11 *Mauicetus*-like fossils and several mysticetes of uncertain affinities (Fordyce,  
12 1991:1256-1257). Altogether, six eomysticetids are present in Duntroonian strata in  
13 New Zealand as well as several additional mysticetes; this diversity is suggestive of  
14 similar species richness in extant balaenopterids.

15

## 16 **Eomysticetids as Transitional Mysticetes**

17 During the past three decades, a series of spectacular fossil skeletons of archaeocete  
18 whales have been reported from the Eocene of Egypt, Indo-Pakistan, and eastern  
19 North America, beautifully demonstrating various skeletal changes that occurred  
20 during the land-to-sea transition in early Cetacea (Uhen, 2010). Although the tempo  
21 and mode of aquatic adaptation in archaeocetes is well known, the archaeocete-  
22 mysticete transition is comparatively less well known. Archaic toothed mysticetes  
23 from the Oligocene such as Mammalodontidae (*Janjucetus*, *Mammalodon*), the  
24 Aetiocetidae (*Aetiocetus*, *Ashorocetus*, *Chonecetus*, *Morawanacetus*), and *Llanocetus*  
25 include well-preserved crania primitively retaining teeth, poorly “telescoped” skulls,

1 firm rather than clearly kinetic rostral sutures, and derived mysticete characteristics  
2 (e.g. thin lateral edge of maxilla, triangular occipital shield, thickened basioccipital  
3 crests; Barnes et al., 1995; Fitzgerald, 2006; 2010; Deméré et al., 2008; Deméré and  
4 Berta, 2008). Despite being morphologically intermediate between archaeocetes and  
5 later mysticetes, a large morphological gulf still exists between this rather  
6 taxonomically diverse grade and the better-known “cetotheres” *sensu lato* and  
7 Cetotheriidae of the Miocene. Eomysticetids such as *Eomysticetus* and *Tokarahia*  
8 exhibit many features intermediate between toothed mysticetes and Miocene  
9 Chaemysticeti, including an intermediate stage of cranial “telescoping”, incipient  
10 rostral kinesis, as well as being putatively edentulous or having a highly reduced  
11 dentition (e.g. Okazaki, 2012). Critically, few toothed mysticetes with well preserved  
12 tympanoperiotics are preserved, otherwise relegating our knowledge of the most  
13 primitive tympanoperiotic morphology relatively high on the mysticete tree, within  
14 Miocene Chaemysticeti. New fossil material like *Tokarahia kauaeroa* supplement  
15 the anatomical information present in *Eomysticetus whitmorei* and contributes  
16 significantly to the eomysticetid “archetype”, illuminating the morphology of the  
17 earliest chaemysticetes, and serving as an excellent point of comparison (Fig. 32)  
18 between toothed Mysticeti and more derived chaemysticetes (=Balaenomorpha).  
19 One critical example of transitional feature elucidated by *Tokarahia* is the partial  
20 rotation of the tympanic bulla; in archaeocetes and toothed mysticetes, the outer lip of  
21 the bulla faces laterally, whilst in crown Mysticeti the outer lip faces ventrally and the  
22 bulla is rotated approximately 90° (Bouetel and Muizon, 2006). *Tokarahia* preserves a  
23 bulla rotated approximately 45° from the primitive condition, and demonstrates that  
24 rotation of the bulla began prior to fusion of the anterior and posterior pedicles and  
25 loss of differentiation between the medial and lateral lobes.

1           Perhaps the most profound change in the archaeocete-mysticete transition is  
2 that of feeding adaptations: archaeocetes retain a piercing and shearing dentition,  
3 whilst extant mysticetes lack teeth and uniquely possess keratinous racks of baleen for  
4 filter feeding on fish, krill, amphipods, and other zooplankton from the water column  
5 and seafloor. The feeding ecology of certain toothed mysticetes has been robustly  
6 investigated, identifying the mammalodontids *Janjucetus* and *Mammalodon* as  
7 macrophagous predators and benthic suction feeders (respectively; Fitzgerald, 2006;  
8 2010). Notably, the identification of palatal vascular foramina and sulci in several  
9 aetiocetids (e.g. *Aetiocetus weltoni*) has led to the discovery that some aetiocetids may  
10 have possessed baleen or a baleen-like structure, perhaps engaging in some form of  
11 filter feeding (Deméré et al., 2008). However, as eomysticetids either lacked teeth or  
12 possessed a rudimentary dentition, they are arguably the earliest diverging mysticete  
13 clade to have been obligatory filter feeders. In this context, a robust interpretation of  
14 the feeding adaptations of eomysticetids is crucial for identifying the primitive mode  
15 of filter feeding in Chaecomysticeti. It is apparent that *Tokarahia* did not feed in a  
16 manner analogous to extant Balaenopteridae (e.g. high-volume lunge feeding; see  
17 above), but the preserved features do not distinguish between the other two modes of  
18 feeding utilized by other extant mysticetes (e.g. skim feeding, Balaenidae  
19 and ?Neobalaenidae; benthic suction feeding, Eschrichtiidae). A more robust  
20 interpretation of eomysticetid feeding ecology awaits the description of a new genus  
21 and species of eomysticetid even more completely preserved than *Tokarahia*  
22 *kauaeroa*, preliminarily reported by Boessenecker and Fordyce (2013). However  
23 *Tokarahia* may have filter fed, its transversely narrow and dorsoventrally shallow  
24 rostrum with an anteriorly placed blowhole would not have resembled any extant  
25 mysticete (Fig. 33).

1

## 2 CONCLUSIONS

3 New fossil material including a well-preserved skull, tympanoperiotics, mandibles,  
4 and postcrania is described as a new genus and species *Tokarahia kauaeroa* within  
5 the archaic chaemysticete family Eomysticetidae. The problematic taxon  
6 “*Mauicetus*” *lophocephalus* is transferred to this new genus and recombined as  
7 *Tokarahia lophocephalus*, resolving decades of uncertainty regarding the taxonomic  
8 affinities and phylogenetic significance of this historically puzzling taxon. Referred  
9 material suggests that both species existed at the same time from at least 27.3-25.2 Ma  
10 and were perhaps sympatric. Phylogenetic analysis using a large and exhaustive  
11 dataset of extant and extinct Mysticeti places both species of *Tokarahia* within  
12 Eomysticetidae, and robustly confirms the monophyly of Eomysticetidae.  
13 *Micromysticetus* is also confirmed as an eomysticetid and removed from the  
14 Cetotheriopsidae, which is not possible to diagnose and at present is restricted to the  
15 holotype of *Cetotheriopsis lintianus*. Incipient rostral fusion and a delicate and  
16 synovial tempromandibular joint seem to preclude lunge feeding in *Tokarahia* and  
17 other eomysticetids, but the uniquely elongate rostrum and comparatively enormous  
18 temporal fossae and crests for temporalis attachment suggest an uncertain but highly  
19 specialized adaptation for an as-yet unidentified feeding strategy.

20

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14

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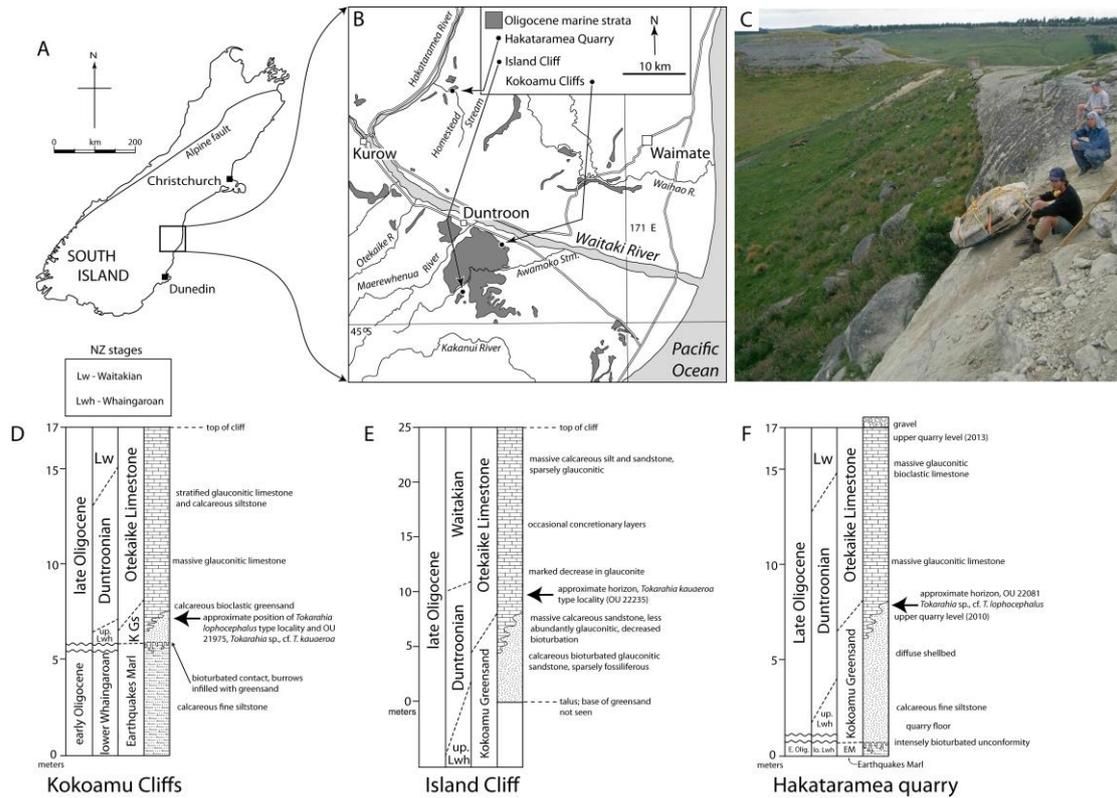
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2 **Figure 1. Location and stratigraphy of *Tokarahia*-bearing localities, South Island,**

3 **New Zealand.** A, map of South Island with inset showing position of B; B,

4 map of the Waitaki Valley region showing positions of three *Tokarahia*

5 localities; C, excavation at type locality of *Tokarahia kauaeroa*, Island Cliff,

6 North Otago (© R.E. Fordyce); D, Oligocene stratigraphy at Kokoamu Cliffs,

7 modified from Gage (1957) and Boessenecker and Fordyce (In Press); E,

8 Oligocene stratigraphy at Island Cliff, modified from Gottfried and Fordyce

9 (2001); F, Oligocene stratigraphy at Hakataramea Quarry, modified from

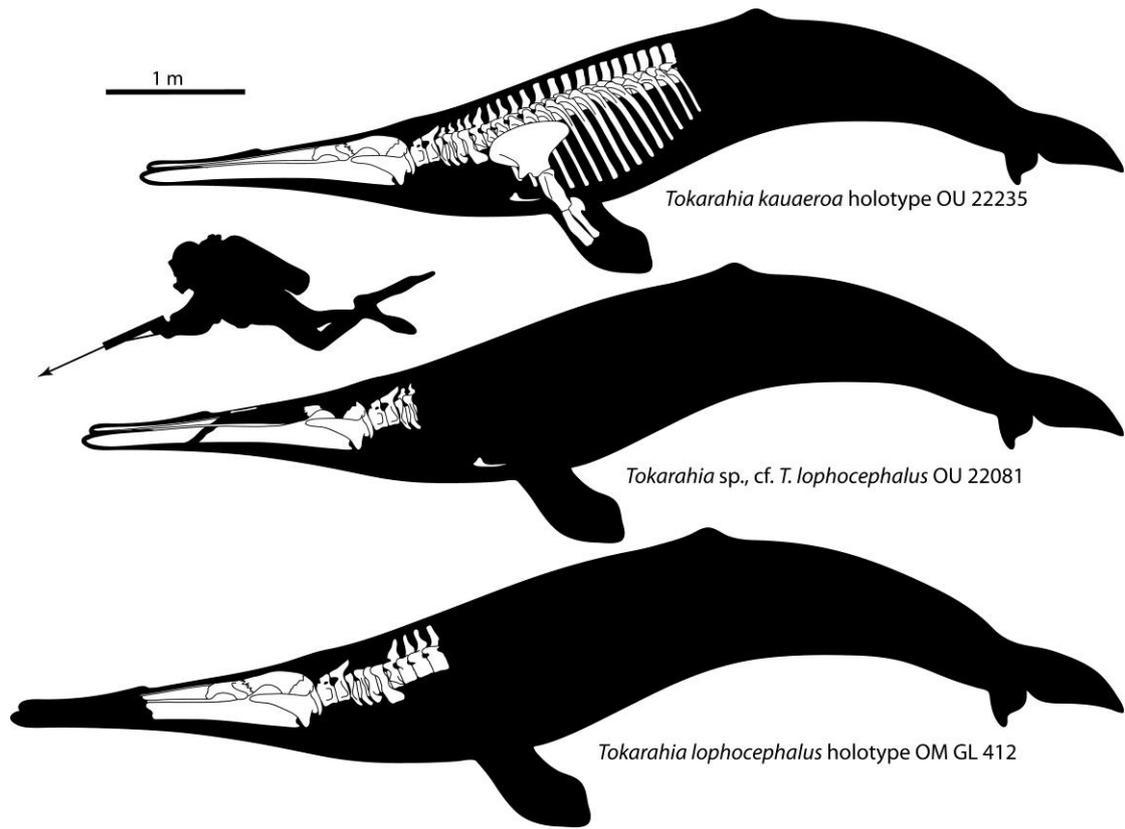
10 Gottfried et al. (2012).

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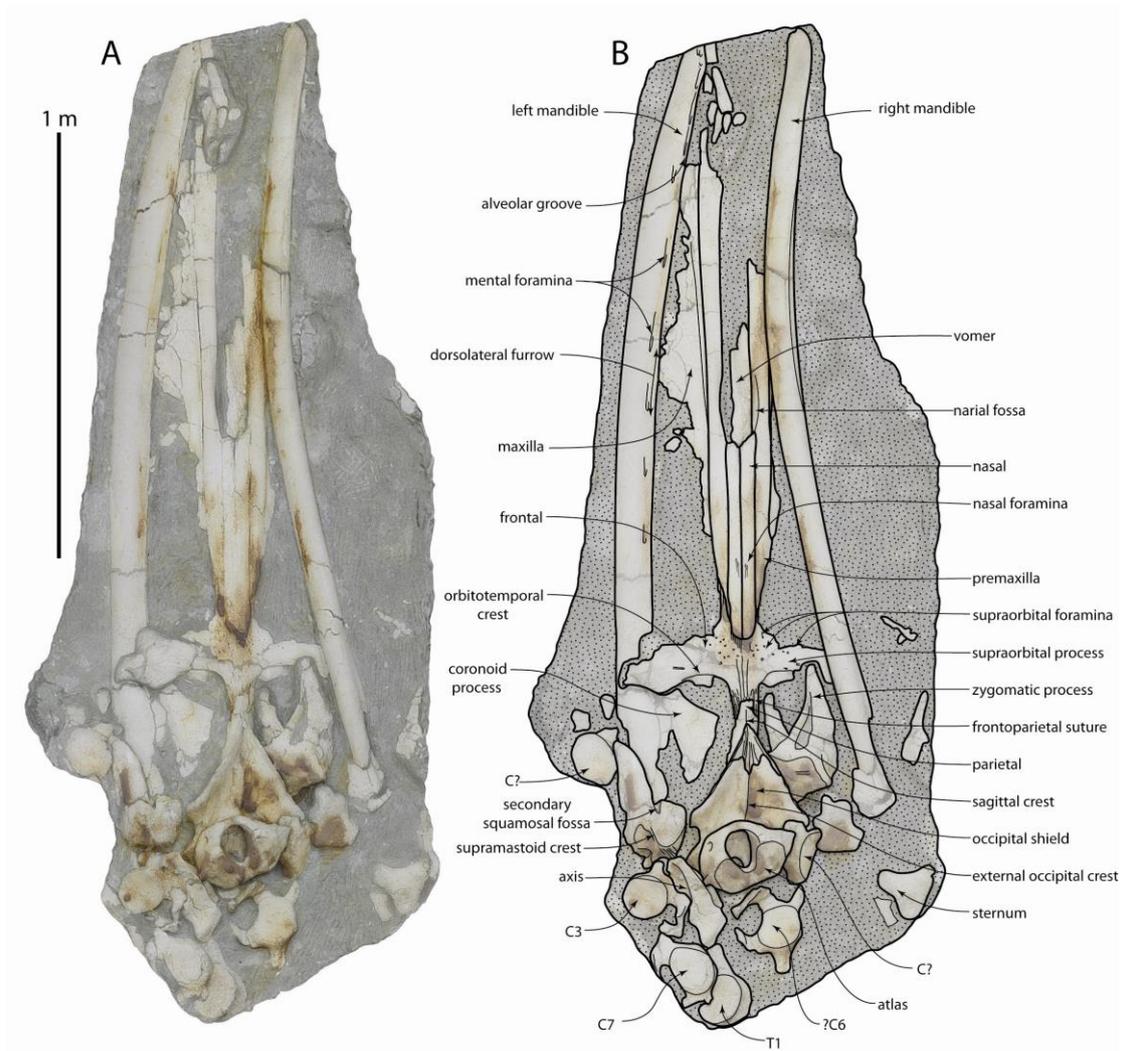
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**Figure 2. Excavation of the *Tokarahia kauaeroa* holotype skull and skeleton, showing A, exposure of the skull and mandibles in a ventral up position, and B, removal of the large jacket containing the skull.**



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**Figure 3. Silhouetted skeletal reconstructions of the three primary specimens of *Tokarahia* described in this study with human for scale. Skeletal reconstruction based in part on *Eomysticetus whitmorei* and *Yamatocetus canaliculatus*.**

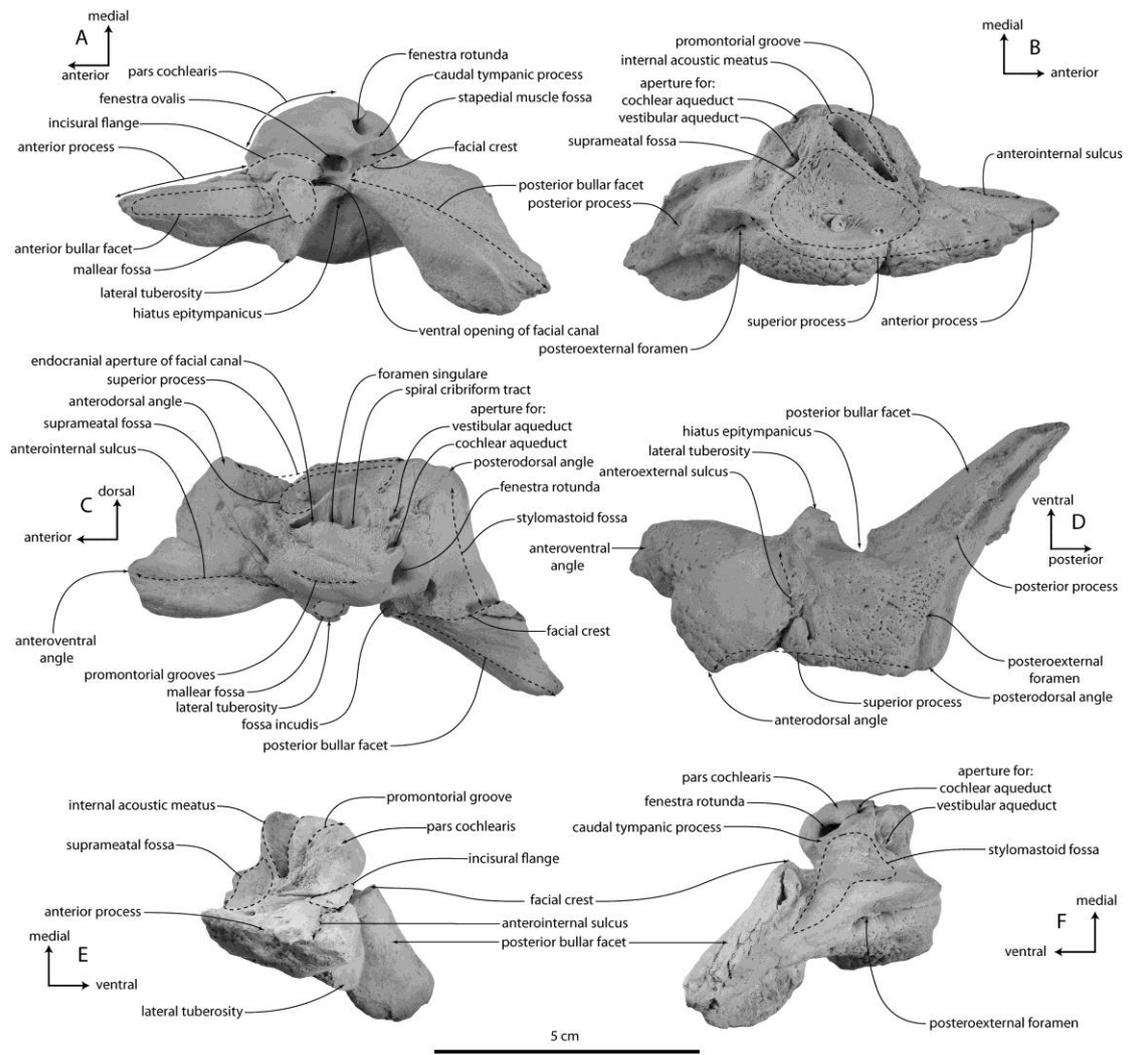


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2 **Figure 4. Cast of holotype (OU 22235) skull, mandibles, vertebrae, and sternum**

3 **of *Tokarahia kauaeroa*. A, photograph, B, interpretive line drawing.**

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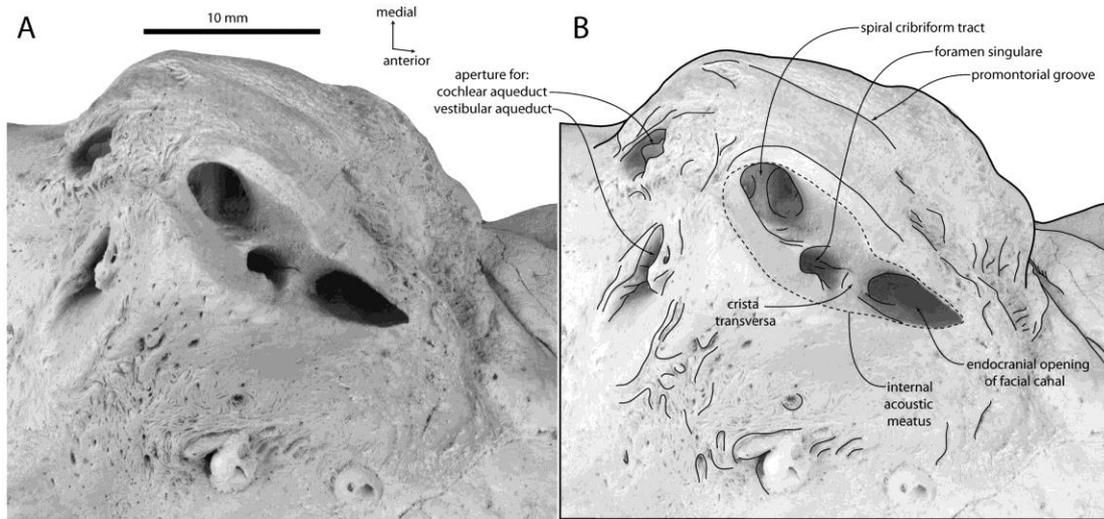
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2 **Figure 5. Holotype right periotic (OU 22235) of *Tokarahia kauaeroa*, whitened**

3 **with ammonium chloride. A, ventral; B, dorsal; C, medial; D, lateral; E,**

4 **anterior; F, posterior.**

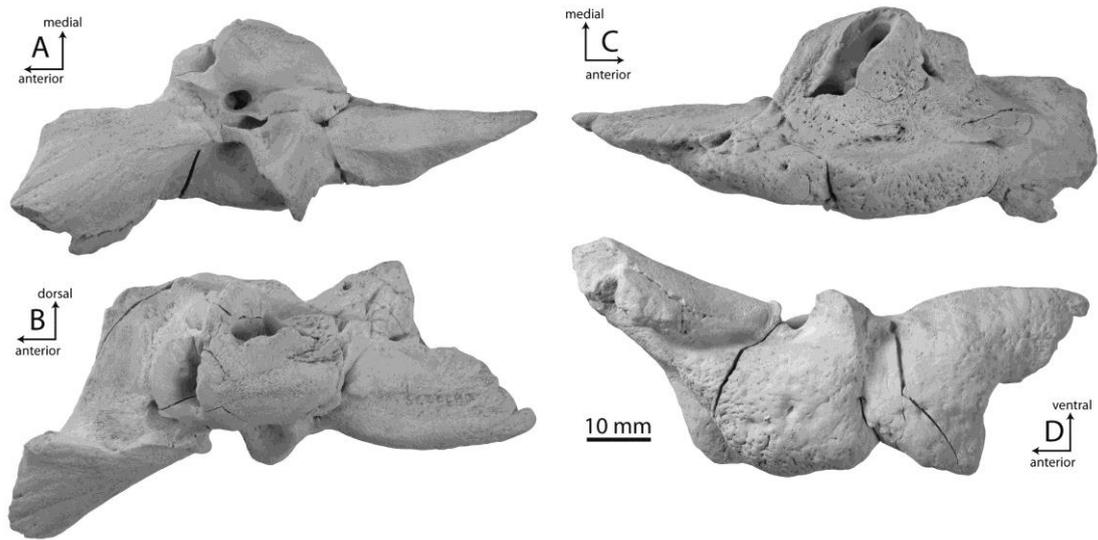
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**Figure 6. Detail of internal acoustic meatus of *Tokarahia kauaeroa* holotype (OU 22235) right periotic. A, photograph, B, interpretive line drawing.**

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**Figure 7. Holotype left periotic (OU 22235) of *Tokarahia kauaeroa*,**

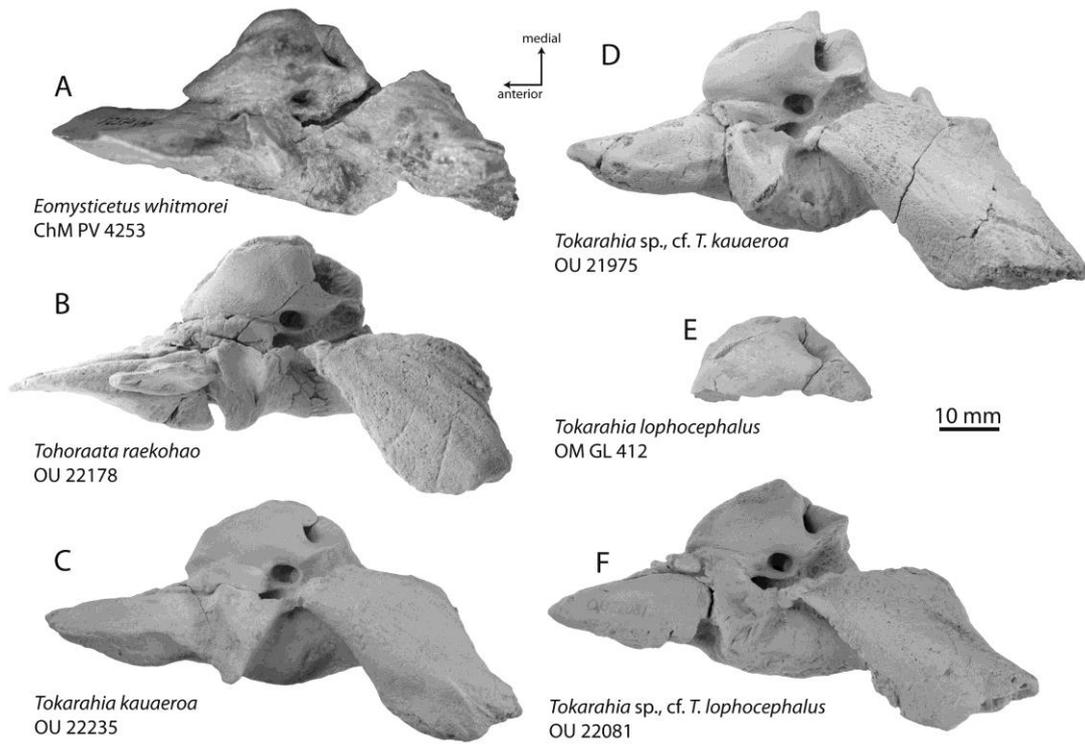
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**whitened with ammonium chloride. A, ventral; B, dorsal; C, medial; D,**

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**lateral.**

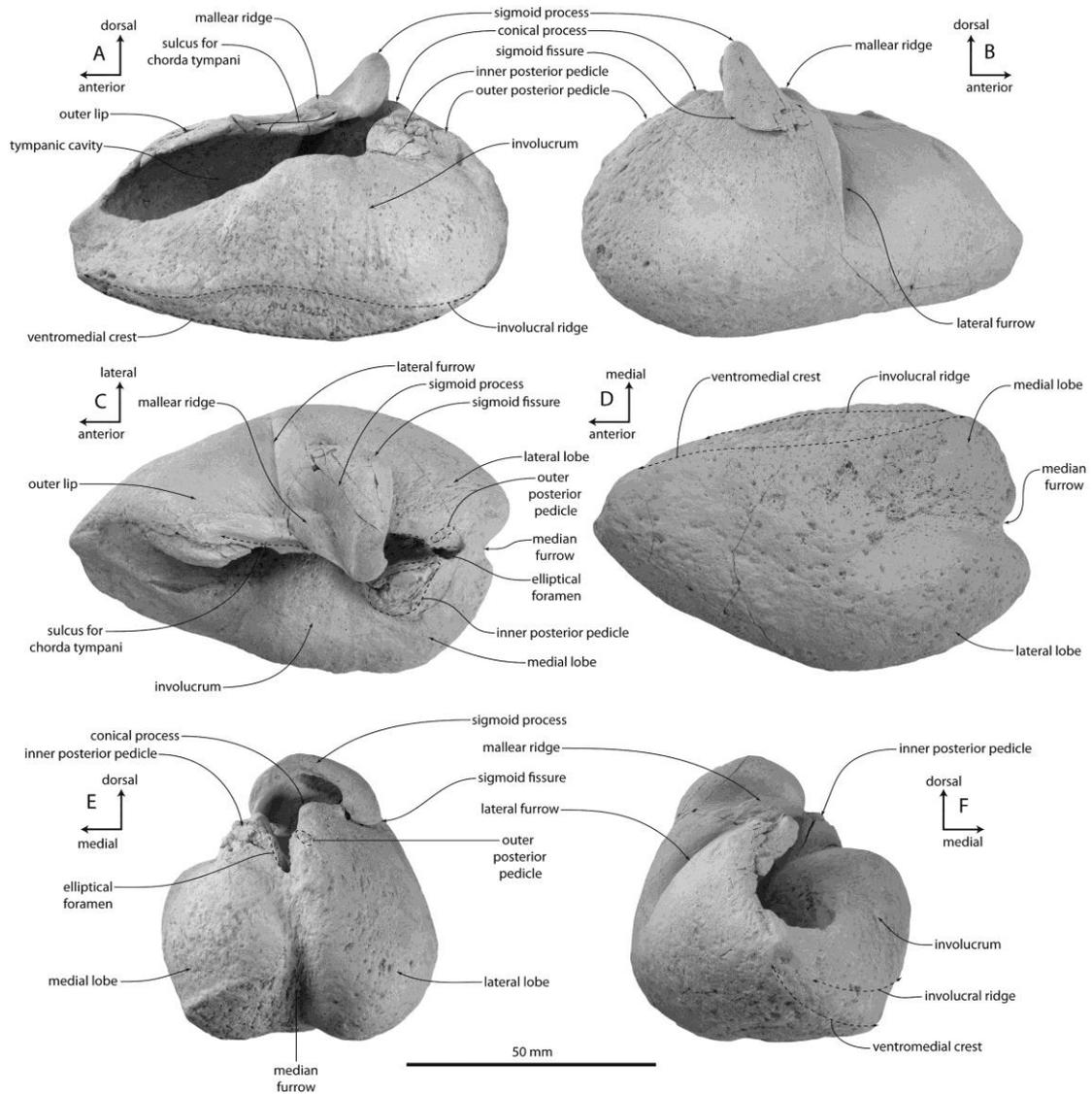
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**Figure 8. Comparison of eomysticetid periotics in ventral view, whitened with ammonium chloride.** A, holotype left periotic of *Eomysticetus whitmorei* (reversed); B, holotype right periotic of *Tohoraata raekohao*; C, holotype right periotic of *Tokarahia kauaeroa*; D, referred right periotic of *Tokarahia* sp., cf. *T. kauaeroa*; E, holotype right pars cochlearis of *Tokarahia lophocephalus*; F, referred right periotic of *Tokarahia* sp., cf. *T. lophocephalus*.

