

Oligocene Dawn Baleen Whales in Mexico (Cetacea, Eomysticetidae) and Palaeobiogeographic Notes

Ballenas del Alba en el Oligoceno de México (Cetacea, Eomysticetidae) y Notas Paleobiogeográficas

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Abstract

Eomysticetids are an extinct basal taxon of baleen whales (Mysticeti: Chaeomysticeti - 'true whales'), which appeared during the Oligocene and reflected a transitional stage between the origin of baleen and the loss of teeth, a trait that characterizes extant baleen whales. The eomysticetids are recognized as a diverse and widely distributed lineage with a rich record in the Australasia region (Australia and New Zealand). Several features of their palaeobiology, such as ontogenetic growth and ecological feeding, have been discussed; however, traits related to their biogeography and inherent speciation (origin and extinction) have only been briefly reviewed. In this context, the present study addresses biogeographic aspects based on a new fossil from the eastern North Pacific belonging to the records of the El Cien Formation of Baja California Sur, Mexico. Our description and phylogenetic analysis classify this new specimen of eomysticetid within the genus *Eomysticetus* (cf. *Eomysticetus* sp.). In addition, we identify the biogeographic relationship between the (eastern) North Pacific and the (western) North Atlantic, which indicates a possible exchange of their Oligocene cetacean faunas. Furthermore, the presence of the Gaarlandia terrestrial arc during the Oligocene indicate vicariance events, which likely led to allopatric speciation within Eomysticetidae in the North Hemisphere. Lastly, the Oligocene cetacean fossil record from Baja California Sur, unique in Mexico, might explain several aspects of the eomysticetids palaeobiology, considering the several unnamed specimens housed in the local collections.

Keywords: Baja California Sur, El Cien Formation, Eomysticetidae, Gaarlandia, Palaeobiogeography.

Resumen

Los eomisticetidos son un taxón basal extinto de las ballenas barbadas (Mysticeti: Chaeomysticeti - "ballenas verdaderas"), los cuales aparecieron durante el Oligoceno y reflejan una etapa de transición entre el origen de las barbas y la pérdida de dientes, rasgo que caracteriza a las ballenas actuales. Los eomisticetidos son considerados un linaje diverso y ampliamente distribuido con un rico registro en la región de Australasia (Australia y Nueva Zelanda). Varios aspectos de su paleobiología como el crecimiento ontogenético y ecología alimenticia han sido discutidos; sin embargo, elementos relacionados con su biogeografía e inherente especiación (origen y extinción) sólo han sido brevemente revisados. En este contexto, el presente estudio aborda aspectos biogeográficos a partir de un nuevo fósil del Pacífico Norte oriental perteneciente a los registros de la Formación El Cien de Baja California Sur, México. Nuestra descripción y análisis filogenético clasifica a este nuevo ejemplar de eomisticetido dentro del género *Eomysticetus* (cf. *Eomysticetus* sp.). Asimismo, identificamos la relación biogeográfica entre el Pacífico Norte (este) y el Atlántico Norte (oeste), lo que indica un posible intercambio de sus faunas de cetáceos durante el Oligoceno. Además, la presencia del arco terrestre de Gaarlandia durante el Oligoceno indica eventos de vicarianza, que probablemente condujeron a la especiación alopatrica dentro de Eomysticetidae en el Hemisferio Norte. Por último, el registro fósil de cetáceos de edad Oligoceno presente en Baja California Sur, único en México, podría aclarar varios aspectos acerca de la paleobiología de los eomisticetidos considerando los varios especímenes sin nominar en las colecciones locales.

Palabras clave: Baja California Sur, Eomysticetidae, Formación El Cien, Gaarlandia, Paleobiogeografía

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1. Introduction

Eomysticetidae represents an archaic lineage of Oligocene ‘toothless’ mysticetes (Chaeomysticeti), which appeared during the second evolutionary radiation among cetaceans, the rise time of the clade Neoceti (Fordyce, 2009; Fordyce & Marx, 2018). Eomysticetids were contemporaneous to the tooth-bearing mysticetes, archaic odontocetes and relict archaeocetes (Keenodontidae; Fordyce & Marx, 2018), and show a widespread distribution in the Pacific, Atlantic, and perhaps Mediterranean-Paratethys seas (Boessenecker & Fordyce, 2017). At present, eleven eomysticetid species have been described mainly from the New Zealand fossil record from the Southern Hemisphere (Boessenecker & Fordyce, 2016, 2017). However, their diversity and palaeobiology are still far from being completed, as shown by the discussion on the origin of the baleen (Boessenecker & Fordyce, 2015c, 2016; Peredo *et al.*, 2018; Ekdale & Deméré, 2022) and the several unnamed fossils from the North Hemisphere (e.g., Hernández-Cisneros *et al.*, 2017).

On the other hand, the fossil record of late Oligocene marine mammals from Baja California Sur, Mexico indicates a rich evidence of Oligocene Chaeomysticeti from El Cien and San Gregorio formations (Hernández-Cisneros *et al.*, 2017; Hernández-Cisneros, 2018). Such fossils include several eomysticetids species promising new interpretations of their palaeobiology. Herein, we describe a new eomysticetid specimen for the North Pacific, which belongs to the southernmost fossil assemblage of Oligocene cetaceans in North America (Barnes, 1998). Its morphology is similar to the Atlantic species (*Eomysticetus* and *Micromysticetus*; Sanders & Barnes, 2002a, 2002b; Boessenecker & Fordyce, 2016), but the fragmented material makes difficult to identify a likely new species. Nonetheless, the phylogenetic analysis supports a biogeographic relationship between the North Pacific and the North Atlantic, allowing interpretations regarding distributional patterns.

1.1 Abbreviations

MHN-UABCS (MU), Museo de Historia Natural de la Universidad Autónoma de Baja California Sur, Baja California Sur, Mexico.

