A possible enigmatic kekenodontid (Cetacea, Kekenodontidae) from the Oligocene of Mexico

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Abstract

Kekenodontidae is a taxon of unresolved affinity in Cetacea; whether it belongs to Mysticeti or archaeocetes remains uncertain, mainly due to the poor fossil record from the Oligocene. Here, we report a left periotic, identified as a kekenodontid from the Oligocene (Chattian) of Baja California Sur, Mexico. This periotic is phenetically similar to *Kekenodon onamata* in the presence of: broad and deep anteroexternal sulcus, broad oblique furrow on the anterior half of the ventral surface of the pars cochlearis, a transversally narrow pars cochlearis, deeply excavated mallear fossa, and present but indistinct stylomastoid fossa. In the light of the highly diagnostic periotic in Cetacea, this fossil, an isolated left periotic, is currently recognized as a kekenodontid. Thus, this fossil is the first possible kekenodontid recognized from the North Pacific, suggesting a global distribution of Kekenodontidae during the Oligocene.

Keywords: *Kekenodon onamata*, Baja California Sur, whale, periotic, fossil.

Resumen

La familia Kekenodontidae es un taxón con una posición taxonómica no resuelta dentro del grupo Cetacea, cuya relación con el grupo Mysticeti y los arqueocetos se mantiene incierta debido a la pobreza del registro fósil concerniente al Oligoceno. En este estudio reportamos un hueso del complejo auditivo (periótico izquierdo) identificado como un animal kekenodontido del Oligoceno (Chattiano) de Baja California Sur, México. Este periótico es fenéticamente similar a <u>Kekenodon onamata</u> *en la presencia de: un amplio y profundo surco anteroexterno, una hendidura o surco sobre la superficie media-anterior del par coclear, un par coclear transversalmente estrecho, una fosa maleolar profundamente escavada, y una fosa estilomastoidea presente pero tenue. A la luz del alto valor diagnóstico que posee el hueso periótico en cetáceos, este fósil, un periótico izquierdo aislado del Oligoceno de México, es reconocido como un kekenodontido. Como resultado este espécimen representa el primer posible kekenodontido conocido para el Pacífico Norte, sugiriendo una distribución global para el grupo Kekenodontidae durante el Oligoceno.*

Palabras clave: <u>Kekenodon onomata</u>*, Baja California Sur, cetáceo, periótico, fósil.*

1. Introduction

Kekenodontidae, currently only known from the Late Oligocene (28–23 million years ago), is a taxonomically and phylogenetically unresolved group in Cetacea (whales, dolphins and porpoises), as it has been recognized as archaeocetes (*e.g.* Kellogg, 1936; Uhen, 2008) and mysticetes (*e.g.* Fordyce, 1992; Fordyce and de Muizon, 2001). Hector (1881) described the isolated teeth, left tympanic bulla and periotic (holotype: NMNZ Ma. 306) from the Oligocene of New Zealand, and accordingly named a new taxon: *Kekenodon onamata*. Later, Kellogg (1936) re-described the holotype *K. onamata* in further detail, and Mitchell (1989) established a new subfamily: Kekenodontinae based on the holotype; now, it is widely recognized as an independent family: Kekenodontidae. However, since the recognition of enigmatic kekenodontids, no new kekenodontid fossils have been formally described.

The holotype of *K. onamata* illustrated by Hector (1881) includes teeth and ear bones (left periotic and tympanic bulla). Other specimens tentatively referred to kekenodontids are *Phococetus vasconum* Delfortrie, 1874 from the Oligocene of France (Uhen, 2008), and '*Squalodon*' *gambierensis* Glaessner, 1955 from the Oligocene of Australia (Fitzgerald, 2010). However, *P. vasconum* and '*S.*' *gambierensis* are poorly known due to the fact that both taxa were named based on an isolated, single tooth; thus, it remains largely uncertain whether they should be placed in the Kekenodontidae. The taxonomic affinity of *P. vasconum* and '*S.*' *gambierensis* to *K. onamata* is beyond the scope of this study; on this account, we follow the suggestions of Uhen (2008) and Fitzgerald (2010) in including both taxa in the Kekenodontidae, and plotting the kekenodontid distribution during the Oligocene accordingly (Figure 1). Here we report a left periotic from the Late Oligocene of Baja California Sur, Mexico. This new fossil is phenetically similar to the periotic of *K. onamata*. Note that the periotic (part of earbone) is morphologically distinct and diagnostic, and is commonly used to recognize cetacean species taxonomically (*e.g.* Kasuya, 1973; Steeman, 2010; Ekdale *et al.*, 2011; Tsai and Fordyce, 2016). Thus, this fossil is identified as the first fossil record of Kekenodontidae from Mexico, and the whole North Pacific.