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**Figure 9. Holotype right tympanic bulla (OU 22235) of *Tokarahia***

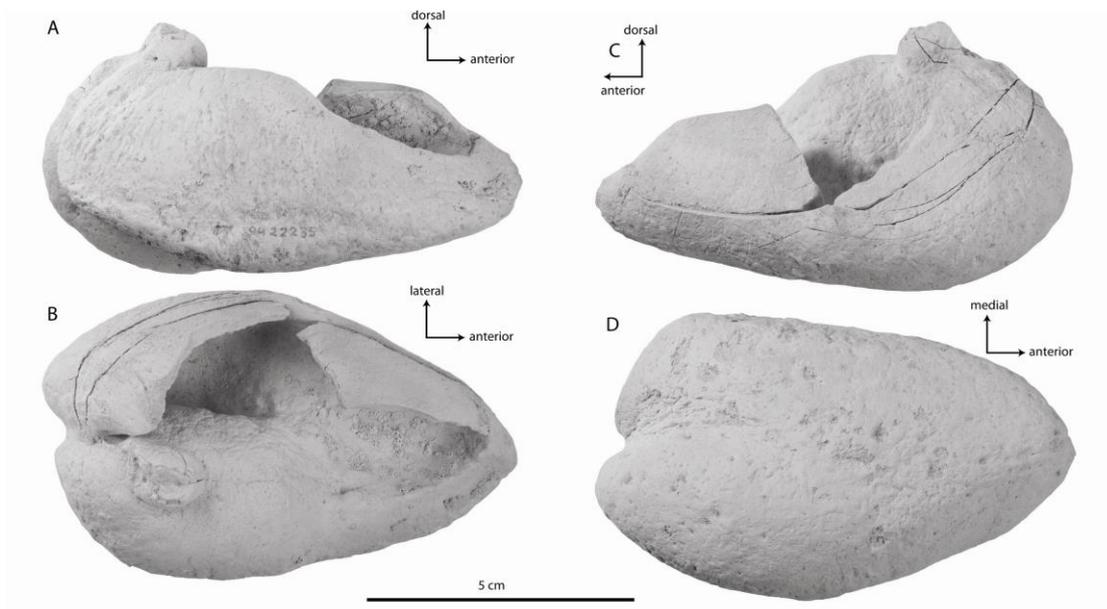
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***kauaeroa*, whitened with ammonium chloride. A, medial; B, lateral; C,**

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**dorsal; D, ventral; E, posterior; F, anterior.**

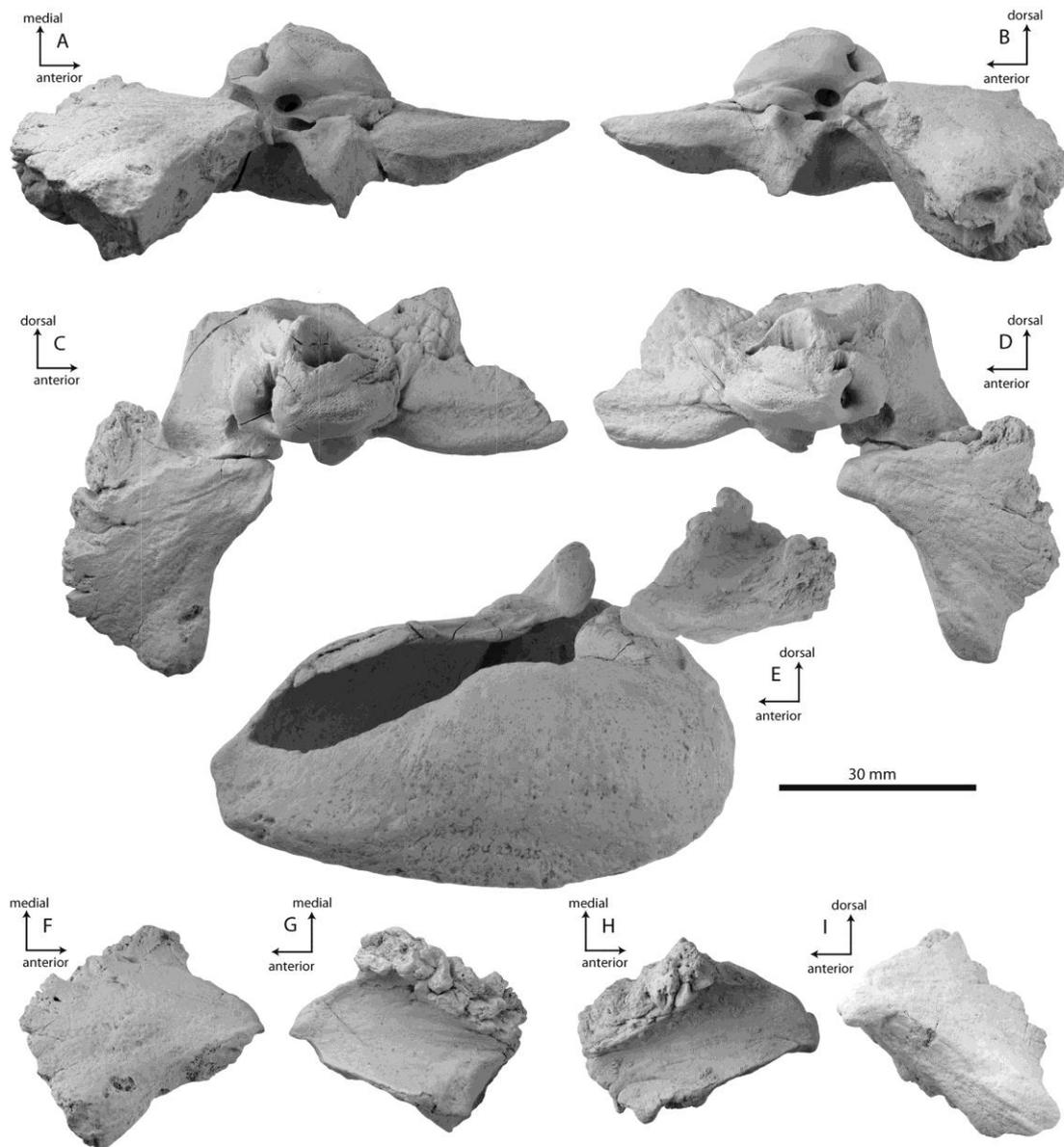
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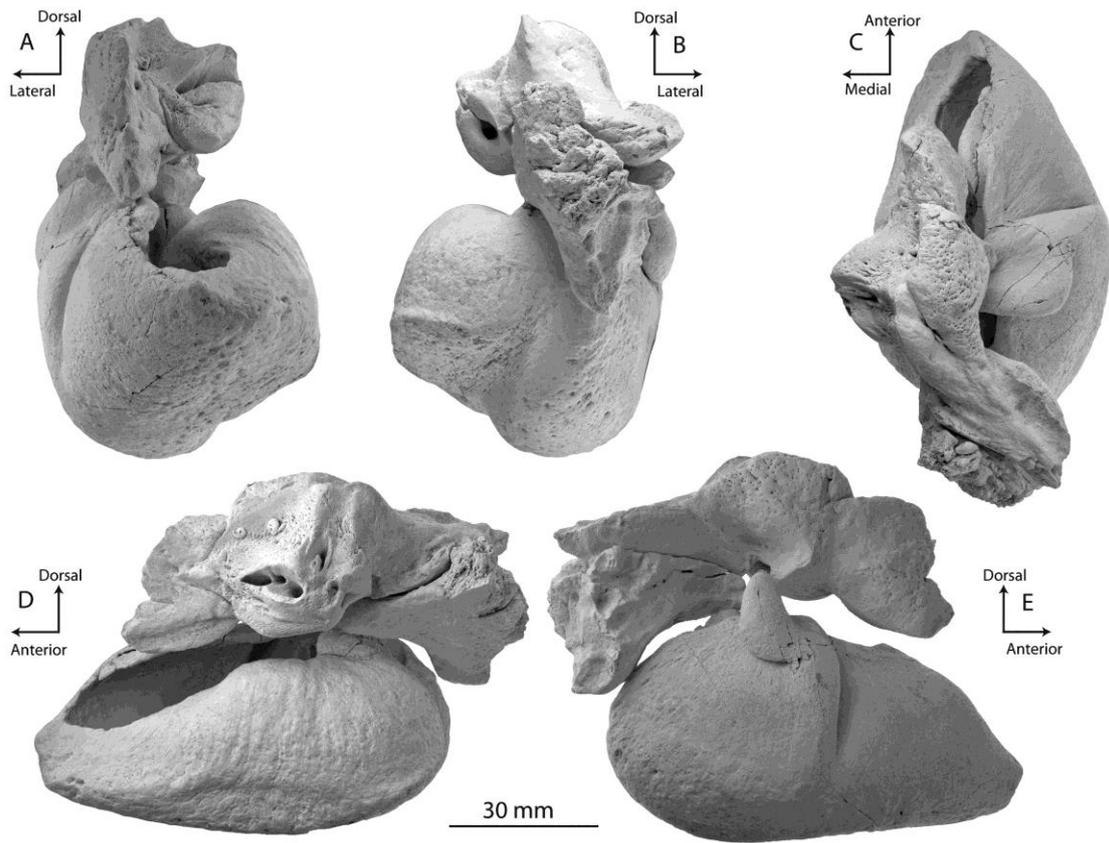
2 **Figure 10. Holotype left tympanic bulla (OU 22235) of *Tokarahia kauaeroa*,**  
3 **whitened with ammonium chloride. A, medial; B, lateral; C, dorsal; D,**  
4 **ventral.**

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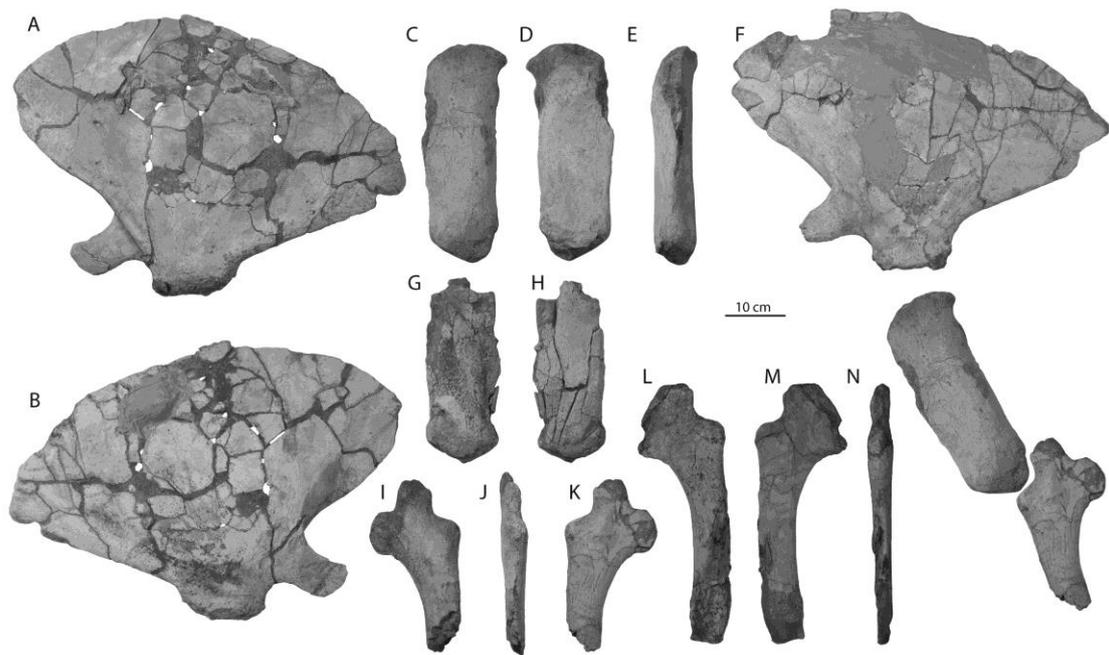
2 **Figure 11. Holotype (OU 22235) left and right periotics, right tympanic bulla,**  
 3 **and posterior processes of the tympanic bulla of *Tokarahia kauaeroa*,**  
 4 **whitened with ammonium chloride. A, left periotic with articulated posterior**  
 5 **process of bulla in ventral view; B, right periotic with posterior process of**  
 6 **bulla in ventral view; C, left periotic with articulated posterior process of bulla**  
 7 **in medial view; D, right periotic with articulated posterior process of bulla**  
 8 **in medial view; E, right tympanic bulla with posterior process in medial view; F,**  
 9 **left posterior process of bulla in ventromedial view G, and dorsal view, H;**  
 10 **right posterior process of bulla in dorsal view and I, ventromedial view.**



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2 **Figure 12.** Articulated tympanoperiotic of *Tokarahia kauaeroa* holotype (OU  
 3 **22245).** A, anterior; B, posterior; C, dorsal (relative to bulla); D, medial  
 4 (relative to bulla); and E, lateral view (relative to bulla).

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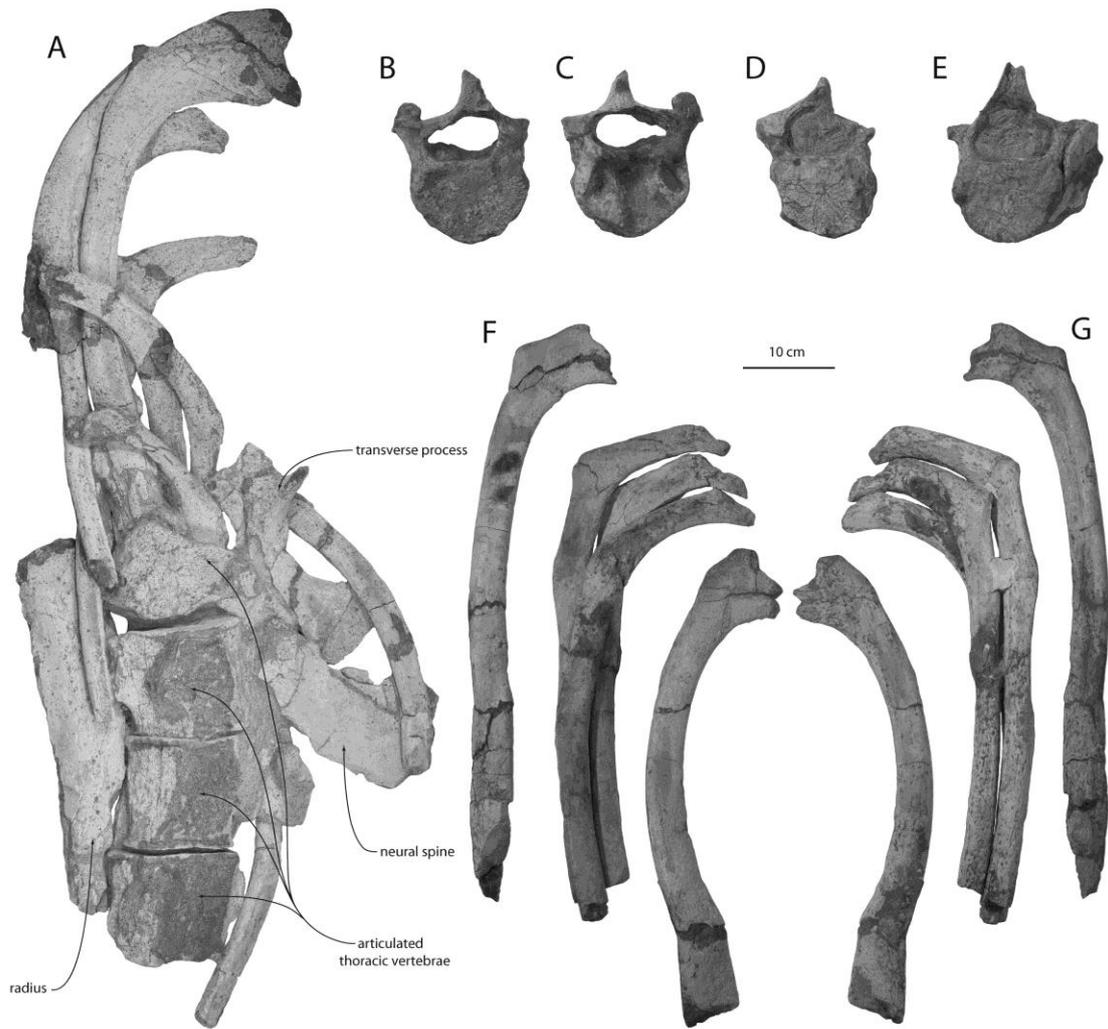


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2 **Figure 13. Axial skeleton and radius of *Tokarahia kauaeroa* holotype (OU 22235).**

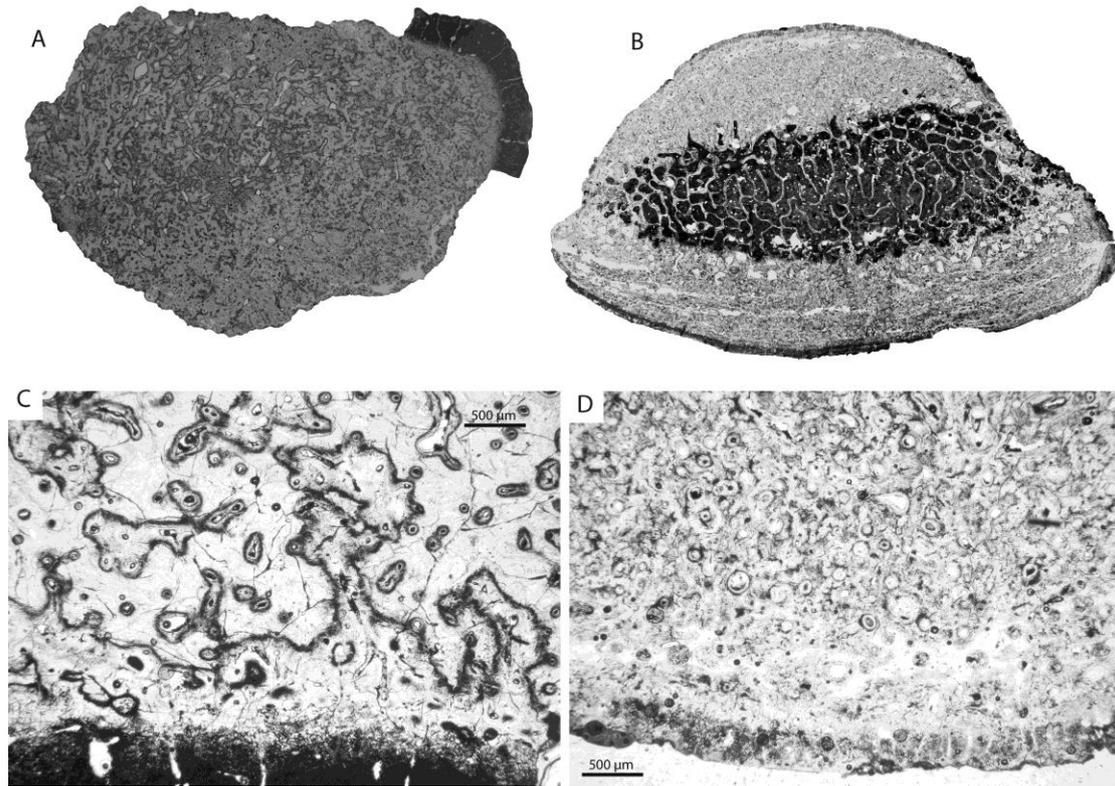
3 A, associated and articulated ribs, thoracic vertebrae, and radius. B, thoracic  
 4 vertebra I in anterior view, A, and posterior view, B. Thoracic vertebra B and  
 5 C in anterior view (D, E). Left ribs in posterior, F, and anterior view, G.

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**Figure 14. Appendicular skeleton of *Tokarahia kauaeroa* holotype (OU 22235).** A, right scapula in medial view; B, right scapula in lateral view; C, left humerus in lateral, D, medial, and E, anterior view; F, left scapula, humerus, and ulna in approximate articulation in lateral view; G, right humerus in lateral and H, medial view; I, left ulna in medial, J, anterior, and K, lateral view; L, right ulna in lateral, M, medial, and N, anterior view.



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2 **Figure 15. Rib histology of *Tokarahia*.** A, complete thin section of *Tokarahia* sp., cf.

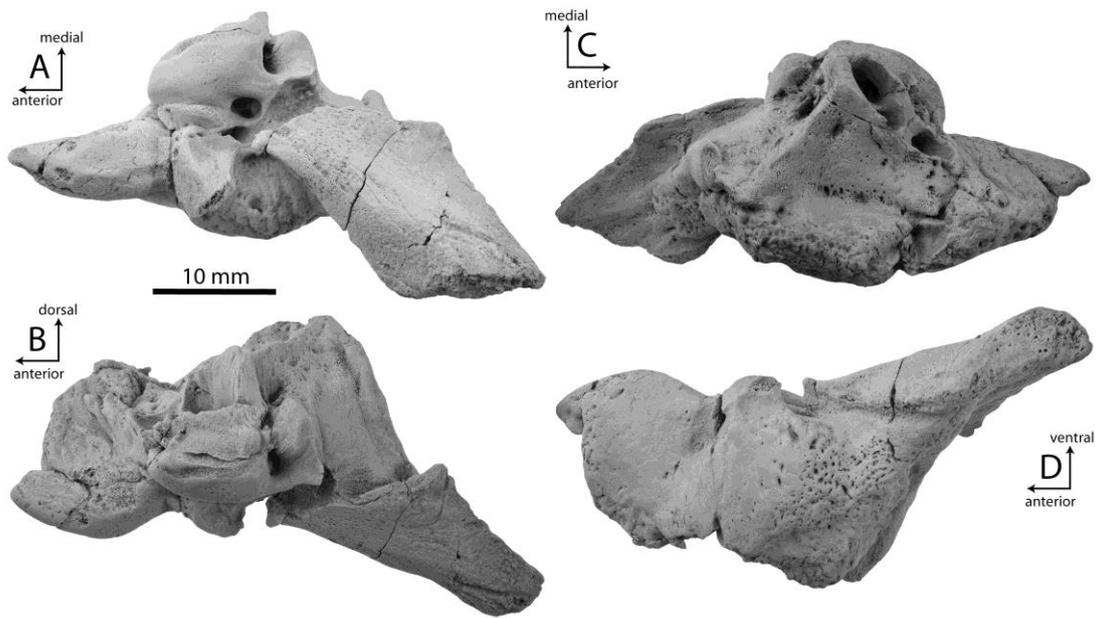
3 *T. lophocephalus* (OU 22081); B, complete thin section of *Tokarahia kauaeroa*

4 (OU 22235) C, photomicrograph of cortex of OU 22081; D, photomicrograph

5 of cortex of OU 22235.

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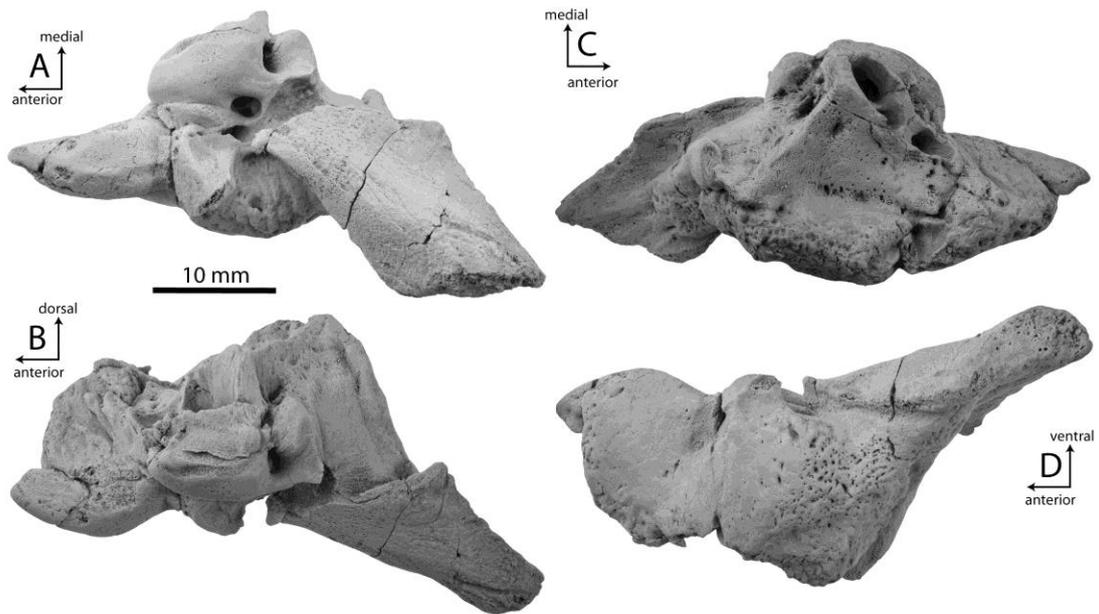
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3 **Figure 16. Referred right periotic (OU 21975) of *Tokarahia* sp., cf. *T. kauaeroa*,**

4 **whitened with ammonium chloride. A, ventral; B, medial; C, dorsal; D,**

5 **lateral.**

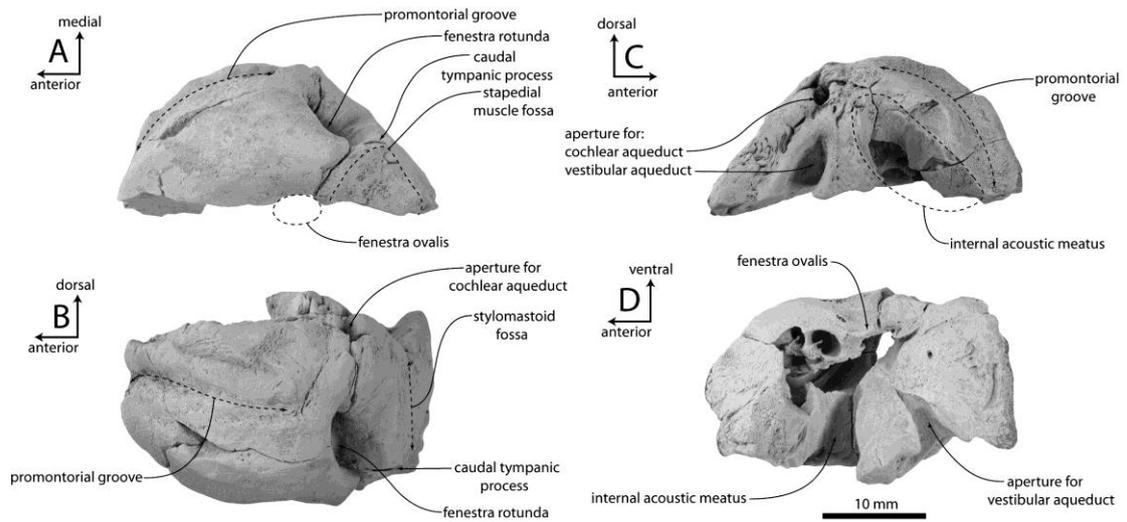
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2 **Figure 17. Holotype skull and skeleton of *Tokarahia lophocephalus* (OM GL 412),**  
3 **reproduced from Marples (1956). A, prepared skull in dorsal view; B,**  
4 **specimen as excavated in field.**

5



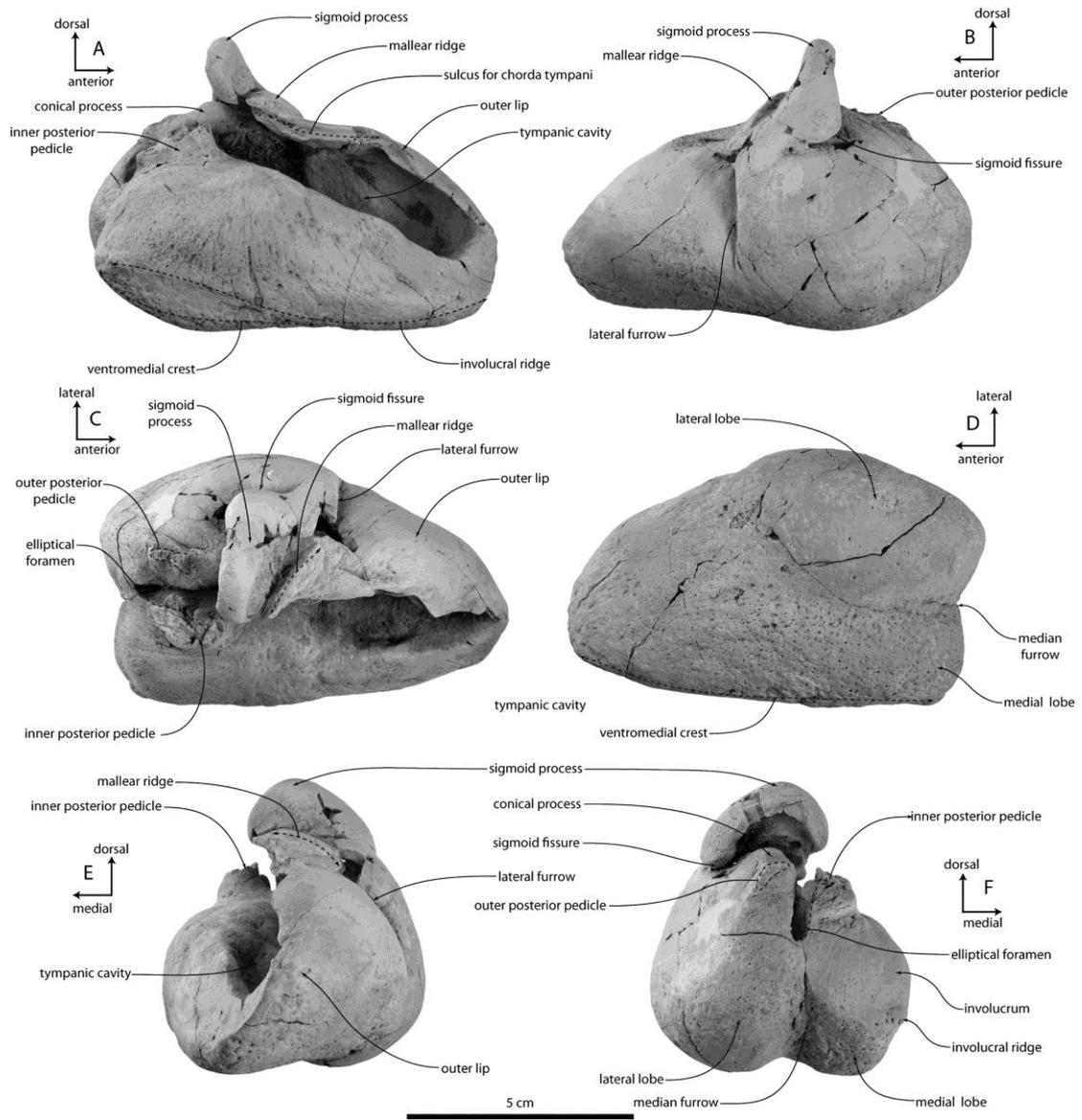
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2 **Figure 18. Holotype pars cochlearis of *Tokarahia lophocephalus* (OM GL 412),**