2. Methods

The specimen MU_EcSj1/29/142 belongs to the palaeontological collection of the Universidad Autónoma de Baja California Sur, in La Paz, Baja California Sur, Mexico. The fossil materials (partial skull and postcranial elements) were prepared using pneumatic chisels, hand tools, coated and glued with polyvinyl acetate. Vertebrae set are fragmented and unprepared. Thus, only three cervical (include atlas and axis) and three thoracic vertebrae are illustrated with diagnostic

features. The positions of some sutures were confirmed using a magnifying glass. Photographs were taken with a Canon PowerShot G10 camera. The used anatomical terms follow that of Mead and Fordyce (2009). The taxonomic classification follows the current criteria of the inclusion of Cetacea within Artiodactyla (Waddell *et al.*, 1999; Gatesy *et al.*, 2013; O’Leary *et al.*, 2020; Prothero *et al.*, 2021). Measurements from the skull and vertebrae are in Tables 1 and 2.

The fossil MU_EcSj1/29/142 was coded into the matrix published by Hernández-Cisneros and Velez-Juarbe (2021; derived initially from Marx & Fordyce, 2015) with 272 characters and 112 terminal taxa. The character 83 in *Tohoroata*, *Tokarahia* and *Matapanui* were changed from 0 to 1 (according to the distinctive feature, the parasagittal and oval temporal fossa present in eomysticetids; Boessenecker & Fordyce, 2016). Morphological coding is as follows (?=missing or inapplicable).

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The phylogenetic analysis was focused on the relationship of MU_EcSj1/29/142 within Eomysticetidae. The cladistic analysis was performed using T.N.T. v.1.5 software (Goloboff & Catalano, 2016) under the heuristic parsimony analysis (‘traditional search’). Characters were treated under equal weights and implied weights, applying a backbone constraint tree (see Hernández-Cisneros & Velez-Juarbe, 2021). The concavity constant ($k = 18.374024$) was calculated with the script setk (Goloboff *et al.*, 2008; Goloboff *et al.*, 2018). Only the strict consensus tree under implied weights was illustrated –the phylogenetic relationship of MU_EcSj1/29/142 is the same in both strict consensus tree under equal weights and implied weights. The analysis settings include 10,000 random stepwise-addition replicate (in Memory option) and Tree Bisection Reconnection (TBR) branch swapping with ten trees per replicate. Support values were obtained by symmetric resampling based on 1000 replicates (Goloboff *et al.*, 2003).

Our interpretation follows the concept of the biotic components as the basic unit in biogeography (‘sets of spatiotemporally integrated taxa that coexist in given areas’; Morrone, 2009). The area cladogram was obtained following the main steps of the cladistic biogeographic approach: i) construction of taxon-area cladograms from taxon cladograms by replacing their terminal taxa with the areas they inhabit; ii) obtaining resolved area cladograms (if necessary); and iii) getting the general area cladogram (Morrone & Carpenter, 1994; Morrone, 2009). We resolved the area cladogram based on the redundant distributions criteria (see Ebach, 2005; Morrone, 2009; Parenti & Ebach, 2009).

Table 1. Skull measurements of cf. *Eomysticetus* sp., MU_EcSj1/29/142, (in mm; following Boessenecker & Fordyce, 2015). (~) denotes estimated measurement.

Anteroposterior length preserved	1100
Premaxilla length as preserved	695
Nasal length	285
Greatest length of the temporal fossa, frontal to nuchal crest	420
Length of parietal, occipital apex to frontoparietal suture	100
Greatest transverse width of the premaxilla	~53.6
Transverse width of the anteriormost nasal	24
Transverse width of the posteriormost nasal	12
Width of the intertemporal region	85.9

Table 2. Vertebrae measurements of cf. *Eomysticetus* sp., MU_EcSj1/29/142, in mm. (~) denotes estimated measurement.

	Length of body	Transverse width of the body	Dorsoventral depth of the body	Total height	Width of vertebra at transverse process
Atlas (C1)	55	~160	~85	~123.5	260
Axis (C2)	53.2	~130	~82	~185	220
Cervical C3	---	---	---	---	---
Thoracic (?T5)	---	68	---	---	---
Thoracic (?T6)	---	75	---	---	---
Thoracic (?T7)	~106	~80.5	---	---	---

3. Geological Setting

The fossil MU_EcSj1/29/142 was collected from the San Juan Member outcrops (El Cien Formation, late Oligocene; Fischer *et al.*, 1995) at the locality Mesa del Tesoro (24.47366 N, -110.69646 W), which is a rich fossiliferous site 10 km north of San Juan de la Costa village in Bahía de La Paz, located ~50 km northwest from La Paz city, Baja California Sur, Mexico (Figure 1). The San Juan Member is the lower section of the El Cien Formation, which is composed of mudstones, siltstones, sandstones, conglomerates, coquinas, tuffs and phosphorites (Fischer *et al.*, 1995). The strata show multiple transgressive and regressive sedimentary cycles, which end at the Oligocene/Miocene boundary (Fischer *et al.*, 1995), and indicate coastal environments not deeper than 200 m suggesting shelf environments, coastal lagoons, estuaries and deltas (Schwennicke, 1994). The age of the San Juan Member has been estimated at ~28 to 25 Ma (Hausback, 1984; Applegate, 1986; Kim & Barron, 1986; Smith, 1991; Fischer *et al.*, 1995; Drake *et al.*, 2017; Galván-Escovedo *et al.*, 2020).