Institutional Abbreviation: MHN-UABCS, Museo de Historia Natural de la Universidad Autónoma de Baja California Sur, México; **NMNZ**, National Museum of New Zealand, Wellington.

2. Material and methods

The fossil MHN-UABCS EcSj5/16/267 was prepared with various hand tools and polyvinyl acetate, and photographed with a Canon PowerShot G10. The illustrations of MHN-UABCS EcSj5/16/267 were prepared and edited in Adobe Photoshop/Illustrator© and CorelDraw©. Standard views of the periotic are used for further comparison across the Cetacea: dorsal is the surface of dorsal margin of the internal acoustic meatus (see Boessenecker and Fordyce, 2015; Tsai and Fordyce, 2015). Anatomical terminology follows standardized terms in Cetacea (Mead and Fordyce, 2009).

3. Systematic Palaeontology

Cetacea Brisson, 1762
Kekenodontidae Mitchell, 1989
Gen. *et* sp. indet.
(Figures 2, 3, 4)

Material. MHN-UABCS_EcSj5/16/267, an isolated left periotic. Collected by Gerardo González Barba, Lawrence G. Barnes and Arturo Cruz Marín in March, 1993.

Locality and Geological Settings. MHN-UABCS EcSj5/16/267 was collected in the San Juan de la Costa area at the El Saladito locality (24.44307 N, -110.70136 W, see Figure 1), where the Late Oligocene fossiliferous outcrop belongs to the San Juan Member of the El Cien Formation (Fischers *et al.*, 1995). Field notes indicate that this fossil was collected from the mine spoils associated with the phosphatic Humboldt bed (the phosphorite source mainly exploited by mining activity). According to the trace of grayish mudstone and silt-sandstone from MHN-UABCS EcSj5/16/267, this fossil is likely to belong to the horizon above the Humboldt bed. We therefore interpret that MHN-UABCS EcSj5/16/267 originally comes from the mudstones/silt-sandstones layer above the Humboldt bed (see Schwennicke, 1994; Fischers *et al.*, 1995). Given the planktonic foraminifera correlated with the P21/P22 transition above the Humboldt bed (Fischer *et al.*, 1995; Berggren *et al.*, 1995), the geological age of MHN-UABCS EcSj5/16/267 is about 27 Ma (early Chattian).

Diagnosis and Remarks. The left periotic MHN-UABCS EcSj5/16/267 shares morphological similarities with *K. onamata* in the presence of: broad and deep anteroexternal sulcus, broad oblique furrow on the anterior half of the ventral surface of the pars cochlearis, narrow pars cochlearis, deeply excavated mallear fossa, and indistinct stylomastoid fossa; but it differs from *K. onamata* (Hector 1881; Kellogg 1936) in having: pars cochlearis more inflated posteriorly, thinner anterior process (mediolaterally), and the superior process slightly higher than the suprameatal area.