3 **whitened with ammonium chloride. A, ventral; B, medial; C, dorsal; D,**

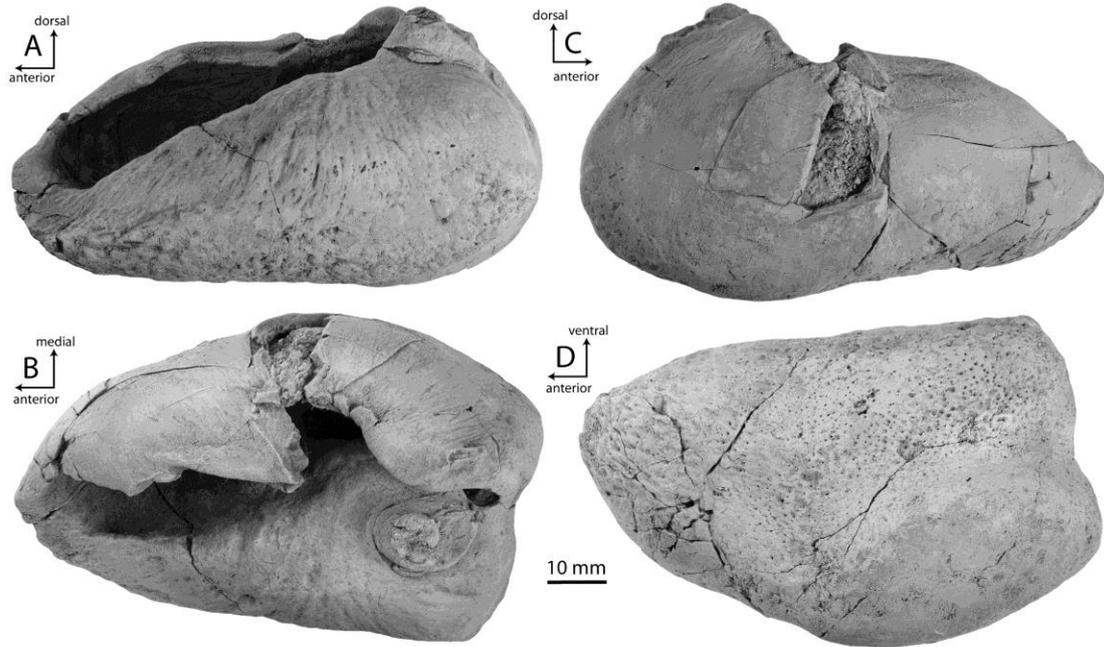
4 **lateral.**

5



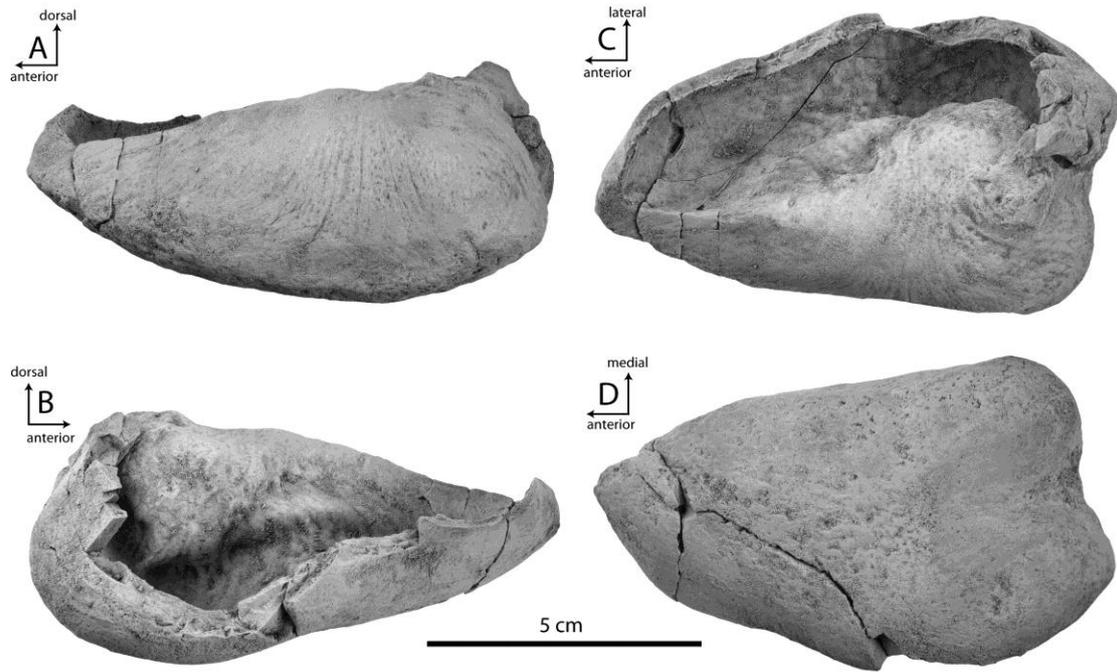
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**Figure 19. Holotype left tympanic bulla of *Tokarahia lophocephalus* (OM GL 412), whitened with ammonium chloride. A, medial; B, lateral; C, dorsal; D, ventral; E, anterior; F, posterior.**



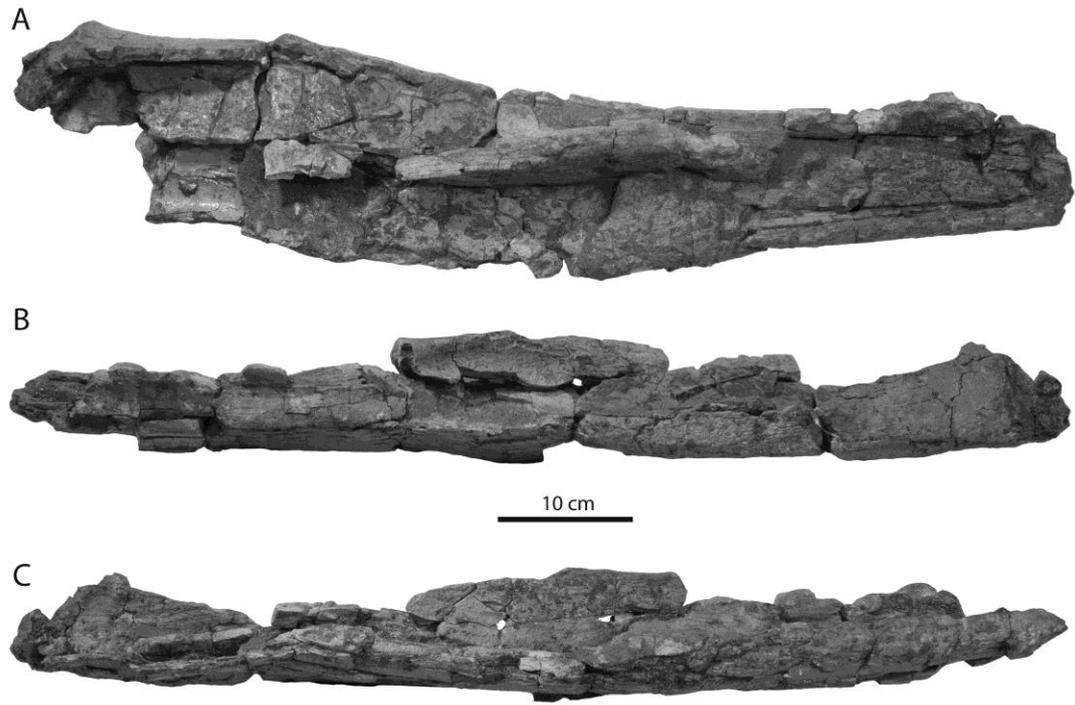
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**Figure 20. Holotype right tympanic bulla of *Tokarahia lophocephalus* (OM GL 412), whitened with ammonium chloride. A, medial; B, lateral; C, dorsal; D, ventral.**



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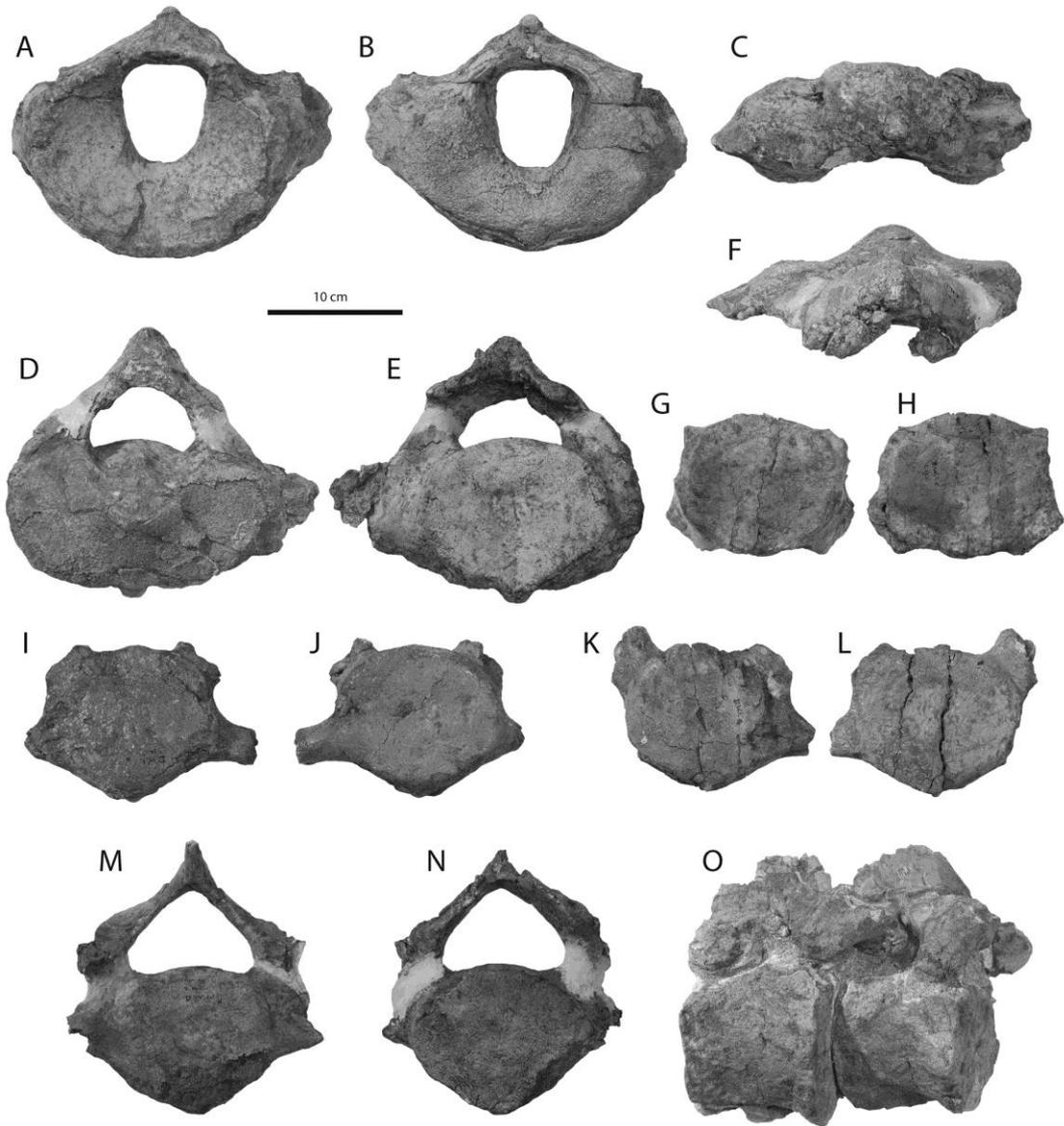
**Figure 21. Referred tympanic bulla of *Tokarahia lophocephalus* (OM GL 443), whitened with ammonium chloride. A, medial; B, lateral; C, dorsal; D, ventral.**



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**Figure 22. Holotype left mandible of *Tokarahia lophocephalus* (OM GL 412). A,**  
dorsal; B, lateral; C, medial.

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**Figure 23. Holotype vertebrae of *Tokarahia lophocephalus* (OM GL 412).**

4

Atlas in A, anterior, B, posterior, and C, dorsal view; axis in D, anterior, E,

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posterior, and F, dorsal view; ?C3 in G, anterior, and H, posterior view; ?C4 in

6

I, anterior, and J, posterior view; ?C5 in K, anterior, L, posterior view; C7 in

7

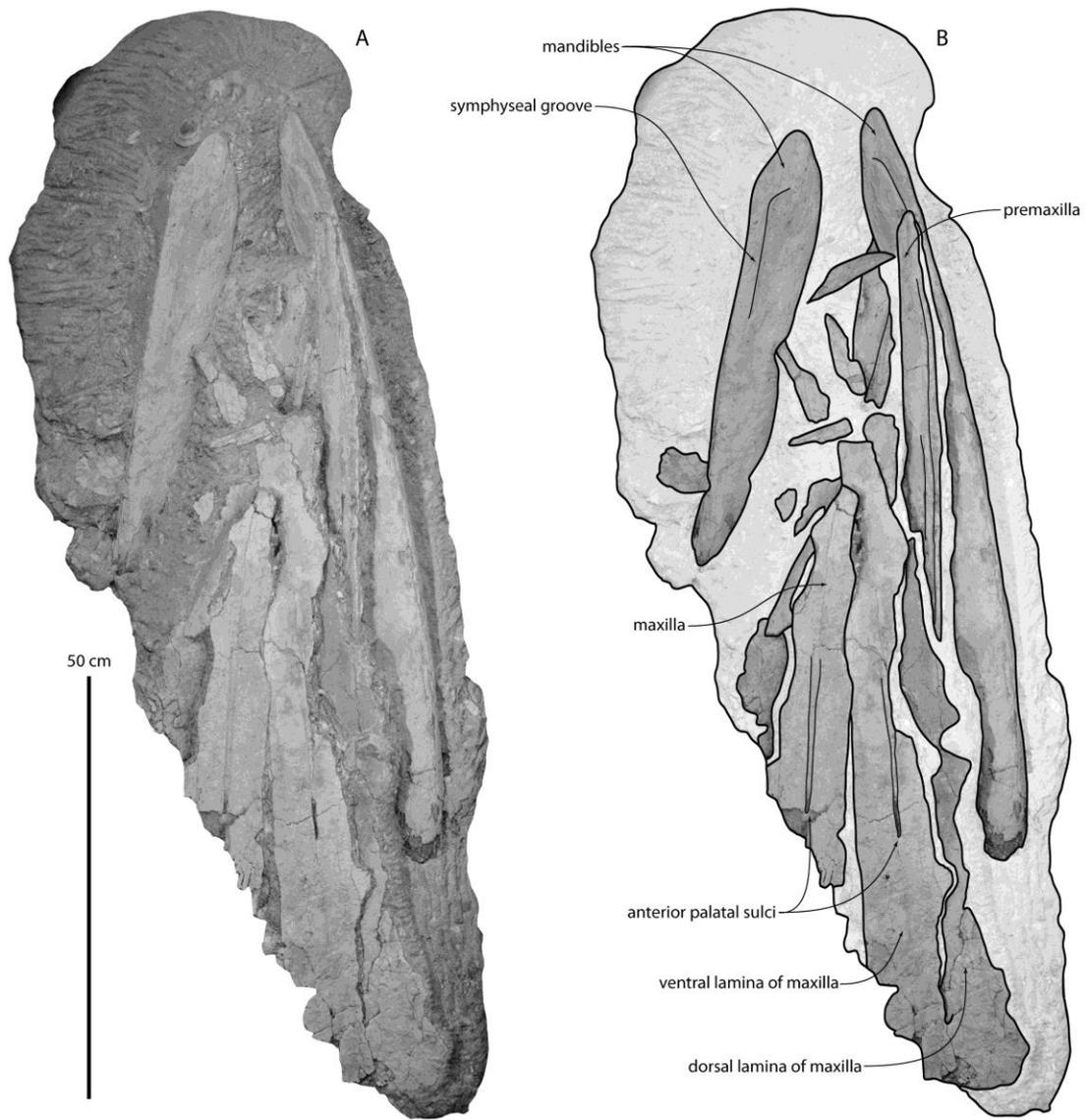
M, anterior, and N, posterior view; articulated thoracic vertebrae in O, lateral

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view.

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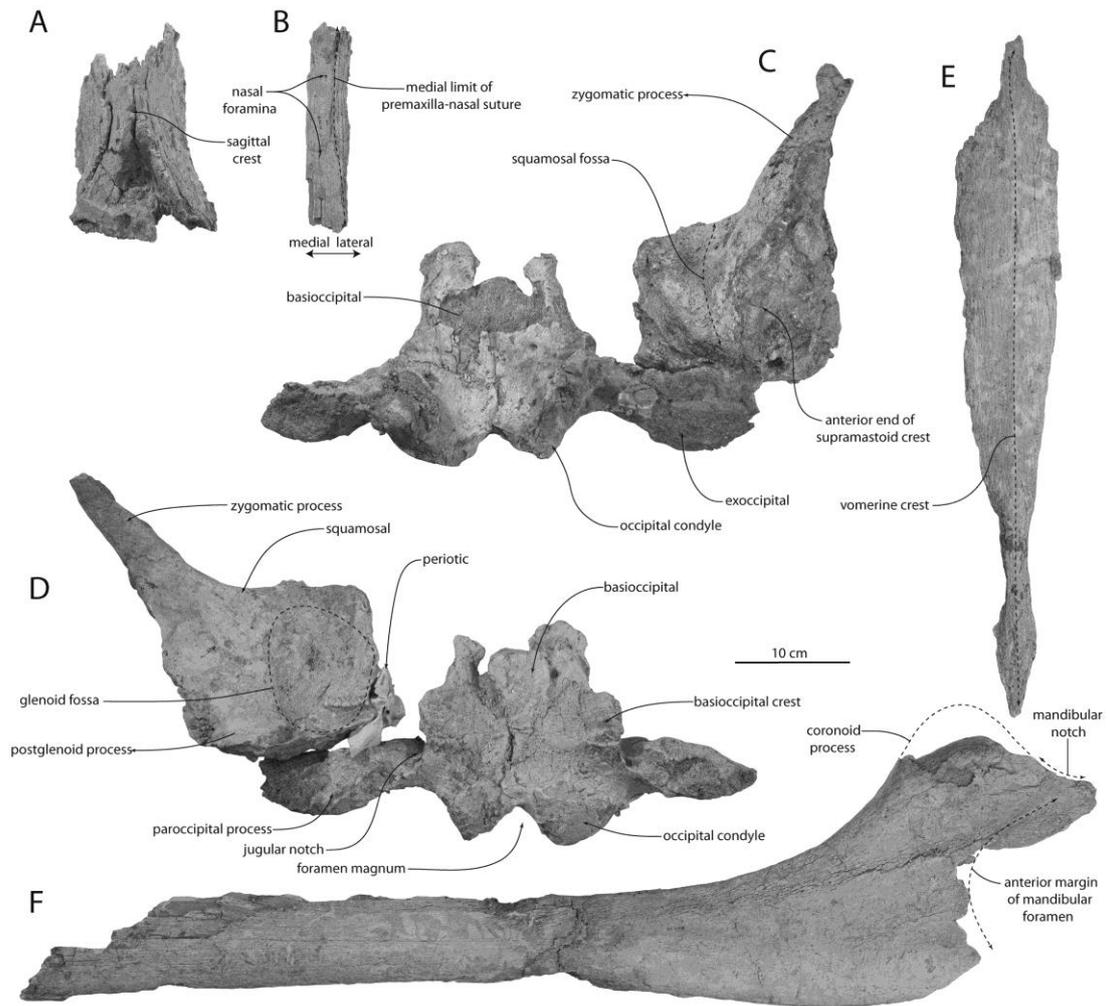
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**Figure 24. Partial rostrum and mandibles *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081) *in situ* within block of matrix. A, photograph, B, interpretive line drawing.**

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**Figure 25. Referred cranial elements and mandible of *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081).**

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**A, fragmentary intertemporal region in dorsal**

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**view; B, right nasal in dorsal view; C, fragmentary basicranium in dorsal view;**

6

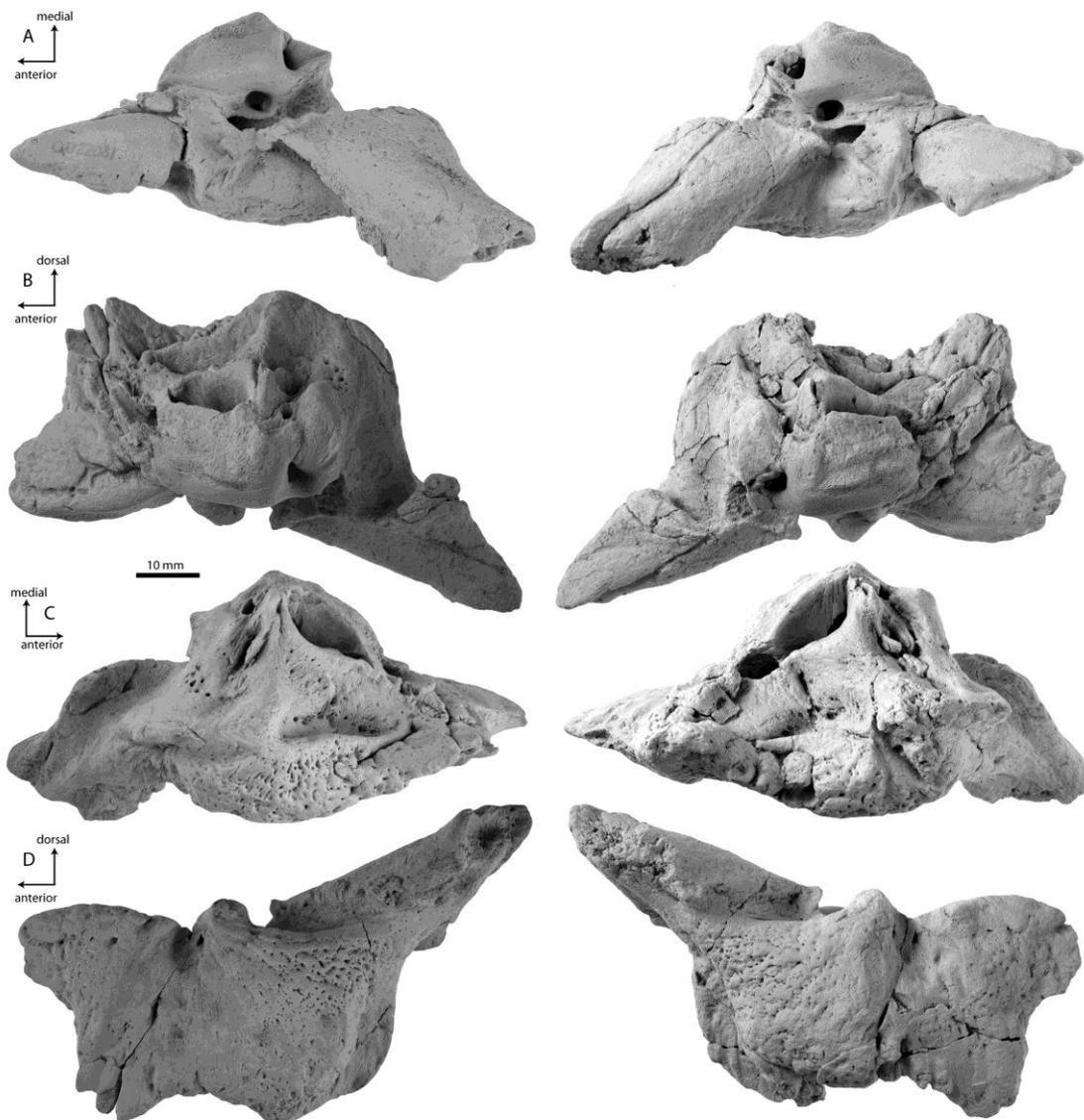
**D, fragmentary basicranium in ventral view; E, vomer in ventral view; F, right**

7

**mandible in medial view.**

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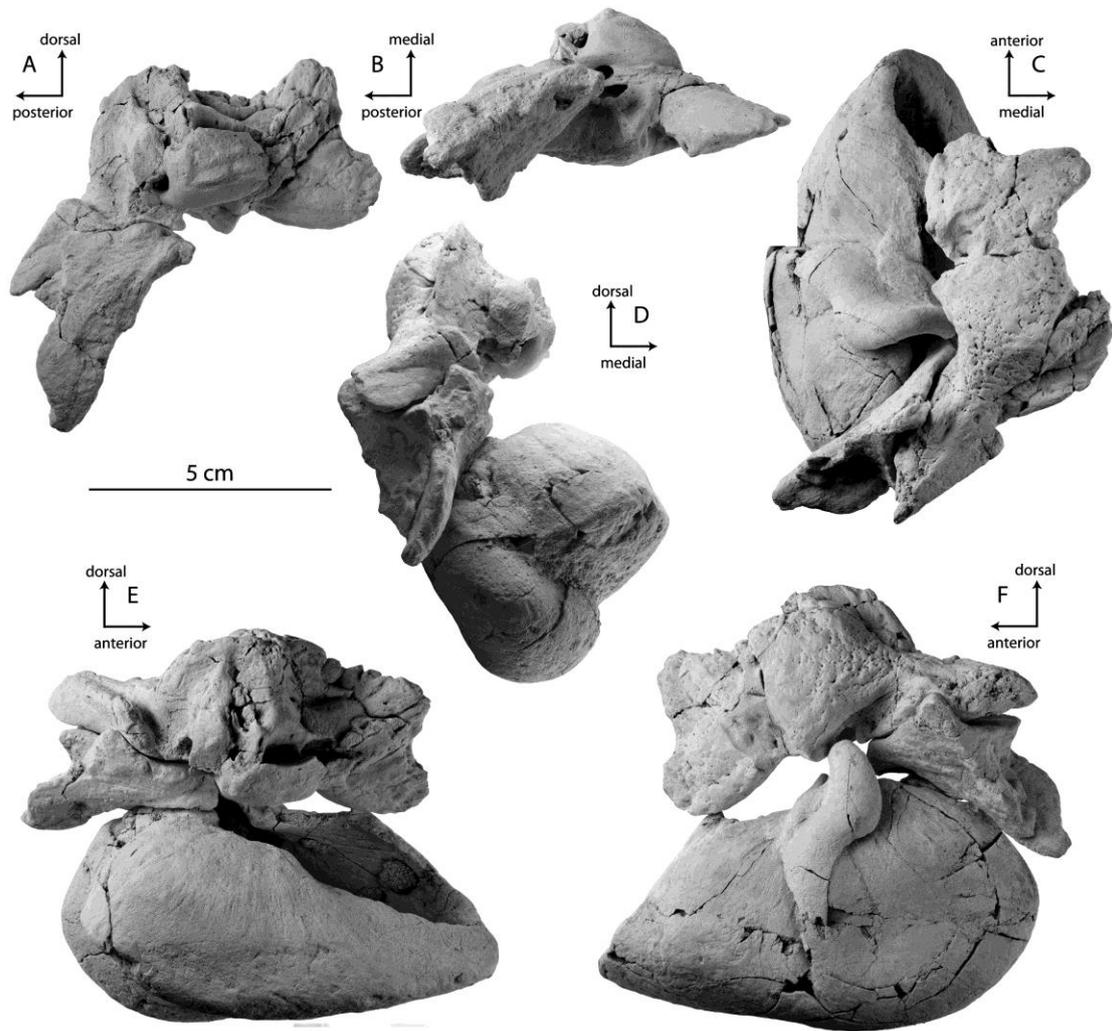
3 **Figure 26. Referred periotic of *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081),**

4 **whitened with ammonium chloride. A, ventral; B, medial; C, dorsal; D,**

5 **lateral.**

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3 **Figure 27. Articulated left tympanoperiotic of *Tokarahia* sp., cf. *T. lophocephalus***

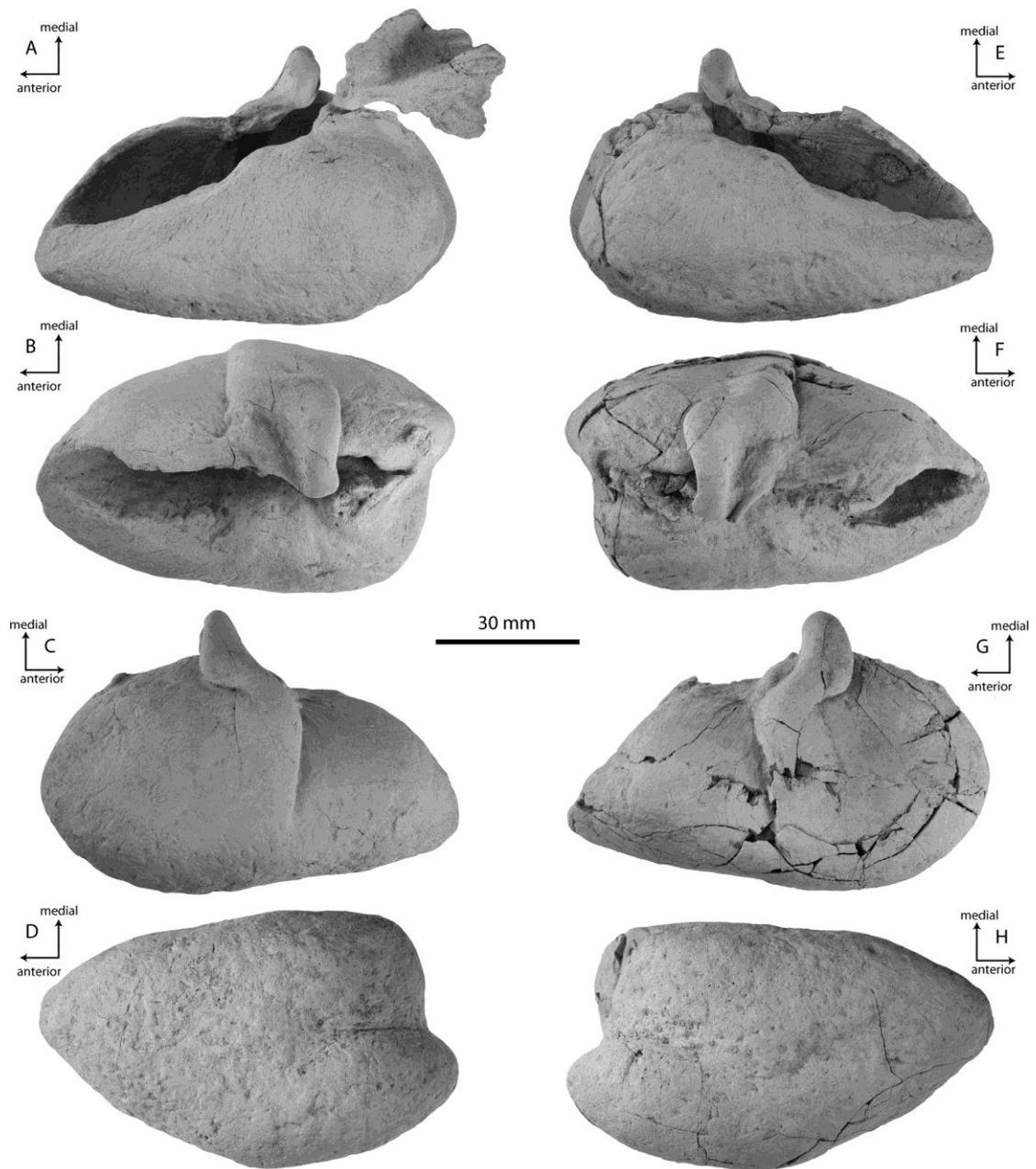
4 **(OU 22081), whitened with ammonium chloride.** Articulated periotic and

5 posterior process of bulla in medial, A; and ventral view, B. Articulated

6 tympanoperiotic in C, dorsal view (relative to bulla); D, posterior view; E,

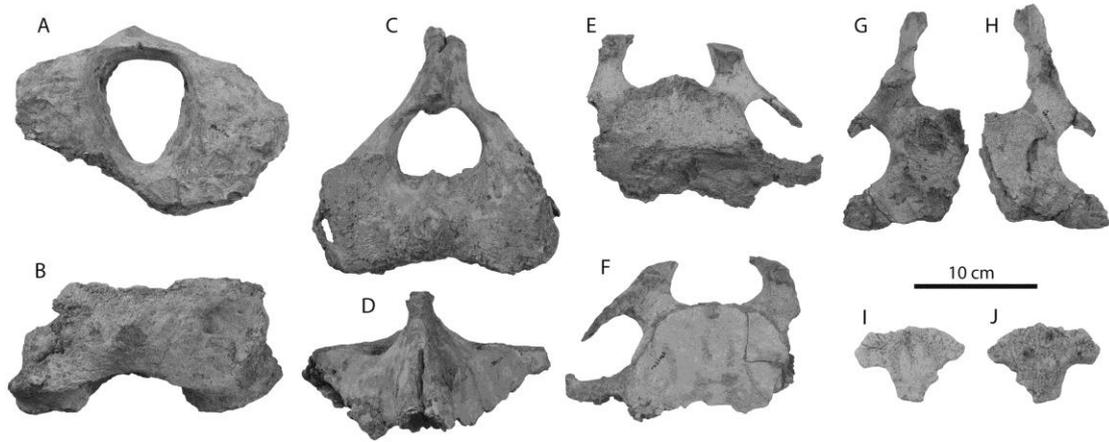
7 medial view (relative to bulla), and F, lateral view (relative to bulla).