In the San Juan de la Costa area, many cetacean fossils have been found within the numerous phosphatic beds from the San Juan Member's middle section due to the mining activity that exploits the phosphatic beds and from palaeontological research (Hernández-Cisneros *et al.*, 2017; Hernández-Cisneros, 2018). However, several records lack stratigraphic data because they were obtained from reworked material or are by-product mine spoils, *e.g.*, MU_EcSj1/29/142. The eomysticetid,

MU_EcSj1/29/142, likely belongs to an unknown phosphatic bed from the middle part of the stratigraphic section at the Mesa del Tesoro, perhaps close to the Humboldt bed, the main exploited phosphatic bed at the San Juan de la Costa zone (see Fischer *et al.*, 1995; Hernández-Cisneros, 2018). Hence, due to the unknown stratigraphic data, we give an age between 25 to 28 Ma for MU_EcSj1/29/142 same as the estimated age for the San Juan Member at San Juan de la Costa area (Fischer *et al.*, 1995; Drake *et al.*, 2017; Galván-Escovedo *et al.*, 2020).

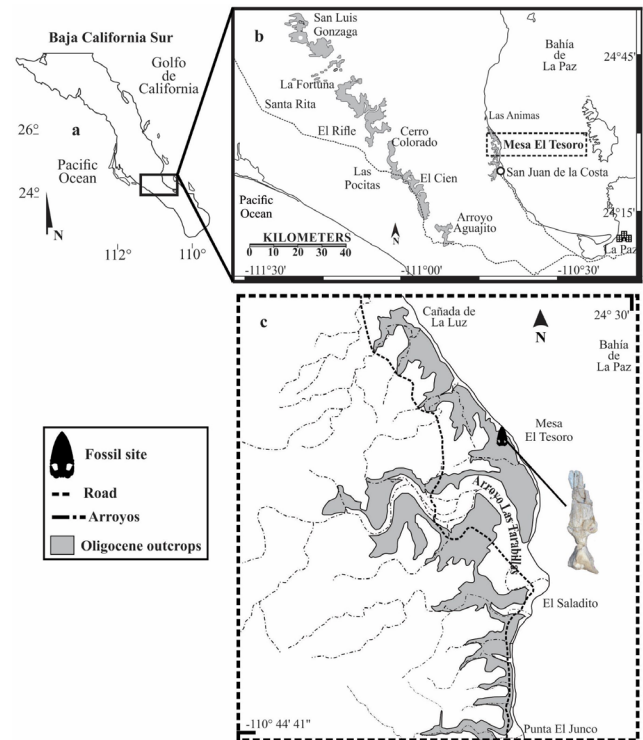


Figure 1. Map with the fossil site of MU_EcSj1/29/142 (cf. *Eomysticetus* sp.). (a) State of Baja California Sur, (b) Distribution of the San Juan Member outcrops, and (c) Locality of Mesa El Tesoro (map modified from Hernández-Cisneros, 2018; original map base Romero-Rojas, 2002)

4. Systematic Palaeontology

Order Artiodactyla, Owen (1848)
 Suborder Whippomorpha, Waddell *et al.* (1999)
 Infraorder Cetacea, Brisson (1762)
 Pavorder Mysticeti, Gray (1864)
 Section Chaemysticeti, Mitchell (1989)
 Family Eomysticetidae, Sanders and Barnes (2002b)
 Genus *Eomysticetus*, Sanders and Barnes (2002b)
 cf. *Eomysticetus* sp.
 Figures 2–8.

4.1 Material

MHN-UABCS_EcSj1/29/142, partial skull, atlas and axis, third and fourth cervical vertebrae, eight incomplete thoracic vertebrae, approximately fourth

fragmented lumbar vertebrae and several bone fragments. The specimen is housed in the palaeontological collection from the Universidad Autónoma de Baja California Sur. The specimen was collected by Gerardo González Barba, Lawrence G. Barnes and James Goedert, in November of 1999.

4.2 Locality

Mesa del Tesoro, San Juan de la Costa, La Paz, Baja California Sur, Mexico. (24.47366 N, -110.69646 W). San Juan Member, El Cien Formation.

4.3 Horizon

From an unknown phosphatic bed of the middle section at Mesa del Tesoro, around 35 to 60 m level in the stratigraphic column of the San Juan Member (see Hernández-Cisneros, 2018).

4.4 Age

Late Oligocene, ~28 to 25 Ma (Fischer *et al.*, 1995; Drake *et al.*, 2017; Galván-Escovedo *et al.*, 2020).

4.5 Diagnosis

The specimen, MU_EcSj1/29/142, is classified as an eomysticetid animal (Sanders & Barnes, 2002b;

Boessenecker & Fordyce, 2016) by having: long and slender skull, an elongate and transversally narrow intertemporal region with exposures of the frontal and parietal, elongate nasal bones; narrow and elongated rostrum, oval and long temporal fossa. The specimen MU_EcSj1/29/142 share with *Eomysticetus whitmorei* Sanders & Barnes, 2002b: an anterolaterally concave margin of the occipital shield in dorsal view (an autapomorphy for *Eomysticetus whitmorei*; Boessenecker & Fordyce, 2016), a nasal lateral process and a sharp triangular

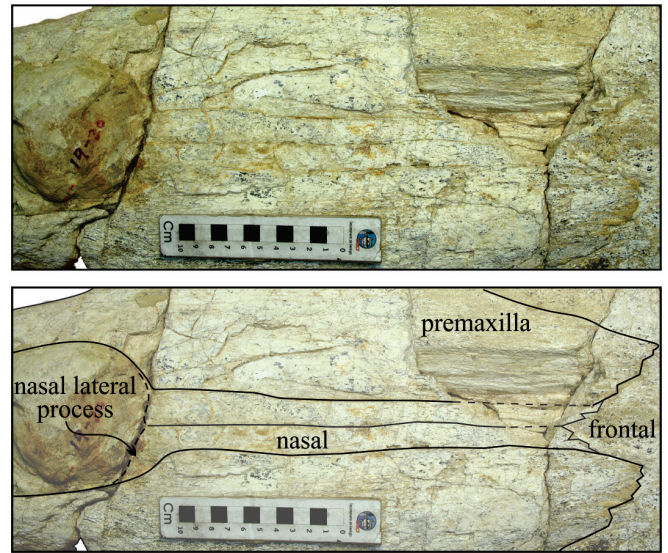


Figure 3. Nasal region, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.), skull, dorsal view.

