New Simocetidae (Cetacea, Odontoceti) from the Pysht Formation in Washington State, U.S.A. (#80454)

First submission

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New Simocetidae (Cetacea, Odontoceti) from the Pysht Formation in Washington State, U.S.A.

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Odontocetes first appeared by the early Oligocene and their early evolutionary history can provide clues as to how some of their unique adaptations, such as echolocation, evolved. Here, three new specimens from the middle Oligocene Pysht Formation are described further increasing our understanding of richness and diversity of early odontocetes, particularly for the North Pacific region. Phylogenetic analysis shows that the new specimens are part of a more inclusive, redefined Simocetidae, which now includes *Simocetus rayi*, *Olympicetus* sp. 1, *Olympicetus avitus*, *O. thalassodon* sp. nov.,, and a large unnamed taxon, all part of an endemic, North Pacific clade. Of these, *Olympicetus thalassodon* sp. nov. represents one of the best known simocetids, offering new information on the cranial and dental morphology of early odontocetes. Additionally, the inclusion of CCNHM 1000, here considered to represent a neonate of *Olympicetus* sp., as part of the Simocetidae, suggests that this group represents a clade of non-echolocating odontocetes, further implying that some morphological features that have been correlated with the capacity to echolocate appeared before the acquisition of ultrasonic hearing. Thedentition of simocetids is interpreted as being plesiomorphic, with a tooth count more akin to that of basilosaurids and early toothed mysticetes, while other features of the skull and hyoid suggests various forms of prey acquisition, including raptorial or combined feeding and in *Olympicetus* spp., and suction feeding in *Simocetus*. Finally, body size estimates show that small to moderately large taxa are present in Simocetidae, with a largest taxon represented by LACM 124104 with an estimated body length of 3 meters, which places it as the largest known simocetid, and amongst the largest Oligocene odontocetes. The new specimens described here add to a growing list of Oligocene marine tetrapods from the North Pacific, further promoting faunistic comparisons across other contemporaneous and younger assemblages, that will allow for an improved understanding of the evolution of marine faunas in the region.

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Abstract

Odontocetes first appeared by the early Oligocene and their early evolutionary history can provide clues as to how some of their unique adaptations, such as echolocation, evolved. Here, three new specimens from the middle Oligocene Pysht Formation are described further increasing our understanding of richness and diversity of early odontocetes, particularly for the North Pacific region. Phylogenetic analysis shows that the new specimens are part of a more inclusive, redefined Simocetidae, which now includes *Simocetus rayi*, *Olympicetus* sp. 1, *Olympicetus avitus*, *O. thalassodon* sp. nov., and a large unnamed taxon, all part of an endemic, North Pacific clade. Of these, *Olympicetus thalassodon* sp. nov. represents one of the best known simocetids, offering new information on the cranial and dental morphology of early odontocetes. Additionally, the inclusion of CCNHM 1000, here considered to represent a neonate of *Olympicetus* sp., as part of the Simocetidae, suggests that this group represents a clade of non-echolocating odontocetes, further implying that some morphological features that have been correlated with the capacity to echolocate appeared before the acquisition of ultrasonic hearing. The dentition of simocetids is interpreted as being plesiomorphic, with a tooth count more akin to that of basilosaurids and early toothed mysticetes, while other features of the skull and hyoid suggest~~s~~ various forms of prey acquisition, including raptorial or combined feeding and in *Olympicetus* spp., and suction feeding in *Simocetus*. Finally, body size estimates show that small to moderately large taxa are present in Simocetidae, with ~~a~~ largest taxon represented by LACM 124104 with an estimated body length of 3 meters, which places it as the largest known simocetid, and amongst the largest Oligocene odontocetes. The new specimens described here add to a growing list of Oligocene marine tetrapods from the North Pacific, further promoting faunistic comparisons across other contemporaneous and younger assemblages, that will allow for an improved understanding of the evolution of marine faunas in the region.

Introduction

The Eastern North Pacific Region is recognized as one of the best sources for early marine mammals belonging to various groups, particularly desmostylians, pinnipeds, and early mysticetes ~~mysticetes~~ (Emlong, 1966; Russell, 1968; Domning et al., 1986; Berta, 1991; Ray et al., 1994; Barnes et al., 1995; Beatty, 2006; Beatty and Cockburn, 2015; Marx et al., 2015, 2016b; Peredo and Uhen, 2016; Peredo and Pyenson, 2018; Peredo et al., 2018; Poust and Boessenecker, 2018; Shipps et al., 2019; Solis-Añorve et al., 2019; Hernández-Cisneros, 2018, 2022; Hernández-Cisneros and Nava-Sánchez, 2022). However, while odontocetes have also been found in these units, and have been remarked in the literature in non-taxonomic context (e.g. Whitmore and Sanders, 1977; Goedert et al., 1995; Barnes, 1998; Barnes et al., 2001; Kiel et al., 2013; Hernández Cisneros et al., 2017), only a handful are described (Fordyce, 2002; Boersma and Pyenson, 2016; Vélez-Juarbe, 2017). These include *Simocetus rayi* Fordyce, 2002, from the early Oligocene Alsea Formation, in Oregon, U.S.A., the platanistoid *Arktocara yakataga* Boersma and Pyenson, 2016, from the middle Oligocene Poul Creek Fm., in Alaska, U.S.A., and the more recently described, *Olympicetus avitus* Vélez-Juarbe, 2017, from the middle Oligocene Oligocene Pysht Fm., in Washington State. The presence of stem (i.e. *Simocetus*, *Olympicetus*) and crown (*Arktocara*) odontocetes in similar-aged rocks point to a complex early history for odontocetes, hence the description of new material will advance our current understanding of odontocete evolution.

In this work three additional specimens of stem odontocetes collected from the mid-Oligocene Pysht Formation of Washington are described. The morphology of these new specimens show similariries with *Simocetus* and *Olympicetus*, and provide further insight into the diversity of early odontocetes in the North Pacific. The Pysht Fm. has a rich fossil record of marine tetrapods, including plotopterids (Olson, 1980; Dyke et al., 2011; Mayr and Goedert, 2016), desmostylians (Domning et al., 1986), aetiocetids (Barnes et al., 1995; Shipps et al., 2019), stem mysticetes (Peredo and Uhen, 2016), and many others still remaining to be described (Whitmore and Sanders, 1977; Hunt and Barnes, 1994; Barnes et al., 2001; Marx et al., 2016b). The fossils described in this work demonstrate that stem odontocetes were ~~much~~ more diverse in the North Pacific Region and hint at the presence of clade of stem odontocetes that were geographically confined to this region that parallels aetiocetid mysticetes (Hernández Cisneros and Vélez-Juarbe, 2021).

Abbreviations—c., character state as described and numbered by Sanders and Geisler (2015) and subsequent works, e.g. (c.15[0]) refers to state 0 of character 15; **LACM**, Vertebrate Paleontology Collection, Natural History Museum of Los Angeles County, Los Angeles, CA, U.S.A.; **KMNH VP**, Kitakyushu Museum of Natural History, Kitakyushu City, Japan; **USNM**, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Materials & Methods

Phylogenetic analysis

The phylogenetic analysis was performed using the morphological matrix of Albright et al. (2018) as modified recently by Boessenecker et al. (2020), with the addition of two new characters. The first one (c.335) refers to the presence of a transverse cleft on the apex of the zygomatic process of the squamosal (first noted by Racicot et al., 2019), while the other new character (c.336) relates to the morphology of the thyrohyoid/thyrohyal, for a total of 336 characters (see Supplemental File 1). Besides LACM 124104, LACM 124105 and LACM 158720, one additional odontocete from the Pysht Fm. was added, CCNHM 1000, based on the description from Racicot et al. (2019:S1). All otherwise undescribed specimens in earlier versions of this matrix were removed from this analysis as their character/states cannot be independently corroborated, resulting in a total of three outgroup and 106 ingroup taxa. The matrix was analyzed using PAUP* (v. 4.0a169; Swofford, 2003), all characters were treated as unordered and with equal weights. A heuristic search of 10000 replicates was performed using the tree bisection-reconnection (TBR) algorithm and using a backbone constraint based on the phylogenetic tree from McGowen et al. (2020); bootstrap values were obtained by performing 10000 replicates.

Taxonomy

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Systematic Paleontology

CETACEA Brisson, 1762

ODONTOCETI Flower, 1867

SIMOCETIDAE Fordyce, 2002

Type—*Simocetus rayi* Fordyce, 2002.

Included Species—*Simocetus rayi*; *Olympicetus avitus* Velez-Juarbe, 2017; *Olympicetus thalassodon* sp. nov.; *Olympicetus* sp. 1; Simocetidae gen. et sp. A.

Range—early-late Oligocene (Rupelian–early Chattian) of the eastern North Pacific.