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**Figure 28. Referred tympanic bullae of *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081).** Right tympanic bulla in medial view with posterior process, A; dorsal, B; lateral, C; ventral, D; left tympanic bulla in medial view, E; dorsal, F; lateral, G; ventral, H.



1

2 **Figure 29. Vertebrae of *Tokarahia* sp., cf. *T. lophocephalus* (OU 22081). A, atlas**

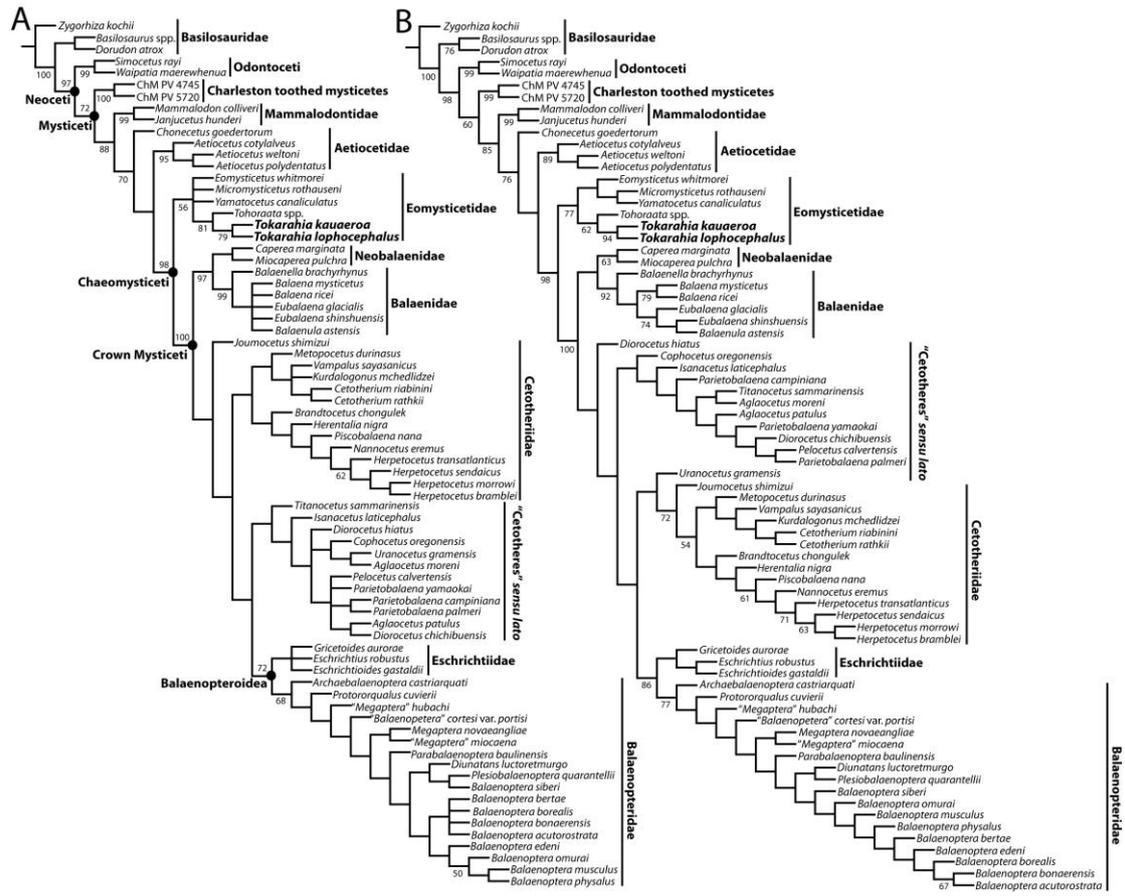
3 in posterior view; B, atlas in dorsal view; C, axis in anterior view; D, axis in

4 dorsal view; E, cervical vertebra in anterior view and F, posterior view; G,

5 partial cervical vertebra in anterior view and H, posterior view; I, sternum in

6 dorsal view and J, ventral view.

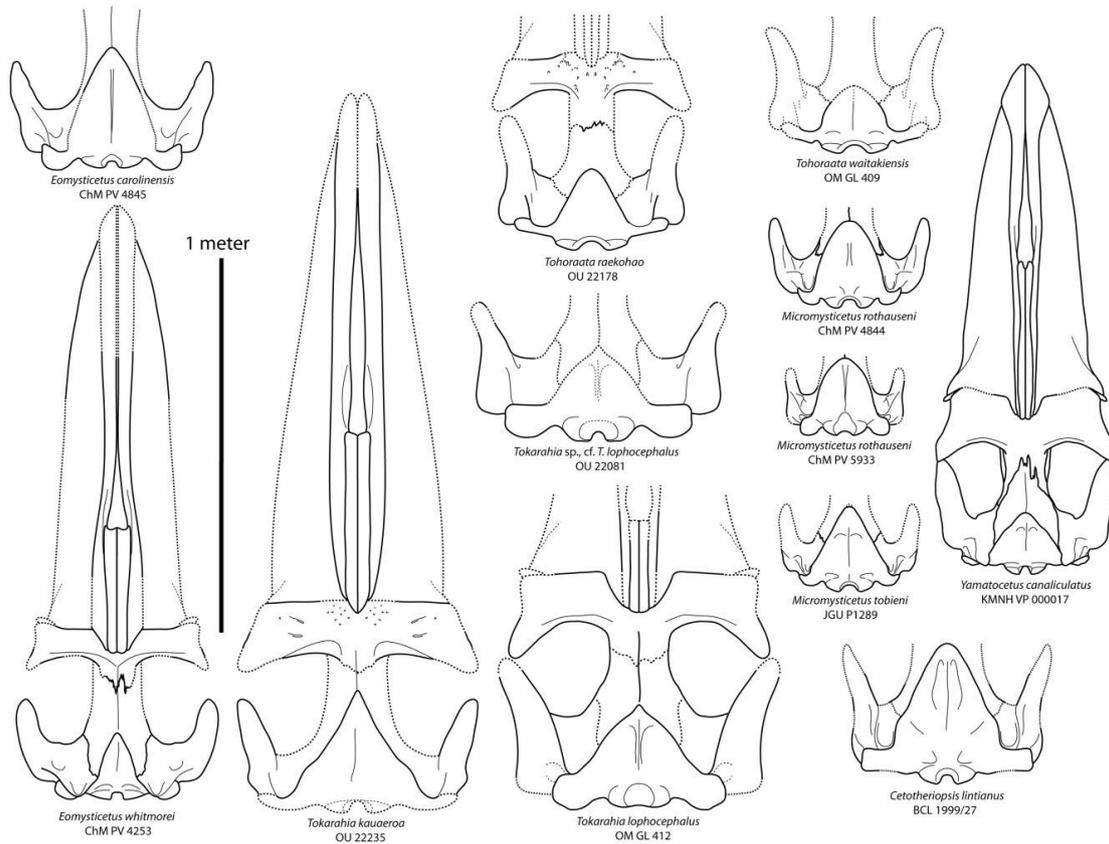
7



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**Figure 30. Phylogenetic relationships of *Tokarahia* and the Eomysticetidae.**

Cladograms shown are strict consensus trees with branch support shown as GC frequency values mapped on. A, strict consensus of 37 equally most parsimonious trees recovered under equal weighting. B, single most parsimonious tree recovered under implied weighting.



1

2 **Figure 31. Interpretive reconstructions of crania of described eomysticetids,**  
 3 **drawn to scale with missing parts indicated by dashed lines and preserved**  
 4 **portions symmetrically flipped. Reconstruction of *Tokarahia lophocephalus***  
 5 **based on published photograph from Marples (1956).**

6





1

2 **Figure 33. Life restoration of *Tokarahia kauaeroa*.** Artwork by Christopher Gaskin,

3                   © Geology Museum, University of Otago.

4

1 Table 1. Cranial measurements of *Tokarahia* spp. (in cm). Measurements to nearest  
 2 millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
 3 incomplete preparation). (e) denotes estimated measurements.  
 4

	<i>Tokarahia kauaeroa</i> (OU 22235)	<i>Tokarahia</i> sp., cf. <i>T. lophocephalus</i> (OU 22081)
Greatest skull length	200 (e)	-
Rostrum, length	140.5*	-
Premaxilla, anteroposterior length	137*	-
Premaxilla, greatest transverse width	5.2	-
Nasal, anteroposterior length	50.4	-
Nasal, greatest transverse width	3.4	-
Frontal, greatest transverse width	56*	-
Frontal, anteroposterior length of medial supraorbital process	14.0	-
Anteroposterior separation of nasals and parietal	12.0	-
Anteroposterior separation of nasals and occipital	18.9	-
Anteroposterior separation of frontal and occipital	7.7	-
Intertemporal region, narrowest transverse width	6.8*	-
Occipital shield, anteroposterior length	30.7	-
Occipital shield, transverse width	28*	-
Exoccipital, greatest transverse width	54	45.2
Temporal fossa, greatest anteroposterior length	31(e)	-
Bizygomatic width	50(e)	64.8
Zygomatic process, length	17.4	17.8
Basioccipital crest, transverse width	-	5(e)
Basioccipital crests, width across crests	-	17.2
Occipital condyles, transverse width across condyles	-	19
Glenoid fossa, maximum diameter	-	14.0
Glenoid fossa, minimum	-	9.8

diameter		
Vomer, anteroposterior length	-	60*

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2

- 1 Table 2. Measurements of periotics of *Tokarahia* (in mm). Measurements given to  
 2 nearest hundredth of a millimeter. Asterisk denotes incomplete measurement (owing  
 3 to breakage or incomplete preparation). (e) denotes estimated measurements.

	<i>T. kauaeroa</i> (OU 22235)	<i>T.sp., cf.</i> <i>T.kauaeroa</i> (OU 21975)	<i>T.</i> <i>lophocephalus</i> (OM GL 412)	<i>T. sp., cf. T.</i> <i>lophocephalus</i> (OU 22081)
Greatest anteroposterior length	83.76	87.51	-	81.63
Length, anteroventral angle to posterodorsal angle	59.49	58.68	-	61.46
Pars cochlearis, anteroposterior length	27.67	26.78	24.75	28.57
Pars cochlearis, dorsoventral depth	21.11	24.13	18.88	20.56
Pars cochlearis, transverse width	10.45	9.95	12.14	13.51
Anteroposterior length of pars cochlearis anterior to fenestra ovalis	15.28	13.95	14.03*	14.35
Anteroposterior length of pars cochlearis anterior to fenestra rotunda	21.31	20.27	18.95*	20.32
Internal acoustic meatus, anteroposterior length	15.87	20.85	-	21.10
Internal acoustic meatus, transverse width	4.98	5.83	8(e)	8.24
Depth of crest between foramen singulare and spiral cribriform tract	7.39	9.5	-	8.72

within meatus				
Stapedial muscle fossa, anteroposterior length	8.39	8.16	-	8.70
Anterior process, greatest length	23.26	23.32	-	23.12
Anterior process, transverse width	13.16	11.90	-	12.91
Distance anteroventral to anterodorsal angle	27.73	28.06	-	33.13
Posterior bullar facet, greatest length	44.53	48.88	-	49.69
Posterior bullar facet, transverse width	20.68	25.48	-	24.53

1

2

1 Table 3. Measurements of bullae of *Tokarahia* (in mm). Measurements given to  
 2 nearest hundredth of a millimeter. Asterisk denotes incomplete measurement (owing  
 3 to breakage or incomplete preparation). Values in bold denote estimated  
 4 measurements.

	<i>T. kauaeroa</i> (OU 22235)	<i>T.</i> <i>lophocephalus</i> (OM GL 412)	<i>T.</i> <i>lophocephalus</i> (OM GL 443)	<i>T. sp., cf. T.</i> <i>lophocephalus</i> (OU 22081)
Anteroposterior length	86.73	89.30	95.61	92.17
Greatest transverse width	53.46	54.16	54.25*	55.98
Involucrum, dorsoventral depth anterior to inner posterior pedicle	35.15	38.87	35.54	40.45
Dorsoventral depth at sigmoid process	55.40	61.88	-	58.80
Anteroposterior length of tympanic cavity anterior to malleus	53.51	56.65	-	52.45
Anteroposterior length, dorsal lateral furrow to posterior edge of lateral lobe	51.48	53.24	-	54.46
Medial lobe, transverse width	22.85	24.85	25.05	22.98
Lateral lobe, transverse width	19.03	25.21	26*	26.32
Distance, posterior elliptical foramen to anterior margin of inner posterior pedicle	19.86	23.33	21.13	20.94
Sigmoid process, transverse width	24.91	27.74	-	24.16

5

6

1 Table 4. Measurements of mandibles of *Tokarahia* (in cm). Measurements given to  
 2 nearest millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
 3 incomplete preparation). Values in bold denote estimated measurements.

	<i>Tokarahia kauaeroa</i> (OU 22235)	<i>Tokarahia</i> sp., cf. <i>T. lophocephalus</i> (OU 22081)
Total length (linear)	184	-
Total length (curvilinear)	186.5	-
Dorsoventral depth at coronoid process	23.4	23.9
Greatest depth at symphysis	-	8.7
Dorsoventral depth of mandibular foramen	-	<b>16.5</b>

4  
 5

1 Table 5. Measurements of atlases of *Tokarahia* (in cm). Measurements given to  
 2 nearest millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
 3 incomplete preparation). Values in bold denote estimated measurements.  
 4

	<i>Tokarahia kuaeroa</i> (OU 22235)	<i>T. lophocephalus</i> (OM GL 412)	<i>Tokarahia</i> sp., cf. <i>T. lophocephalus</i> (OU 22081)
Transverse width of anterior articular facets	20.5	18.0	9.3
Dorsoventral depth of atlas	15.0	16.9	<b>15</b>
Body, anteroposterior length	9.4	7.5	9.6
Neural canal, transverse width	6.4	5.8	6.4
Neural canal, dorsoventral depth	9.3	7.6	7.7
Greatest transverse width	27.2	-	-

5  
6

1 Table 6. Measurements of axes of *Tokarahia* (in cm). Measurements given to nearest  
 2 millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
 3 incomplete preparation). Values in bold denote estimated measurements.  
 4

	<i>Tokarahia kuaeroa</i> (OU 22235)	<i>T. lophocephalus</i> (OM GL 412)	<i>Tokarahia</i> sp., cf. <i>T. lophocephalus</i> (OU 22081)
Greatest transverse width	-	-	-
Anterior articular facets, transverse width	-	17.7	19.4*
Posterior articular surface, transverse width	-	12.8	-
Body, dorsoventral depth (posterior)	8.6	11.5	9.9
Body, anteroposterior length at odontoid	-	8.1	-
Neural canal, transverse width		7.0	8.0
Neural canal, dorsoventral depth		4.4	7.1

5  
 6

1 Table 7. Measurements of seventh cervical vertebra (in cm). Measurements given to  
2 nearest millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
3 incomplete preparation). Values in bold denote estimated measurements.  
4

	<i>Tokarahia kauaeroa</i> (OU 22235)	<i>T. lophocephalus</i> (OM GL 412)
Body, dorsoventral depth	9.5	10.0
Body, transverse width	12.5	12.5
Neural canal, dorsoventral depth	-	6.1
Neural canal, transverse width	4.6	7.8

5  
6

1 Table 8. Measurements of sterna of *Tokarahia* (in cm). Measurements given to  
2 nearest millimeter. Asterisk denotes incomplete measurement (owing to breakage or  
3 incomplete preparation). Values in bold denote estimated measurements.

	<i>Tokarahia kuaeroa</i> (OU 22235)	<i>Tokarahia</i> sp., cf. <i>T. lophocephalus</i> (OU 22081)
Total length	13*	6.3
Transverse width	12.9	8.8

4  
5  
6

1 Table 9. Measurements of forelimb elements of Tokarahia kauaeroa (OU 22235, in  
 2 cm). Measurements given to nearest millimeter. Asterisk denotes incomplete  
 3 measurement (owing to breakage or incomplete preparation). Values in bold denote  
 4 estimated measurements.

Scapula, anteroposterior length	67.0
Scapula, dorsoventral depth	46.5
Distal scapula, anteroposterior length	13.5
Scapula, dorsoventral depth of acromion	6.6
Humerus, total length	38.5
Humerus, anteroposterior width of distal end	11.0
Humerus, transverse width of distal end	5.6
Ulna, total length	43.3
Ulna, total length (to humeral articulation)	35.8
Ulna, transverse width at humeral articulation	4.1
Ulna, anteroposterior length at olecranon	15.1
Ulna, transverse proximodistal length of olecranon	13.7
Radius, total length	37.4

5

6

1 **ELECTRONIC SUPPLEMENTARY INFORMATION**

2  
3 R.W. Boessenecker and R.E. Fordyce. A new genus and species of eomysticetid  
4 (Cetacea: Mysticeti) and a reinterpretation of “*Mauicetus*” *lophocephalus* Marples,  
5 1956: transitional baleen whales from the upper Oligocene of New Zealand.

6 **List of morphological characters used in cladistic analysis.**

7  
8 1. Cranium, length. Modified from Bisconti (2000: 72), Deméré et al. (2005: 83),  
9 Bisconti (2008: 56), Marx (2011: 26), Churchill et al. (2012: 114).

10  
11 0=less than 1/3 body length.

12 1=approximately 1/3 body length.

13  
14 2. Cranium, dorsal profile posterior to orbit. Modified from Bisconti (2005: 63),  
15 Fitzgerald (2010: 55), Churchill et al. (2012: 1), El Adli et al. (2014: 8).

16  
17 0=dorsal edge of skull ascends steeply towards vertex, vertex forms >10° angle  
18 between anterior edge of occipital shield and anterior skull bones

19 1=dorsal edge of skull is low or flat, forming <10° at the vertex

20  
21 3. Cranium, facial plane. Modified from Bisconti (2000: 1, 2), Kimura and Ozawa  
22 (2002: 8), Geisler and Sanders (2003: 63), Dooley et al. (2004: 33), Deméré et al.  
23 (2005: 1), Bouetel and Muizon (2006: 1), Fitzgerald (2006: 65), Bisconti (2008: 33),  
24 Deméré et al. (2008: 1), Fitzgerald (2010: 37), Kimura and Hasegawa (2010: 1),  
25 Churchill et al. (2012: 1, 4), Bisconti et al. (2013: 5, 6), El Adli et al. (2014: 1).

26  
27 0=straight

28 1=concave

29 2=convex

30  
31 4. Premaxilla, anterior part in dorsal aspect. Modified from Fitzgerald (2006: 8),  
32 Geisler and Sanders (2003: 8), Bisconti (2008: 106), Fitzgerald (2010: 6), Kimura and  
33 Hasegawa (2010: 9), Marx (2011: 7), Bisconti et al. (2013: 33), Fordyce and Marx  
34 (2013: 4, 7).

35  
36 0=narrows anteriorly or with parallel margins

37 1=anteriorly widens

38  
39 5. Premaxilla, posterior part in lateral aspect. Modified from Bouetel and Muizon  
40 (2006: 2), Steeman (2007: 14), Marx (2011: 8), Fordyce and Marx (2013: 5).

41  
42 0=shallower dorsoventrally or same depth as anteriorly

43 1=dorsoventrally deeper posteriorly

44  
45 6. Premaxilla, overhang of maxilla. Modified from Kimura and Ozawa (2002: 17),  
46 Geisler and Sanders (2003: 110), Fitzgerald (2006: 9, 100), Bisconti (2008: 128),  
47 Fitzgerald (2010: 49), Marx (2011: 9), Fordyce and Marx (2013: 7).

1  
2 0=do not overhang maxilla adjacent to narial fossa  
3 1=premaxilla overhangs maxilla  
4  
5 7. Premaxilla, premaxillary foramen. Modified from Kimura and Ozawa (2002: 16),  
6 Geisler and Sanders (2003: 69), Fitzgerald (2006: 71), Fitzgerald (2010: 40), Marx  
7 (2011: 43), Bisconti et al. (2013: 32).  
8  
9 0=absent  
10 1=present  
11  
12 8. Premaxilla, posterior extension relative to maxilla. Modified from Bouetel and  
13 Muizon (2006: 18), Fitzgerald (2010: 41), Kimura and Hasegawa (2010: 5), Marx  
14 (2011: 49), Bisconti et al. (2013: 34).  
15  
16 0=anterior to anteriormost supraorbital process of frontal  
17 1=at level of anterior half or midpoint of supraorbital process of frontal  
18 2=at level of posterior half of supraorbital process of frontal  
19  
20 9. Premaxilla, position of inflection in dorsal view. Modified from Geisler and  
21 Sanders (2003: 107, 108), Bouetel and Muizon (2006: 12), Fitzgerald (2006: 98),  
22 Steeman (2007: 6), Bisconti (2008: 81), Deméré et al. (2008: 18), Marx (2011: 53),  
23  
24 0=within posterior half of rostrum  
25 1=at level of anterior edge or anterior half of supraorbital process of frontal  
26 2=at level of posterior half of supraorbital process or postorbital process  
27  
28 10. Premaxilla, cross section of rostral portion. New character.  
29  
30 0=ventrally flat and contiguous with ventral maxilla  
31 1=ventrally concave  
32 2=medially and ventrally concave  
33 3=medially concave, ventrally/laterally convex  
34  
35 11. Premaxilla, exposure in palate. Modified from Fitzgerald (2010: 13), Fordyce and  
36 Marx (2013: 17).  
37  
38 0=present posterior to anteriormost tip of maxilla, medial to maxilla  
39 1=only exposed anterior to maxilla  
40  
41 12. Premaxilla, rostral process. Modified from Bisconti (2000: 10), Geisler and  
42 Sanders (2003: 68), Fitzgerald (2006: 70), Fitzgerald (2010: 39).  
43  
44 0=convex transversely  
45 1=flat or concave, forming premaxillary sac fossa  
46  
47 13. Premaxilla, medial contact of premaxillae along anterior 2/3 of rostrum. Modified  
48 from Geisler and Sanders (2003: 5, 9, 67), Bouetel and Muizon (2006: 22), Fitzgerald  
49 (2006: 10), Fitzgerald (2010: 7), Kimura and Hasegawa (2010: 6), Bisconti et al.  
50 (2013: 13).

1  
2 0=medially fused along most of rostrum  
3 1=separated along most of rostrum, medially fused at anterior tip  
4 2=separated along entire length of rostrum  
5 3=widely separated, greater than or equal to transverse width of premaxilla  
6  
7 14. Premaxilla, posterior end. Modified from Geisler and Sanders (2003: 112),  
8 Fitzgerald (2006: 102), Fitzgerald (2010: 50).  
9  
10 0=faces anterolaterally  
11 1=faces anteriorly  
12 2=faces anteromedially  
13  
14 15. Maxilla, length of rostral portion. Modified from Kimura and Ozawa (2002: 9),  
15 Geisler and Sanders (2003: 3), Deméré et al. (2005: 3), Fitzgerald (2010: 2), Kimura  
16 and Hasegawa (2010: 26), Marx (2011: 1), Churchill et al. (2012: 3), Bisconti et al.  
17 (2013: 1), Fordyce and Marx (2013: 1), El Adli et al. (2014: 3).  
18  
19 0=intermediate, 40-49% of CBL  
20 1=short, <40% of CBL  
21 2=long, >50% of CBL  
22 3=very long, >60% of CBL  
23  
24 16. Maxilla, lateral edge. Modified from Kimura and Ozawa (2002: 12), Geisler and  
25 Sanders (2003: 4), Deméré et al. (2005: 4, 5), Bouetel and Muizon (2006: 6),  
26 Fitzgerald (2006: 4), Deméré and Berta (2008: 45), Deméré et al. (2008: 3, 4),  
27 Fitzgerald (2010: 3), Kimura and Hasegawa (2010: 12, 13), Marx (2011: 3), Churchill  
28 et al. (2012: 7, 10), Bisconti et al. (2013: 26, 27), El Adli et al. (2014: 4).  
29  
30 0=thick lateral edge, >45° in cross section along length of maxilla  
31 1=thin lateral edge posteriorly, <45°, anterior half of maxilla steeper and  
32 approximately 45° or more  
33 2=thin lateral edge along entire maxilla, <45°  
34 3=thin lateral edge posteriorly, transverse width of dorsal surface of maxilla in  
35 anterior half is less than ½ transverse width of ventral surface  
36  
37 17. Maxilla, lateral border anterior to antorbital process. Modified from Fitzgerald  
38 (2006: 3), Bisconti (2008: 107), Marx (2011: 5), Bisconti et al. (2013: 3, 4)  
39  
40 0=straight  
41 1=continuously convex  
42 2=posteriorly parasagittal, anteriorly straight and converging at rostrum tip  
43 3=posterior 3/4 parallel and narrowing in anterior 1/4  
44  
45 18. Maxilla, steep face on antorbital process separating it from rostral portion.  
46 Modified from Geisler and Sanders (2003: 13), Bouetel and Muizon (2006: 9),  
47 Fitzgerald (2006: 14), Bisconti (2008: 7), Deméré and Berta (2008: 39), Fitzgerald  
48 (2010: 10), Kimura and Hasegawa (2010: 16), Marx (2011: 11), Bisconti et al. (2013:  
49 10).  
50

- 1 0=absent  
2 1=present  
3  
4 19. Maxilla, anterior border of antorbital process. Modified from Fitzgerald (2010: 9),  
5 Marx (2010: 12), Fordyce and Marx (2013: 10).  
6  
7 0=maxilla closely approximates or underlies frontal  
8 1=separated by a basin  
9  
10 20. Maxilla, posterior portion. Modified from Kimura and Ozawa (2002: 15), Deméré  
11 et al. (2005: 14), Deméré and Berta (2008: 46), Deméré et al. (2008: 13). Fitzgerald  
12 (2010: 44), Kimura and Hasegawa (2010: 19), Marx (2011: 14), Fordyce and Marx  
13 (2013: 12), El Adli et al. (2014: 16).  
14  
15 0=situated lateral to frontal  
16 1=situated lateral to nasal  
17 2=situated lateral to nasals and premaxilla  
18  
19 21. Maxilla, posterior end of ascending process. Modified from Geisler and Sanders  
20 (2003: 14), Deméré et al. (2005: 20), Bouetel and Muizon (2006: 12), Fitzgerald  
21 (2006: 15), Steeman (2007: 6), Bisconti (2008: 77), Deméré et al. (2008: 18),  
22 Fitzgerald (2010: 43), Kimura and Hasegawa (2010: 20), Marx (2011: 15), Churchill  
23 et al. (2012: 8), Fordyce and Marx (2013: 13), El Adli et al. (2014: 24).  
24  
25 0=lateral edges convergent, process tapers to point  
26 1=lateral edges parallel  
27 2=lateral edges divergent, process transversely expanded at posterior end  
28  
29  
30 22. Maxilla, antorbital notch. Modified from Kimura and Ozawa (2002: 11), Bouetel  
31 and Muizon (2006: 8), Steeman (2007: 16), Bisconti (2008: 80), Kimura and  
32 Hasegawa (2010: 15), Marx (2011: 16), Churchill et al. (2012: 9), Bisconti et al.  
33 (2013: 10, 11), Fordyce and Marx (2013: 9, 14).  
34  
35 0=antorbital notch absent  
36 1=antorbital notch present  
37  
38 23. Maxilla, antorbital process. Modified from Bouetel and Muizon (2006: 10),  
39 Kimura and Hasegawa (2010: 17), Marx (2011: 17), Bisconti et al. (2013: 8, 9, 10,  
40 11).  
41  
42 0= does not extend anterior to notch  
43 1=extends anterior to antorbital notch  
44  
45 24. Maxilla, nutrient foramina and sulci. Modified from Geisler and Sanders (2003:  
46 17), Bouetel and Muizon (2006: 4), Fitzgerald (2006: 18), Steeman (2007: 2), Deméré  
47 and Berta (2008: 16), Deméré et al. (2008: 38), Fitzgerald (2010: 14), Kimura and  
48 Hasegawa (2010: 11), Marx (2011: 20), Churchill et al. (2012: 16), Bisconti et al.  
49 (2013: 12), Fordyce and Marx (2013: 19), El Adli et al. (2014: 50).  
50