The periotic MHN-UABCS EcSj5/16/267 differs from basilosaurid archaeocetes in its: long and straight periotic body, longer anterior process, less inflated and rounded pars cochlearis, oval suprameatal area, and low superior process. The periotic MHN-UABCS EcSj5/16/267 differs from Oligocene Mammalodontidae (Fitzgerald, 2006, 2010), Aetiocetidae (Marx *et al.*, 2015; Tsai and Ando, 2016), Eomysticetidae (*e.g.* Boessenecker and Fordyce, 2015,
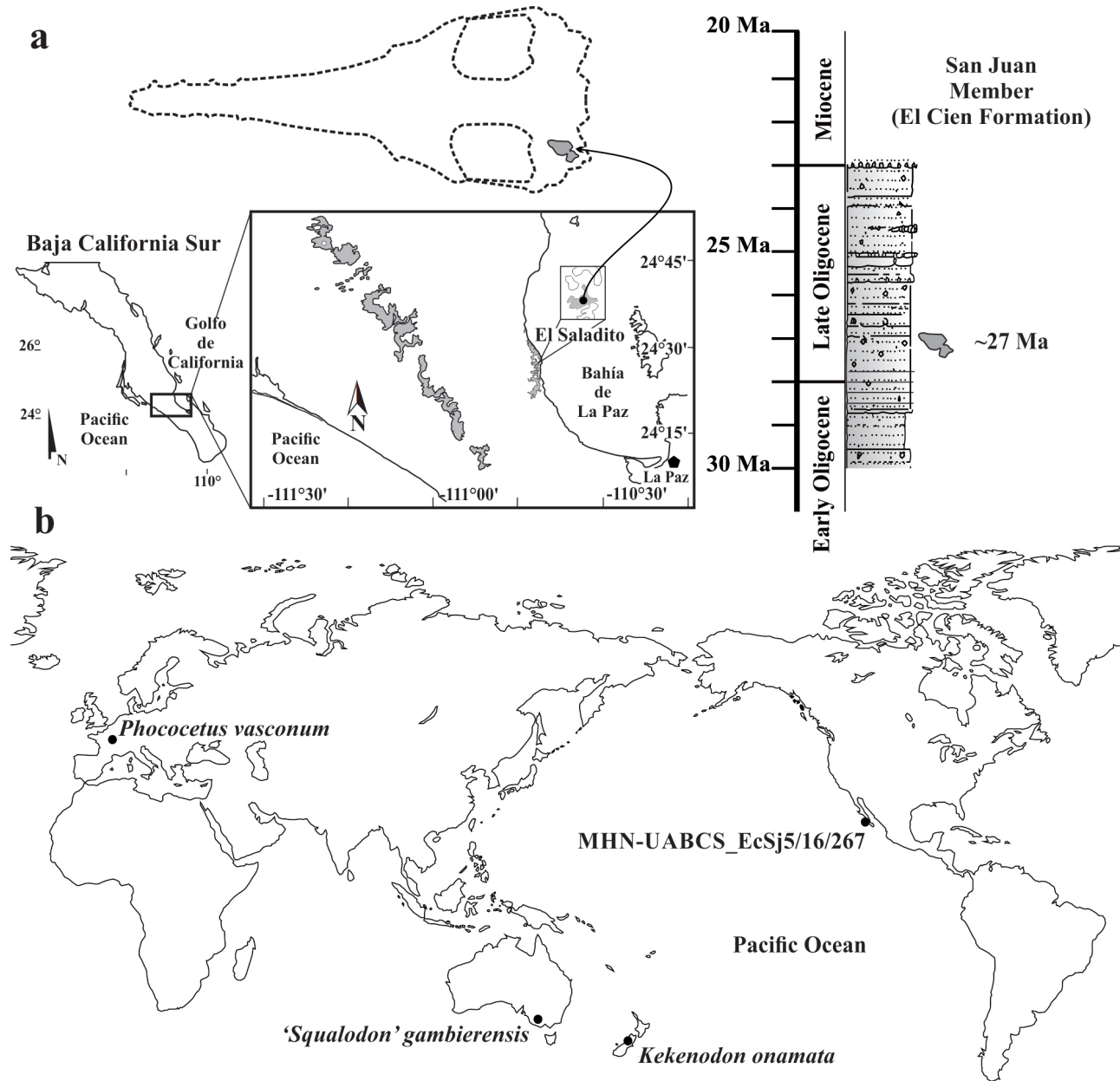
Figure 1. Geographical map and general stratigraphical column. a, locality and the possible horizon of producing MHN-UABCS_EcSj5/16/267; b, distribution of Oligocene kekenodontids: *Kekenodon onamata* from New Zealand, '*Squalodon*' *gambierensis* from Australia, *Phococetus vasconum* from France, and MHN-UABCS_EcSj5/16/267 from Mexico.