Emended Diagnosis—Stem odontocetes displaying a mosaic of plesiomorphic and derived characters that sets them apart from other basal odontocetes, particularly the Xenorophidae, Patriocetidae and Agorophidae. Characterized by the following combination of characters: rostrum fairly wide (c.7[1]; shared with *Ashleycetus planicapitis* Sanders and Geisler, 2015,

Agorophius pygmaeus [Müller, 1849], and *Ankylorhiza tiedemani* [Allen, 1887]); palatine/maxilla suture anteriorly bowed (21[0]; shared with *Patriocetus kazakhstanicus* Dubrovo and Sanders, 2000); seven to eight teeth completely enclosed by the maxilla (c.25[1]); lacrimal restricted to below the supraorbital process of frontal (c.52[0]; shared with *A. planicapitis*, *P. kazakhstanicus* and *An. tiedemani*); relatively small ventral (orbital) exposure of the lacrimal (c.56[0]; shared with *A. planicapitis*, *Archaeodelphis patrius* Allen, 1921, and *P. kazakhstanicus*); postorbital process of frontal relatively long and oriented posterolaterally and ventrally (c.62[0]; shared with *A. planicapitis*, *Mirocetus riabinini* and *P. kazakhstanicus*); lack of a rostral basin (c.66[0]), differing from most xenorophids which have a well-defined basin; presence of a long posterolateral sulcus extending from the premaxillary foramen (c.73[2]; shared with *A. planicapitis*); maxilla only partially covering supraorbital processes (c.77[1]; shared with *A. planicapitis* and *Ar. patrius*); posteriormost edge of nasals in line with the anterior half of the supraorbital processes (c.123[1]); frontals slightly lower than nasals (c.125[0]; shared with *Cotylocara macei* Geisler et al., 2014); supraoccipital at about the same level as the nasals (c.129[1]), differing from xenorophids where the supraoccipital is higher; intertemporal region with an ovoid cross section (c.137[1]; shared with *A. planicapitis*, *Echovenator sandersi* Churchill et al., 2016, and *C. macei*); floor of squamosal fossa thickens posteriorly (c.149[1]); distal end of postglenoid process is anteroposteriorly wide (c.152[2]); anterior end of supraoccipital is semicircular (c.153[1]; shared with *P. kazakhstanicus*); occipital shield with distinct sagittal crest (c.156[1]; shared with *Albertocetus meffordorum* Uhen, 2008, *P. kazakhstanicus*, *Ag. pygmaeus*, and *An. tiedemani*); a nearly transverse pterygoid-palatine suture (c.163[1]; shared with *Ar. patrius*); long and subconical hamular process of the pterygoid (c.173[1]); hamular processes unkeeled (c.174[0]); hamular processes extending to a point in line with the middle of the zygomatic processes (c.175[3]); cranial hiatus constricted by medial projection of the parietal (c.184[2]); absent to poorly defined rectus capitus anticus muscle fossa (c.193[0]), differing from the well-defined fossa of xenorophids; posteroventral end of basioccipital crest forming a posteriorly oriented flange (c.194[2]); anterior process of periotic short (c.204[2]; shared with *C. macei*); anterior process of periotic with well-defined fossa for contact with tympanic (c.210[3]); lateral tuberosity of periotic forming a bulbous prominence lateral to mallear fossa (c.212[1]); tegment tympani at the base of the anterior process unexcavated (c.232[0]), differing from the excavated surface in xenorophids; articular surface of the posterior process of periotic is smooth (c.242[0]) and concave (c.243[0]); posterolateral sulcus of premaxilla deeply entrenched (c.310[1]).

SIMOCETIDAE GEN. ET SP. A

(Figs. 1-5; Tables 1-2)

Material—LACM 124104, posterior part of ~~skull~~ skull, missing most parts anterior to the frontal/parietal suture and the left squamosal; including one molariform tooth and partial atlas, axis and third cervical vertebrae. Collected by J. L. Goedert and G. H. Goedert March 21, 1984.

Locality and Horizon—LACM Loc. 5123, Murdock Creek, Clallam Co., Washington, U.S.A. (48º 09' 25"N, 123º 52' 10"W; = locality JLG-76). At this locality specimens are found as concretions along a beach terrace about 40 m north of the mouth of Murdock Creek. Besides LACM 124104, additional specimens known from this locality include the desmostylian *Behemotops proteus* (LACM 124106; Ray et al., 1994), additional material of the simocetid *Olympicetus* spp. (LACM 124105 and LACM 158720; described below), aff. *Olympicetus* sp. (Racicot et al., 2019), and the aetiocetid *Borealodon osedax* (Shipps et al., 2019).
Formation and Age—Pysht Formation, between 30.5–26.5 Ma (Oligocene: late Rupelian-early Chattian; Prothero et al., 2001; Vélez-Juarbe, 2017).
Range—Oligocene of Washington, U.S.A.

Description

The partial skull, LACM 124104, is missing most parts anterior to the fronto-parietal suture, the left squamosal, and some parts of the palatines and earbones (Figs. 1-4). The preserved portion of the skull has a pachyostotic appearance, in comparison with the other described simocetids. The estimated bizygomatic width, 322 mm (c.333[2]), suggests a body length of around 3 m (based on equation "i" from Pyenson and Sponberg, 2011), which is larger than any of the other described simocetids.
Vomer—Most of the palatal surface of the vomer is missing as is much of the rostrum. Posteriorly, it seems to have been exposed along an elongated, diamond-shaped, window between the palatines and pterygoids as in other simocetids (Fig. 2C-D; Fordyce, 2002; Vélez-Juarbe, 2017; see below). From this point, the vomerine keel extends posterodorsally, separating the choanae along the midline and extending to about 20 mm from the posterior edge of the bone (Fig. 2C-D). The horizontal plate extends posteriorly to a point in line with the anterior end of the basioccipital crests, thus covering the suture between the basisphenoid and basioccipital (c.191[0]; Fig. 2C-D). The choanal surface of the horizontal plate forms a ventrally concave choanal roof, with its lateral edges slightly flared and forming a nearly continuous surface with the internal lamina of the pterygoid.
Palatine—Only the posteriormost parts of the palatines are preserved, these are separated along the midline by the vomer, resembling the condition of other simocetids (Fig. 2C-D; Fordyce, 2002; see below). In anterior view, the palatines formed the ventral and lateral surface of the internal nares, while the vomer formed the medial and dorsal surfaces. Ventrolaterally, the palatines form a vertical to semilunar contact with the pterygoids, best observed in ventral, ventrolateral and lateral views (c.163[1]; Figs. 2C-D, 3-4), resembling the contact in *Simocetus rayi* and *Olympicetus* spp. (Fordyce, 2002; Vélez-Juarbe, 2017). An elongated groove along the ventrolateral end of the left palatine seems to have been part of the palatine foramen/canal.
Frontal—Only the posteriormost portion of the frontals are preserved, but are eroded (Fig. 1). Dorsally, the interfrontal suture seems to have been completely fused, and posteriorly formed a broad V-shaped contact with the parietals, which continues as a vertical contact along the temporal surface (Fig. 3).

Parietal—As in other simocetids, the parietals are broadly exposed dorsally, and the interparietal is either absent or fused early in ontogeny (c.135[0], 136[1]; Fig. 1). The parietals do not extend anterolaterally, resembling *Simocetus rayi*, and differing from *Olympicetus* where the parietals extend into the base of the supraorbital processes. The parietal exposure in the intertemporal region is anteroposteriorly short and broad in dorsal view, with an ovoid cross section (c.137[1]). Posterodorsally, the parietal-supraoccipital contact is broad and anteriorly convex, while along the temporal surface, it forms a vertical contact with the frontal~~s~~ (c.134[0];Fig. 1), and seems to have formed part of the posterior edge of the optic infundibulum; abaft to this point the parietal~~s~~ become laterally convex towards the contact with the squamosal~~s~~ (Figs. 3-4). Anteroventrally, on the temporal surface, the parietal descend to contact the orbitosphenoid, a portion of the dorsal lamina of the pterygoid, the alisphenoid, and the squamosal, with which it forms part of the subtemporal crest (Fig. 4). Its contact with the squamosal on the temporal surface becomes an interdigitated, dorsally arched suture posterior to this point. In ventral view the parietal~~s~~ contact the squamosal medially, partially constricting the cranial hiatus (c.184[2]; Figs. 2C-D, 4).

Supraoccipital—The anterior half of the supraoccipital is not preserved, bu based on its contact with the parietal, it anterior edge formed a gentle semicircular arch that reached anteriorly to a level in line with the anterior half of the squamosal fossa (c.140[0], 153[1]; Fig. 1), resembling the condition observed in *Olympicetus* spp. The preserved portion of the supraoccipital forms a gently concave surface that seems to have lacked ~~the~~ sagittal crest (c.156[?0], 311[0]; Figs. 1, 2A-B) observed in other simocetids. The nuchal crest ~~are~~ oriented dorsolaterally (c.154[1], c.155[0]), and seem to have been gently sinuous, descending posterolaterally to meet the supramastoid crest (Figs. 1,2A-B, 3).