- 1 0=absent  
2 1=present  
3  
4 25. Maxilla, geometry of lateral nutrient foramina and sulci. Modified from Deméré et  
5 al. (2005: 41), Deméré et al. (2008: 54), Marx (2011: 45), Churchill et al. (2012: 16),  
6 El Adli et al. (2014: 51).  
7  
8 0=posterior foramina with radially arranged sulci, no associated open maxillary  
9 groove  
10 1=posterior foramina coincide with open maxillary groove  
11 2=foramina restricted to posterior 2/3 of palate, with isolated posterior foramina  
12 without sulci and 1-2 bilateral pairs of large foramina with elongate sulci anteriorly  
13 3=posterior foramina present in two rows without well developed sulci  
14  
15 26. Maxilla, infraorbital plate. Modified from Bisconti (2000: 71), Geisler and  
16 Sanders (2003: 59), Bisconti (2005: 5, 58, 64), Deméré et al. (2005: 17), Bouetel and  
17 Muizon (2006: 7), Fitzgerald (2006: 60), Bisconti (2008: 6, 141), Deméré and Berta  
18 (2008: 29), Deméré et al. (2008: 16), Fitzgerald (2010: 34), Kimura and Hasegawa  
19 (2010: 14), Marx (2011: 39), Churchill et al. (2012: 12, 13), Bisconti et al. (2013:  
20 114), Fordyce and Marx (2013: 30), El Adli et al. (2014: 23).  
21  
22 0=absent  
23 1=present  
24  
25 27. Maxilla, window adjacent to infraorbital plate. Modified from Deméré et al. (2005:  
26 40), Deméré et al. (2008: 37), Marx (2011: 40), Churchill et al. (2012: 14), Fordyce  
27 and Marx (2013: 31), El Adli et al. (2014: 49).  
28  
29 0=absent  
30 1=present  
31  
32 28. Maxilla, angle between anterior margin of supraorbital process of frontal and  
33 ascending process of maxilla. Modified from Bisconti (2000: 26), Kimura and Ozawa  
34 (2002: 13), Geisler and Sanders (2003: 49), Bisconti (2005: 59), Bouetel and Muizon  
35 (2006: 25), Fitzgerald (2006: 50), Steeman (2007: 9), Bisconti (2008: 110, 130),  
36 Kimura and Hasegawa (2010: 24), Marx (2011: 28, 42), Bisconti et al. (2013: 20, 21) ,  
37 Fordyce and Marx (2013: 23).  
38  
39 0=larger than 90°, frontal-maxilla suture trends posteromedially towards vertex  
40 1=larger than 90°, frontal-maxilla suture transverse or trends anteromedially towards  
41 vertex  
42 2= less than 90°  
43  
44 29. Maxilla, posterior edge of ascending process. Modified from Kimura and Ozawa  
45 (2002: 1), Geisler and Sanders (2003: 76), Dooley et al. (2004: 37), Bisconti (2005:  
46 25), Deméré et al. (2005: 16), Bouetel and Muizon (2006: 11), Fitzgerald (2006: 78),  
47 Deméré and Berta (2008: 3), Deméré et al. (2008: 15), Fitzgerald (2010: 42), Kimura  
48 and Hasegawa (2010: 18), Marx (2011: 44), Bisconti et al. (2013: 18), El Adli et al.  
49 (2014: 22).  
50

- 1 0=at level of anterior half of supraorbital process of frontal or in line with halfway  
2 point  
3 1=at level of posterior half or at position of postorbital process  
4 2=extends posterior to postorbital process  
5 3=well anterior to orbit  
6  
7 30. Maxilla, posterior edge of ascending process. Modified from Marx (2011: 47).  
8  
9 0=anterior to orbitotemporal crest  
10 1=posterior to anteriormost point of orbitotemporal crest  
11  
12 31. Maxilla, medial contact of ascending processes. Modified from Bouetel and  
13 Muizon (2006: 13), Kimura and Hasegawa (2010: 22), Marx (2011: 48), Bisconti et al.  
14 (2013: 23), Fordyce and Marx (2013: 34).  
15  
16 0=absent, maxillae widely separated  
17 1=processes contacting at tips or nearly contacting  
18 2=long medial contact of ascending processes, anteroposteriorly longer than dorsal  
19 exposure of nasal  
20  
21 32. Maxilla, posterior border of ascending process. Modified from Marx (2011: 50).  
22  
23 0=transversely oriented or medial corner more posterior  
24 1=lateral corner more posterior  
25  
26 33. Maxilla, posterior border of ascending process. Modified from Geisler and  
27 Sanders (2003: 14), Bouetel and Muizon (2006: 12), Fitzgerald (2006: 15), Steeman  
28 (2007: 6), Bisconti (2008: 81), Deméré et al. (2008: 18), Marx (2011: 51), Bisconti et  
29 al. (2013: 18).  
30  
31 0=pointed or rounded  
32 1=squared off  
33  
34 34. Maxilla, ascending process in dorsal aspect. Modified from Geisler and Sanders  
35 (2003: 129), Steeman (2007: 7), Bouetel and Muizon (2006: 21), Marx (2011: 60),  
36 Bisconti et al. (2013: 24).  
37  
38 0=posteriormost point anterior to supraoccipital  
39 1=posterior to anteriormost point of supraoccipital  
40  
41 35. Maxilla and Mandible, open alveolar groove. New character.  
42  
43 0=dentition present, not implanted in alveolar groove  
44 1=alveolar groove developed (dentition absent or present)  
45 2=dentition and alveolar groove absent  
46  
47 36. Maxilla, dorsal infraorbital foramina. Modified from Kimura and Ozawa (2002:  
48 14), Geisler and Sanders (2003: 64), Fitzgerald (2006: 66), Fitzgerald (2010: 38),  
49 Churchill et al. (2012: 11).  
50

- 1 0=single  
2 1=two  
3 2=three or more  
4  
5 37. Maxilla, foramina in ascending process. New character.  
6  
7 0=foramina absent  
8 1=large dorsally oriented foramen or pair of foramina in ascending process  
9  
10 38. Maxilla, relative position of posterior edge. Modified from Bouetel and Muizon  
11 (2006: 14), Fitzgerald (2006: 80), Deméré and Berta (2008: 38), Bisconti et al. (2013:  
12 22), Fordyce and Marx (2013: 35).  
13  
14 0=at level of or posterior to posterior edge of nasal  
15 1=anterior to posterior edge of nasal  
16  
17 39. Maxilla, development of ascending process. Modified from Bisconti (2005: 23).  
18  
19 0=short, approximately as long as wide  
20 1=absent or indistinct, transversely wider than long or not clearly differentiated from  
21 rostral portion of maxilla  
22 2=long and narrow, approximately twice as long as wide or longer  
23  
24 40. Rostrum, proximal portion in lateral aspect. Modified from Bisconti (2008: 142),  
25 Marx (2011: 2), Fordyce and Marx (2013: 2).  
26  
27 0=below SOS and frontal  
28 1=at or above level of SOS and frontal  
29  
30 41. Rostrum, curvature in lateral aspect. Modified from Bisconti (2005: 62), Bisconti  
31 (2008: 139), Marx (2011: 4), Bisconti et al. (2013: 7).  
32  
33 0=regular  
34 1=anterior 1/4 abruptly deflected ventrally  
35  
36 42. Rostrum, width at antorbital notch. Modified from Geisler and Sanders (2003: 7),  
37 Deméré et al. (2005: 2), Fitzgerald (2006: 7), Bisconti (2008: 67), Deméré and Berta  
38 (2008: 1, 40), Deméré et al. (2008: 2), Fitzgerald (2010: 5), Kimura and Hasegawa  
39 (2010: 4), Marx (2011: 6), Churchill et al. (2012: 2), Bisconti et al. (2013: 2), El Adli  
40 et al. (2014: 2).  
41  
42 0=wide, 40-54% of BZW  
43 1=narrow, <40% of BZW  
44 2=very wide, >55% of BZW  
45  
46 43. Rostrum, posterior rostral edge in dorsal aspect. Modified from Geisler and  
47 Sanders (2003: 11), Fitzgerald (2006: 12), Deméré et al. (2008: 78), Marx (2011: 10),  
48 Bisconti et al. (2013: 11), El Adli et al. (2014: 25).  
49  
50 0=straight or gently concave

1 1=bowed laterally forming V or U shaped antorbital notch  
2  
3 44. Rostrum, maxilla-frontal contact. Modified from Deméré et al. (2008: 17),  
4 Fitzgerald (2010: 9), Kimura and Hasegawa (2010: 27), Marx (2011: 13), Bisconti et  
5 al. (2013: 29, 31), Fordyce and Marx (2013: 11).  
6  
7 0=maxilla and frontal contact along ankylosed suture  
8 1=frontal-maxilla contact is loose, groove developed  
9 2=contact is loose with large vertical gap or pocket present anteromedially  
10  
11 45. Rostrum, palatal surface. Modified from Geisler and Sanders (2003: 16), Deméré  
12 et al. (2005: 39), Bouetel and Muizon (2006: 5), Fitzgerald (2006: 17), Steeman (2007:  
13 23), Bisconti (2008: 25), Deméré and Berta (2008: 41), Deméré et al. (2008: 36),  
14 Fitzgerald (2010: 12), Kimura and Hasegawa (2010: 3, 33), Marx (2011: 18),  
15 Churchill et al. (2012: 5), Fordyce and Marx (2013: 15, 16), El Adli et al. (2014: 48).  
16  
17 0=flat or gently concave  
18 1=longitudinal keel formed by vomer and maxilla present, gently rounded in cross  
19 section and confined to posterior ½ of palate  
20 2=longitudinal keel present, narrow and sharp in cross section and present along at  
21 least ¾ of rostrum  
22  
23 46. Rostrum, maxilla/palatine suture in ventral aspect. Modified from Geisler and  
24 Sanders (2003: 20), Deméré et al. (2005: 43), Fitzgerald (2006: 21), Deméré et al.  
25 (2008: 40), Kimura and Hasegawa (2010: 32), Marx (2011: 21), Churchill et al. (2012:  
26 29), Fordyce and Marx (2011: 20).  
27  
28 0=straight and transverse or anteriorly bowed  
29 1=V-shaped suture with maxillae medially separating palatines  
30  
31 47. Rostrum, anterior edge of narial fossa. Modified from Bisconti (2000: 4), Deméré  
32 et al. (2005: 7), Deméré and Berta (2008: 35), Marx (2011: 22).  
33  
34 0=located in posterior 3/4 of rostrum  
35 1=located in anterior 1/4 of rostrum  
36  
37 48. Rostrum, lateral aspect. Modified from Bouetel and Muizon (2006: 2), Steeman  
38 (2007: 14), Fitzgerald (2010: 47), Kimura and Hasegawa (2010: 2, 7? ), Marx (2011:  
39 23), Fordyce and Marx (2013: 21), El Adli et al. (2014: 5).  
40  
41 0=step-like profile, depressed anterior to nasals  
42 1=smooth profile  
43  
44 49. Rostrum, shape. Modified from Marx (2011: 24), Bisconti et al. (2013: 2)  
45  
46 0=narrow, width at antorbital notches <80% of rostrum length  
47 1=broad, width >80% of rostrum length  
48  
49 50. Rostrum, geometry of cranial and rostral element contact. Modified from Bisconti  
50 (2008: 140), Marx (2011: 52).

- 1  
2 0=smooth or angular transition  
3 1=two sets of bones form distinct apex  
4  
5 51. Rostrum, fusion of maxilla-premaxilla suture. Modified from Geisler and Sanders  
6 (2003: 10), Deméré et al. (2005: 6), Fitzgerald (2006: 11), Deméré and Berta (2008:  
7 44), Deméré et al. (2008: 5), Fitzgerald (2010: 8), Kimura and Hasegawa (2010: 25),  
8 El Adli et al. (2014: 6).  
9  
10 0=firmly ankylosed  
11 1=firmly ankylosed, deep longitudinal groove present  
12 2=not sutured  
13  
14 52. Rostrum, embrasure pits on palate. New character.  
15  
16 0=present  
17 1=absent  
18  
19 53. Rostrum, scalloped edge on maxilla and premaxilla. New character.  
20  
21 0=present  
22 1=absent  
23  
24 54. Vomer, exposure in palate. Modified from Deméré and Berta (2008: 13), Deméré  
25 et al. (2008: 96), Fitzgerald (2010: 15), Marx (2011: 19), Fordyce and Marx (2013:  
26 18), El Adli et al. (2014: 55).  
27  
28 0=not exposed  
29 1=exposed in palatal window  
30  
31 55. Vomer, ventral border in ventral view. Modified from Bisconti (2005: 40),  
32 Deméré et al. (2005: 44), Deméré et al. (2008: 41), Churchill et al. (2012: 33),  
33 Fordyce and Marx (2013: 78), El Adli et al. (2014: 53).  
34  
35 0=posteriormost portion projects beyond posterior tips of palatine and is visible in  
36 ventral view  
37 1=completely covered by palatine  
38  
39 56. Lacrimal, dorsal aspect. Modified from Geisler and Sanders (2003: 50), Deméré et  
40 al. (2005: 21), Fitzgerald (2006: 51), Bisconti (2008: 165), Deméré and Berta (2008:  
41 12), Deméré et al. (2008: 19), Fitzgerald (2010: 11, 121), Marx (2011: 38), Bisconti et  
42 al. (2013: 45), El Adli et al. (2014: 67).  
43  
44 0=entirely lateral to ascending maxilla  
45 1=extends medially between ascending maxilla and rostral portion of maxilla  
46  
47 57. Lacrimal, articulation with maxilla and frontal. New character.  
48  
49 0=sutured to maxilla and frontal  
50 1=unsutured

- 1  
2 58. Nasal, lateral edges anterior to preorbital process. Modified from Bouetel and  
3 Muizon (2006: 19), Fitzgerald (2010: 52), Kimura and Hasegawa (2010: 38), Bisconti  
4 et al. (2013: 41), El Adli et al. (2014: 19).  
5  
6 0=converge anteriorly  
7 1=parallel  
8 2=diverge anteriorly  
9
- 10 59. Nasal, length. Modified from Bisconti (2000: 13), Deméré et al. (2005: 8),  
11 Deméré et al. (2008: 7), Kimura and Hasegawa (2010: 40), Marx (2011: 54),  
12 Churchill et al. (2012: 17), Bisconti et al. (2013: 43), Fordyce and Marx (2013: 36), El  
13 Adli et al. (2014: 10).  
14  
15 0=long, >40% BZW  
16 1=short, <40% BZW  
17 2=very long, >65% BZW  
18
- 19 60. Nasal, posterior edge. Modified from Kimura and Ozawa (2002: 26), Geisler and  
20 Sanders (2003: 122), Deméré et al. (2005: 13), Fitzgerald (2006: 112), Bisconti (2008:  
21 111), Deméré and Berta (2008: 28), Deméré et al. (2008: 12), Fitzgerald (2010: 54),  
22 Marx (2011: 55), Bisconti et al. (2013: 57), Fordyce and Marx (2013: 41), El Adli et  
23 al. (2014: 17).  
24  
25 0=at level of anterior half of supraorbital process or halfway point  
26 1=at level of posterior half of supraorbital process or postorbital process  
27 2=posterior to postorbital process  
28 3=just anterior to supraorbital process  
29
- 30 61. Nasals, dorsal profile of anterior tip. New character.  
31  
32 0=flat  
33 1=anterodorsally flaring  
34
- 35 62. Nasals, transverse arching. New character.  
36  
37 0=nasals and premaxillae transversely arched  
38 1=nasals and adjacent rostral elements dorsally flat in cross section  
39
- 40 63. Nasal, longitudinal foramina. New character.  
41  
42 0=absent  
43 1=present  
44
- 45 64. Nasals, anterior edge. Modified from Fitzgerald (2010: 72), Bisconti et al. (2013:  
46 38), El Adli et al. (2014: 9).  
47  
48 0=in line with p1 or anterior 4/5 of rostrum  
49 1=in line with p2 or posterior 1/5 of rostrum  
50 2=just anterior or at level of anterior edge of supraorbital process

1 3=in line with anterior half or midpoint of supraorbital process  
2  
3 65. Nasal, posterior portion. Modified from Bisconti et al. (2013: 40), Fordyce and  
4 Marx (2013: 37), El Adli et al. (2014: 18).  
5  
6 0=blocky or triangular with medially converging lateral margins  
7 1=transversely thin sheet barely exposed dorsally  
8  
9 66. Nasal, dorsal surface. Modified from Deméré et al. (2005: 12), Deméré et al.  
10 (2008: 11), Kimura and Hasegawa (2010: 43), Churchill et al. (2012: 22), Bisconti et  
11 al. (2013: 44), Fordyce and Marx (2013: 39), El Adli et al. (2014: 15).  
12  
13 0=flattened  
14 1=forms sagittal keel  
15  
16 67. Nasal, anterior margin. Modified from Deméré et al. (2005: 10), Fitzgerald (2006:  
17 106), Bisconti (2008: 100), Deméré et al. (2008: 9), Kimura and Hasegawa (2010: 42),  
18 Churchill et al. (2012: 20), Bisconti et al. (2013: 42), Fordyce and Marx (2013: 38), El  
19 Adli et al. (2014: 13).  
20  
21 0=roughly straight or U shape  
22 1=forms posteriorly pointing W shape  
23 2=with point on midline and gap between nasal and premaxilla  
24  
25  
26 68. Orbit, anteroposterior diameter. Modified from Marx (2011: 27).  
27  
28 0= <25% BZW  
29 1= >25% BZW  
30  
31 69. Orbit, dorsal edge in dorsal aspect. Modified from Kimura and Ozawa (2002: 5),  
32 Bouetel and Muizon (2006: 30, 34), Deméré and Berta (2008: 6), Kimura and  
33 Hasegawa (2010: 52), Marx (2011: 35).  
34  
35 0=roughly straight or slightly concave  
36 1=deeply notched  
37  
38 70. Orbit, dorsal edge relative to lateral edge of rostrum. Modified from Geisler and  
39 Sanders (2003: 47), Bouetel and Muizon (2006: 33), Fitzgerald (2006: 48), Kimura  
40 and Hasegawa (2010: 53), Marx (2011: 37), Fordyce and Marx (2013: 28).  
41  
42 0=orbit elevated above rostrum edge  
43 1=orbit low, in line with edge or slightly above  
44 2=below rostrum edge  
45  
46 71. Frontal, posterior margin of supraorbital process. Modified from Geisler and  
47 Sanders (2003: 60), Bouetel and Muizon (2006: 29), Fitzgerald (2006: 61), Fitzgerald  
48 (2010: 35), Kimura and Hasegawa (2010: 50), Marx (2011: 30), Bisconti et al. (2013:  
49 49), Fordyce and Marx (2013: 24).  
50

- 1 0=concave  
2 1=straight  
3  
4 72. Frontal, supraorbital process. Modified from Bisconti (2000: 25), Kimura and  
5 Ozawa (2002: 3), Geisler and Sanders (2003: 46), Dooley et al. (2004: 29), Bisconti  
6 (2005: 20), Deméré et al. (2005: 25), Bouetel and Muizon (2006: 28), Fitzgerald  
7 (2006: 47), Steeman (2007: 11), Bisconti (2008: 24), Deméré and Berta (2008: 31),  
8 Deméré et al. (2008: 23), Fitzgerald (2010: 32), Kimura and Hasegawa (2010: 49),  
9 Marx (2011: 31), Churchill et al. (2012: 24?, 25?, 26), Bisconti et al. (2013: 46),  
10 Fordyce and Marx (2013: 25), El Adli et al. (2014: 32).  
11  
12 0=horizontal  
13 1=gradually slope ventrolaterally from vertex  
14 2=abruptly depressed below vertex  
15  
16 73. Frontal, anterior border of supraorbital process in dorsal aspect. Modified from  
17 Marx (2011: 32),  
18  
19 0=bordered by lacrimal and maxilla  
20 1=bordered by lacrimal only  
21  
22 74. Frontal, supraorbital process in dorsal aspect. Modified from Deméré et al. (2005:  
23 24), Bouetel and Muizon (2006: 26), Steeman (2007: 10), Bisconti (2008: 108, 152),  
24 Deméré et al. (2008: 22), Fitzgerald (2010: 31), Marx (2011: 33), Bisconti et al. (2013:  
25 50).  
26  
27 0=medial portion as long as lateral portion  
28 1=medial portion distinctly shorter, SOPF is triangular  
29 2=medial portion longer than lateral  
30  
31 75. Frontal, anteroposterior length of supraorbital process. Modified from Kimura and  
32 Ozawa (2002: 6, 7), Bisconti (2005: 18), Bouetel and Muizon (2006: 27), Steeman  
33 (2007: 19), Bisconti (2008: 2), Deméré and Berta (2008: 22), Kimura and Hasegawa  
34 (2010: 48), Marx (2011: 34), Bisconti et al. (2013: 47, 48), Fordyce and Marx (2013:  
35 26), El Adli et al. (2014: 29).  
36  
37 0=roughly as long as wide  
38 1=wider than long  
39 2=more than twice as long as wide  
40  
41  
42 76. Frontal, position of line joining anteriormost points of supraorbital process.  
43 Modified from Geisler and Sanders (2003: 80), Bouetel and Muizon (2006: 23),  
44 Fitzgerald (2006: 83), Steeman (2007: 4), Bisconti (2008: 112), Deméré et al. (2008:  
45 6), Kimura and Hasegawa (2010: 39), Marx (2011: 36), Fordyce and Marx (2013: 27).  
46  
47 0=passing through nasals  
48 1=posterior to or at posterior edge of nasals  
49 2=at anterior edge of nasals  
50 3=anterior to nasals

1  
2  
3 77. Frontal, anteromedial corner of supraorbital process. Modified from Marx (2011:  
4 41), Fordyce and Marx (2013: 32).  
5  
6 0=lacks anterior projection  
7 1=triangular projection present  
8  
9 78. Frontal, maxilla/frontal overlap. Modified from Kimura and Ozawa (2002: 1),  
10 Geisler and Sanders (2003: 12, 76, 127), Dooley et al. (2004: 37), Deméré et al. (2005:  
11 18), Fitzgerald (2006: 13, 78, 117), Deméré and Berta (2008: 3), Deméré et al. (2008:  
12 17), Kimura and Hasegawa (2010: 23), Marx (2011: 44), Churchill et al. (2012: 15),  
13 Fordyce and Marx (2013: 42).  
14  
15 0=maxilla overlaps anteromedial corner of supraorbital process of frontal  
16 1=maxilla almost completely overlaps frontal  
17  
18 79. Frontal, orbitotemporal crest. Modified from Bisconti (2000: 34), Geisler and  
19 Sanders (2003: 131), Bisconti (2005: 3, 57), Bouetel and Muizon (2006: 24),  
20 Fitzgerald (2006: 121), Steeman (2007: 19), Bisconti (2008: 3, 19, 90), Deméré and  
21 Berta (2008: 43), Deméré et al. (2008: 79), Kimura and Hasegawa (2010: 46), Marx  
22 (2011: 56), Churchill et al. (2012: 23), Bisconti et al. (2013: 51, 52), Fordyce and  
23 Marx (2013: 43), El Adli et al. (2014: 33).  
24  
25 0=forms posterior margin of supraorbital process  
26 1=anteriorly retracted from posterior margin, within posterior 50% of SOPF  
27 2=positioned within anterior 50% of SOPF  
28 3=indistinct  
29  
30 80. Frontal, orbitotemporal crest, shape. Modified from Bisconti (2008: 151), Marx  
31 (2011: 57), Bisconti et al. (2013: 52), Fordyce and Marx (2013: 44).  
32  
33 0=straight  
34 1=distal half abruptly projecting posterolaterally  
35  
36 81. Frontal, supraorbital process. New character.  
37  
38 0=foramina absent  
39 1=numerous foramina and sulci present on dorsal surface  
40  
41 82. Frontal, triangular extension of frontal anteriorly separating nasals. Modified from  
42 Geisler and Sanders (2003: 121), Deméré et al. (2005: 11), Bouetel and Muizon (2006:  
43 20), Fitzgerald (2006: 111), Deméré et al. (2008: 10), Fitzgerald (2010: 53), Kimura  
44 and Hasegawa (2010: 45), Churchill et al. (2012: 21), Fordyce and Marx (2013: 40),  
45 El Adli et al. (2014: 14).  
46  
47 0=present  
48 1=absent  
49

- 1 83. Frontal, preorbital process. Modified from Fitzgerald (2010: 33), El Adli et al.  
2 (2014: 30).  
3  
4 0=anterior edge of preorbital process has squared off or slightly concave margin  
5 1=rounded off, anteriorly convex margin  
6  
7 84. Frontal, postorbital ridge. Modified from Geisler and Sanders (2003: 62),  
8 Fitzgerald (2006: 64), Fitzgerald (2010: 36).  
9  
10 0=present, forms well defined ridge posterior to optic canal  
11 1=no well defined ridge, smoothly convex surface  
12  
13 85. Frontal, position of optic groove. Modified from Bisconti et al. (2013: 115).  
14 0=positioned about anteromedial midpoint of supraorbital process  
15 1=positioned in posterior 1/3 of supraorbital process  
16  
17  
18 86. Frontal, height relative to nasals. Modified from Geisler and Sanders (2003: 124),  
19 Bisconti (2005: 19), Fitzgerald (2006: 114), Fitzgerald (2010: 56), Churchill et al.  
20 (2012: 25).  
21  
22 0=higher than nasals  
23 1=same height as nasals  
24  
25 87. Frontal, orbitotemporal crest roofs over entire temporal fossa. Modified from  
26 Fitzgerald (2006: 122), Fitzgerald (2010: 58).  
27  
28 0=absent  
29 1=present  
30  
31 88. Cranium, shape of temporal fossa. Modified from Bisconti (2000: 30, 31), Bouetel  
32 and Muizon (2006: 32), Steeman (2007: 12), Kimura and Hasegawa (2010: 77), Marx  
33 (2011: 58), Fordyce and Marx (2013: 45).  
34  
35 0=longer than wide, or roughly equidimensional  
36 1=wider than long  
37  
38 89. Parietal, intertemporal constriction. Modified from Bisconti (2000: 32), Bisconti  
39 (2005: 31), Fitzgerald (2006: 127), Bisconti (2008: 126), Deméré and Berta (2008: 8),  
40 Kimura and Hasegawa (2010: 59, 60), Marx (2011: 59), Bisconti et al. (2013: 63, 69,  
41 70), Fordyce and Marx (2013: 46), El Adli et al. (2014: 31).  
42  
43 0=longer anteroposteriorly than transversely wide, straight medial margins of  
44 temporal fossae  
45 1=longer anteroposteriorly than transversely wide, concave medial margins of  
46 temporal fossae  
47 2=wider transversely than long  
48

- 1 90. Parietal and interparietal. Modified from Bisconti (2008: 22), Deméré and Berta  
2 (2008: 4), Deméré et al. (2008: 95), Marx (2010: 61), Bisconti et al. (2013: 77),  
3 Fordyce and Marx (2013: 47).  
4  
5 0=anteriormost point behind supraorbital process of frontal or at level of postorbital  
6 process  
7 1=anteriormost point in line with supraorbital process  
8  
9 91. Parietal, dorsal aspect. Modified from Bisconti (2000: 41), Geisler and Sanders  
10 (2003: 134), Deméré et al. (2005: 27), Bouetel and Muizon (2006: 35), Fitzgerald  
11 (2006: 124), Bisconti (2008: 34, 74), Deméré et al. (2008: 25), Fitzgerald (2010: 59),  
12 Kimura and Hasegawa (2010: 55, 59), Marx (2011: 62), Churchill et al. (2012: 36),  
13 Bisconti et al. (2014: 78), El Adli et al. (2014: 34).  
14  
15 0=contact medially or separated by interparietal  
16 1=present in skull roof as small triangular exposures in intertemporal constriction  
17 2=completely absent in skull roof  
18  
19 92. Parietal and Interparietal, anteriormost point. Modified from Kimura and Ozawa  
20 (2002: 28), Geisler and Sanders (2003: 133), Deméré et al. (2005: 22), Fitzgerald  
21 (2006: 123), Bisconti (2008: 163), Marx (2011: 63), Deméré et al. (2008: 20), Kimura  
22 and Hasegawa (2010: 21), Bisconti et al. (2013: 56, 76), Fordyce and Marx (2013: 49),  
23 El Adli et al. (2014: 27).  
24  
25 0=posterior to or at position of posteriormost ascending maxilla  
26 1=more anterior  
27  
28 93. Parietal, intertemporal constriction. Modified from Bisconti (2000: 33), Fitzgerald  
29 (2006: 126), Bisconti (2008: 79), Bisconti et al. (2013: 64).  
30  
31 0=high sagittal crest present  
32 1=sagittal crest absent or present as low ridge  
33  
34 94. Parietal, orbitotemporal crest. New character.  
35  
36 0=extends posteriorly onto parietal  
37 1=on frontals only  
38  
39 95. Alisphenoid, contacts in temporal fossa. Modified from Geisler and Sanders (2003:  
40 141), Fitzgerald (2006: 131), Bisconti (2008: 113, 114), Marx (2011: 66), Churchill et  
41 al. (2012: 32), Bisconti et al. (2013: 97) Fordyce and Marx (2013: 53).  
42  
43 0=contacts frontal, squamosal, parietal, palatine, and pterygoid  
44 1=contacts frontal, squamosal, parietal, pterygoid, not palatine  
45 2=contacts squamosal, parietal, pterygoid, not frontal or palatine  
46 3=contacts parietal and pterygoid, not squamosal, palatine, or frontal  
47 4=no alisphenoid exposed  
48  
49 96. Alisphenoid, exposure. Modified from Fitzgerald (2006: 132), Bisconti (2008:  
50 114), Bisconti et al. (2013: 96).