2016), and *Horopeta umarere*, Tsai and Fordyce, 2015 in its: inflated pars cochlearis, less developed stylomastoid fossa, anterior process extended more anteriorly and dorsoventrally, reduced suprameatal area, and low superior process. The left periotic MHN-UABCS EcSj5/16/267 differs from all crown-ward mysticetes (Balaenidae, Balaenopteridae, Cetotheriidae/Neobalaenidae, and Eschrichtiidae), ranging from the Miocene to Recent in: presence of the superior process, united internal acoustic meatus, indistinct lateral tuberosity and the presence of fovea epitubaria for receiving the accessory ossicle.

Considering these similarities and differences, we currently identify MHN-UABCS EcSj5/16/267 as Kekenodontidae gen. *et* sp. indet.

Description. Left periotic (Figures 2, 3, 4; measurements are listed in Table 1).– The anteroventral angle of the anterior process is broken; the anterior process is trapezoidal to slightly irregular in medial view, with vertical anterior keel extending ventrally from the anterodorsal angle. The anterior keel is straight vertically. The anteroexternal sulcus is present, forming a broad groove and extending diagonally from the posteroventral margin of the anterior
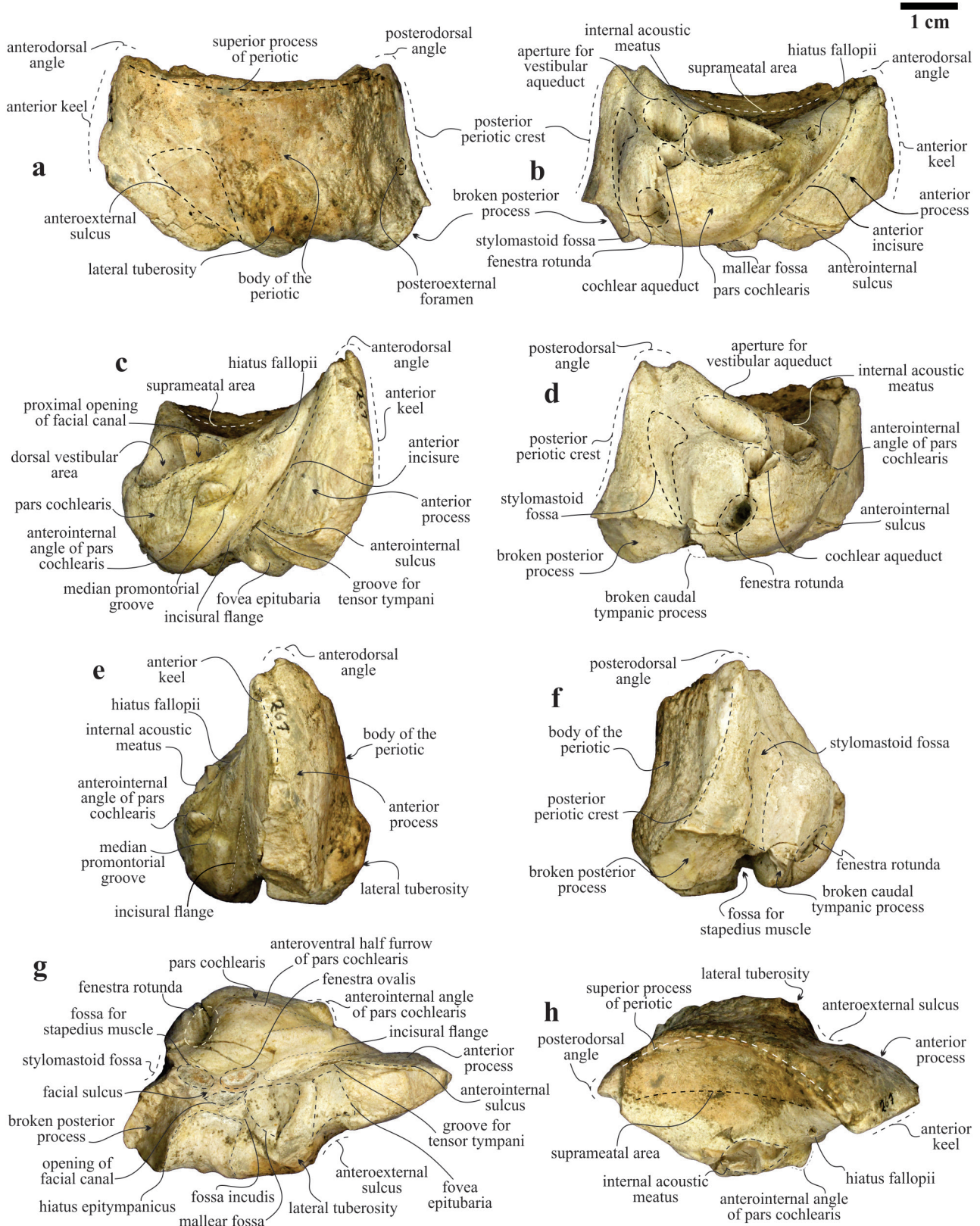