Exoccipital—The occipital condyles are semilunar in outline, with well-defined edges, and bounded dorsally by shallow, transversely oval supracondylar fossae (c.157[1]; Fig. 2A-B) as in *Simocetus rayi* and *Olympicetus avitus*. The foramen magnum has an oval outline, being slightly wider than high. The paroccipital processes are transversely broad and oriented posteroventrally, approximating the posterior edge of the condyles (c.198[1]; Fig. 2). The ventral edge of the paroccipital processes ~~are~~ anteroposteriorly broad, becoming thinner medially towards the broad jugular notch (c.197[0]). The hypoglossal foramen is rounded (~4 mm in diameter), located ventrolateral to the occipital condyle~~s~~ and well separated from the jugular notch (c.196[0]; Fig. 2).

Basioccipital—The basioccipital crests are short, transversely thin, oriented ventrolaterally, and diverging posteroventrally at an angle between 58-60º (c.192[0], 195[2]; Fig. 2). ~~The~~ crest contacts the posterior lamina of the pterygoid along a posteroventrally oriented suture. The ventral surface between the crest is flat, with no distinct Rectus capitus anticus fossa (c.193[0]). Anteriorly the contact with the basisphenoid is obscured by the vomer (Fig. 2C-D).

Squamosal—The squamous portion is flat to gently convex, contacting the parietal~~s~~ along a dorsally arched suture that extends along a sinuous path to form the posteromedial edge of the subtemporal crest (Figs. 1, 3). Only the right zygomatic process is preserved, although incompletely, missing its anterolateral corner. The process is long, oriented anteriorly, robust and

somewhat cylindrical when viewed dorsally, constricting the squamosal fossa (c.143[0], 189[3]; Figs. 1, 2C-D, 3-4). The squamosal fossa is relatively deep, with a moderately sigmoidal outline and gently sloping anteriorly (c.147[2], 148[1], 149[1]; Fig. 1). When viewed laterally, the dorsal edge of the zygomatic process is flat to gently convex (c.144[0]), while its ventral edge was concave (c.151[0]; Fig. 3-4). The supramastoid crest is more prominent proximally, continuing posteromedially to join the nuchal crest (c.150[0]). The sternomastoid muscle fossa on the posterior edge of the zyogomatic process is a large, shallow oval depression, broadly visible in posterior or lateral view (c.145[1]; Figs. 2A-B, 3). The squamosal exposure lateral to the paroccipital processes is moderate in posterior view (c.146[1]; Fig. 2A-B). Ventrally, the postglenoid process is incompletely preserved, but seems to have been broad as in other simocetids. Posterior to the base of the postglenoid process, the external auditory meatus seems to have been broad (c.190[?0]; the posttympanic process is not preserved). The glenoid fossa is shallowly concave with nearly indistinct borders. Medial to the glenoid fossa is a shallow, oval tympanosquamosal recess (c.179[2]; Fig. 2C-D). The falciform process is anteroposteriorly long (c.177[0]; Figs. 2C-D, 3-4). The periotic fossa is partially obscured by a fragment of periotic; the anterior part of the fossa contains a small foramen spinosum close to the medial suture with the parietal (c.187[1]; Fig. 2C-D), resembling the condition observed in *Olympicetus avitus*. Anteromedially, the squamosal contacts the alisphenoid along anterolaterally oriented suture that follows the anterodorsal edge of the groove for the mandibular branch of the trigeminal nerve (c.181[1]); the groove wraps around the posterior end of the pterygoid sinus fossa, opening anteriorly (c.182[1]; Figs. 2C-D, 4).

Pterygoid—The pterygoids are incompletely preserved, missing the hamular processes (Fig. 2C-D). As in other simocetids, the palatal surface seems to have been separated along the midline by a diamond-shaped palatal exposure of the vomer (Fig. 2C-D). Anteriorly, the contact between the pterygoids and palatine is nearly vertical in lateral view. The pterygoid sinus fossa is anteroposteriorly long (99 mm) and dorsoventrally deep (at least 63 mm on the left side), transversely narrower anteriorly (25 mm) and becoming broader posteriorly (46 mm) (Fig. 2C-D, 4). The anterior edge of the pterygoid sinus fossa is at the level of the pterygo-palatine suture, extending posteriorly to the anterior edge of the foramen ovale (c.164[2]; Fig. 2C-D). The dorsal lamina contacts the orbitosphenoid anterodorsally, the frontal and the alisphenoid posterodorsally, along an irregularly sinuous contact, and forms the roof of the pterygoid sinus (c.166[0]; Fig. 4). The lateral lamina seems to have descended ventromedially, but its full extent is unknown (c.165[?0]; Figs. 2C-D, 3-4). The medial lamina is incompletely preserved, but medially contacts the lateral flanges of the horizontal plate of the vomer to form the lateral wall of the choana, while laterally ~~they~~ form the medial wall of the sinus fossa (Figs. 2C-D, 3-4).

Alisphenoid—Only a small portion of the alisphenoid can be observed on the temporal wall, where its exposure is small, wedged in between the squamosal, frontal and lateral lamina of the pterygoid (c.142[1]; Figs. 3-4). Ventrally, its suture with the squamosal runs along the anterior border of the sulcus for the mandibular branch of the trigeminal nerve; its more anteromedal portions are covered by sediment.

Orbitosphenoid/Optic Infundibulum—The orbitosphenoid is exposed on the temporal wall where it is in contact with the parietal dorsally and palatine and pterygoid ventrally. Medially, the bones are eroded and the distinct features of the optic infundibulum cannot be properly interpreted.

Mandible—The mandible is missing for the most part, with the exception of the left coronoid process (Fig. 1). The process has a subtriangular outline, as preserved being about as long as high, with the dorsal edge slightly recurved medially. The general outline resembles the coronoid process of *Olympicetus avitus* (Velez-Juarbe, 2017:fig. 7A–B).

Dentition—Only a double-rooted molariform is preserved in association with the specimen (Fig. 5A-C). The mesial root is mostly missing, but seems to have been buccolingually broader than the distal root, which is more cylindrical and slightly recurved buccally. The crown (length = 10 mm; height = 7 mm; width =8 mm) is worn, and is longer than tall, and buccolingually broader on its anterior half, somewhat resembling tooth 'mo3' of *Olympicetus avitus* (see Vélez-Juarbe, 2017:fig.7O,Bb), however, differing by lacking a well-defined buccal ridge with denticles. The crown has three denticles, with the apical one being slightly larger than the two on the distal carina, while there are no denticles on the blunter, mesial carina (Fig. 5A-C). There ~~are~~ no buccal cingul~~a~~, and only a nearly inconspicuous cingul~~a~~ is present on the distolingual corner of the base of the crown.

Cervical Vertebrae—Only the first three cervical vertebrae are preserved and are unfused (c.279[0], 280[?0] ; Fig. 5D-I). The dorsal arch of the atlas is missing, as ~~are~~ the distal end of the transverse processes. The anterior articular facets have a semilunar outline, and are shallowly concave, with relatively poorly defined ventrolateral and medial edges. The posterior facets for articulation with the axis have a suboval outline, with gently convex articular surfaces and sharp, well-defined edges. The posterior facets gently merge ventromedially with the articular surface for the odontoid (Fig. 5E). The ventral arch has a more prominent hypapophysis than that observed in *Olympicetus* spp. (Fig. 5E). The base of the transverse processes flare posterolaterally.

The axis is missing most of the apex and left half of the dorsal arch and the left transverse process (Fig. 5F-G). The pedicle is anteroposteriorly broad, and flat transversely, ~~t~~the postzygapophysis is oriented posterolateroventrally, forming a flat, smooth surface (Fig. 5G). The anterior articular surface is broad, with a suboval outline, and raised edges~~.~~ the surface is shallowly concave, merging ventromedially with the ventral surface of the odontoid (Fig. 5F). The odontoid is short, broad and blunt, with a mid-dorsal ridge that extends along the dorsal surface of the centrum, reaching the distal end (Fig. 5F). Posteriorly, the centrum has a cardiform outline ~~and t~~the epiphysis is fused, and its surface is concave, ~~and has~~ a mid-ventral cleft that slightly bifurcates its posteroventral end. The ventral surface of the centrum has a mid-ventral keel that becomes broader and more prominent towards the posterior end of the centrum. The transverse process is anteroposteriorly flat, and oriented mainly laterally, ~~t~~there are no transverse foramina (Fig. 5F-G).