- 1  
2 0=small or not exposed  
3 1=hypertrophied  
4  
5 97. Braincase, frontoparietal suture. Modified from Fitzgerald (2010: 60), Bisconti et  
6 al. (2013: 55), El Adli et al. (2014: 36).  
7  
8 0=transversely oriented  
9 1=suture is strongly V or U-shaped, with sutures converging posteriorly and frontal  
10 penetrating between parietals  
11  
12 98. Braincase, posterior apex of nuchal crest. Modified from Bisconti (2008: 83),  
13 Marx (2011: 65), Bisconti et al. (2013: 73) Fordyce and Marx (2013: 51).  
14  
15 0=anterior to or at level of posteriormost point of occipital condyles  
16 1=posterior to condyles  
17  
18 99. Braincase, postparietal foramen. Modified from Bisconti et al. (2013: 71).  
19  
20 0=absent  
21 1=present  
22  
23 100. Braincase, shape of parieto-squamosal suture. Modified from Bisconti (2005: 4?),  
24 Bouetel and Muizon (2006: 37), Bisconti (2008: 4?), Churchill et al. (2012: 38),  
25 Bisconti et al. (2013: 74), Fordyce and Marx (2013: 59).  
26  
27 0=ridge absent  
28 1=present and low  
29 2=present and distinctly elevated  
30  
31 101. Braincase, squamosal-alisphenoid suture. Modified from Geisler and Sanders  
32 (2003: 180), Fitzgerald (2006: 170), Bisconti (2008: 115), Fitzgerald (2010: 75).  
33  
34 0=anterior to external foramen ovale  
35 1=courses along branch of trigeminal nerve  
36 2=just medial to anterior edge of squamosal fossa  
37  
38 102. Braincase, tubercle on parieto-squamosal suture. Modified from Fordyce and  
39 Marx (2013: 52).  
40  
41 0=absent  
42 1=tubercle developed at junction of suture and occipital shield  
43  
44 103. Occipital, anteriormost point of supraoccipital. Modified from Bisconti (2000:  
45 42), Kimura and Ozawa (2002: 2), Geisler and Sanders (2003: 139), Deméré et al.  
46 (2005: 29), Bouetel and Muizon (2006: 39), Fitzgerald (2006: 129), Steeman (2007:  
47 5), Bisconti (2008: 78), Deméré et al. (2008: 27), Fitzgerald (2010: 62), Kimura and  
48 Hasegawa (2010: 78), Marx (2011: 64), Churchill et al. (2012: 49), Bisconti et al.  
49 (2013: 56, 98), Fordyce and Marx (2013: 50), El Adli et al. (2014: 37).  
50

1 0=at level of braincase between subtemporal crest and posteriormost skull  
 2 1=at level of gap between postorbital process and subtemporal crest  
 3 2=at level of posterior half of supraorbital process or postorbital process  
 4 3=at level of anterior half of supraorbital process  
 5 4=anterior to or at level of anterior edge of supraorbital process  
 6  
 7 104. Occipital, paired tubercles on occipital shield. Modified from Bisconti (2000: 51),  
 8 Marx (2011: 76).  
 9  
 10 0=absent  
 11 1=present  
 12  
 13 105. Occipital, lateral margins of occipital shield in dorsal aspect. Modified from  
 14 Deméré et al. (2005: 31), Bisconti (2008: 62), Deméré et al. (2008: 29), Kimura and  
 15 Hasegawa (2010: 81), Marx (2011: 77), Churchill et al. (2012: 50), Bisconti et al.  
 16 (2013: 107, 109), Fordyce and Marx (2013: 69), El Adli et al. (2014: 39).  
 17  
 18 0=convex  
 19 1=straight or concave  
 20 2=sinuuous  
 21  
 22 106. Occipital, paroccipital process in dorsal aspect. Modified from Bisconti (2000:  
 23 55), Kimura and Ozawa (2002: 29), Geisler and Sanders (2003: 197), Bisconti (2005:  
 24 28), Deméré et al. (2005: 46), Bouetel and Muizon (2006: 55), Fitzgerald (2006: 187),  
 25 Deméré et al. (2008: 43), Fitzgerald (2010: 78), Kimura and Hasegawa (2010: 83),  
 26 Marx (2011: 83), Churchill et al. (2012: 35), Bisconti et al. (2013: 110), Fordyce and  
 27 Marx (2013: 81), El Adli et al. (2014: 60).  
 28  
 29 0=extends anterior to posterior edge of condyles  
 30 1=at level of or posterior to posterior edge of condyles  
 31  
 32 107. Occipital, nuchal crests in dorsal view. Modified from Bisconti (2000: 40, 47),  
 33 Geisler and Sanders (2003: 153, 154), Bouetel and Muizon (2006: 54), Fitzgerald  
 34 (2006: 143, 144), Bisconti (2008: 82, 132), Deméré and Berta (2008: 34), Fitzgerald  
 35 (2010: 69), Kimura and Hasegawa (2010: 80), Churchill et al. (2012: 55), Bisconti et  
 36 al. (2013: 67, 68).  
 37  
 38 0=vertical and posteriorly or dorsally directed, not obscuring temporal fossa  
 39 1=subvertical to horizontal and anterolaterally directed, obscuring temporal wall but  
 40 not temporal fossa  
 41 2=subvertical to horizontal and anterolaterally directed, obscuring temporal fossa  
 42  
 43 108. Occipital, paroccipital process. New character.  
 44  
 45 0=forms a vertical, plate-like process  
 46 1=anteroposteriorly swollen in ventral aspect  
 47 2=anteroposteriorly swollen with anteroventral pit for stylohyoid  
 48  
 49 109. Occipital, shape in posterior view. Modified from Bisconti (2005: 69).  
 50

1 0=trefoil shaped  
2 1=triangular or subtriangular  
3  
4 110. Supraoccipital, shape of apex. Modified from Bisconti (2000: 48), Geisler and  
5 Sanders (2003: 152), Bisconti (2005: 60), Deméré et al. (2005: 30), Bouetel and  
6 Muizon (2006: 53), Fitzgerald (2006: 142), Bisconti (2008: 63), Deméré et al. (2008:  
7 28), Fitzgerald (2010: 68), Kimura and Hasegawa (2010: 79), Churchill et al. (2012:  
8 51), Bisconti et al. (2013: 105, 106), El Adli et al. (2014: 38).  
9  
10 0=rounded or triangular  
11 1=flattened apex  
12  
13 107. Cranium, dorsally highest part. Modified from Geisler and Sanders (2003: 128),  
14 Bouetel and Muizon (2006: 38), Fitzgerald (2006: 118), Bisconti (2008: 164).  
15  
16 0=apex of occipital shield  
17 1=nuchal crest elevated above occipital apex  
18 2=rostral elements elevated above occipital  
19  
20 111. Occipital, external occipital crest. Modified from Bisconti (2000: 49, 50), Geisler  
21 and Sanders (2003: 155), Bisconti (2005: 22, 68), Bouetel and Muizon (2006: 40),  
22 Fitzgerald (2006: 145), Bisconti (2008: 145?, 157), Fitzgerald (2010: 70), Kimura and  
23 Hasegawa (2010: 82), Churchill et al. (2012: 52, 54), Bisconti et al. (2013: 103),  
24 Fordyce and Marx (2013: 70).  
25  
26 0=sharp ridge present dividing shield into two concave fossae  
27 1=blunt ridge dividing anterior half of shield into two dorsolaterally sloping facets  
28 2=absent  
29  
30 112. Occipital, dorsal condyloid fossae. Modified from Geisler and Sanders (2003:  
31 156), Fitzgerald (2006: 146), Fitzgerald (2010: 71), Kimura and Hasegawa (2010: 85).  
32  
33 0=present  
34 1=absent  
35  
36 114. Occipital, posterior margin of exoccipital. New character.  
37  
38 0=straight  
39 1=posteriorly convex and bulbous  
40  
41 115. Squamosal, zygomatic process. Modified from Geisler and Sanders (2003: 142),  
42 Deméré et al. (2005: 32), Bouetel and Muizon (2006: 42), Fitzgerald (2006: 132),  
43 Bisconti (2008: 91), Deméré et al. (2008: 30), Fitzgerald (2010: 63), Kimura and  
44 Hasegawa (2010: 64), Marx (2011: 67), Churchill et al. (2012: 41, 45), Bisconti et al.  
45 (2013:92), Fordyce and Marx (2013: 54), El Adli et al. (2014: 40).  
46  
47 0=directed anteromedially  
48 1=directed anteriorly  
49 2=directed anterolaterally  
50

- 1 116. Squamosal, zygomatic process in lateral aspect. Modified from Deméré and  
2 Berta (2008: 10), Fitzgerald (2010: 64), Marx (2011: 68), Fordyce and Marx (2013:  
3 55), El Adli et al. (2014: 45).  
4  
5 0=dorsal and ventral margins convergent  
6 1=zygomatic expanded anteriorly and posteriorly with constriction in middle  
7
- 8 117. Squamosal, zygomatic process. Modified from Kimura and Ozawa (2002: 21),  
9 Deméré et al. (2005: 23), Bouetel and Muizon (2006: 31), Bisconti (2008: 93),  
10 Deméré and Berta (2008: 11), Deméré et al. (2008: 21), Fitzgerald (2010: 65), Kimura  
11 and Hasegawa (2010: 62), Marx (2011: 69), Churchill et al. (2012: 46), Bisconti et al.  
12 (2013: 54), Fordyce and Marx (2013: 56), El Adli et al. (2014: 28).  
13  
14 0=does not contact postorbital process, entirely posterior to frontal  
15 1=does not contact postorbital process, anterior tip is lateral to frontal  
16 2=contacts or situated below postorbital process  
17
- 18 118. Squamosal, supramastoid crest. Modified from Bisconti (2000: 39), Bisconti  
19 (2005: 14), Bouetel and Muizon (2006: 43), Fitzgerald (2006: 139), Bisconti (2008:  
20 18, 134?, 158), Kimura and Hasegawa (2010: 65), Marx (2011: 70), Churchill et al.  
21 (2012: 40), Bisconti et al. (2013: 87, 88), Fordyce and Marx (2013: 57).  
22  
23 0=present along length of zygomatic  
24 1=extends past posterior margin of temporal fossa but not to tip of zygomatic  
25 2=does not extend anterior to posterior margin of temporal fossa  
26
- 27 119. Squamosal, axis of development. Modified from Bisconti (2000: 68), Kimura  
28 and Ozawa (2002: 19), Bisconti (2005: 33), Deméré et al. (2005: 35), Bisconti (2008:  
29 35), Deméré et al. (2008: 33), Marx (2011: 71), Churchill et al. (2012: 42), Bisconti et  
30 al. (2013: 86), Fordyce and Marx (2013: 58), El Adli et al. (2014: 43).  
31  
32 0=anteroposterior  
33 1=dorsoventral  
34
- 35 120. Squamosal, transverse width lateral to exoccipital (posterior aspect). Modified  
36 from Geisler and Sanders (2003: 145), Deméré et al. (2005: 36), Fitzgerald (2006:  
37 135), Deméré et al. (2008: 34), Fitzgerald (2010: 66), Kimura and Hasegawa (2010:  
38 73), Marx (2011: 72), Fordyce and Marx (2013: 61), El Adli et al. (2014: 44).  
39  
40 0=intermediate width, 10-40% of distance from midline to lateral edge of exoccipital  
41 1=wide, 35-49% of distance  
42 2=very wide, >50% of distance  
43 3=narrow, <10% of distance  
44
- 45 121. Squamosal, orientation of postglenoid process in lateral aspect. Modified from  
46 Bouetel and Muizon (2006: 45), Marx (2011: 73), Bisconti et al. (2013: 94), Fordyce  
47 and Marx (2013: 63).  
48  
49 0=subvertical to anteriorly projecting  
50 1=subvertical to posteroventrally projecting

- 1 2=concave posterior margin, horizontal and posteriorly directed postglenoid process  
2  
3 122. Squamosal, orientation of postglenoid process in ventral view. Modified from  
4 Bouetel and Muizon (2006: 46), Kimura and Hasegawa (2010: 67), Marx (2011: 74),  
5 Fordyce and Marx (2013: 65), El Adli et al. (2014: 46).  
6  
7 0=ventrally oriented  
8 1=ventrolaterally oriented  
9  
10 123. Squamosal, squamosal cleft. Modified from Bisconti (2005: 26), Deméré et al.  
11 (2005: 34), Bisconti (2008: 69), Deméré et al. (2008: 32), Kimura and Hasegawa  
12 (2010: 70), Marx (2011: 75), Churchill et al. (2012: 43), Bisconti et al. (2013: 80),  
13 Fordyce and Marx (2013: 68), El Adli et al. (2014: 42).  
14  
15 0=absent  
16 1=present  
17  
18 124. Squamosal, twisting of postglenoid process in ventral aspect. Modified from  
19 Bouetel and Muizon (2006: 47), Kimura and Hasegawa (2010: 68), Marx (2011: 78),  
20 Fordyce and Marx (2013: 67).  
21  
22 0=not twisted, oriented transversely  
23 1=twisted clockwise on left and counterclockwise on right  
24  
25 125. Squamosal, zygomatic shape in dorsal aspect. Modified from Bouetel and  
26 Muizon (2006: 41).  
27  
28 0=zygomatic tapers anteriorly  
29 1=medial and lateral margins parallel  
30  
31 126. Squamosal, subtemporal crest. Modified from Deméré and Berta (2008: 33).  
32  
33 0=well developed horizontal crest that is anterolaterally convex or bulges into  
34 temporal fossa  
35 1=well developed anterolaterally concave horizontal crest  
36 2=crest absent, squamosal is anteroventrally smooth and convex  
37  
38 127. Squamosal, secondary squamosal fossa. Modified from Bisconti (2008: 162).  
39  
40 0=absent  
41 1=developed as a pit or trough lateral to squamosal fossa  
42  
43 128. Squamosal, glenoid fossa. Modified from Bisconti (2000: 23), Kimura and  
44 Ozawa (2002: 22), Bisconti (2005: 15, 55), Bouetel and Muizon (2006: 49), Bisconti  
45 (2008: 20, 36), Kimura and Hasegawa (2010: 72), Bisconti et al. (2013: 84).  
46  
47 0=margins of fossa clearly developed  
48 1=absent, margins of fossa indistinct or convex  
49

- 1 129. Squamosal, squamosal prominence on supramastoid crest. Modified from Geisler  
2 and Sanders (2003: 149), Fitzgerald (2006: 139), Fordyce and Marx (2013: 60).  
3  
4 0=absent  
5 1=developed as large knob or tubercle  
6 2=developed as a dorsally arched, narrow flange  
7  
8 130. Squamosal, ventromedial fossa on zygomatic process. New character.  
9  
10 0=fossa absent  
11 1=ventral or ventromedial fossa present at apex  
12 2=longitudinal groove for masseter insertion present on ventral surface of zygomatic  
13 base  
14  
15 131. Squamosal, longitudinal twisting of zygomatic process. Modified from Bisconti  
16 et al. (2013: 93).  
17  
18 0=absent  
19 1=zygomatic process twisted so that lateral surface faces dorsolaterally  
20  
21 132. Squamosal, curvature of zygomatic process in dorsal view. Modified from  
22 Bisconti (2000: 38).  
23  
24 0=lateral margin is straight or laterally convex, concave medial margin  
25 1=medially bowed with laterally concave medial and lateral margins  
26  
27 133. Squamosal, postglenoid process in lateral view. Modified from Bouetel and  
28 Muizon (2006: 48), Fitzgerald (2006: 141), Fitzgerald (2010: 67), Kimura and  
29 Hasegawa (2010: 66), Churchill et al. (2012: 48).  
30  
31 0=anteroposteriorly flattened  
32 1=anteroposteriorly inflated  
33  
34 134. Squamosal, squamosal crease. Modified from Bisconti (2008: 149).  
35  
36 0=absent  
37 1=present  
38  
39 135. Squamosal, proportions of zygomatic process in lateral view. Modified from  
40 Bisconti (2000: 37), Geisler and Sanders (2003: 188), Bisconti (2005: 27, 38), Bouetel  
41 and Muizon (2006: 41), Fitzgerald (2006: 178), Bisconti (2008: 37), Kimura and  
42 Hasegawa (2010: 63), Churchill et al. (2012: 44), Bisconti et al. (2013: 89).  
43  
44 0=anteroposterior length is twice as long as dorsoventral depth at base of process or  
45 longer  
46 1=dorsoventral depth and anteroposterior length are approximately equal  
47 2=dorsoventrally deeper than long  
48  
49 136. Squamosal, dorsal arching in lateral view. Modified from Bisconti (2013: 90).  
50

- 1 0=absent  
2 1=present  
3  
4 137. Squamosal, tympanosquamosal recess. Modified from Geisler and Sanders (2003:  
5 178, 260), Fitzgerald (2006: 168, 250), Fitzgerald (2010: 74).  
6  
7 0=absent, but small pit for sigmoid process is present  
8 1=absent  
9 2=present  
10  
11 138. Squamosal, shape of lateral skull border. Modified from Fordyce and Marx  
12 (2013: 42).  
13  
14 0=lateral skull border forms an angle  
15 1=continuous lateral skull border  
16  
17 139. Squamosal, length of squamosal fossa. Modified from Geisler and Sanders (2003:  
18 146, 147, 148), Deméré et al. (2005: 33), Fitzgerald (2006: 136, 137, 138), Deméré  
19 and Berta (2008: 17), Deméré et al. (2008: 31), Kimura and Hasegawa (2010: 74, 75),  
20 Fordyce and Marx (2013: 62), El Adli et al. (2014: 41).  
21  
22 0=length of fossa equal to or exceeds width of temporal fossa  
23 1=length of fossa is 3/4 of temporal fossa width or longer  
24 2=length of squamosal fossa is under 3/4 of temporal fossa width  
25  
26 140. Squamosal, ventral extension of postglenoid process. Modified from Bisconti  
27 (2008: 120, 133), Fordyce and Marx (2013: 64).  
28  
29 0=ventral edge of postglenoid process approximately in line with or dorsal to ventral  
30 edge of exoccipital  
31 1=extends ventral to ventral edge of exoccipital  
32  
33 141. Squamosal, outline of postglenoid process in anterior or posterior view. Modified  
34 from Geisler and Sanders (2003: 151), Fordyce and Marx (2013: 66).  
35  
36 0=parabolic  
37 1=parabolic but with parallel or concave lateral and medial edges  
38 2=triangular  
39 3=trapezoidal with ventrally deflected medial border  
40  
41 142. Squamosal, base of postglenoid process in ventral view. Modified from Steeman  
42 (2007: 19), Bisconti (2008: 76?), Kimura and Hasegawa (2010: 69), Bisconti et al.  
43 (2013: 111), Fordyce and Marx (2013: 77).  
44  
45 0= in line with center of tympanic bulla  
46 1= in line with anterior half of tympanic bulla or further anterior  
47 2= posterior to the longitudinal midpoint of the tympanic bulla  
48  
49 143. Pterygoid, ventral aspect. Modified from Kimura and Ozawa (2002: 18),  
50 Bisconti (2005: 48, 50), Deméré et al. (2005: 42), Steeman (2007: 22), Bisconti (2008:

1 46), Deméré and Berta (2008: 15), Deméré et al. (2008: 39), Kimura and Hasegawa  
2 (2010: 31), Marx (2011: 79), Churchill et al. (2012: 30), Bisconti et al. (2013: 117),  
3 Fordyce and Marx (2013: 71), El Adli et al. (2014: 52).  
4  
5 0=exposed for entire or most of their length  
6 1=anterior half covered by palatines  
7 2=almost entirely covered by palatines  
8  
9 144. Pterygoid, shape of hamulus. Modified from Geisler and Sanders (2003: 172),  
10 Fitzgerald (2006: 162), Bisconti (2008: 150), Deméré et al. (2008: 80), Kimura and  
11 Hasegawa (2010: 35), Churchill et al. (2012: 31), Fordyce and Marx (2013: 74), El  
12 Adli et al. (2014: 58).  
13  
14 0=fingerlike  
15 1=expanded into dorsoventrally flattened plate partially flooring pterygoid sinus fossa  
16 2=reduced in size or almost absent  
17  
18 145. Braincase, foramen pseudovale. Modified from Bisconti (2000: 59, 60), Bisconti  
19 (2005: 8), Deméré et al. (2005: 38), Bouetel and Muizon (2006: 52), Bisconti (2008:  
20 11, 117), Deméré et al. (2008: 35), Kimura and Hasegawa (2010: 76), Marx (2011:  
21 80), Bisconti et al. (2013: 121), Fordyce and Marx (2013: 75), El Adli et al. (2014:  
22 47).  
23  
24 0=absent  
25 1=within pterygoid  
26 2=between squamosal and pterygoid  
27  
28 146. Basioccipital, basioccipital crest. Modified from Bisconti (2000: 65), Geisler and  
29 Sanders (2003: 191), Deméré et al. (2005: 45), Bouetel and Muizon (2006: 50, 51),  
30 Fitzgerald (2006: 181), Steeman (2007: 21), Bisconti (2008: 8), Deméré and Berta  
31 (2008: 42), Deméré et al. (2008: 42), Fitzgerald (2010: 76), Kimura and Hasegawa  
32 (2010: 84), Marx (2011: 81), Churchill et al. (2012: 34), Fordyce and Marx (2013: 79),  
33 El Adli et al. (2014: 59).  
34  
35 0= transversely narrow  
36 1= wide and bulbous  
37  
38 147. Basioccipital, basioccipital crest orientation. Modified from Geisler and Sanders  
39 (2003: 194), Fitzgerald (2006: 184), Deméré and Berta (2008: 18), Fitzgerald (2010:  
40 77), Marx (2011: 82), Bisconti (2008: 194), Marx (2011: 82), Fordyce and Marx  
41 (2013: 80),  
42  
43 0= diverging posteriorly  
44 1= parallel or subparallel  
45  
46 148. Basioccipital, width relative to basisphenoid. New character.  
47  
48 0=basisphenoid abruptly narrower than basioccipital,  $<2/3$  basioccipital width  
49 1=basisphenoid and basioccipital roughly equivalent,  $>2/3$  basioccipital width  
50

1 149. Periotic, cerebral elongation of pars cochlearis. Modified from Geisler and Luo  
2 (1996: 12), Kimura and Ozawa (2002: 61), Geisler and Sanders (2003: 230), Dooley  
3 et al. (2004: 12), Bisconti (2005: 81), Deméré et al. (2005: 50), Bouetel and Muizon  
4 (2006: 77), Fitzgerald (2006: 220), Steeman (2007: 75), Deméré and Berta (2008: 46),  
5 Deméré et al. (2008: 46), Fitzgerald (2010: 98), Kimura and Hasegawa (2010: 92,  
6 94?), Ekdale et al. (2011: 27), Marx (2011: 84), Churchill et al. (2012: 69), Bisconti et  
7 al. (2013: 134), Fordyce and Marx (2013: 84), El Adli et al. (2014: 86).

8

9 0=absent

10 1=present, pars cochlearis dorsoventrally longer than anteroposteriorly wide

11

12 150. Periotic, contact of anterior process with tympanic bulla. Modified from Geisler  
13 and Luo (1996: 3, 5, 6, 27), Kimura and Ozawa (2002: 53, 55), Geisler and Sanders  
14 (2003: 209, 253, 255), Dooley et al. (2004: 3, 6), Fitzgerald (2006: 199, 243, 245),  
15 Bisconti (2008: 29), Fitzgerald (2010: 114), Marx (2011: 85), Churchill et al. (2012:  
16 63), Fordyce and Marx (2013: 91).

17

18 0=little or no contact, or contact with accessory ossicle

19 1=fused into anterior pedicle

20

21 151. Periotic, lateral tuberosity. Modified from Geisler and Luo (1996: 4, 11), Kimura  
22 and Ozawa (2002: 54, 60?), Geisler and Sanders (2003: 210, 211), Dooley et al. (2004:  
23 4, 11?), Bisconti (2005: 53), Deméré et al. (2005: 51), Bouetel and Muizon (2006: 69),  
24 Fitzgerald (2006: 200, 201), Steeman (2007: 28), Bisconti (2008: 55), Deméré et al.  
25 (2008: 47), Fitzgerald (2010: 85), Kimura and Hasegawa (2010: 89), Ekdale et al.  
26 (2011: 18), Marx (2011: 86), Churchill et al. (2012: 65), Bisconti et al. (2013: 152,  
27 154), Fordyce and Marx (2013: 92), El Adli et al. (2014: 78).

28

29 0=absent or blunt projection

30 1=conical and laterally projecting

31 2=long, ventrally directed blade-like projection half the length of the anterior process  
32 or longer

33 3=flattened triangular shelf, anteroposteriorly longer than wide

34

35 152. Periotic, hiatus epitympanicus. Modified from Geisler and Luo (1996: 8),  
36 Kimura and Ozawa (2002: 57), Dooley et al. (2004: 8), Marx (2011: 87).

37

38 0=present

39 1=absent or indistinct

40

41 153. Periotic, facial canal, internal acoustic meatus and perilymphatic foramen  
42 aligned. Modified from Geisler and Luo (1996: 20), Steeman (2007: 39), Marx (2011:  
43 88).

44

45 0=absent

46 1=present

47

48 154. Periotic, aperture for cochlear aqueduct. Modified from Geisler and Sanders  
49 (2003: 227), Marx (2011: 89), Fordyce and Marx (2013: 102).

50

1 0=smaller than aperture for vestibular aqueduct  
2 1=approximately similar in size  
3  
4 155. Periotic, facial canal. Modified from Kimura and Ozawa (2002: 69), Geisler and  
5 Sanders (2003: 238), Dooley et al. (2004: 20), Deméré et al. (2005: 56), Bouetel and  
6 Muizon (2006: 75), Fitzgerald (2006: 228), Deméré et al. (2008: 52), Fitzgerald (2010:  
7 105), Kimura and Hasegawa (2010: 105), Ekdale et al. (2011: 47), Marx (2011: 90),  
8 Bisconti et al. (2013: 131, 132), Fordyce and Marx (2013: 105).  
9  
10 0=roughly circular and contiguous with broad hiatus fallopii  
11 1=continuous with fissure-like hiatus fallopii  
12  
13 156. Periotic, articulation with tympanic bulla. Modified from Kimura and Ozawa  
14 (2002: 76), Geisler and Sanders (2003: 241), Dooley et al. (2004: 27), Bouetel and  
15 Muizon (2006: 62), Fitzgerald (2006: 231), Steeman (2007: 37), Bisconti (2008: 28),  
16 Fitzgerald (2010: 107), Marx (2011: 91), Churchill et al. (2012: 66), Fordyce and  
17 Marx (2013: 107).  
18  
19 0=unfused  
20 1=fused in adults  
21  
22 157. Periotic, facial sulcus distal to stylomastoid notch. Modified from Geisler and  
23 Luo (1996: 26), Kimura and Ozawa (2002: 75), Geisler and Sanders (2003: 244),  
24 Dooley et al. (2004: 26), Bouetel and Muizon (2006: 83), Fitzgerald (2006: 234),  
25 Bisconti (2008: 105), Fitzgerald (2010: 108), Kimura and Hasegawa (2010: 111),  
26 Marx (2011: 92), Bisconti et al. (2013: 158), Fordyce and Marx (2013: 108).  
27  
28 0=short, no sulcus posterior to notch  
29 1=long but relatively shallow sulcus, disappearing distally  
30  
31 158. Periotic, morphology of compound posterior process. Modified from Geisler and  
32 Luo (1996: 23, 28), Kimura and Ozawa (2002: 72, 77), Geisler and Sanders (2003:  
33 245, 248, 249), Dooley et al. (2004: 23, 28), Bouetel and Muizon (2006: 84, 85),  
34 Fitzgerald (2006: 239, 235, 238), Steeman (2007: 35), Bisconti (2008: 23), Fitzgerald  
35 (2010: 109, 112), Kimura and Hasegawa (2010: 107, 112, 113), Marx (2011: 93),  
36 Bisconti et al. (2013: 155, 156), Fordyce and Marx (2013: 110, 111), El Adli et al.  
37 (2014: 103).  
38  
39 0=short, processes not exposed or barely exposed on skull wall  
40 1=conical-tetrahedral process exposed laterally, widening distally  
41 2=process exposed and cylindrical or flattened  
42  
43 159. Periotic, neck of posterior process. Modified from Geisler and Luo (1996: 24),  
44 Kimura and Ozawa (2002: 73), Geisler and Sanders (2003: 247), Dooley et al. (2004:  
45 24), Bouetel and Muizon (2006: 56), Fitzgerald (2006: 237), Steeman (2007: 36),  
46 Kimura and Hasegawa (2010: 109), Marx (2011: 94), Churchill et al. (2012: 67).  
47  
48 0=transversely constricted  
49 1=transversely and dorsoventrally constricted  
50 2=absent

- 1  
2 160. Periotic, apex of anterior process. Modified from Geisler and Sanders (2003:  
3 208), Fitzgerald (2006: 198), Bisconti (2008: 82, 127), Kimura and Hasegawa (2010:  
4 88), Ekdale et al. (2011: 20), Bisconti et al. (2013: 147), El Adli et al. (2014: 80).  
5  
6 0=transversely blunt or massive  
7 1=conical or sharply bladelike  
8  
9 161. Periotic, superior process. Modified from Geisler and Luo (1996: 17), Geisler  
10 and Sanders (2003: 231?, 232, 233), Fitzgerald (2006: 221?, 222, 223), Bisconti (2008:  
11 66, 75?), Fordyce and Marx (2013: 103), El Adli et al. (2014: 84, 91).  
12  
13 0=continuous, well developed  
14 1=discontinuous with anterior and posterior apices  
15 2=discontinuous, posterior apex only, anterior apex missing  
16 3=absent or poorly developed  
17  
18 162. Periotic, conical projection on dorsal surface posteriorly adjacent to IAM.  
19 Modified from Geisler and Sanders (2003: 235), Fitzgerald (2006: 225), Fitzgerald  
20 (2010: 103).  
21  
22 0=absent  
23 1=present  
24  
25 163. Periotic, vestibular and cochlear nerve canals. Modified from Geisler and  
26 Sanders (2003: 236), Fitzgerald (2006: 226), Fitzgerald (2010: 101, 104).  
27  
28 0=separated by crest, crest is dorsally higher than crista transversa  
29 1=separated by crest  
30 2=confluent, or separated by crest deeply recessed within internal acoustic meatus  
31  
32 164. Periotic, posterior bullar facet. Modified from Geisler and Sanders (2003: 242),  
33 Fitzgerald (2006: 232).  
34  
35 0=flat  
36 1=transversely concave  
37 2=transversely convex  
38  
39 165. Periotic, pars cochlearis. Modified from Geisler and Sanders (2003: 221),  
40 Fitzgerald (2006: 211), Fitzgerald (2010: 92), Ekdale et al. (2011: 30), El Adli et al.  
41 (2014: 102).  
42  
43 0=longitudinal ridge present on ventral surface  
44 1=ridge absent, pars cochlearis smooth and convex  
45  
46 166. Periotic, anterior process. Modified from Geisler and Luo (1996: 2), Kimura and  
47 Ozawa (2002: 52), Dooley et al. (2004: 2).  
48  
49 0=Deep pit present on lateral surface  
50 1=pit shallow or absent

- 1  
2 167. Periotic, position of fenestra ovalis. New character.  
3  
4 0=present ~2/3 of a/p distance from anterior margin of pars cochlearis  
5 1=present within anterior 2/3 of pars cochlearis  
6  
7 168. Periotic, incisural flange appressed to anterior pars cochlearis. New character.  
8  
9 0=absent  
10 1=present  
11  
12 169. Periotic, posterior bullar facet divided into two distinct facets divided by  
13 transverse hingeline. Modified from Geisler and Sanders (2003: 243), Fitzgerald  
14 (2006: 233).  
15  
16 0=absent  
17 1=present  
18 2=posterior processes fused  
19  
20 170. Periotic, position of malleolar fossa relative to lateral tuberosity. New character.  
21  
22 0=posterior to lateral tuberosity  
23 1=medial to lateral tuberosity  
24  
25 171. Periotic, orientation of anterolateral sulcus. Modified from Fitzgerald (2010: 82).  
26  
27 0=transverse  
28 1=anterolaterally  
29  
30 172. Periotic, groove on dorsal side of posterior process. Modified from Geisler and  
31 Sanders (2003: 239), Fitzgerald (2006: 229).  
32  
33 0=absent  
34 1=groove on dorsomedial side of posterior process  
35 2=grooves present on dorsomedial and dorsolateral sides of posterior process  
36 3=deep dorsolateral groove, poorly developed dorsomedial groove  
37  
38 173. Periotic, longitudinal grooves on posterior bullar facet. New character.  
39  
40 0=absent  
41 1=present  
42  
43 174. Periotic, anteromedial margin of pars cochlearis. Modified from Geisler and  
44 Sanders (2003: 219), Fitzgerald (2006: 209), Fitzgerald (2010: 90), Kimura and  
45 Hasegawa (2010: 91), Fordyce and Marx (2013: 94).  
46  
47 0=forms corner  
48 1=smoothly convex  
49  
50 175. Periotic, posteroexternal foramen. New character.