Figure 2. Left periotic, MHN-UABCS_EcSj5/16/267, a, lateral view; b, medial view; c, anteromedial view; d, posteromedial view; e, anterior view; f, posterior view; g, ventral view; and h, dorsal view
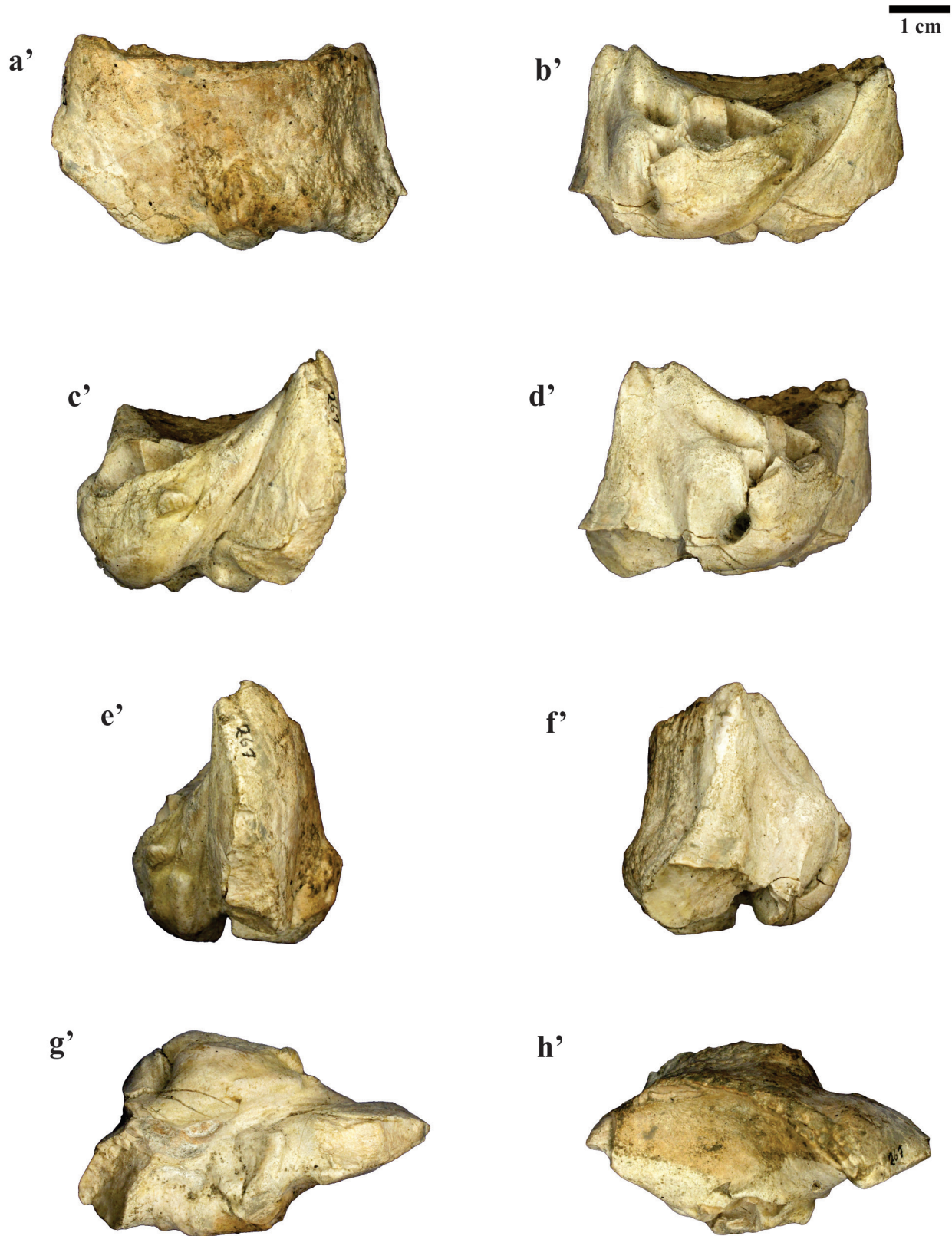
Figure 3. Left periotic, MHN-UABCS_EcSj5/16/267, a', lateral view; b', medial view; c', anteromedial view; d', posteromedial view; e', anterior view; f', posterior view; g', ventral view; and h', dorsal view.
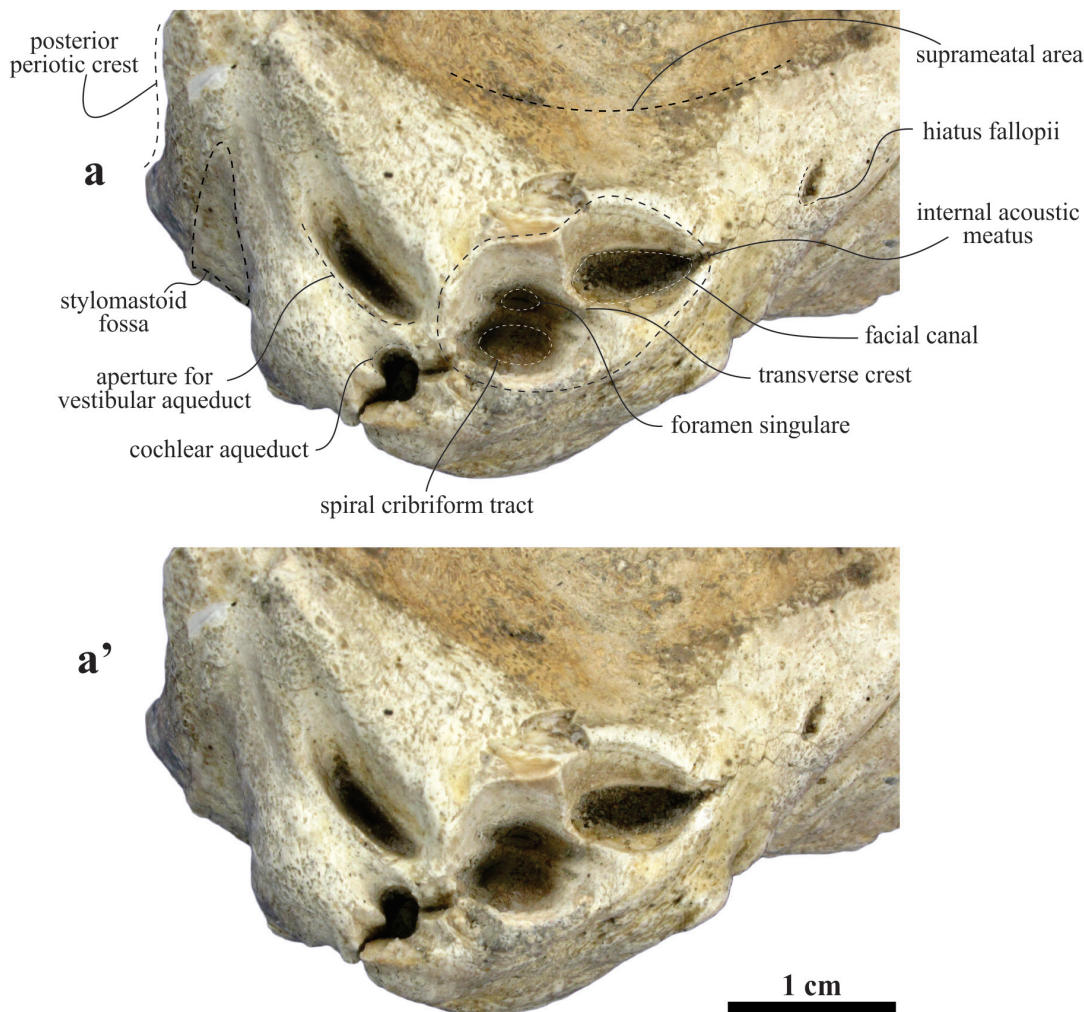
Figure 4. Internal/endocranial view and anatomical features of the left periotic, MHN-UABCS_EcSj5/16/267, internal acoustic meatus.