The third cervical preserves only a portion of the right neural arch; the pedicle is anteroposteriorly flat and transversely broad, both, anterior and posterior, epiphyses are fused (Fig.5H-I). The prezygapophysis consists of a rounded, flat surface that is oriented anterodorsomedially, complementing its counterpart in the axis. The transverse foramen is large, being slightly broader than tall (16 mm x 11 mm). The transverse process is mainly oriented laterally, its posterior surface forms a low keel that extends from the base to the apex, and its anteroventral edge is flared (Fig. 5I). The centrum is rounded, anteroposteriorly short, with shallowly concave proximal and distal articular surfaces. Low midline keels are present along the ventral and dorsal surfaces of the centrum. A pair of small (~4 mm) nutrient foramina are present on each side of the middorsal keel.

Remarks—LACM 124104 represents the largest known simocetid, with an estimated bizygomatic width of 322 mm, in comparison with that of *Simocetus rayi* (238 mm), which (using equation "i" from from Pyenson and Sponberg, 2011) results in estimated body lengths of about 3 m and 2.3 m, respectively, both which are larger than those estimated for *Olympicetus* spp. (see below). This large simocetid shows a unique combination of characters, some which are shared with *Olympicetus* spp. such as the more retracted position of the supraoccipital (c.140[0]), the dorsolateral orientation of the lambdoidal crest (c.154[1]), a shallow tympanosquamosal recess (c.179[1,2]), an alisphenoid/squamosal suture that courses along the groove for the mandibular branch of the trigeminal nerve (c.181[1]). At the same time, some of the preserved characters seem to be unique to this taxon amongst simocetids, such as a deep squamosal fossa (c.147[2]) and the path of the groove for the mandibular branch of the trigeminal nerve which wraps around the posterior end of the pterygoid sinus fossa (c.182[1]). This specimen does preserve a remarkable amount of details of the size and morphology of the pterygoid sinus fossa, which together with other simocetids, suggest that they had a well developed, large fossae, particularly when compared to those of other early odontocetes, such as *Archaeodelphis patrius*, which seems to have a much shorter fossa (pers. obs. LACM 149261, cast of type). LACM 124104 resembles, and may be congeneric, with an odontocete skull from the early Oligocene Lincoln Creek Formation of Washington State, briefly described by Barnes et al. (2001), in many characters of its morphology, including its large size (bizygomatic width = 265 mm) and the pachyostotic appearance of some of the cranial bones, and will be addressed in more detail in a follow-up study.

OLYMPICETUS Velez-Juarbe, 2017

Type—*Olympicetus avitus* Velez-Juarbe, 2017.

Included Species—*Olympicetus avitus*; *Olympicetus thalassodon* sp. nov., *Olympicetus* sp. 1.

Range—Oligocene (late Rupelian–early Chattian; 33.7–26.5 Ma;) of Washington, U.S.A.

Emended Diagnosis—Small odontocetes, with bizygomatic width ranging from 145–220 mm (c.333[0,1]), with symmetric skulls and heterodont dentition, resembling *Simocetus rayi* Fordyce, 2002. Differs from *Simocetus*, other simocetids, and other stem odontocetes by the following combination of characters: having a concave posterior end of the palatal surface of the

rostrum (c.19[0]; shared with Xenorophidae); posterior buccal teeth closely spaced (c.26[0]; shared with *Ashleycetus planicapitis*, *Patriocetus kazakhstanicus*, *Agorophius pygmaeus* and *Ankylorhiza tiedemani*), differing from the widely-spaced teeth of *S. rayi*; buccal teeth with ecto- and entocingula (c.32[1], 33[0]; shared with *Xenorophus sloani* Kellogg, 1923, *Echovenator sandersi*, *Cotylocara macei* and *P. kazakhstanicus*), and unlike *S. rayi* where these features are absent; lacrimal and jugal separated (c.54[0]; shared with CCNHM 1000, Xenorophidae, *P. kazakhstanicus*, *Ag. pygmaeus* and *An. tiedemani*); presence of a short maxillary infraorbital plate (c.60[1]; shared with CCNHM 1000 and *Archaeodelphis patrius*); infratemporal crest of the frontal forming a well-defined ridge along the posterior edge of the sulcus for the optic nerve (c.63[0]; shared with Xenorophidae); posteriormost end of the nasal process of the premaxilla in line with the anterior half of the supraorbital process of the frontal (c.75[2]), differing from the longer process of *S. rayi*; absence of a posterior dorsal infraorbital foramen (= maxillary foramen; c.76[0]), differing from *S. rayi* which has two foramina on each side located medial to the orbit; posteriormost end of the ascending process of the maxilla in line with the posterior half of the supraorbital process of the frontal (c.78[2]; shared with *Ashleycetus planicapitis* and *Archaeodelphis patrius*); lack of a premaxillary cleft (c.110[0]; present in *S. rayi*); anteriormost point of the supraoccipital in line with the floor of the squamosal fossa (c.140[0]), differing from the more anterior position in *S. rayi*; having a relatively shallow squamosal fossa (c.147[1]; shared with *Ar. patrius* and *P. kazakhstanicus*), thus differing from the deeper fossae of *Simocetus rayi* and Simocetidae gen. et sp. A; involucrum of the tympanic bulla lacking a transverse groove (c.272[1]; shared with *C. macei*); dorsal process of atlas larger than ventral process (c.278[2]); presence of three mesial and four distal denticles on main molars (c.328[1], 329[2]); presence of a transverse cleft on the apex of the zygomatic process of the squamosal (c.335[1]); arched palate, and, saddle-like profile of the skull roof (when viewed laterally).

OLYMPICETUS THALASSODON, sp. nov.
(Figs. 6-13; Tables 1-5)

Holotype—LACM 158720, partial skull with articulated mandibles, including 18 teeth, tympanic bullae, cervical vertebrae 1–6, and hyoids; missing distal end of rostrum/mandible. Collected by J. L. Goedert and G. H. Goedert, July 30, 1983.

Type Locality and Horizon—LACM Loc. 5123, Murdock Creek, Clallam Co., Washington, U.S.A. (48º 09’ 25”N, 123º 52’ 10”W). See above for additional details.

Formation and Age—Pysht Formation, between 30.5–26.5 Ma (Oligocene: late Rupelian-early Chattian; Prothero et al., 2001; Velez-Juarbe, 2017).

Range—Oligocene of Washington, U.S.A.

Differential Diagnosis—Species of relatively small bodied odontocete with bizygomatic width of about 220 mm (c. 333[1]), differing from other simocetids by the following combination of characters: posterior wall of the antorbital notch formed by the lacrimal (c.16[1]; shared with *Simocetus rayi* and Xenorophidae); mandible with a relatively straight profile in lateral view (c.39[0]), differing from the more strongly arched mandible of *S. rayi*; mandibular condyle

positioned at about the same level as the alveolar row (c.46[1]); dorsal edge or orbit relatively low (c.48[2]; shared with *Olympicetus avitus*, *Ashleycetus planicapitis* and *Xenorophus* spp.); dorsolateral edge of ventral infraorbital foramen formed by lacrimal (c.58[2]; shared with *Archaeodelphis patrius*, *Albertocetus meffordorum* and *Inermorostrum xenops* Boessenecker et al., 2017), differing from *Olympicetus* sp. 1 where it is formed by the maxilla, and *O. avitus* where it is formed by the maxilla and lacrimal; posterior edge of zygomatic process forming nearly a right angle with the dorsal edge of the process (c.145[0]); lack of a well-defined dorsal condyloid fossa (c.157[0]; otherwise present on other simocetids); posterior process of the periotic exposed on the outside of the skull (c.250[0]); tympanic bulla proportionately narrow and long (c.252[0]; shared with *Echovenator sandersi* and *Cotylocara macei*), differing from the shorter, wider bulla of *Olympicetus avitus* and *Olympicetus* sp. 1; moderately large bizygomatic width (c.333[2]; shared with *S. rayi*), differing from the smaller size of *O. avitus* and *Olympicetus* sp. 1, or the relatively larger Simocetidae gen. et sp. A; parietals not forming part of the supraorbital processes, differing from *O. avitus* where they extend into the posteromedial part of the process, nasals contacting the maxillae along their posterolateral corners; longer paroccipital and postglenoid processes; teeth with more conical cusps, contrasting with the more lanceolate ones of *O. avitus*; and, thyrohyals tubular and not fused to basihyal (c.336[0]).

Etymology—Combination of *thalasso-* from the Greek word 'thalassa' meaning 'sea' and *-odon* from the Greek word 'odon' meaning 'tooth', in reference to the marine habitat of the species and its particular tooth morphology.

Description

Description is based on the holotype (LACM 158720), which consists of a nearly complete skull of an adult individual with articulated mandibles and preserving 18 teeth, cervical vertebrae and hyoid elements (Figs. 6-13). Some of the preserved mandibular and maxillary teeth are in situ, allowing for determination of associated, loose teeth. The estimated body length is ~2.15 m, based on equation "i" for stem Odontoceti in Pyenson and Sponberg (2011). The terminology used herein follows Mead and Fordyce (2009).