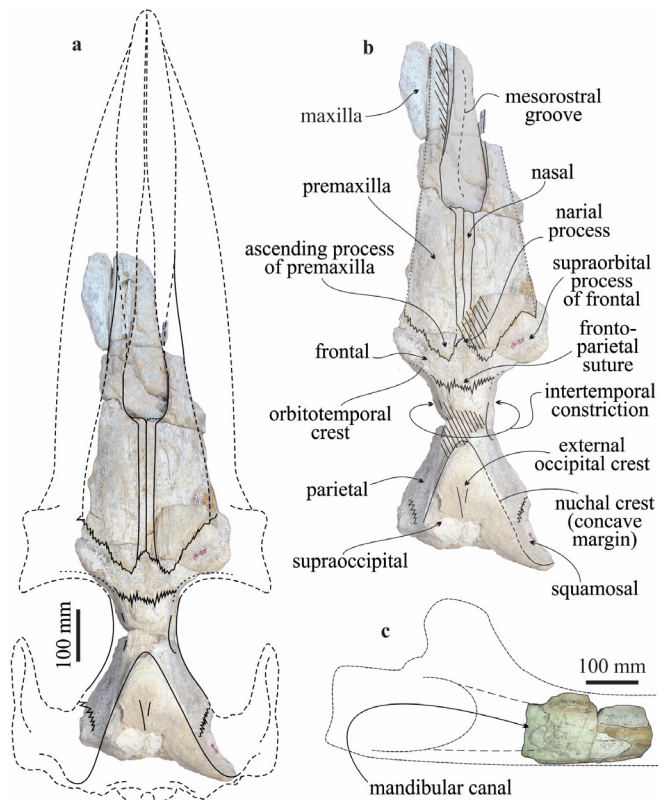


Figure 2. Skull, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.), dorsal view. (a) Reconstruction lines of the skull based on the preserved material. (b) Anatomical details. (c) Fragment of the left mandible, medial view.

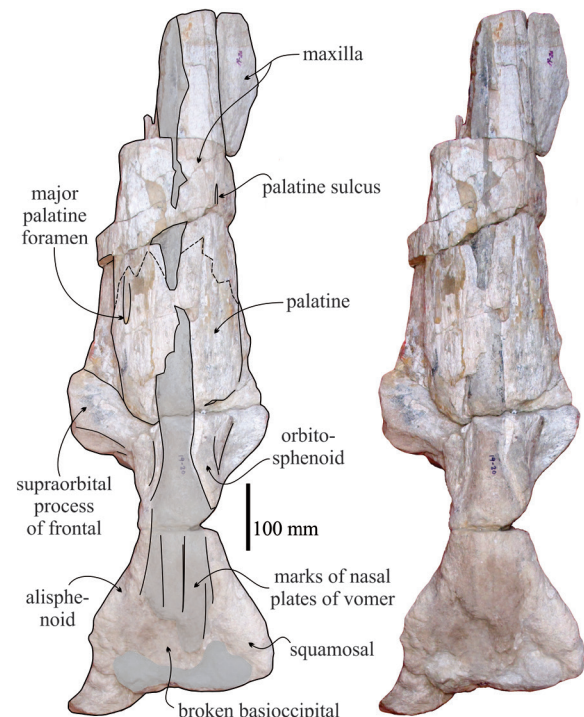


Figure 4. Skull, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.), ventral view and anatomical details.

supraoccipital. Also, the specimen, MU_EcSj1/29/142, has similar morphology with *Eomysticetus carolinensis* Sanders and Barnes, 2002b. However, the holotype of *Eomysticetus carolinensis* represents a possible juvenile ontogenetic state and a likely synonym regarding *Eomysticetus whitmorei* (Boessenecker and Fordyce, 2016). Thus, it is a challenge to suggest morphological affinities due to ontogenetic changes (Tsai & Fordyce, 2014; Boessenecker & Fordyce, 2015c). On the other hand, it is similar to *Micromysticetus rothauseni* Sanders & Barnes, 2002a, because it has a relatively short intertemporal region, broad and parallel premaxilla along nasals (Sanders & Barnes, 2002a; Boessenecker & Fordyce, 2016). Furthermore, the specimen, MU_EcSj1/29/142, is different from other eomysticetids by having a wide mesorostral groove, a broad premaxilla with an ascending process extended farther than the posterior ending of the nasals, long rectangular nasal bones with wedge posterior end, narial process, and a neural spine with an elliptical foramen and bifurcated end.

The following features separate the specimen MU_EcSj1/29/142 from the crown Mysticeti: transversely narrow intertemporal region, extremely long nasals (> 65% bizygomatic width), rigid nasals and premaxillae sutures, a dorsoventrally shallow palatal keel, and axis without vertebral arterial canal (for an extensive review of Eomysticetidae see Boessenecker & Fordyce, 2015a; 2016).

5. Description

5.1 Ontogenetic age and size

The specimen, MU_EcSj1/29/142, display well-developed and fused cranial sutures, well-fused vertebral epiphyses and neural arches, and a bifurcated neural spine in the axis indicating likely physical maturity of an adult animal (Perrin, 1975; Walsh & Berta, 2011; Boessenecker & Fordyce, 2015a). The body size is difficult to estimate due to the fragmented material but based on the preserved skull, we suggest that the specimen's total body length may vary around 5 to 6 m long, similar to *Tokarahia* (Boessenecker & Fordyce, 2015b).