- 1  
2 0=small pore  
3 1=foramen opens into anteroposteriorly directed fissure or furrow  
4  
5 176. Periotic, ventral margin of anterior process in medial view. Modified from  
6 Geisler and Sanders (2003: 202), Bouetel and Muizon (2006: 64), Fitzgerald (2006:  
7 129), Fitzgerald (2010: 80).  
8  
9 0=at same level or dorsal to ventral edge of pars cochlearis  
10 1=well ventral to ventral edge of pars cochlearis, process is ventrally deflected  
11  
12 177. Periotic, length of anterior process. Modified from Geisler and Luo (1996: 1),  
13 Kimura and Ozawa (2002: 51), Geisler and Sanders (2003: 203), Dooley et al. (2004:  
14 1), Bouetel and Muizon (2006: 63), Fitzgerald (2006: 193), Fitzgerald (2010: 81),  
15 Kimura and Hasegawa (2010: 86), Ekdale et al. (2011: 37), Bisconti et al. (2013: 146),  
16 Fordyce and Marx (2013: 87), El Adli et al. (2014: 95).  
17  
18 0=present but very short, length <36% of the length of the pars cochlearis  
19 1=short, length between 59 and 94% of pars cochlearis length.  
20 2=approximately same length as pars cochlearis, 100-134%  
21 3=long, length between 141% and 174% of pars cochlearis length  
22 4=very long, >212% of pars cochlearis length  
23  
24 178. Periotic, angle formed by dorsal and posterior margins. Modified from Geisler  
25 and Sanders (2003: 246), Fitzgerald (2006: 236), Fitzgerald (2010: 110), Fordyce and  
26 Marx (2013: 109).  
27  
28 0=broadly rounded or forms corner >90°  
29 1=forms corner ≤ 90°  
30  
31 179. Periotic, shape of dorsal margin of anterior process (between anteroventral and  
32 anterodorsal angles). New character.  
33  
34 0=straight or dorsally convex  
35 1=dorsally concave  
36  
37 180. Periotic, position of dorsoventrally deepest part of anterior process. Modified  
38 from Geisler and Sanders (2003: 201), Bisconti (2005: 30), Bouetel and Muizon  
39 (2006: 70), Fitzgerald (2006: 191), Bisconti (2008: 84), Bisconti et al. (2013: 148).  
40  
41 0= within posterior 50% of anterior process, process is rounded in medial/lateral view  
42 1=within anterior 50% of anterior process, or dorsal and ventral margins parallel  
43 2=within posterior 50% of anterior process, process is triangular in medial/lateral  
44 view  
45  
46 181. Periotic, lateral face of anterior process. New character.  
47  
48 0=surface anterior to anterolateral sulcus smooth or smoothly convex  
49 1=distinct tubercle present immediately anterior to anterolateral sulcus and lateral  
50 tuberosity

- 1  
2 182. Periotic, shape of lateral face of posterior process (if exposed on lateral skull  
3 wall). New character.  
4  
5 0=oval or circular  
6 1=triangular  
7  
8 183. Periotic, lateral face of posterior process. New character.  
9  
10 0=convex or tapering  
11 1=flat or concave  
12  
13 184. Periotic, shape of facial and vestibulocochlear canals if separated by crista  
14 transversa. New character.  
15  
16 0=circular  
17 1=oval, transversely compressed and anteroposteriorly aligned  
18  
19 185. Periotic, squamosal flange. New character.  
20  
21 0=absent  
22 1=secondary squamosal flange present lateral to fossa for stapedial muscle  
23  
24 186. Periotic, relative size of facial and vestibulocochlear canals. Modified from  
25 Ekdale et al. (2011: 40), Fordyce and Marx (2013: 106), El Adli et al. (2014: 97).  
26  
27 0=approximately equal  
28 1=facial canal measures less than or equal to 2/3 transverse diameter of  
29 vestibulocochlear canal  
30  
31 187. Periotic, articulation with squamosal. New character.  
32  
33 0=petrosal and squamosal share vertical butt joint  
34 1=lateral projection of falciform process fits into groove on anterior margin of lateral  
35 tuberosity  
36  
37 188. Periotic, lateral portion of facial sulcus. New character.  
38  
39 0=distinct or indistinct sulcus  
40 1=sulcus nearly encircled by bone  
41  
42 189. Periotic, thickness of crista transversa. Modified from Bouetel and Muizon (2006:  
43 74), Kimura and Hasegawa (2010: 104), Bisconti et al. (2013: 128, 129), El Adli et al.  
44 (2014: 93).  
45  
46 0=anteroposteriorly thin or absent  
47 1=anteroposteriorly as thick or thicker than transverse width of facial canal  
48 2=facial canal and IAM separated by approximately 200% of maximum IAM  
49 diameter  
50

- 1 190. Periotic, relative size of facial canal and aperture for vestibular aqueduct.  
2 Modified from Steeman (2007: 40).  
3  
4 0=facial canal larger than or similar in size to endolymphatic foramen  
5 1=endolymphatic foramen transversely wider than facial canal  
6
- 7 191. Periotic, transversely thickest part of body in ventral view. New character.  
8  
9 0=apex of lateral margin positioned posterior to or at level of pars cochlearis  
10 1=apex of lateral margin positioned anterior to or at anterior margin of pars cochlearis  
11
- 12 192. Periotic, ventral margin of anterior process. Modified from Bouetel and Muizon  
13 (2006: 64), Fitzgerald (2006: 194), Bisconti (2008: 103?), Kimura and Hasegawa  
14 (2010: 87), Bisconti et al. (2013: 150).  
15  
16 0=straight or convex in medial view  
17 1=concave, apex of anterior process is ventrally deflected  
18
- 19 193. Periotic, lateral surface. Modified from Geisler and Sanders (2003: 216),  
20 Fitzgerald (2006: 206).  
21  
22 0=smooth  
23 1=rugose  
24 2=rugose anterior to anterolateral sulcus only  
25
- 26 194. Periotic, malleolar fossa. Modified from Geisler and Luo (1996: 9), Kimura and  
27 Ozawa (2002: 58), Geisler and Sanders (2003: 214), Dooley et al. (2004: 9), Bouetel  
28 and Muizon (2006: 78), Fitzgerald (2006: 204), Steeman (2007: 42), Bisconti (2008:  
29 27), Fitzgerald (2010: 86), Kimura and Hasegawa (2010: 96), Ekdale et al. (2011: 43),  
30 El Adli et al. (2014: 100).  
31  
32 0=present as distinct pit  
33 1=absent or poorly defined  
34
- 35 195. Periotic, ventrolateral ridge. Modified from Geisler and Luo (1996: 16), Kimura  
36 and Ozawa (2002: 65), Geisler and Sanders (2003: 215), Dooley et al. (2004: 16),  
37 Bouetel and Muizon (2006: 66), Fitzgerald (2006: 205), Fitzgerald (2010: 87).  
38  
39 0=absent  
40 1=present  
41 2=present and expanded  
42
- 43 196. Periotic, shape of fenestra rotunda. Modified from Geisler and Sanders (2003:  
44 222), Bouetel and Muizon (2006: 68), Fitzgerald (2006: 212), Fitzgerald (2010: 93),  
45 Kimura and Hasegawa (2010: 93).  
46  
47 0=oval  
48 1=teardrop with fissure directed toward aperture for cochlear aqueduct  
49

- 1 197. Periotic, caudal tympanic process. Modified from Geisler and Sanders (2003:  
2 225), Bouetel and Muizon (2006: 82), Fitzgerald (2006: 215), Steeman (2007: 32),  
3 Fitzgerald (2010: 94), Kimura and Hasegawa (2010: 101), Ekdale et al. (2011: 26),  
4 Fordyce and Marx (2013: 98), El Adli et al. (2014: 85).  
5  
6 0=low, semicircular in medial view  
7 1=prominent, forms an acute point in medial view  
8  
9 198. Periotic, caudal tympanic process in posteromedial view. Modified from Kimura  
10 and Ozawa (2002: 64), Geisler and Sanders (2003: 226), Dooley et al. (2004: 15),  
11 Fitzgerald (2006: 216), Fitzgerald (2010: 95), Kimura and Hasegawa (2010: 100?),  
12 Bisconti et al. (2013: 144), Fordyce and Marx (2013: 96), El Adli et al. (2014: 101).  
13  
14 0=separated from crista parotica, no division between stapedia muscle fossa and  
15 stylomastoid fossa  
16 1=narrow separation or contact, clear separation of fossae  
17  
18 199. Periotic, fundus of IAM. Modified from Geisler and Luo (1996: 19), Kimura and  
19 Ozawa (2002: 68), Geisler and Sanders (2003: 234), Dooley et al. (2004: 19), Bisconti  
20 (2005: 37), Bouetel and Muizon (2006: 73), Fitzgerald (2006: 224), Bisconti (2008:  
21 59), Fitzgerald (2010: 102), Kimura and Hasegawa (2010: 103).  
22  
23 0=funnel-shaped  
24 1=tube-shaped  
25  
26 200. Periotic, orientation of caudal tympanic process in ventral view. New character.  
27  
28 0=posteromedially divergent  
29 1=parallel with longitudinal axis of pars cochlearis  
30  
31 201. Periotic, suprameatal area. Modified from Kimura and Ozawa (2002: 67),  
32 Dooley et al. (2004: 18), Bouetel and Muizon (2006: 67), Deméré et al. (2008: 50),  
33 Ekdale et al. (2011: 33), El Adli et al. (2014: 91).  
34  
35 0=smooth or rugose compact bone  
36 1=distinct pit floored by cancellous bone  
37 2=cancellous bone exposed along dorsal surface of pars cochlearis and suprameatal  
38 area  
39  
40 202. Periotic, dorsal surface of pars cochlearis. Modified from Geisler and Luo (1996:  
41 18), Bisconti et al. (2013: 141).  
42  
43 0=dorsal surface is flat or convex and aligned anteroposteriorly  
44 1=pars cochlearis is anterodorsally extended, entire dorsal surface visible in posterior  
45 view  
46  
47 203. Periotic, fenestra rotunda. Modified from Steeman (2007: 31?).  
48  
49 0=bone dorsally adjacent to fenestra rotunda is smooth

- 1 1=tubercle with transverse sulci and ridges bulging into dorsal margin of fenestra  
2 rotunda  
3
- 4 204. Periotic, anterior margin of fenestra rotunda.  
5
- 6 0=anterior margin is posterior to or at level of posterior margin of fenestra ovalis  
7 1=anterior margin of fenestra rotunda overlaps fenestra ovalis in ventral view  
8
- 9 205. Periotic, pinching of IAM. New character.  
10
- 11 0=high crista transversa present, or margins of IAM not pinched  
12 1=crista transversa absent and medial and lateral projections from IAM rim pinch the  
13 IAM between the facial canal and foramen singulare  
14
- 15 206. Periotic, sharp transverse crest between stylomastoid and suprameatal fossae.  
16 New character.  
17
- 18 0=absent  
19 1=present  
20 2=present as small semicircular ridge ventrally encircling small stylomastoid fossa,  
21 suprameatal fossa indistinct  
22
- 23 207. Periotic, attachment of anterior process to pars cochlearis in taxa with cranially  
24 elongated pars cochlearis. Modified from Ekdale et al. (2011: 19), Fordyce and Marx  
25 (2013: 88), El Adli et al. (2014: 79).  
26
- 27 0=absent  
28 1=present  
29
- 30 208. Periotic, anteroexternal sulcus. Modified from Geisler and Sanders (2003: 205),  
31 Bouetel and Muizon (2006: 65), Fitzgerald (2006: 195), Ekdale et al. (2011: 23),  
32 Fordyce and Marx (2013: 89).  
33
- 34 0=present  
35 1=absent  
36
- 37 209. Periotic, distinct ridge delimiting insertion surface of tensor tympani. Modified  
38 from Geisler and Luo (1996: 7), Kimura and Ozawa (2002: 56), Geisler and Sanders  
39 (2003: 217), Dooley et al. (2004: 7), Bisconti (2005: 82), Deméré et al. (2005: 52),  
40 Bouetel and Muizon (2006: 80), Fitzgerald (2006: 207), Bisconti (2008: 148), Deméré  
41 et al. (2008: 48), Fitzgerald (2010: 88), Kimura and Hasegawa (2010: 98), Ekdale et  
42 al. (2011: 28), Churchill et al. (2012: 72), Bisconti et al. (2013: 138), Fordyce and  
43 Marx (2013: 93), El Adli et al. (2014: 87).  
44
- 45 0=absent  
46 1=absent, but insertion is excavated  
47 2=present  
48
- 49 210. Periotic, promontorial groove. Modified from Geisler and Luo (1996: 13),  
50 Kimura and Ozawa (2002: 62), Dooley et al. (2004: 13), Deméré et al. (2005: 53),

- 1 Bouetel and Muizon (2006: 81), Deméré et al. (2008: 49), Kimura and Hasegawa  
2 (2010: 99), Ekdale et al. (2011: 29), Churchill et al. (2012: 70), Fordyce and Marx  
3 (2013: 95), El Adli et al. (2014: 88, 137).  
4  
5 0=present  
6 1=present and deeply excavated  
7 2=absent  
8  
9 211. Periotic, anteroposterior alignment of apertures for cochlear and vestibular  
10 aqueducts. Modified from Ekdale et al. (2011: 38), Fordyce and Marx (2013: 100).  
11  
12 0=absent  
13 1=present  
14  
15 212. Periotic, path of anterointernal sulcus. Modified from Ekdale et al. (2011: 21), El  
16 Adli et al. (2014: 81).  
17  
18 0=sulcus absent  
19 1=directed towards anteroventral angle  
20 2=directed towards anterodorsal angle or ascends dorsally at level of anterior pars  
21 cochlearis  
22  
23 213. Periotic, aperture for vestibular aqueduct. New character.  
24  
25 0=opens dorsally  
26 1=forms laterally directed elongate sulcus  
27  
28 214. Periotic, accessory promontorial groove immediately medial to IAM. New  
29 character.  
30  
31 0=absent  
32 1=present  
33  
34 215. Periotic, shape of posterior bullar facet. New character.  
35  
36 0=oval or quadrate  
37 1=teardrop shaped, narrowing proximally and broadly rounded distally  
38 2=diamond-shaped, narrowing proximally and distally and widest in middle with  
39 medial and lateral apices  
40  
41 216. Periotic, posteromedial corner of pars cochlearis in ventral view. Modified from  
42 Geisler and Luo (1996: 21), Kimura and Ozawa (2002: 70), Geisler and Sanders  
43 (2003: 228), Dooley et al. (2004: 21), Deméré et al. (2005: 55), Fitzgerald (2006: 218),  
44 Bisconti (2008: 92), Deméré et al. (2008: 51), Kimura and Hasegawa (2010: 95),  
45 Ekdale et al. (2011: 32), Bisconti et al. (2013: 139), Fordyce and Marx (2013: 97), El  
46 Adli et al. (2014: 90).  
47  
48 0=pars cochlearis visible medial to fenestra rotunda  
49 1=dorsally ascending sulcus begins at fenestra rotunda, pars cochlearis not visible

1 2=as in state 1, but fenestra rotunda is confluent with aperture for cochlear aqueduct  
2 or connected by deep sulcus  
3  
4 217. Periotic, stylomastoid fossa. Modified from Geisler and Luo (1996: 14), Kimura  
5 and Ozawa (2002: 63), Geisler and Sanders (2003: 224), Dooley et al. (2004: 14),  
6 Bisconti (2005: 51), Steeman (2007: 29), Bisconti (2008: 53, 54), Kimura and  
7 Hasegawa (2010: 106), Ekdale et al. (2011: 31), Churchill et al. (2012: 75), Bisconti  
8 et al. (2013: 143), El Adli et al. (2014: 89).  
9  
10 0=absent or poorly developed  
11 1=developed on much of posterior “base” of pars cochlearis  
12 2=extends distally onto posterior process  
13  
14 218. Periotic, suprameatal fossa. Modified from Bouetel and Muizon (2006: 71),  
15 Ekdale et al. (2011: 33, 34), Bisconti et al. (2013: 133), El Adli et al. (2014: 91, 92).  
16  
17 0=deep  
18 1=shallow or absent  
19  
20 219. Periotic, crista transversa and internal acoustic meatus. Modified from Bisconti  
21 (2005: 21), Bouetel and Muizon (2006: 72), Bisconti (2008: 65), Kimura and  
22 Hasegawa (2010: 102), Ekdale et al. (2011: 35), Churchill et al. (2012: 71), Bisconti  
23 et al. (2013: 129), El Adli et al. (2014: 93).  
24  
25 0=crista transversa elevated and easily seen within meatus or elevated to meatal rim  
26 1=crista transversa deeply recessed within meatus or poorly developed  
27  
28 220. Tympanic bulla, orientation of main axis in ventral aspect. Modified from  
29 Bouetel and Muizon (2006: 56), Kimura and Hasegawa (2010: 115), Marx (2011: 95),  
30 El Adli et al. (2014: 75).  
31  
32 0=parallel  
33 1=diverging posteriorly  
34 2=diverging anteriorly  
35  
36 221. Tympanic bulla, orientation of outer lip. Modified from Bouetel and Muizon  
37 (2006: 61), Marx (2011: 96), Fordyce and Marx (2013: 115).  
38  
39 0=faces laterally  
40 1=faces ventrolaterally to ventrally  
41  
42 222. Tympanic bulla, sigmoid fissure curving anteriorly. Modified from Geisler and  
43 Sanders (2003: 2593), Fitzgerald (2010: 115), Kimura and Hasegawa (2010: 120),  
44 Marx (2011: 97), Fordyce and Marx (2013: 119).  
45  
46 0=present as distinct horizontal crease that curves anteriorly past level of sigmoid  
47 process tip  
48 1=absent, present as vertical sigmoid fissure  
49

- 1 223. Tympanic bulla, elliptical foramen. Modified from Geisler and Sanders (2003:  
2 261), Fitzgerald (2006: 251), Bisconti (2008: 31), Marx (2011: 98, 99), Bisconti et al.  
3 (2013: 165), Fordyce and Marx (2013: 121).  
4  
5 0=present as distinct notch separating two pedicles  
6 1=elliptical foramen absent, single posterior pedicle present  
7
- 8 224. Tympanic bulla, medial lobe. Modified from Dooley et al. (2004: 41), Steeman  
9 (2007: 44), Ekdale et al. (2011: 5), Marx (2011: 100), Churchill et al. (2012: 61),  
10 Bisconti et al. (2013: 173), El Adli et al. (2014: 66).  
11  
12 0=present and distinct from lateral lobe, separated by median furrow on posterior  
13 surface  
14 1=present as robust dorsal posterior prominence on posterior surface of involucrum  
15 2=dorsal posterior prominence not developed, medial lobe indistinct  
16
- 17 225. Tympanic bulla, eustachian opening in anterior aspect. Modified from Marx  
18 (2011: 101), Bisconti et al. (2013: 163).  
19  
20 0=well-developed groove, ventrally depressed below dorsal margin of involucrum  
21 1=above or at level of dorsal margin of involucrum  
22
- 23 226. Tympanic bulla, sigmoid process in lateral aspect. Modified from Marx (2011:  
24 102).  
25  
26 0=overlaps anterior half or more of conical process  
27 1=no overlap or slight overlap, gap between sigmoid and apex of conical process  
28
- 29 227. Tympanic bulla, transverse ridge dividing tympanic cavity. Modified from  
30 Geisler and Sanders (2003: 272), Fitzgerald (2006: 262), Bisconti (2008: 154),  
31 Fitzgerald (2010: 118), Marx (2011: 103).  
32  
33 0=present  
34 1=absent  
35
- 36 228. Tympanic bulla, ventral surface. Modified from Kimura and Ozawa (2002: 32),  
37 Geisler and Sanders (2003: 266), Deméré et al. (2005: 49), Bouetel and Muizon (2006:  
38 59), Fitzgerald (2006: 256), Deméré et al. (2008: 45), Fitzgerald (2010: 116), Kimura  
39 and Hasegawa (2010: 118), Ekdale et al. (2011: 4), Marx (2011: 104), Churchill et al.  
40 (2012: 59), Bisconti et al. (2013: 166), Fordyce and Marx (2013: 132), El Adli et al.  
41 (2014: 65).  
42  
43 0=transversely concave  
44 1=flat or convex  
45
- 46 229. Tympanic bulla, medial lobe. Modified from Geisler and Sanders (2003: 252,  
47 267), Fitzgerald (2006: 242, 257), Bisconti (2008: 153), Fordyce and Marx (2013:  
48 124).  
49  
50 0=horizontal crest present on posterior surface

- 1 1=crest absent  
2
- 3 230. Tympanic bulla, posterior margin in ventral aspect. Modified from Geisler and  
4 Sanders (2003: 266), Bouetel and Muizon (2006: 57), Fitzgerald (2006: 256),  
5 Steeman (2007: 43), Bisconti (2008: 30), Deméré et al. (2008: 45), Kimura and  
6 Hasegawa (2010: 116, 117), Ekdale et al. (2011: 16), Churchill et al. (2012: 59),  
7 Fordyce and Marx (2013: 122), El Adli et al. (2014: 76).  
8
- 9 0=lateral lobe extends posterior to medial lobe, not separated by notch  
10 1=lateral lobe extends posterior to medial lobe, separated by notch  
11 2=medial and lateral lobes not clearly differentiated  
12
- 13 231. Tympanic bulla, involucral ridge. Modified from Geisler and Sanders (2003:  
14 273), Fitzgerald (2006: 263).  
15
- 16 0=present as sharp ventromedial ridge  
17 1=low ridge or absent  
18
- 19 232. Tympanic bulla, articular facet for basioccipital. New character.  
20
- 21 0=present  
22 1=absent  
23
- 24 233. Tympanic bulla, inner posterior pedicle. New character.  
25
- 26 0=present as thin flange  
27 1=present on swollen tubercle  
28
- 29 234. Tympanic bulla, anterior margin in medial view. New character.  
30
- 31 0=ventral and dorsal margins form near right angle  
32 1=evenly curved, oval-shaped anterior margin  
33
- 34 235. Tympanic bulla, posterior margin of medial lobe in medial view. New character.  
35
- 36 0=forms sharp corner, posterior and ventral margins form  $\leq 90^\circ$  angle  
37 1=forms corner or rounded margins, posterior and ventral margins form  $> 90^\circ$  angle  
38
- 39 236. Tympanic bulla, posterior spur on medial lobe. New character.  
40
- 41 0=absent  
42 1=ventral spur present on posteroventral tip of medial lobe  
43
- 44 237. Tympanic bulla, position of main ridge in ventral view. Modified from Ekdale et  
45 al. (2011: 3), El Adli et al. (2014: 67).  
46
- 47 0=main ridge positioned on lateral half of ventral surface  
48 1=main ridge divides medial and lateral sides of bulla  
49 2=main ridge and involucral ridge positioned close to medial edge  
50

- 1 238. Tympanic bulla, involucrel and main ridges in medial view. Modified from  
2 Ekdale et al. (2011: 6), Fordyce and Marx (2013: 117), El Adli et al. (2014: 67).  
3  
4 0=involucrel ridge present along ventral margin  
5 1=involucrel ridge retracted medially along entire ventral margin  
6  
7 239. Tympanic bulla, anteromedial shelf. Modified from Ekdale et al. (2011: 7),  
8 Fordyce and Marx (2013: 134), El Adli et al. (2014: 68, 72).  
9  
10 0=absent  
11 1=vertical, anteriorly directed flange developed  
12  
13 240. Tympanic bulla, anterior lobe in dorsal view. Modified from Bisconti (2008: 44),  
14 Fordyce and Marx (2013: 112).  
15  
16 0=convex, continuous with curvature of posterior lobe  
17 1=strongly convex, deviates from curvature of posterior lobe  
18 2=forms right angle, forming rectangular anterior margin of bulla  
19  
20 241. Tympanic bulla, longitudinal furrow lateral to main ridge. New character.  
21  
22 0=absent  
23 1=present  
24  
25 242. Tympanic bulla, proportions. Modified from Kimura and Ozawa (2002: 31),  
26 Geisler and Sanders (2003: 251), Bisconti (2005: 34, 36), Deméré et al. (2005: 47, 48),  
27 Bouetel and Muizon (2006: 60), Fitzgerald (2006: 241), Steeman (2007: 49), Bisconti  
28 (2008: 41), Deméré et al. (2008: 44), Fitzgerald (2010: 113), Kimura and Hasegawa  
29 (2010: 119), Ekdale et al. (2011: 2), Churchill et al. (2012: 58), El Adli et al. (2014:  
30 63).  
31  
32 0=wide, width of bulla >65% of length  
33 1=narrow, width of bulla <65% of length  
34 2=very narrow, width of bulla <50% of length  
35  
36 243. Tympanic bulla, involucrel. Modified from Geisler and Sanders (2003: 271),  
37 Fitzgerald (2006: 261), Fitzgerald (2010: 117), Bisconti et al. (2013: 171), El Adli et  
38 al. (2014: 71).  
39  
40 0=dorsal margin is stepped, divided into narrow anterior part and bulbous posterior  
41 part  
42 1=smooth dorsal margin  
43  
44 244. Tympanic bulla, width of medial lobe. Modified from Fordyce and Marx (2013:  
45 126).  
46  
47 0=medial lobe transversely wider than lateral lobe  
48 1=equivalent in width  
49

- 1 245. Tympanic bulla, anterior end in dorsal or ventral view. Modified from Fordyce  
2 and Marx (2013: 112).  
3  
4 0=pointed or rounded  
5 1=squared  
6
- 7 246. Tympanic bulla, position of dorsal origin of lateral furrow. Modified from  
8 Ekdale et al. (2011: 14), Fordyce and Marx (2013: 113), El Adli et al. (2014: 74).  
9  
10 0=located along posterior 2/3 of bulla  
11 1=located in anterior 1/3 of bulla  
12
- 13 247. Tympanic bulla, orientation of lateral furrow. Modified from Fordyce and Marx  
14 (2013: 114).  
15  
16 0=vertical  
17 1=anteroventrally oriented  
18
- 19 248. Tympanic bulla, separation of sigmoid process and malleus. Modified from  
20 Fordyce and Marx (2013: 118).  
21  
22 0=separated from pedicle of malleus  
23 1=confluent with pedicle of malleus  
24
- 25 249. Tympanic bulla, shape of conical process. Modified from Bisconti (2005: 35),  
26 Ekdale et al. (2011: 8, 9), Churchill et al. (2012: 62), Fordyce and Marx (2013: 120),  
27 El Adli et al. (2014: 69, 70).  
28  
29 0=well developed and dorsally convex  
30 1=reduced to a low ridge or absent  
31 2=developed as robust triangular process  
32
- 33 250. Tympanic bulla, orientation of crest on posterior surface of medial lobe.  
34 Modified from Fordyce and Marx (2013: 125).  
35  
36 0=horizontal  
37 1=ventromedially sloping  
38
- 39 251. Tympanic bulla, anteriormost point of involucral ridge. Modified from Ekdale et  
40 al. (2011: 17), Fordyce and Marx (2013: 127), El Adli et al. (2014: 77).  
41  
42 0=extends anteriorly to form the anteriormost point of the bulla  
43 1=in line with posterior or anterior border of the bulla  
44
- 45 252. Hyoid, cross section of stylohyal. Modified from Churchill et al. (2012: 91),  
46 Fordyce and Marx (2013: 82).  
47  
48 0=cylindrical  
49 1=flattened  
50

1 253. Hyoid, ankylosed basihyal and thyrohyals. Modified from Deméré et al. (2008:  
2 92), Kimura and Hasegawa (2010: 155), Fordyce and Marx (2013: 83), El Adli et al.  
3 (2014: 129).  
4  
5 0=absent  
6 1=present  
7  
8 254. Mandible, medial surface of middle part. Modified from Kimura and Ozawa  
9 (2002: 42), Bouetel and Muizon (2006: 91), Bisconti (2008: 94), Deméré et al. (2008:  
10 88), Kimura and Hasegawa (2010: 124), Marx (2011: 105), Fordyce and Marx (2013:  
11 135).  
12  
13 0=flat or convex, similar to lateral surface  
14 1=distinctly flattened relative to lateral surface  
15  
16 255. Mandible, symphysis. Modified from Bisconti (2000: 17), Kimura and Ozawa  
17 (2002: 33), Geisler and Sanders (2003: 40), Bisconti (2005: 6), Deméré et al. (2005:  
18 57, 58), Bouetel and Muizon (2006: 88), Fitzgerald (2006: 41), Bisconti (2008: 9),  
19 Deméré and Berta (2008: 26), Deméré et al. (2008: 53), Fitzgerald (2010: 26), Kimura  
20 and Hasegawa (2010: 121), Marx (2011: 106), Churchill et al. (2012: 82), Bisconti et  
21 al. (2013: 174), Fordyce and Marx (2013: 136), El Adli et al. (2014: 104).  
22  
23 0=sutured or fused  
24 1=not sutured  
25  
26 256. Mandible, condyle and neck. Modified from Deméré et al. (2005: 59), Deméré et  
27 al. (2008: 55), Marx (2011: 108), Fordyce and Marx (2013: 137), El Adli et al. (2014:  
28 105).  
29  
30 0=forms part of curvature of horizontal ramus  
31 1=medially curved giving mandible sinusoidal profile in dorsal aspect  
32  
33 257. Mandible, curvature of horizontal ramus in dorsal aspect. Modified from  
34 Bisconti (2000: 20), Deméré et al. (2005: 61), Fitzgerald (2010: 27), Kimura and  
35 Hasegawa (2010: 125), Marx (2011: 109), Churchill et al. (2012: 76), Bisconti et al.  
36 (2013: 198), Fordyce and Marx (2013: 138).  
37  
38 0=medially bowed  
39 1=straight or slightly bowed laterally, line connecting anterior and posterior tips stays  
40 within body of mandible  
41 2=strongly bowed laterally, line connecting anterior and posterior tips medial to  
42 ramus  
43  
44 258. Mandible, anterior extremity relative to middle portion. Modified from Kimura  
45 and Ozawa (2002: 39), Bisconti (2005: 46), Bouetel and Muizon (2006: 89), Steeman  
46 (2007: 60), Bisconti 2008: 50), Deméré et al. (2008: 89), Kimura and Hasegawa  
47 (2010: 122), Marx (2011: 110), Churchill et al. (2012: 78), Bisconti et al. (2013: 190),  
48 Fordyce and Marx (2013: 139), El Adli et al. (2014: 109).  
49  
50 0=vertical

1 1=twisted with the ventral edge shifted medially  
2 2=apex of mandible rotated nearly horizontally  
3  
4 259. Mandible, height of ramus in lateral aspect. Modified from Kimura and Ozawa  
5 (2002: 43), Bouetel and Muizon (2006: 90), Bisconti (2008: 95), Fitzgerald (2010:  
6 120), Kimura and Hasegawa (2010: 123), Marx (2011: 111), Churchill et al. (2012:  
7 77), Fordyce and Marx (2013: 140), El Adli et al. (2014: 117).  
8  
9 0=constant height  
10 1=dorsoventrally constricted in middle portion  
11 2=ramus increases in height posteriorly  
12  
13 260. Mandible, mandibular foramen. Modified from Kimura and Ozawa (2002: 38),  
14 Deméré et al. (2005: 62), Bouetel and Muizon (2006: 98), Steeman (2007: 58),  
15 Bisconti (2008: 26?, 159), Deméré et al. (2008: 58), Fitzgerald (2010: 28), Kimura  
16 and Hasegawa (2010: 132), Marx (2011: 112), Bisconti et al. (2013: 193), Fordyce  
17 and Marx (2013: 141), El Adli et al. (2014: 107).  
18  
19 0=dorsoventral height approximates that of mandible  
20 1=dorsoventral height about half that of mandible or less  
21  
22 261. Mandible, anterior margin of mandibular foramen. Modified from Bisconti (2008:  
23 160), Marx (2011: 113), Bisconti et al. (2013: 194), Fordyce and Marx (2013: 142).  
24  
25 0=round  
26 1=triangular  
27  
28 262. Mandible, satellite process. Modified from Marx (2011: 114), Bisconti et al.  
29 (2013: 181, 182).  
30  
31 0=absent  
32 1=present  
33  
34 263. Mandible, relative position of anterior margin of mandibular foramen. Modified  
35 from Bouetel and Muizon (2006: 97), Fitzgerald (2006: 58), Deméré et al. (2008: 87),  
36 Kimura and Hasegawa (2010: 129, 130), Marx (2011: 115), Bisconti et al. (2013:  
37 178), Fordyce and Marx (2013: 143), El Adli et al. (2014: 111).  
38  
39 0=anterior to apex of coronoid process  
40 1=at level of tip or posterior edge of coronoid  
41 2=posterior to coronoid process  
42  
43 264. Mandible, subcondylar furrow. Modified from Bisconti (2005: 17), Bouetel and  
44 Muizon (2006: 95), Steeman (2007: 59), Deméré et al. (2008: 86), Kimura and  
45 Hasegawa (2010: 138), Fordyce and Marx (2013: 144), El Adli et al. (2014: 112).  
46  
47 0=absent  
48 1=only present medially  
49 2=deep groove posteriorly separating condyle and angular process  
50

1 265. Mandible, coronoid process. Modified from Bisconti (2000: 22), Kimura and  
2 Ozawa (2002: 34), Geisler and Sanders (2003: 44), Dooley et al. (2004: 30), Bisconti  
3 (2005: 41), Deméré et al. (2005: 64), Bouetel and Muizon (2006: 92), Fitzgerald  
4 (2006: 45), Steeman (2007: 56), Bisconti (2008: 32, 121), Deméré and Berta (2008:  
5 27), Deméré et al. (2008: 60), Fitzgerald (2010: 29), Kimura and Hasegawa (2010:  
6 128), Marx (2011: 117), Churchill et al. (2012: 81), Bisconti et al. (2013: 176, 177),  
7 Fordyce and Marx (2013: 145), El Adli et al. (2014: 108).