Premaxilla—The part of the premaxillae anterior to the premaxillary foramen is not preserved. Each premaxillae preserve a single, small (diam. = 3 mm) foramen located far anterior to the antorbital notch (c.70[1], 71[0], 72[0]; Fig. 6) The ascending process adjacent to the external nares is divided by a long posterolateral sulcus (c.73[2]) and a short, incipient, posteromedial sulcus (c.319[1]), both which extend from the premaxillary foramen, forming the lateral and anteromedial limits of the premaxillary sac fossa (Fig. 6). The premaxillary sac fossae are flat to shallowly concave, transversely narrow and anteroposteriorly long (c.69[0]; 320[0], 324[1]), resembling the condition observed in *O. avitus*. The premaxilla forms the lateral edges of the external nares and mesorostral canal (c.74[0]). Posterior to the premaxillary sac fossae, the ascending process extends posteriorly as a transversely thin flange, reaching a level just beyond the preorbital process of the frontal (c.75[2]), leaving a narrow gap where the premaxilla contacts the nasal. In contrast, in *O. avitus* the ascending process extends farther posteriorly, to a point

closer to the middle of the supraorbital processes, separating the nasal~~s~~ from the maxilla~~e~~ (Velez-Juarbe, 2017).

Maxilla—As preserved, the palatal surface is anteroposteriorly concave and transversely convex to flat (c.17[0]). Anteriorly the vomer is exposed ventrally through an elongated window between the maxillae as in *Simocetus rayi*~~,~~ similarly, a pair of major palatine foramina are located on each side at the proximal end of this opening (c.18[0]; Fig. 7C-D). Posteriorly, the maxilla contacts the palatines along an anteriorly-bowed contact (c.20[0], 21[0]). The alveolar row diverge posteriorly (c.23[0]); it is incompletely preserved anteriorly, but based on the preserved dentition and visible alveoli, there were at least seven closely-spaced maxillary teeth, with the most posterior six representing double-rooted P1-4, M1-2, with the most anterior of the preserved alveoli representing an anteroventrally-oriented single rooted ?canine (c.24[4], 26[0]; Fig. 8). Posteriorly, the maxillary tooth row extends beyond the antorbital notch, forming a short infraorbital plate (c.60[1]; Fig. 9). The ventral infraorbital foramen has an oval outline (15mm wide by 9mm high) and is bounded laterally and dorsally by the lacrimal and ventrally and medially by the maxilla (c.58[2], 59[0]; Fig. 9).

Proximally, the rostrum is wide, relative to the width across the orbits (c.7[1]) and the lateral edges of the maxillae are bowed out, giving the antorbital notch a 'V'-shaped outline (c.12[1]; Fig. 6). The surface of the maxillae anterior and anteromedial to the orbits is flat to shallowly convex (c.66[0]) lacking the rostral basin observed in some xenorophids (e.g. *Cotylocara macei*; Geisler et al., 2014). As in *O. avitus*, this surface has cluster~~s~~ of three to four anterior dorsal infraorbital foramina with diameters ranging between 4-6 mm with the posteriormost foramen located dorsomedial to the antorbital notch~~es~~ (c.65[3]). However, in contrast to *O. avitus* the maxilla~~e~~ does not extend anterolaterally to form the posterior wall of the antorbital notch (c.16[1]; Figs. 6, 8), thus more closely resembling the condition observed in *Simocetus rayi*. Posteromedial to the antorbital notch~~es~~, the maxilla~~e~~ extends over the supraorbital process~~es~~, covering a little more than the anterior half of the process~~es~~ and laterally to within 12 mm of the edge of the orbit, while medially ~~they~~ contact the ascending process of the premaxilla~~e~~ and the nasal~~s~~, forming a gently sloping dorsolaterally-facing surface (c. 49[0], 77[1], 78[], 79[0], 80[0], 130[0], 308[1]; Figs. 6, 8).

Vomer—Dorsally the vomer forms the ventral and lateral surfaces of the mesorostral fossa, which seems to have been dorsally open, at least for the length of the rostrum that is preserved, and has a V- to U-shaped cross section, having a more acute ventral edge anteriorly (c. 5[0]; Fig. 6). Anteriorly, along the palatal surface of the rostrum, the vomer is exposed through a narrow elongate window mostly between the maxillae and the premaxillae distally, resembling the condition in *S. rayi* and possibly, *Olympicetus avitus* (Fig. 7C-D; Fordyce, 2002; Velez-Juarbe, 2017). The vomer is exposed again towards the posterior end of the palate along a diamond-shaped window between the palatines and the pterygoids, resembling *S. rayi* (Fig. 7C-D; Fordyce, 2002)~~,~~ similarly, the vomer seems to have been exposed posteriorly in *O. avitus*, although the window may have been comparably smaller. The choanae are not prepared thus making it impossible to determine the posterodorsal extension of the vomer (c. 191[?]).

Palatine—As in *Simocetus* and *Olympicetus avitus* the anterior edge of the horizontal plate of the palatine~~s~~ extend to about 10 mm anterior to the level of the antorbital notches, forming the shallowly concave proximal surface of the palate (Fig. 7C-D). The posterior edge of the palatines are separated in the midline by the vomer even more than in *Simocetus* (Fig. 7C-D; Fordyce, 2002). Posterolaterally there is an elevated palatal crest that originates at the contact with the pterygoid hamul~~i~~ and extends anterodorsally on the orbital lamina, approximating, but not reaching, the infundibulum for the sphenopalatine and infraorbital foramina, it instead become a shallow groove that reaches the sphenopalatine foramen as in *O. avitus* (Figs. 7C-D, 8). The orbital lamina of the palatine contacts the frontal dorsally to form the posteroventral edge of the sphenopalatine foramen, and the maxilla anteriorly, and forms the ventral edge of the infundibulum for the sphenopalatine and infraorbital foramina (Figs. 8-9). In posterolateral view, the infundibulum has an oval outline, measuring 28 x 15 mm, while the rounded sphenopalatine foramen has a diameter of about 8 mm. Ventrally and laterally, ~~the~~ palatine~~s~~ ~~have~~ a nearly transverse contact with the pterygoid~~s~~ (c. 163[1]; Figs. 7C-D, 8), resembling the condition observed in *O. avitus*, *Simocetus rayi* and *Archaeodelphis patrius*.

Nasal—The nasals are poorly preserved and seem to have formed the highest point of the vertex (c. 114[?0], 124[0], 125[0], 312[0]; Figs. 6, 8) as in *Olympicetus avitus* and *Simocetus*). Anteriorly, the nasals reach to about 24 mm beyond the antorbital notches, while posteriorly they are in line with the preorbital process of the frontals (c. 81[3], 123[1]; Fig. 6). The nasals are anteroposteriorly elongated, facing dorsally, forming a low transversely convex arch, are dorsoventrally thin (<3 mm) and are separated posteriorly by the narial process of the frontal (c. 116[0], 118[0], 120[1], 121[2], 122[1], 312[0], 321[0]). ~~The~~ nasal~~s~~ seem to contact the ascending process of the premaxilla~~e~~ for most of ~~their~~ length~~s~~ with only ~~their~~ posterolateral corner~~s~~ contacting the maxilla, differing from *Olympicetus avitus* where the premaxilla extend beyond the posterior edge of the nasal~~s~~ (Velez-Juarbe, 2017).

Frontal—Dorsally along the midline, the frontals are wedged between the maxillae and posterior edge of the nasals forming a large semi-rectangular surface (c. 126[1]; Fig. 6). Abaft to this point, the frontals are shallowly depressed towards their contact with the parietals, forming a saddle-like outline of the skull roof in lateral view, resembling the condition observed in *O. avitus* (Fig. 8). The interfrontal suture is completely fused; dorsally the frontals form a broad, V-shaped contact with the parietals, while ~~its~~ contact along the temporal surface is nearly vertical. The supraorbital processes gently slope ventrolaterally from the midline (c. 47[0]), and only their anterior half is covered by the ascending process of the maxillae (Fig. 6, 8). The preorbital processes are rounded and only partially covered by the maxilla and are thus exposed dorsally; anteriorly they contact the maxilla and the lacrimals ~~anteroventrally~~. The postorbital process~~es~~ ~~are~~ blunt, longer and oriented posterolaterally and ventrally to a level nearly in line with the lacrimal~~s~~ when viewed laterally (c. 62[0]; Fig. 8). The orientation of the postorbital process~~es~~ give the orbit a slight anterolateral orientation in dorsal view, while in lateral view, the orbit~~s~~ ~~are~~ highly arched and positioned high relative to the rostral maxillary edge as in *O. avitus* (c. 48[2]; Figs. 6, 8). The posterior edge of the supraorbital process is defined by a relatively sharp

orbitotemporal crest that becomes blunter towards its contact with the orbital process~~es~~ of the parietal~~s~~.