5.2 Skull

In dorsal view, the rostrum as preserved lacks most of the maxilla (Figures 2, 4, 6), but some fragments are attached to the premaxilla. On the other hand, the premaxilla is a distinctive feature of MU_EcSj1/29/142, mainly by the broad ascending process of the premaxilla readily distinct from other known eomysticetids. At the level of the narial fossa, the premaxilla is the wall of a wide mesorostral groove and inflected medially

towards the nasal opening. In the anterior end of the nasal bones, the premaxilla is broad with a convex dorsal surface at the level of the nasal. It extends posteriorly to form the ascending process of the premaxilla, which lays on the medial part of the frontal. The posterior end of the ascending process extends far from the rear of the nasal bones, and the premaxilla/frontal suture is relatively tight (Figure 3). Premaxillae were

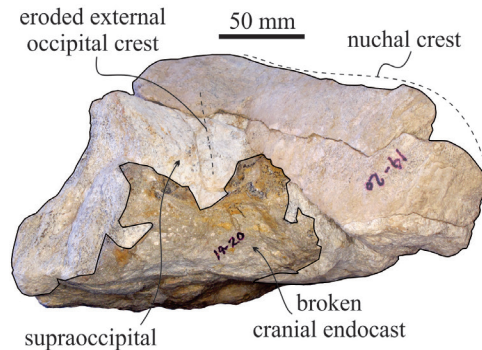


Figure 5. Cranium in posterior view with anatomical details, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.).

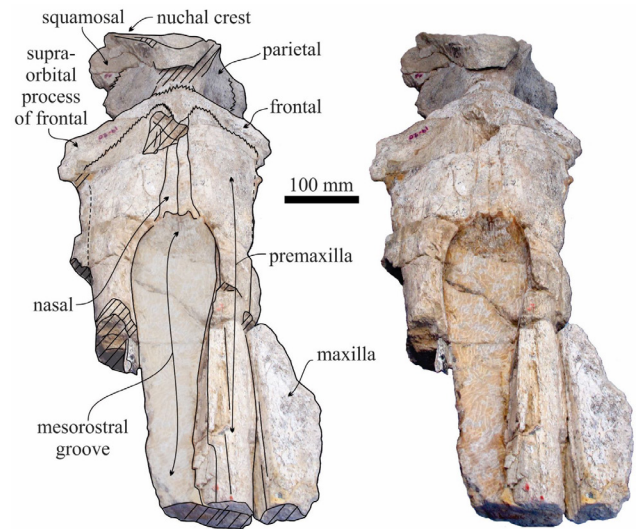


Figure 6. Skull, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.), anterodorsal view and anatomical details.

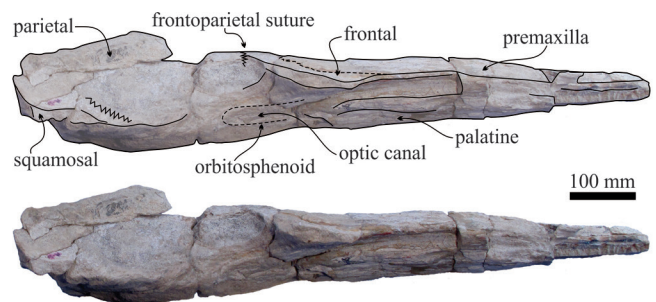


Figure 7. Skull, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.), right lateral view and anatomical details.

wrapped laterally by the maxilla, but the contact and contribution of the maxilla are unclear.

In a lateral view, the rostrum is straight with not well preserved maxillary, and its lateral edge lay below the apex of the supraoccipital (Figure 7). However, the suture of the maxilla/palatine, plus the palatine sulcus and major palatine foramen, are visible. The nasal

bones, like in other stem mysticetes, are longer and anterior to the antorbital notch. Their dorsal surface is flat, transversely narrow and rectangular. The anterolateral end of the nasals shows a more or less preserved short lateral process like a wedge (Figure 3), similar to *Eomysticetus whitmorei*. The nasal bones are joined tightly between the premaxillae, and the posterior suture