process up to the anterodorsal angle. A narrow sulcus of the fossa for the tensor tympanic muscle occurs medially in the posteroventral part of the anterior process, perpendicular to the anterior incisure and above the fovea epitubaria, and is directed anteroventrally to the broken anteroventral angle. The ventral margin of the anterior process is roughly at the same level as the ventral margin of the pars cochlearis. On the ventral margin, the fovea epitubaria, anterior to the mallear fossa, is prominently anteroposteriorly concave, semispherical in medial view and rectangular in ventral view. The accessory ossicle is missing.

The superior process is reduced and horizontal to slightly concave at the dorsal margin, extending from anterodorsal angle to posterodorsal angle. The suprameatal area is oval, concave and smooth, with a few very small foramina posteriors to the internal acoustic meatus. In ventral view, the lateral tuberosity is blunt, bulbous and indistinct; the apex of the lateral tuberosity is broken. The mallear fossa is rounded, concave with well-defined margin, and oriented posteroventrally. The fossa incudis is irregular to rounded

and indistinct. The fenestra ovalis is elliptical, oriented ventrally and located anteromedial to the distal opening of the facial canal.

The pars cochlearis is crescent in medial view. The anterior surface of the pars cochlearis gradually tilts onto the medial surface of the anterior process, with a slight step (anterointernal angle of pars cochlearis) posterior to the anterior incisure; ventral to the anterointernal angle is a short median promontorial groove most prominent at the anteroventral margin of the pars cochlearis, which is continuous to the anteroventral half furrow of the pars cochlearis. The anterior incisure slightly curves up to the anterodorsal angle from the ventral surface of the pars cochlearis. The hiatus Fallopii is small, elliptical and anterodorsal to the proximal opening of the facial canal (Figure 4). The proximal opening of the facial canal, the dorsal vestibular area, and the aperture for the cochlear aqueduct are roughly in a straight line oriented anterolaterally. The proximal opening of the facial canal and the dorsal vestibular area are both rounded and similar

Table 1. Measurements in mm, left periotic, MHN-UABCS EcSj5/16/267.

Greatest anteroposterior length	51
Anteroposterior length, from anterodorsal angle to posterodorsal angle.	45
Greatest anteroposterior length of anterior process	21
Maximum anteroposterior length of pars cochlearis	31
Maximum anteroposterior length of internal acoustic meatus	13
Anteroposterior length of the mallear fossa	10
Anteroposterior length of stapedial muscle fossa	7.1
Transverse width of base of anterior process	11
Transverse width of pars cochlearis	15
Maximum transverse width of internal acoustic meatus	6.5
Maximum transverse width of the suprameatal area	19
Maximum transverse width of periotic, internal face of pars cochlearis to apex of lateral tuberosity	28
Transverse width of mallear fossa	7.1
Dorsoventral depth of pars cochlearis	22
Maximum dorsoventral depth of anterior process	31
Dorsoventral depth of the periotic at level of the mallear fossa	26

in size (~7mm). The aperture for the cochlear aqueduct is rounded and smaller than the aperture for the vestibular aqueduct. The aperture for the vestibular aqueduct is long, slit-like, and oriented anteromedially. The fenestra rotunda, at the posteromedial corner of the pars cochlearis, is oval in outline. The connection between the fenestra rotunda and the aperture for the cochlear aqueduct is an open fissure. The posteroventral margin of the caudal tympanic process is broken, but it broadly forms a triangular and rounded flange posterior to the fenestra rotunda. The posterior process is missing. The gentle depression on the posterior surface of the pars cochlearis marks the presence of the stylomastoid fossa.