Ventrally, in the orbital region, the frontal~~s~~ contact lacrimal~~s~~ anterolaterally to form the anterior edge of the orbit~~s~~ (Figs. 8-9). More medially the frontal~~s~~ contact the maxilla~~e~~ and palatine~~s~~, forming the posterodorsal border of the infundibulum for the sphenopalatine and infraorbital foramina (Figs. 8-9). Medially, the optic foramen has an oval outline (~10 x 5 mm) and is oriented anterolaterally; the posterior edge of the optic foramen and infundibulum is defined by a low infratemporal crest (c. 63[0]; Fig. 9). As in *Simocetus rayi* and *O. avitus* a small (~3 mm diameter) ethmoid foramen (sensu Fordyce, 2002) is located anterolateral to the optic foramen, while a series of additional, smaller foramina (1-2 mm) are located more laterally.

Lacrimal + Jugal—Only a small, cylindrical portion of the proximal end of the jugal is preserved, it is set in a close-fitting socket formed by the lacrimal anterodorsally, and the maxilla anteriorly and ventrally (c. 54[0], 55[0]; Figs. 8-9). As preserved, the jugal is visible only in lateral or ventral views, as dorsally it is covered by the lacrimal, and resembles the condition observed in cf. *Olympicetus* sp. of Racicot et al. (2019). The lacrimal~~s~~ ~~are~~ enlarged and shaped like a thick rod that covers the anterior surface of the preorbital process~~es~~ of the frontal~~s~~ (c. 51[1], 52[0], 53[1]; Figs. 6, 8-9). The lacrimals are broadly visible in dorsal view as they are not covered by the maxilla as in *Olympicetus avitus*, thus resembling the condition observed in *Simocetus rayi*; ventrally their exposure is anteroposteriorly short relative to the length of the supraorbital process of the frontal (c. 56[0]), but are elongated mediolaterally, forming the dorsolateral and dorsal edges of the ventral infraorbital foramen (c. 58[2]), differing from *O. avitus* where it is formed by the maxilla and lacrimal.

Parietal—The parietals are broadly exposed in dorsal view, with no clear indication of the presence of an interparietal (c. 135[0], 136[1]; Fig. 6), although it is visible in some ontogenetically young specimens that can be referred to *Olympicetus* (Racicot et al., 2019; see discussion). Anteriorly in dorsal view, the parietals meet the frontals along a broad V-shaped suture, with ~~its~~ anterolateral corners extending for a short distance along the base of the postorbital processes of the frontals, although not as far as in *Olympicetus avitus*. Posterior to the frontal-parietal suture there is a low incipient crest that gives the intertemporal region an ovoid cross section (c. 137[1]), similar to the condition in *O. avitus* and *Simocetus rayi*. As in *O. avitus*, the parietals contact the supraoccipital along an anteriorly convex suture when viewed dorsally. The temporal surface of the parietal is flat to shallowly concave anteriorly, with a near vertical suture with the frontal (c. 134[0]; Fig. 9) as it descends to form the posterior wall of the optic infundibulum; the temporal surface of the parietal ~~then~~ becomes more inflated posteriorly and posteroventrally where it contacts the squamosal and alisphenoid (Figs. 6, 8). The anteroventral edge of the parietal~~s~~ form a semilunar notch that likely contacted part of the alisphenoid and the dorsal lamina of the pterygoid, then continuing posteriorly to form part of the subtemporal crest.

Supraoccipital—The anterior edge of the supraoccipital form a semicircular arch when viewed posteriorly and dorsally, extending as far anteriorly ~~to nearly~~ the anterior edge of the squamosal fossa (c.140[0], 153[1]) as in *Olympicetus avitus* and *Simocetus rayi* (Figs. 6-7A-B). The

posterior surface is incompletely preserved, but seems to have had a low sagittal crest (c.156[?1], 311[?0]). The nuchal crest ~~are~~ oriented dorsolaterally (c.154[1]), curving posteriorly and ventrally to meet the supramastoid crest of the squamosal~~s~~ (Figs. 6, 7A-B, 8).

Exoccipital—The occipital condyles have a semilunar outline and are transversely and dorsoventrally convex, with sharp dorsal and lateral edges. Although the bone is poorly preserved, there is no indication for the presence of well-defined dorsal condyloid fossae (c.157[0]), differing from *Olympicetus avitus* (Fig. 7A-B). The surface lateral to the condyle~~s~~ is shallowly convex transversely and the paroccipital process~~es~~ ~~are~~ broad, oriented posteroventrally to a point nearly, but not reaching the posterior edge of the condyles (c.198[2]; Fig. 6).

Basioccipital—The basioccipital is partially covered by part of the atlas posteriorly and hyoids posteroventrally (Fig. 7). The basioccipital crest are oriented ventrolaterally, diverging posteriorly at about an angle ~~of~~ between 60-70º, and seem to have been transversely narrow (c.192[0]); 195[2]), with their posteroventralmost end forming a small flange as in *Simocetus rayi* (c.194[2]; Fig 7C-D). No well-developed Rectus capitus anticus fossa is discernible on the ventral surface (c.193[0]).

Squamosal—The zygomatic processes are partially eroded, more so on the left side, however, its general morphology is conserved. The processes are oriented anteriorly (c.143[0]) and seem~~s~~ to have been relatively long (c.189[?3]). In lateral view the dorsal edge of the zygomatic process is greatly convex dorsally (c.144[0]), while ventrally ~~they are~~ strongly concave (c.151[0]) (Fig. 8). The apex of the zygomatic process has a transverse cleft (best preserved on the right side; c.335[1]; Fig. 8), which is present in the type of *Olympicetus avitus* as well as in CCNHM 1000, and may as well be a unique feature of the genus (Racicot et al., 2019). Posteriorly the sternomastoid fossa is nearly absent (c.145[0]), contrasting with the deeper fossa observed in *O. avitus* and *Olympicetus* sp. A (see below). In dorsal view, the zygomatic process~~es~~ ~~are~~ mediolaterally broad, forming a transversely narrow and relatively shallow squamosal fossa as in *O. avitus* (c.147[1]; Fig. 6). The floor of the squamosal fossa is slightly sigmoidal, sloping gently towards its anterior end (c.148[1], 149[0]), and is bounded laterally and posteriorly by a fairly continuous supramastoid crest (c.150[0]), which extends medially to join the nuchal crest (Fig. 6). Medially, the squamous portion is flat, with an interdigitated suture with the parietal~~s~~ that slope anteroventrally at about 45º towards the anterior edge of the squamosal fossa and subtemporal crest and contacting the alisphenoid. Posteroventrally, the postglenoid process is long, more so than in *Simocetus rayi* and *O. avitus*, and anteroposteriorly broad, with near parallel anterior and posterior borders that end in a squared-off ventral end (c.152[2]; Figs. 7C-D, 8). Abaft the postglenoid process, the external auditory meatus is deep and anteroposteriorly broad (c.190[0]), bounded anteriorly by a low anterior meatal crest, that, as in *O. avitus*, seems to have formed the posterior edge of a fossa for the reception of the sigmoid process of the squamosal. The posttympanic process does not extend as far ventrally as the postglenoid process; its ventral surface is well sutured to the posterior process of the tympanic bulla (Figs. 7C-D, 8). In ventral view, the glenoid fossa is poorly defined, although medially there is a very shallow, nearly indistinguishable tympanosquamosal recess (c.179[?1,2]), as in *O. avitus* and *S. rayi*.

Anteromedially the falciform process anteroposteriorly broad with a nearly square outline (about 15 mm by 15 mm; c.177[0]), contacting most of the anterior process of the periotic (fig. 10C). In posterior view, the squamosal has a relatively small exposure lateral to the exoccipital~~s~~ (c. 146[1]; Fig. 7A-B).

Pterygoid—In ventral view, the pterygoids form robust, cylindrical hamular processes that are not excavated by the pterygoid sinus (c.173[1], 174[0]) and are separated anteriorly along the midline by a diamond-shaped exposure of the vomer, resembling the condition observed in *Simocetus rayi* (Fig. 7; Fordyce, 2002:fig. 4). The hamuli are long, extending posteriorly as far as the level of the middle of the zygomatic processes (c.175[3]). Although not preserved, the lateral lamina likely formed the anterior and lateral surfaces of the pterygoid sinus fossa. The dorsal lamina extends dorsally, reaching the frontal, and, judging from the preserved sutures, posteriorly, to join the parietal and alisphenoid, forming the roof of the sinus fossa as in *Olympicetus avitus* (c.166[0]; Fig. 8-9). As in *Simocetus rayi*, the ventralmost point of the pterygoid sinus fossa is at the base of the hamuli just anterior to the eustachian notch, suggesting that the nasal passages were underlaid by the sinus fossa (Fig. 7C-D). The medial lamina forms the deep eustachian notch, and bulges laterally at this point; posteriorly, it extends to contact the basioccipital crest~~s~~. The pterygoid sinus fossa is dorsoventrally ~~broad~~ (~45 mm ~~high),~~ and somewhat compressed mediolaterally (~23 mm wide), extending forwards to the level of the posterior edge of the supraorbital process of the frontal (c. 164[2]; Figs. 7C-D, 8-9).