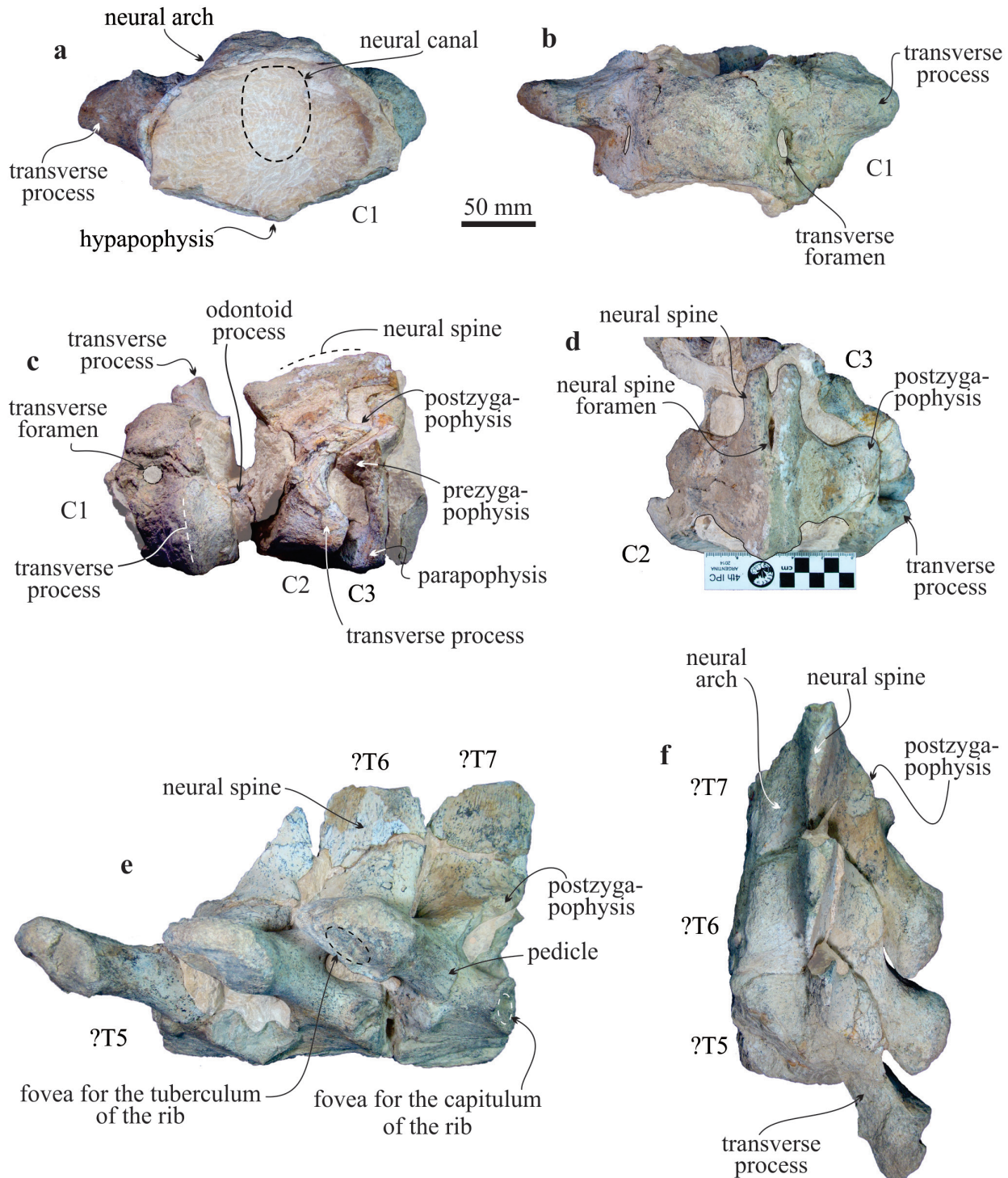


Figure 8. Vertebrae and anatomical details, MU_EcSj1/29/142 (cf. *Eomysticetus* sp.). (a–b) Atlas (C1), anterior and dorsal view. (c) Atlas (C1), Axis (C2), and third cervical vertebra (C3) in left lateral view. (d) Axis (C2) in dorsal view. (e–f) Thoracic vertebrae, likely fifth to the seventh vertebra (?T5–T7), left lateral and dorsal view respectively.

is relatively tight with the frontal. The frontal is incomplete, the right supraorbital process conserves part of the orbital roof, the dorsal surface lacks supraorbital foramina, and the joint with the parietal has an irregular suture. The orbitotemporal crest is present in the posteromedial part of the frontal and near to the posterior edge. In the ventral view can be seen traces of the optical canal in the medial part of the frontal.

The parietals are widely exposed in the temporal region. The elongate dorsal surface of the intertemporal region is broken; the cross-section is semicircular to elliptic in shape. The parietal surface is slightly convex on the braincase, and the supraoccipital joint with the parietal forms the slightly concave edges of the nuchal crest. In lateral view, the parietal/squamosal suture down obliquely above the incomplete alisphenoid. The supraoccipital is triangular with a relatively concave surface and displays an eroded external occipital crest (Figures 2, 5). The broken surface of the occipital shield allows observing part of the cranial endocast. Ventrally, the cranium lacks details of the basioccipital, squamosal, pterygoid, sphenoid bones.

5.3 Vertebrae

Around 16 vertebrae are partially preserved and require preparation. Only the atlas, axis, and thoracic vertebrae (?T5–T7) allow identifying morphological features (Figure 8). The atlas shape is similar to other vertebrae found in different eomysticetids (e.g., *Yamatocetus*, *Eomysticetus*, *Tokarahia*), with an approximately elliptical to rounded profile in anterior view. The transverse process is prominent and thick (akin to the present in *Yamatocetus* or *Tokarahia*). The hypapophysis and a rounded transverse foramen are present in the atlas. On the other hand, the axis contrasts widely with the known fossils mainly by having a bifurcated neural spine with defined lobules and a foramen (Figure 8d). These features are distinct to the medial sulcus and small tubercles present in the neural spine of *Micromysticetus rothauseni* (a youth animal, ChM PV4844; Sanders & Barnes, 2002a; Boessenecker & Fordyce, 2016) and *Tokarahia* sp., cf. *Tokarahia lophocephalus* (a likely subadult animal, OU 22081; Boessenecker & Fordyce, 2015b).

The thoracic vertebrae ?T5–T7, as preserved (Figures 8e, 8f), have a dense and long transverse process, distinct to the short process present in the first four anterior thoracic vertebrae (e.g., *Tohoraata* and *Waharoa*; Boessenecker & Fordyce, 2015a, 2015c). The length of the incomplete centrum of the vertebra ?T7 (106 mm), the relatively high pedicle, the size and position of the fovea for the tuberculum and capitulum of the ribs, plus the lateral shape of the neural spine similar to the thoracic vertebrae 6–7 from *Yamatocetus canaliculatus* Okazaki, 2012, indicate a middle position in the thoracic vertebrae set (see Okazaki, 2012; Martínez-Cáceres *et al.*, 2017).