8  
9 0=anterior margin convex and merging into a horizontal dorsal margin, posterior  
10 margin vertical; length of coronoid greater than height  
11 1=anterior and posterior margins parallel, coronoid posterodorsally directed  
12 overhanging neck, coronoid higher than long  
13 2=triangular process, anterior and posterior margins convergent, higher than or equal  
14 to length  
15 3=triangular process, anteroposteriorly longer than high

16  
17 266. Mandible, postcoronoid elevation. Modified from Bisconti (2008: 64), Deméré et  
18 al. (2008: 82), Kimura and Hasegawa (2010: 131), Marx (2011: 118), Bisconti et al.  
19 (2013: 179), Fordyce and Marx (2013: 146).

20  
21 0=absent  
22 1=present

23  
24 267. Mandible, articular surface of condyle. Modified from Bisconti (2000: 24),  
25 Kimura and Ozawa (2002: 35), Bisconti (2005: 42), Deméré et al. (2005: 63), Bouetel  
26 and Muizon (2006: 99), Steeman (2007: 57), Bisconti (2008: 38), Deméré et al. (2008:  
27 59), Fitzgerald (2010: 30), Kimura and Hasegawa (2010: 136), Marx (2011: 119),  
28 Churchill et al. (2012: 80), Fordyce and Marx (2013: 148).

29  
30 0=posterior or posterodorsal  
31 1=directed dorsally, neck and angular process not elevated above ventral margin of  
32 mandible  
33 2=directed dorsally, neck and angular process directed dorsoventrally and elevated  
34 above ventral margin

35  
36 268. Mandible, gingival foramina. Modified from Steeman (2007: 61), Marx (2011:  
37 120), Bisconti et al. (2013: 196).

38  
39 0=absent  
40 1=present

41  
42 269. Mandible, sulcus for mylohyoid muscle attachment. Modified from Bisconti  
43 (2000: 19), Bisconti (2005: 45), Deméré et al. (2005: 60), Bisconti (2008: 49),  
44 Deméré et al. (2008: 56), Marx (2011: 121), Churchill et al. (2012: 79), Bisconti et al.  
45 (2013: 191), Fordyce and Marx (2013: 149).

46  
47 0=absent  
48 1=present

49

- 1 270. Mandible, angular process. Modified from Bisconti (2005: 16, 17), Bouetel and  
2 Muizon (2006: 94), Kimura and Hasegawa (2010: 134), Bisconti et al. (2013: 186),  
3 Fordyce and Marx (2013: 147), El Adli et al. (2014: 118).  
4  
5 0=positioned below condyle  
6 1=projects far posterior to condyle  
7
- 8 271. Mandible, mandibular condyle. Modified from Bouetel and Muizon (2006: 101),  
9 Steeman (2007: 57), Deméré et al. (2008: 83), Kimura and Hasegawa (2010: 137),  
10 Bisconti et al. (2013: 189), El Adli et al. (2014: 115).  
11  
12 0=convex articular surface  
13 1=flattened condyle  
14
- 15 272. Mandible, orientation of coronoid process. Modified from Bouetel and Muizon  
16 (2006: 92).  
17  
18 0=vertical  
19 1=laterally hooked  
20
- 21 273. Mandible, height of condyle. Modified from Geisler and Sanders (2003: 45),  
22 Bouetel and Muizon (2006: 10), Fitzgerald (2006: 46).  
23  
24 0=condyle at or slightly above level of ramus anterior to coronoid process  
25 1=dorsal margin of ramus elevated far above condyle  
26 2=condyle elevated far above tip of coronoid process  
27
- 28 274. Mandible, orientation of angular process. Modified from Deméré et al. (2008:  
29 84), Kimura and Hasegawa (2010: 135), Bisconti et al. (2013: 186), El Adli et al.  
30 (2014: 114).  
31  
32 0=horizontal (posteriorly directed)  
33 1=posteroventrally curved  
34
- 35 275. Mandible, longitudinal furrow on dorsomedial surface of proximal ramus. New  
36 character.  
37  
38 0=absent  
39 1=present  
40
- 41 276. Mandible, apex of mandibular terminus. New character.  
42  
43 0=mandible tapers gradually  
44 1=apex positioned closer to dorsal margin  
45 2=positioned halfway between dorsal and ventral margins  
46
- 47 277. Mandible, shape of mandibular terminus. New character.  
48  
49 0=rounded or rectangular in lateral view  
50 1=spear-shaped in lateral view

- 1  
2 278. Mandible, symphyseal groove. Modified from Geisler and Sanders (2003: 41),  
3 Deméré et al. (2005: 57), Fitzgerald (2006: 42), Bisconti et al. (2013: 175).  
4  
5 0=absent in adults  
6 1=prominent in adults  
7  
8 279. Mandible, angular process. Modified from Bisconti (2005: 16), Bouetel and  
9 Muizon (2006: 93), Bisconti (2008: 84), Kimura and Hasegawa (2010: 133), Bisconti  
10 et al. (2013: 187).  
11  
12 0=dorsoventrally flattened and flange-like  
13 1=developed as a swollen tubercle  
14  
15 280. Mandible, groove for insertion for internal pterygoid muscle. Modified from  
16 Bouetel and Muizon (2006: 96), Bisconti et al. (2013: 183, 184).  
17  
18 0=absent  
19 1=shallow groove present along medial edge of mandibular foramen  
20  
21 281. Dentition, teeth. Modified from Bisconti (2000: 6, 18), Bisconti (2005: 11),  
22 Deméré et al. (2005: 65, 66), Steeman (2007: 1), Bisconti (2008: 15), Deméré and  
23 Berta (2008: 42), Deméré et al. (2008: 61), Fitzgerald (2010: 17, 25), Kimura and  
24 Hasegawa (2010: 28), Marx (2011: 25), Churchill et al. (2012: 83), Bisconti et al.  
25 (2013: 36, 173), Fordyce and Marx (2013: 22), El Adli et al. (2014: 119).  
26  
27 0=present in adult  
28 1=absent in adult  
29  
30 282. Dentition, orientation of accessory cusps on posterior cheek tooth. New character.  
31  
32 0=parallel with central cusp  
33 1=cusps arranged radially  
34  
35 283. Dentition, extent of division between roots. Modified from Fitzgerald (2010:  
36 123).  
37  
38 0=extends past basalmost enamel of crown  
39 1=does not pass enamel of crown, or does not emerge from alveolus  
40  
41 284. Dentition, upper anterior incisors. Modified from Deméré et al. (2008: 100).  
42  
43 0=procumbent  
44 1=vertical  
45  
46 285. Dentition, lower anterior incisors. Modified from Geisler and Sanders (2003: 35),  
47 Fitzgerald (2006: (36), Deméré et al. (2008: 100).  
48  
49 0=procumbent  
50 1=vertical

- 1  
2 286. Dentition, number of double rooted teeth in maxilla. Modified from Geisler and  
3 Sanders (2003: 23), Fitzgerald (2006: 24), Deméré and Berta (2008: 20, 21), Deméré  
4 et al. (2008: 99), Fitzgerald (2010: 16), El Adli et al. (2014: 122).  
5  
6 0=5 or more  
7 1=1 or 2  
8 2=none  
9  
10 287. Dentition, diastemata. Modified from Geisler and Sanders (2003: 25), Fitzgerald  
11 (2006: 26), Deméré and Berta (2008: 24), Fitzgerald (2010: 18).  
12  
13 0=diastemata absent  
14 1=wide diastemata between cheek teeth  
15  
16 288. Dentition, longitudinal fluting on postcanine teeth. Modified from Geisler and  
17 Sanders (2003: 26), Fitzgerald (2006: 27), Deméré and Berta (2008: 22), Deméré et al.  
18 (2008: 101), Fitzgerald (2010: 19), El Adli et al. (2014: 121).  
19  
20 0=on lingual surface only  
21 1=well developed lingually and labially  
22 2=poorly developed or absent  
23  
24 289. Dentition, shape of posterior cheek teeth. Modified from Geisler and Sanders  
25 (2003: 30), Fitzgerald (2006: 31), Fitzgerald (2010: 20).  
26  
27 0=high, peg-like teeth, crown base is <37% of crown height  
28 1=equilaterally triangular in shape, approximately as high as anteroposteriorly long  
29 2=wide, low teeth, crown base is >120% of crown height  
30  
31 290. Dentition, labial cingulum on upper cheek teeth. Modified from Geisler and  
32 Sanders (2003: 31), Fitzgerald (2006: 32), Fitzgerald (2010: 21).  
33  
34 0=present  
35 1=absent  
36  
37 291. Dentition, lingual cingulum on upper cheek teeth. Modified from Geisler and  
38 Sanders (2003: 32), Fitzgerald (2006: 33), Fitzgerald (2010: 22).  
39  
40 0=present  
41 1=absent  
42  
43 292. Dentition, accessory denticles on posterior cheek teeth. Modified from Geisler  
44 and Sanders (2003: 33), Deméré et al. (2005: 66), Fitzgerald (2006: 34), Deméré and  
45 Berta (2008: 23), Deméré et al. (2008: 102), Fitzgerald (2010: 23), El Adli et al. (2014:  
46 120).  
47  
48 0=absent  
49 1=present  
50

- 1 293. Dentition, central denticle. Modified from Geisler and Sanders (2003: 34),  
2 Fitzgerald (2006: 35), Fitzgerald (2010: 24).  
3  
4 0=larger than accessory denticles  
5 1=subequal  
6  
7 294. Dentition, posteriormost upper tooth. Modified from Fitzgerald (2010: 122).  
8  
9 0=at level of or posterior to antorbital notch  
10 1=anterior to antorbital notch  
11  
12 295. Dentition, heterodonty  
13  
14 0=present, incisors, canine, and anterior cheek teeth incisiform and posterior cheek  
15 teeth are multicuspate  
16 1=homodont, all teeth are incisiform  
17  
18 296. Cervical vertebrae, fusion. Modified from Bisconti (2005: 39), Deméré et al.  
19 (2005: 67), Kimura and Hasegawa (2010: 139), Marx (2011: 124), Churchill et al.  
20 (2012: 93), Fordyce and Marx (2013: 152), Bisconti et al. (2013: 200, 216), El Adli et  
21 al. (2014: 124).  
22  
23 0=separate  
24 1=partially fused  
25 2=fused  
26  
27 297. Atlas and Axis, ventral tubercle/hypophysis. New character.  
28  
29 0=present  
30 1=absent  
31  
32 298. Atlas, base of transverse process. Modified from Marx (2011: 122), Fordyce and  
33 Marx (2013: 150).  
34  
35 0=greater than half height of articular surface, process has dorsal and ventral  
36 processes  
37 1=less than or equal to half height of articular surface, rectangular or triangular,  
38 anteroposteriorly thin  
39 2=greater than half height of articular surface, process is rectangular and  
40 anteroposteriorly thick  
41  
42 299. Atlas, shape of neural canal. New character.  
43  
44 0=circular or rectangular, approximately as wide as high  
45 1=circular or rectangular, transverse width approximately 2/3 of dorsoventral height  
46 2=figure-8 shaped  
47  
48 300. Atlas, dorsoventral thickness of neural canal. New character.  
49

- 1 0=large, neural canal constitutes more than 2/3 of dorsoventral height of arch and  
2 body  
3 1=small, neural canal constitutes 2/3 or less of dorsoventral height of arch and body  
4  
5 301. Atlas, neural arch in dorsal view. New character.  
6  
7 0=arch anteroposteriorly shorter than body, retracted from anterior margin or from  
8 both anterior and posterior margins  
9 1=arch anteroposteriorly shorter than body, positioned anteriorly  
10 2=arch equivalent to anteroposterior length of body  
11  
12 302. Atlas, neural spine. New character.  
13  
14 0=present and small, less than dorsoventral thickness of medial part of arch  
15 1=present and tall, higher than dorsoventral thickness of medial part of arch  
16 2=absent  
17  
18 303. Axis, transverse foramen. Modified from Marx (2011: 123), Fordyce and Marx  
19 (2013: 151).  
20  
21 0=present  
22 1=absent  
23  
24 304. Axis, transverse width relative to atlas. Modified from Steeman (2007: 65),  
25 Kimura and Hasegawa (2010: 141).  
26  
27 0=less than or equal to width of atlas  
28 1=much wider than atlas  
29  
30 305. Axis, shape of neural canal. New character.  
31  
32 0=oval, rectangular, or triangular, flat ventral margin  
33 1=dorsally convex ventral margin giving canal crescent-shape  
34  
35 306. Axis, anterior projection of neural spine. New character.  
36  
37 0=present, extends far anterior to anterior articular surface  
38 1=absent or reduced, does not extend anteriorly past articular surface  
39  
40 307. Axis, lateral margin of pedicle. New character.  
41  
42 0=postzygapophysis extends dorsolaterally, visible as thickening of arch in anterior  
43 view  
44 1=postzygapophysis extends posteriorly, not visible in anterior view  
45  
46 308. Axis, ventral margin of body (excluding tubercle/hypophysis and transverse  
47 process) . New character.  
48  
49 0=straight or convex  
50 1=ventrally concave

- 1  
2 309. Axis, dorsoventral height of neural foramen. New character.  
3  
4 0=less than 2/3 height of anterior articular surface  
5 1=greater than or equal to 2/3 height of anterior articular surface  
6  
7 310. C3-C6, size of lateral vertebral canals. Modified from Bisconti (2013: 211, 212,  
8 213, 214, 215).  
9  
10 0=small, less than dorsoventral thickness of ventral transverse process  
11 1=large, much larger than dorsoventral thickness of ventral transverse process  
12  
13 311. C4-C7, dimensions of neural canal. New character.  
14  
15 0=approximately as transversely wide as dorsoventrally high  
16 1=transversely wide, greater than twice the dorsoventral height  
17  
18 312. C3-C7, shape of neural canal. New character.  
19  
20 0=oval, rectangular, or triangular, flat ventral margin  
21 1=dorsally convex ventral margin giving canal crescent-shape  
22  
23 313. C7, position of transverse process. New character.  
24  
25 0=ventral margin positioned within ventral 50% of body  
26 1=ventral margin positioned within dorsal 50% of body or higher  
27  
28 314. C7, parapophysis. Modified from Fordyce and Marx (2013: 153).  
29  
30 0=present  
31 1=absent  
32  
33 315. Lumbar vertebrae, transverse process. Modified from Geisler and Sanders (2003:  
34 284), Churchill et al. (2012: 96), Fordyce and Marx (2013: 155).  
35  
36 0=ventrolaterally directed  
37 1=laterally directed  
38  
39 316. Lumbar vertebrae, shape of transverse process. Modified from Geisler and  
40 Sanders (2003: 285), Fordyce and Marx (2013: 155).  
41  
42 0=slender and transversely wider than anteroposteriorly long  
43 1=shaped like a broad plate and equidimensional  
44 2=wider than long with distinct projection on anterior margin  
45  
46 317. Sternum, composition. Modified from Bisconti (2005: 9), Kimura and Hasegawa  
47 (2010: 154), Marx (2011: 125), Bisconti et al. (2013: 246), Fordyce and Marx (2013:  
48 156), El Adli et al. (2014: 127).  
49  
50 0=composed of several bones

- 1 1=single element  
2
- 3 318. Sternum, articulation with ribs. Modified from Bisconti (2005: 10), Marx (2011:  
4 126), Bisconti et al. (2013: 235).  
5
- 6 0=several ribs articulate with sternum  
7 1=single pair articulates  
8
- 9 319. Scapula, coracoid process. Modified from Kimura and Ozawa (2002: 48),  
10 Geisler and Sanders (2003: 292), Bisconti (2005: 76), Deméré et al. (2005: 69),  
11 Kimura and Hasegawa (2010: 146), Marx (2011: 127), Churchill et al. (2012: 99),  
12 Bisconti et al. (2013: 222), Fordyce and Marx (2013: 158).  
13
- 14 0=present  
15 1=absent  
16
- 17 320. Scapula, acromion process. Modified from Bisconti (2005: 75), Deméré et al.  
18 (2005: 68), Kimura and Hasegawa (2010: 145), Marx (2011: 128), Churchill et al.  
19 (2012: 98), Bisconti et al. (2013: 221), Fordyce and Marx (2013: 159).  
20
- 21 0=present  
22 1=absent  
23
- 24 321. Scapula, shape. Modified from Bisconti (2005: 77), Bisconti (2008: 68), Kimura  
25 and Hasegawa (2010: 147), Fordyce and Marx (2013: 157).  
26
- 27 0=anteroposterior length equivalent to proximodistal length  
28 1=anteroposteriorly longer than proximodistal length  
29
- 30 322. Scapula, supraspinous fossa. Modified from Geisler and Sanders (2003: 293),  
31 Bisconti et al. (2013: 219), Fordyce and Marx (2013: 160).  
32
- 33 0=present  
34 1=absent or nearly absent with acromion located near anterior edge of scapula  
35
- 36 323. Humerus, length. Modified from Kimura and Ozawa (2002: 50), Geisler and  
37 Sanders (2003: 297), Dooley et al. (2004: 40), Bisconti (2005: 78), Deméré et al.  
38 (2005: 70), Bisconti (2008: 96), Deméré et al. (2008: 66), Kimura and Hasegawa  
39 (2010: 150), Marx (2011: 129), Churchill et al. (2012: 100), Bisconti et al. (2013:  
40 224), Fordyce and Marx (2013: 162), El Adli et al. (2014: 125).  
41
- 42 0=longer than radius/ulna  
43 1=same length  
44 2=shorter than radius/ulna  
45
- 46 324. Humerus, deltopectoral crest. Modified from Geisler and Sanders (2003: 294),  
47 Kimura and Hasegawa (2010: 148), Churchill et al. (2012: 102), Bisconti et al. (2013:  
48 225), Fordyce and Marx (2013: 161).  
49
- 50 0=present as distinct crest

- 1 1=absent or reduced to a variably developed rugosity  
2  
3 325. Humerus, humeral head in lateral or medial view. Modified from Churchill et al.  
4 (2012: 101), Fordyce and Marx (2013: 163).  
5  
6 0=angled  
7 1=vertical  
8  
9 326. Humerus, distal end. Modified from Churchill et al. (2012: 103), Fordyce and  
10 Marx (2013: 164).  
11  
12 0=distal trochlea is narrower than distal shaft  
13 1=distal trochlea is equal to or wider than distal shaft  
14  
15 327. Humerus, head. New character.  
16  
17 0=small, maximum diameter less than 1/3 length of humerus  
18 1=large, maximum diameter approximately 1/2 length of humerus  
19  
20 328. Humerus, position of apex of deltopectoral crest. New character.  
21  
22 0=positioned on distal 1/2 of humerus  
23 1=positioned on proximal 1/2 of humerus  
24  
25 329. Humerus, lesser tuberosity. New character.  
26  
27 0=present  
28 1=absent  
29  
30 330. Humerus, distal trochlea. Modified from Bisconti et al. (2013: 226).  
31  
32 0=single convex articular surface for ulna and radius  
33 1=developed as two oval-rectangular planar facets  
34  
35 331. Radius, curvature. Modified from Bisconti (2005: 79).  
36  
37 0=anteriorly bowed  
38 1=straight  
39  
40 332. Radius, proximal end in lateral view. New character.  
41  
42 0=proximally narrow and abruptly widens in proximal 1/4 of shaft  
43 1=widest proximally, tapers distally  
44 2=roughly parallel anterior and posterior margins  
45  
46 333. Radius, length relative to ulna. New character.  
47  
48 0=shorter than ulna  
49 1=equal to or longer than ulna  
50

- 1 334. Radius and Ulna, shaft (excluding olecranon process). New character.  
2  
3 0=ulna anteroposteriorly wider than radius  
4 1=ulna anteroposteriorly equal to or narrower than radius  
5
- 6 335. Ulna, olecranon process. Modified from Geisler and Sanders (2003: 298),  
7 Bisconti (2005: 74), Marx (2011: 130), Bisconti et al. (2013: 227), Fordyce and Marx  
8 (2013: 165).  
9  
10 0=present  
11 1=absent  
12
- 13 336. Ulna, distal 1/2 of shaft. New character.  
14  
15 0=widens distally  
16 1=parallel margins, rectangular shaft  
17
- 18 337. Ulna, olecranon process. Modified from Churchill et al. (2012: 104).  
19  
20 0=extends proximal to humeral articular surface  
21 1=does not extend proximal to humeral articular surface  
22
- 23 338. Ulna, distal olecranon process. New character.  
24  
25 0=concave posterior margin, smoothly transitions to shaft  
26 1=distinct notch present between olecranon and shaft  
27
- 28 339. Manus, number of digits. Modified from Kimura and Ozawa (2002: 49), Geisler  
29 and Sanders (2003: 299), Dooley et al. (2004: 35), Deméré et al. (2005: 71), Bouetel  
30 and Muizon (2006: 70), Deméré et al. (2008: 67), Kimura and Hasegawa (2010: 151),  
31 Marx (2011: 131), Churchill et al. (2012: 106), Bisconti et al. (2014: 229, 230), El  
32 Adli et al. (2014: 126).  
33  
34 0=pentadactyl  
35 1=tetradactyl  
36
- 37 340. Soft tissue, ventral throat grooves. Modified from Bisconti (2000: 75), Geisler  
38 and Sanders (2003: 301), Deméré et al. (2005: 73), Bisconti (2008: 52), Deméré et al.  
39 (2008: 69), Kimura and Hasegawa (2010: 159), Marx (2011: 132), Churchill et al.  
40 (2012: 112).  
41  
42 0=absent or few (2-10) confined to throat region  
43 1=numerous and terminate midbody  
44 2=numerous and extend to or posterior to umbilicus  
45
- 46 341. Soft tissue, ventral throat pouch. Modified from Deméré et al. (2005: 74),  
47 Deméré et al. (2008: 70), Kimura and Hasegawa (2010: 160), Marx (2011: 133),  
48 Churchill et al. (2012: 110).  
49  
50 0=absent

1 1=present  
2  
3 342. Soft tissue, tongue. Modified from Deméré et al. (2005: 79), Deméré et al. (2008:  
4 75), Kimura and Hasegawa (2010: 161), Marx (2011: 134), Churchill et al. (2012:  
5 109).  
6  
7 0=muscular  
8 1=reduced and predominantly connective tissue  
9  
10 343. Soft tissue, temporomandibular joint. Modified from Marx (2011: 135).  
11  
12 0=synovial  
13 1=non-synovial, fibrocartilaginous pad  
14  
15 344. Soft tissue, longitudinal ridges on rostrum. Modified from Deméré et al. (2005:  
16 85), Deméré et al. (2008: 76), Kimura and Hasegawa (2010: 158), Marx (2011: 136).  
17  
18 0=absent or indistinct  
19 1=single median ridge  
20 2=three longitudinal ridges  
21  
22 345. Soft tissue, dorsal fin. Modified from Geisler and Sanders (2003: 304), Deméré  
23 et al. (2005: 72), Bisconti (2008: 51), Deméré et al. (2008: 68), Marx (2011: 137),  
24 Churchill et al. (2012: 115).  
25  
26 0=present as fin or dorsal hump  
27 1=absent  
28  
29 346. Soft tissue, baleen. Modified from Bisconti (2000: 16), Kimura and Ozawa (2002:  
30 30), Geisler and Sanders (2003: 1), Bisconti (2005: 13), Deméré et al. (2005: 75),  
31 Fitzgerald (2006: 1), Steeman (2007: 1), Bisconti (2008: 17), Deméré et al. (2008: 71),  
32 Marx (2011: 138), Bisconti et al. (2013: 13).  
33  
34 0=absent  
35 1=present  
36  
37 347. Soft tissue, profile of mouth in lateral view. New character.  
38  
39 0=straight or dorsally concave  
40 1=mostly straight and downturned near eye  
41 2=dorsally arched and evenly curved  
42  
43 348. Soft tissue, number of baleen plates. Modified from Deméré et al. (2005: 75),  
44 Churchill et al. (2012: 86).  
45  
46 0=fewer than 200  
47 1=200 to 270  
48 2=greater than 270  
49

1 349. Soft tissue, length of baleen plates. Modified from Bisconti (2005: 54), Bisconti  
2 (2008: 39), Kimura and Hasegawa (2010: 163), Bisconti et al. (2013: 14).  
3  
4 0=shorter than ½ length of rostrum  
5 1=longer than ½ length of rostrum  
6  
7 350. Soft tissue, subrostral gap. Modified from Deméré et al. (2005: 76), Churchill et  
8 al. (2012: 87).  
9  
10 0=absent, baleen racks converge at midline  
11 1=present, baleen racks separated by gap  
12  
13 351. Color patterns, rostral saddle. Modified from Arnold et al. (2005: 1), Marx (2011:  
14 139).  
15  
16 0=absent  
17 1=present  
18 2=well developed  
19  
20 352. Color patterns, blowhole streaks. Modified from Arnold et al. (2005: 2), Marx  
21 (2011: 140).  
22  
23 0=absent  
24 1=present  
25 2=well developed  
26  
27 353. Color patterns, dark nape field. Modified from Arnold et al. (2005: 3), Marx  
28 (2011: 141).  
29  
30 0=absent  
31 1=dark nape present  
32 2=nape light  
33  
34 354. Color patterns, shape of dorsal nape field. Modified from Arnold et al. (2005: 4),  
35 Marx (2011: 142).  
36  
37 0=nape streak absent  
38 1=V-shaped chevron  
39 2=nape blaze linear to diffuse  
40  
41 355. Color patterns, ventral nape streak. Modified from Arnold et al. (2005: 5), Marx  
42 (2011: 143).  
43  
44 0=absent  
45 1=present  
46  
47 356. Color patterns, ear stripe. Modified from Arnold et al. (2005: 6), Marx (2011:  
48 144).  
49  
50 0=absent

1 1=present  
2  
3 357. Color patterns, basal flipper color. Modified from Arnold et al. (2005: 7),  
4 Deméré et al. (2005: 81), Marx (2011: 145).  
5  
6 0=uniformly colored  
7 1=uniform with white leading edge  
8 2=white  
9 3=dark  
10  
11 358. Color patterns, distal flipper color. Modified from Arnold et al. (2005: 8), Marx  
12 (2011: 146).  
13  
14 0=uniformly colored  
15 1=uniform with light leading edge  
16 2=dark grey  
17  
18 359. Color patterns, axillary patch. Modified from Arnold et al. (2005: 9), Marx (2011:  
19 147).  
20  
21 0=absent  
22 1=present  
23  
24 360. Color patterns, thorax field. Modified from Arnold et al. (2005: 10), Marx (2011:  
25 148).  
26  
27 0=body uniformly colored  
28 1=dark dorsum and lighter ventrum, no intermediate gray  
29 2=light gray transitional field present  
30  
31 361. Color patterns, caudal chevron. Modified from Arnold et al. (2005: 11), Marx  
32 (2011: 149).  
33  
34 0=absent  
35 1=single chevron  
36 2=double chevron  
37  
38 362. Color patterns, asymmetry. Modified from Arnold et al. (2005: 13), Deméré et al.  
39 (2005: 82), Marx (2011: 150).  
40  
41 0=absent  
42 1=present but subtle  
43 2=well developed  
44  
45  
46 363. Color patterns, baleen. Modified from Churchill et al. (2012: 89).  
47  
48 0=uniformly light  
49 1=uniformly black or dark grey  
50 2=dark and light, asymmetrical pigmentation  
51



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