Alisphenoid—Only small portions of the alisphenoid~~s~~ can be observed on both sides. In lateral view, only a small portion of the alisphenoid is exposed on the temporal fossa, where it forms the posteromedial part of the subtemporal crest (c.142[1], 166[0]) as in other *Olympicetus* (Velez-Juarbe, 2017; see below).

Orbitosphenoid/Optic Infundibulum—The orbitosphenoid is fused with surrounding bones, unlike the ontogenetically younger specimen of *Olympicetus avitus*. Within the optic infundibulum, the foramen rotundum and orbital fissure seem to have a similar diameter, both being transversely broader (~10 mm) than high (~6 mm) (Fig. 9), with the first located in a slightly more posteromedial position, resembling the condition in *O. avitus* (Fig. 9). However, no distinct groove for the ophthalmic artery is preserved in *Olympicetus thalassodon*, differing from *Simocetus rayi*, *O. avitus* and *Olympicetus* sp. A (Fordyce, 2002:fig.13; Figs. X-X). The foramen rotundum is not prepared, but is inferred that, as in *O. avitus*, it opens ventrolateral to the orbital fissure, with the path for the maxillary nerve (V2) being bound ventrally by the pterygoid and palatine (Fig. 9).

Periotic—Only a small portion is visible on the right side. The anterior process contacts the falciform process anteriorly for about half its length. Posterior to this contact, a portion of the anterior process is visible, as is the epitympanic hiatus, which is bounded posteriorly by a prominent ventrolateral tuberosity (Fig. 10C).

Tympanic Bulla—Both bullae are still articulated with the cranium and mainly visible in ventral view (Fig. 10). The tympanic bullae are transversely narrow and elongated (c.252[0]), differing from the proportionately broader bullae of *Olympicetus avitus* and *O.* sp. A (see below). In

ventral view, the lateral surface is more convex and the ~~more~~ straight medial side~~, anteriorly it~~ is gently convex, with not indications of the presence of a spine (c.251[0]). The posterior surface of the bulla~~e~~ is bilobed, being divided by a broad interprominential notch (c.267[1]) that is divided by a transverse ridge (c.268[0]), differing from the bulla of *Olympicetus avitus*, but resembling that of *Olympicetus* sp. A. Both posterior prominences are level with each other (c.270[0]), the ventromedial keel forms a smooth curve posteriorly (c.253[0]), while more anteriorly it is poorly defined as th~~is~~ surface is nearly flat (c.274[2], 275[?0]). The outer posterior prominence forms a continuous curve along its length, connecting with the conical process.

A vertical, broad lateral furrow can be observed in lateral view (c.257[0], 258[0]), while more dorsally the sigmoid process curves posteriorly at the base, and is nearly vertical and perpendicular to the long axis of the bulla (c.259[0], 260[0]; Fig. 10B-C). Although not entirely visible, the dorsal edge of the sigmoid process likely contacted the sigmoid fossa of the squamosal (c.261[?0]). The posterior process is partially visible at its contact with the posttympanic process and is visible in lateral view (c.250[0]; Figs. 7C-D, 8, 10A-B), and seems to have had more or less the same thickness throughout its length (c.266[0]).

Mandible—Left and right mandibular rami are nearly in articulation with the skull and are only missing coronoid processes and their distal ends, including the symphyseal region (Figs. 7C-D, 8). As preserved, the mandibles are nearly straight, gently arching dorsally at about mid length (c.39[0], 43[1]; Figs. 7C-D, 8), differing from the highly arched mandible of *Simocetus rayi* (Fordyce, 2002). Proximally, the bone seems to be thin, likely forming an enlarged mandibular fossa (c.44[1]). Posterodorsally on the right side, the lateral edge of the condyle can be observed, suggesting that its dorsal surface sits at ~~a~~ level ~~at~~, or below the alveolar row (c.46[1]; Fig. 8). Anteriorly, the right ramus preserved five double-rooted teeth in-situ, which are interpreted as representing p3-4 and m1-3, while the left ramus preserves three, that are interpreted as m1-2 and p4 (Figs. 8-9, 11-12). Multiple mental foramina are longitudinally arranged along the rami below the alveolar row~~,~~ most are oval, ranging in size from 2 to 4 mm in height and up to 10 mm long, with the more posterior ones connected by a fissure as in *Olimpicetus avitus* (Fig. 8; Velez-Juarbe, 2017:fig.7A).

Dentition—Taking a conservative approach to the tooth count, it is interpreted as non-polydont as in *Simocetus rayi* (Fordyce, 2002), although incipient polydonty cannot be entirely ruled out, as it seems to be present on other stem odontocetes from the eastern North Pacific (e.g. LACM 140702; Barnes et al., 2001). Between the teeth and alveoli, the preserved upper and lower dentition is interpreted to represent C, P1-4, M1-2 and p3-4, m1-3 (Figs. 8-9, 11-12). The teeth are proportionately large, heterodont, multicusped, transversely flattened and nearly as high as long (c.31[1], 314[0]), resembling the condition observed in postcanine teeth of *Olympicetus avitus*, *Olympicetus* sp. A and *Simocetus rayi* (Figs. 8-9, 11-12). As in *Olympicetus avitus* and *Simocetus rayi*, the postcanine teeth of *O. thalassodon* have a more concave buccal surface, while being more convex lingually, with the apex of the crowns slightly recurved lingually~~,~~ the base of the crowns ~~are~~ ornamented with vertical striae extending apically from ecto- and entocingula, particularly on the posteriormost upper teeth (c.27[1], 32[1], 33[0]; Figs. 11-12).

The crowns consist of a main apical denticle, and smaller accessory denticles along the mesial and distal edges~~,~~ both apical and accessory denticles are more triangular than the more lanceolate ones observed in *O. avitus* (c.34[0]; 35[0]; Figs. 11-12; Velez-Juarbe, 2017). In double-rooted teeth, the roots become fused proximally, with broad grooves on both~~,~~ buccal and lingual sides that extend to the base of the crown~~s~~, giving ~~them~~ an 8-shaped cross section as in *Simocetus rayi* (Fordyce, 2002). In P4 and M1 the anterior root is cylindrical, tapering distally, while the posterior root~~s~~ ~~are~~ buccolingually broader and oblong in cross section, while in M2 this condition is reversed, with the anterior root being transversely broader; ~~the~~ roots of the lower teeth seem to be subequal in size, both being cylindrical and tapering distally.

The anteriormost end of the right maxilla has a single alveolus (diameter = 6mm) that curves posterodorsally and is interpreted as that of a canine, which is separated by a short interalveolar septum from two adjoining alveoli (each with a diameter ~7mm) for a double-rooted P1 (Figs. 8, 11B). The second (P2) and third (P3) upper premolars are missing on the left side and incompletely preserved on the right~~,~~ they are slightly higher than long, consisting of a main denticle with at least two accessory denticles on the mesial and distal edges, resembling teeth 'ap1' and ap2' of *O. avitus* (Velez-Juarbe, 2017:fig.7D-E, Q-R). Three closely associated teeth that became disarticulated from the maxilla, but still joined by matrix, and three other loose teeth~~,~~ represent left and right P4, M1-2; these are more equilateral, being as long as wide, with stronger lingual and labial cingula and ornamentation along the base of the crowns; P4 and M1 consist of a main apical denticle, with four distal and three mesial accessory denticles that diminish in size towards the base (c.328[1], 329[2]; Figs. 11E-H, 12A-B, 12E-F), their overall morphology resembles that of teeth 'mo1' and 'mo2' of *Olympicetus avitus* (Velez-Juarbe, 2017;fig.7M-N, Z-Aa). The second molar (M2) is the smallest of the series and the crown is longer than tall, ~~it~~ consists of a main apical denticle, four distal and two mesial accessory denticles, the apices of all denticles ~~are~~ slightly slanted distally (Figs. 11D, 11I, 12C-D). As in *Simocetus rayi* and *Xenorophus sloanii*, the mesial and distal keels on the upper posterior postcanines trend towards the buccal side of the teeth so that in occlusal view, the apical and accessory denticles are arranged in an arch (Fordyce, 2002; Uhen, 2008). These characteristics allow for the reassignment of some of the teeth of *Olympicetus avitus*, with teeth 'mo1' and 'mo2' representing right and left M2, respectively, while 'ap1' and 'ap2' represent left upper premolars (Velez-Juarbe, 2017:fig.7). An isolated single-rooted tooth is interpreted as a canine or incisor (FIg. 12H-I). The crown is conical, with vertical striation along its lingual surface and a buccal cingulum; anterior and posterior carinae seem to be present, with larger denticles along the distal edge. Another isolated tooth adjacent to the posterior end of the left maxilla, seems to represent a more anterior upper postcanine tooth (Fig. 12J). Overall, it resembles M2, but it's mesial carina is partially damaged, so it is unclear if any accessory denticles were present, while the distal carina contains three denticles that diminish in size basally~~,~~ however, the denticles are not recurved distally, and is larger than M2, but smaller than M1.