6. Phylogenetic Analysis and Biogeographic Results

6.1 Phylogenetic results

Our phylogenetic result (Figure 9a) is similar to previous phylogenetic analyses (e.g., Boessenecker & Fordyce, 2016; Fordyce & Marx, 2018), which back up the monophyly of the group with branch support ~60 to 90%. The branch support is 72% and includes the known eomysticetid taxa *Matapanui*, *Tokarahia*, *Waharoa*, *Micromysticetus*, *Yamatocetus*, and *Eomysticetus*. We only illustrate the strict consensus tree under implied weights (Figure 9a; strict consensus tree recovered from 20 parsimonious trees, $k = 18.374024$, 42.85138 steps, consistency index CI = 0.250, retention index RI = 0.736, rescaled consistency index RCI = 0.184, tree total length 1448). The following synapomorphic characters support the branch of Eomysticetidae: functional rostrum length more than one and a half times the bizygomatic width (1/2); oval temporal fossa (83/1); the anterior process of periotic in lateral view as two-bladed and L-shaped (146/2); anterior border of the proximal opening of the facial canal is continuous with the hiatus Fallopii and shaped like a fissure (178/2); medial lobe of tympanic bulla subequal in width to the lateral lobe or smaller (202/1); supraspinous fossa of scapula absent or nearly absent, with acromion process located near the anterior edge of the scapula (256/1). The relationship of MU_EcSj1/29/142 (cf. *Eomysticetus* sp.) with *Eomysticetus whitmorei* has branch support of 43% both share a common character, the concave lateral edge of the supraoccipital (112/2), perhaps an unequivocal feature for the genus *Eomysticetus*.

6.2 Biogeographic results

The geographic area relationships based on the phylogenetic results (Figures 9a, 9b) highlight the connection between the (eastern) North Pacific and the (western) North Atlantic concerning the South (western) Pacific Ocean (Figures 9a, 9b). The results illustrate the wide distribution of Eomysticetidae (Figure 9c; Boessenecker & Fordyce, 2017), perhaps linked to their zooplankton food sources (Clementz *et al.*, 2014; Boessenecker & Fordyce, 2015c), but many distributional patterns among eomysticetids species still remain unclear. Furthermore, a relevant point is the presence of two different geographic barriers between the areas: 1) the warm equatorial waters in the Pacific Basin recognized as a crucial barrier regarding the cetacean distribution (Davies, 1963; Hernández-Cisneros & Velez Juarbe, 2021), and 2) the intermittent terrestrial barrier named as Gaarlandia in the Central American Seaway (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). Interestingly, the presence of the Gaarlandia barrier and the oscillation of oceanographic conditions (change on currents flows, temperature, and salinity) in the Central American Seaway (Iturralde-Vinent &

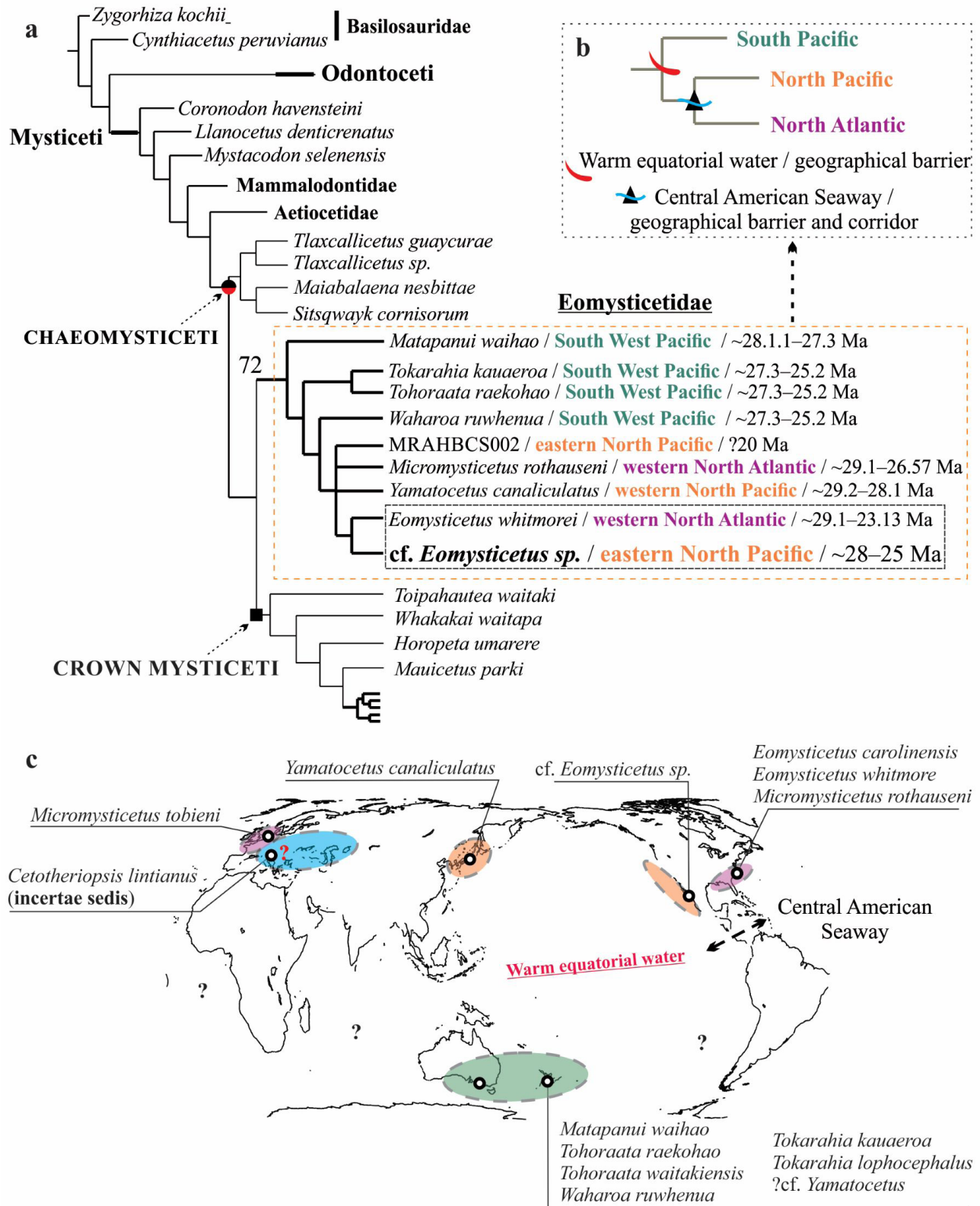


Figure 9. Phylogeny, area cladogram and eomysticetid distribution map. (a) Cladogram showing the phylogenetic relationship of MU_EcSj1/29/142 (cf. *Eomysticetus* sp.) between Eomysticetidae (range ages are from Bossenecker & Fordyce, 2016). (b) The general area cladogram shows the relationship of the areas where eomysticetids are distributed and indicates potential barriers and influence of the Central America corridor. (c) Map with the main eomysticetid species and its distribution, plus *Cetotheriopsis lintianus*, a likely eomysticetid (see Bossenecker & Fordyce, 2016). The black dashed arrow indicates the Central America Seaway corridor.