4. Discussion

The periotic MHN-UABCS EcSj5/16/267 is currently identified as Kekenodontidae gen. *et* sp. indet., and is the first kekenodontid record from the North Pacific. In addition, given the occurrence of *K. onamata* in the Southern Ocean and a putative kekenodontid *P. vasconum* from the Atlantic, this possible Mexican kekenodontid adds to the distribution in the North Pacific, suggesting a global distribution of Kekenodontidae during the Oligocene (Figure 1b). However, it is necessary to reiterate that *P. vasconum* and '*S.*' *gambierensis* are still only known from a single, isolated tooth, making their affinities to *K. onamata* remain an open question; their proper identifications or taxonomic re-evaluations are beyond the scope of this study. For now, we follow the suggestions of Uhen (2008) and Fitzgerald (2010) in tentatively placing *P. vasconum* and '*S.*' *gambierensis* in the Kekenodontidae. Regardless of the present uncertainty, discovery of more complete specimens should resolve the taxonomic problems and the enigmatic evolutionary history of Kekenodontidae.

Interestingly, a well-preserved kekenodontid skull has recently been figured (Clementz *et al.*, 2014, fig. 2), but has yet to be formally described from the Oligocene of New Zealand. Clementz *et al.* (2014) emphasized that *Kekenodon*-like species are of archaeocete architecture without synapomorphies shared with Mysticeti or Odontoceti. Nevertheless, given the uncertainty of kekenodontid affinity in Cetacea, it may be worth noting that the toothed mysticete *Aetiocetus cotylalveus* was first identified as an archaeocete (Emlong, 1966). However, Van Valen (1968) pointed out that *A. cotylalveus* shows some derived features, such as the position of external nares posterior to second upper premolar (P2), which in archaeocetes is far more anterior than P2. If Van Valen's argument remains valid to distinguish Neoceti from archaeocetes, according to the illustration (Clementz *et al.*, 2014, fig. 2), this new *Kekenodon*-like animal also shows far-positioned external nares posterior to P2, which raises the question again whether *Kekenodon*-like species should be identified as mysticetes or archaeocetes.

In addition, the ecological role of kekenodontids in the Oligocene remains largely unknown due to the poor fossil record. The occurrence of MHN-UABCS EcSj5/16/267 from Mexico invites some further consideration. Both sides of the North Pacific occupied a variety of small toothed mysticetes (2 – 4 m long, Aetiocetidae; *e.g.* Barnes *et al.*, 1995; Marx *et al.*, 2015). However, a large aetiocetid (8 m, Tsai and Ando, 2016) suggests a niche partitioning amongst toothed mysticetes in the western North Pacific during the Oligocene. On the other hand, no large Oligocene toothed mysticetes have been reported in the eastern North Pacific. MHN-UABCS EcSj5/16/267 only preserves an isolated periotic, and thus it is not possible to estimate its body size. The range of body size in the Kekenodontidae is unknown, but according to the tooth size of *K. onamata*, kekenodontids may have had larger body sizes than most aetiocetids. If this interpretation is correct, MHN-UABCS EcSj5/16/267

may occupy a similar niche in the eastern North Pacific as a large aetiocetid in the western North Pacific. Future findings of more complete kekenodontids should elucidate this hypothesis.

5. Conclusions

The left periotic MHN-UABCS_EcSj5/16/267 from the Oligocene of Mexico is currently identified as Kekenodontidae gen. *et* sp. indet. Thus, MHN-UABCS_EcSj5/16/267 not only represents the first possible kekenodontid record from Mexico, but also the first in the North Pacific. Kekenodontids are still one of the least known groups in Cetacea and the occurrence of MHN-UABCS_EcSj5/16/267 suggests that kekenodontids may have been distributed globally during the Oligocene. More findings of complete kekenodontids would further elucidate their paleo-distribution, anatomical details, and ecological niche, as well as the unresolved systematics.

Acknowledgements

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