MacPhee, 1999; von der Heydt & Dijkstra, 2006; Zhang *et al.*, 2011; Tremblin *et al.*, 2016) indicate what could have controlled the cetacean dispersal processes during the Oligocene, between the Atlantic and Pacific oceans. In fact, Gaarlandia was almost a complete terrestrial arch during the early Oligocene, and in the late Oligocene, the land arch was mostly an archipelago (Iturralde-Vinent & MacPhee, 1999). Both geological events influenced the distributional patterns of the surrounding marine fauna in the Central American Seaway region (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006; Agnolin *et al.*, 2019). Such a scenario indicates that the Pacific and Atlantic cetacean faunas were subject to vicariance events during the early Oligocene and dispersal events in the late Oligocene. Still, it is unclear if the fauna exchange was unidirectional, from one ocean to another or in both directions. In addition, the relationship of MU_EcSj1/29/142 (cf. *Eomysticetus* sp.) and *Eomysticetus whitmorei* proposes allopatric speciation events in this region (allopatric model I: vicariance; Wiley & Lieberman, 2011).

7. Discussion

The specimen MU_EcSj1/29/142 represents the first eomysticetid animal from the Pacific Coast of North America. However, the new fossil's relevance lies in the biogeographical interpretation of the Eomysticetidae distributional patterns, which are a key to the Mysticeti evolutionary history. Hence, the biogeographical results indicate that eomysticetids are a good indicator of the environmental conditions that drove the origin of the "modern" baleen whales (Chaeomysticeti). The Eomysticetidae distribution and diversity show correspondence within multiple areas with key food sources for the crown Mysticeti evolution (Fordyce, 1977, 1980; Marx & Uhen, 2010; Clementz *et al.*, 2014; Marx & Fordyce, 2015; Marx *et al.*, 2019). Besides, the distributional patterns make it possible to identify likely speciation events between eomysticetids, such as allopatric speciation in the North Hemisphere, which may lead to explain how local environmental conditions and barriers drove cladogenesis of other chaeomysticetes during the Oligocene (e.g., *Horopeta*, *Whakakai*, *Toipahautea*; Tsai & Fordyce, 2015, 2016, 2018).

On the other hand, the new record of MU_EcSj1/29/142 as cf. *Eomysticetus* sp. on the North American west coast indicates a close relationship between the North Pacific and North Atlantic cetacean faunas during the Oligocene. Moreover, the studies of the Oligocene cetacean fauna in the most southern record of North America (Baja California Sur) are still in the first steps, but it is known that the record has representative groups of stem Neoceti and relict taxa such as Kenodontidae (Hernández-Cisneros & Tsai, 2016; Hernández-Cisneros *et al.*, 2017), which are likely related with the North Atlantic faunas. Consequently, these

potential records will allow knowing details on turnover fauna processes and distributional patterns of the cetaceans during the Eocene–Oligocene transition and Oligocene in the North Hemisphere, plus the role of the Central American Seaway corridor and the Gaarlandia barrier in these processes (Iturralde-Vinent & MacPhee, 1999; Leigh *et al.*, 2014).

Lastly, it is noteworthy that the widespread eomysticetid distribution lacks an accurate explanation regarding their ancestral area. The current evidence of the perhaps oldest eomysticetids (e.g., *Yamatocetus*; Marx & Fordyce, 2015) suggests that their common ancestor during the late Eocene likely inhabited the North Hemisphere before colonizing the Southern Hemisphere oceans. However, this idea needs to be supported with more evidences. In addition, the fossil record in Mexico indicates having new eomysticetid species, and propose occurrences of *Eomysticetus whitmorei* (MHN-UABCS_EcTm9/82/254 and MHN-UABCS_EcSj1/29/276; Hernández-Cisneros, 2012; Hernández-Cisneros *et al.*, 2017) and ?*Yamatocetus* species (MHN-UABCS_Sg6/71/208; Hernández-Cisneros *et al.*, 2017; Cedillo-Avila, 2018). Another record perhaps implicates an early Miocene surviving eomysticetid from Baja California Sur, but its geochronological dating is still uncertain (specimen MRAHBCS 002, Figure 9a; AEHC *et al.*, pers. comm.).

8. Concluding remarks

Eomysticetidae fossil record indicates distributional patterns that might help to explain the baleen whales evolution in the oceans. Besides, the fossil record of North America has much to add about eomysticetids and other baleen whales. On the other hand, the Oligocene cetacean fossil record from Baja California Sur will contribute significantly to the Neoceti evolutionary history, which is until now the closes point to the extinct Central American Seaway with Oligocene cetacean record in North America. In addition, it represents a transitional climate point (tropical to temperate) with a rich fossil biota. Lastly, the biogeographical approach offers insight into the cetacean evolution from spatial and geographical scales. It allows establishing a frame to identify environmental variables, biological or geological events, and others processes that might influence the cetacean evolutionary history. The biogeographical approach applied to the cetacean palaeontology is young, but we hope to see more maps illustrating the intricate cetacean evolution.

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Author Contributions

AEHC conceived the study; AEHC and EHNS analysed the data and wrote the paper. Both authors approved the final version of this manuscript and agree to be held accountable for the content therein.

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