The preserved lower dentition includes p3-4, m1-3, and p4, m1-2 on the right and left mandibles, respectively (Figs. 8, 11A-C, 12C). As with the upper premolars, p3-4, m1-3 have a triangular

outline, with mesial and distal carinae aligned vertically, not trending lingually as the upper molars. Furthermore, in p3-4 and m1-2 the mesial carinae has two accessory denticles that are much smaller than the apical denticle, while along the distal carinae there are three to four accessory denticles, with the apical ones being nearly as big as the apical denticle, and then diminish in size towards the base of the crown (Fig. 8, 11A-C, 12C). There is nearly no ornamentation along the buccal side of the lower premolars and molars, with only a few inconspicuous vertical striae, but no prominent cingulum, while lingually striae are more prevalent, and a cingulum is present (Figs. 11A-C, 12G). As in the upper toothrow, m3 is the smallest in the series, seemingly lacking accessory denticles on the mesial carina, and having three subequal ones along the distal carina. As with the preceding teeth, ornamentation is nearly absent on the buccal side (Fig. 11A). The lower postcanine dentition of *Olympicetus thalassodon* then seems to be characterized by having less conspicuous ornamentation on the buccal side, and more vertically aligned carinae, based on these characteristics, it is proposed that teeth 'pp1', 'pp2' and 'pp5', 'pp7' of *Olympicetus avitus* (see Velez-Juarbe, 2017:fig.7F-G, J, L, S-T, W, Y) represent lower anterior molars or premolars from the left and right side respectively.

Hyoid—Most of the hyoid elements are preserved in LACM 158720, including the basihyal, stylohyals and thyrohyals (Fig. 13A-C). The basihyal has a rectangular, blocky outline, with both ends expanded, forming broad, quadrangular rugose surfaces for the articulation of the paired elements (stylo- and thyrohyals). The mid portion is subtriangular cross section, the dorsal surface is shallowly concave transversely, the partial, left thyrohyal obscures the posteroventral surface of the bone. The partial left and the complete right thyrohyals and stylohyals are preserved (Fig. 13A-C). The thyrohyals are not fused to the basihyal and are fairly straight, with a transversely oval cross section at mid-length; overall they are shorter, but more robust than the stylohyals, and not flattened, wing-like as in derived mysticetes and odontocetes (c.336[0]; Fig. 13). The proximal articular surface has a rectangular outline, and the surface is rugose and shallowly convex, distally, the shaft is twisted, so that the distal articular surface is nearly perpendicular to the long axis of the proximal surface. The distal articular surface has a more oval outline that is rugose and shallowly convex. The stylohyals are long and slender, and, on the right side, nearly in articulation with the paroccipital process (Fig. 13A-B). Along the long axis they are bowed laterally, with the shaft having a more flattened, oval cross section along its length, with both, proximal and distal ends expanded, being overall, nearly identical to the stylohyoid of *Olympicetus avitus* (Velez-Juarbe, 2017). The proximal end is transversely expanded with a nearly flat, rugose articular surface, distally, the shaft becomes twisted, so that the distal end is offset at about 45º from the proximal articular surface. The lack of fusion between the thyrohyal and basihyal, and the cylindrical shape of the thyrohyal resemble the condition observed in basilosaurids (e.g. *Durodon atrox* [Andrews, 1906], *Cythiacetus peruvianus* Martínez-Cáceres and de Muizon, 2011; Uhen, 2004; Martínez-Cáceres et al., 2017), some stem mysticetes (e.g. *Mammalodon colliveri* Pritchard, 1939, *Fucaia buelli* Marx et al., 2015, *Mystacodon selenensis* Lambert et al., 2017; Fitzgerald, 2010; Muizon et al., 2019); while in more derived odontocetes (e.g., *Brygmophyseter shigensis* (Hirota and Barnes, 1995), *Kogia*

breviceps (Blainville, 1838), *Albireo whistleri* Barnes, 1984, *Kentriodon nakajimai* Kimura and Hasegawa, 2019, *Tursiops truncatus* (Montagu, 1821); Fig. 13D-G) these bones are partially or completely fused and the thyrohyals tend to be more flattened and plate- or wing-like (Reidenberg and Laitman, 1994; Hirota and Barnes, 1995; Barnes, 2008; Johnston and Berta, 2011; Kimura and Hasegawa, 2019).

Cervical Vertebrae—The atlas, axis and C3-7 are partially preserved, and unfused (c.279[0], 280[0]; Fig. 14; Table 2). The dorsal arch of the atlas has a low, blunt middorsal ridge that extends nearly the whole length of the arch. The vertebral foramen is broken, although it seems to have occupied the same position as that of *Olympicetus avitus* (Velez-Juarbe, 2017). The anterior articular facets are obscured as the atlas is still attached to the skull, while the posterior facets have a reniform outline, and form a dorsoventrally elongate, smooth, flat surface that extends dorsal to the articulation for the odontoid (Fig. 14A). On the ventral arch, the hypapophysis that would have articulated with the odontoid is short as in *O. avitus* and unlike the longer, more robust process of Simocetidae gen. et sp. A, and *Echovenator sandersi* (Churchill et al., 2016). The transverse processes are gently oriented posterolaterally, and are divided into a larger, more robust dorsal process and a smaller, knob-like ventral process that are divided by a broad, rounded notch (c.278[2]; Fig. 14A). The neural canal has an oval outline.

The axis is missing the dorsal arch, the odontoid is short and blunt. The anterior articular surface has a subtriangular outline ~~forming a~~ flat to shallowly concave~~, surface that~~ extend~~s~~ anteroventrally~~,~~ being continuous with the ventral surface of the odontoid (Fig. 14B). The transverse processes are oriented posterolaterally, with a triangular outline when viewed anteriorly~~,~~ their ventral surface is anteroposteriorly broad, forming a flat surface that faces ventrally and slightly posteriorly, with a sharp anterior edge (Fig. 14B-D). Dorsomedially, the posterior surface of the transverse process~~es~~ form a relatively deep, concave surface. Cervicals 3-6 are missing their dorsal arches and transverse processes for the most part, while only a small portion of C7 is preserved. The centra are anteroposteriorly flat and slightly wider than high, the epiphyses are unfused (Fig. 14C-D). The transverse process of C3 is partially preserved and its morphology is similar to that of the axis.

OLYMPICETUS sp. 1

(Figs. 15-19; Tables 1, 3, 6)

Material—LACM 124105, partial skull, including two partial teeth, left tympanic bulla and right periotic; missing distal end of rostrum, zygomatic arches, parts of the neurocranium and mandible. Collected by J. L. Goedert December 17, 1983.

Locality and Horizon—LACM Loc. 5123, Murdock Creek, Clallam Co., Washington, U.S.A. (48º 09’ 25”N, 123º 52’ 10”W). See above for additional information from this locality.

Formation and Age—Pysht Formation, between 30.5–26.5 Ma (Oligocene: late Rupelian-early Chattian; Prothero et al., 2001; Velez-Juarbe, 2017).

Range—Oligocene of Washington, U.S.A.

Description

The description is based solely on LACM 124105 and will focus on morphological characters that differentiate~~s~~ from *Olympicetus avitus* and *O. thalassodon*. As with the type of *Olympicetus avitus*, LACM 124105 seems to represent a subadult individual, showing some partially open sutures. Multiple areas of the skulls show evidence of erosion (e.g. rostrum, skull roof), likely as a result of wave action as specimens from this locality are usually recovered as concretions along the beach.

Premaxillae—Only part of the left ascending process of the premaxilla is preserved (Fig 15). The ascending process borders the external nares as it ascends towards the vertex (c.74[0]), however, its incomplete preservation posterior to the nasals does not permit identification of its posteriormost extent. A relatively deep sulcus extends along its anterior border which is consistent with the placement and morphology of the posterior extent of the posterolateral sulcus in *Olympicetus avitus* (c.73[2); Fig. 15; Velez-Juarbe, 2017).

Maxilla—Only part of the rostral portion of the maxilla is preserved (Figs. 15-17). Ventrally, the palatal surface is incompletely preserved along the midline and along the alveolar rows, however, the parts that are preserved indicate that it was transversely convex, with the alveolar rows slightly more elevated. Posteriorly, the contact between the maxillae and palatines is bowed anteriorly (c.20[?0], 21[1]; Fig. 16) as in other *Olympicetus*. The alveolar row, although incompletely preserved, diverged posteriorly, and had at least three pairs of closely-spaced, double-rooted postcanine teeth (c.23[0], 26[0]). Based on the preserved posterior border of the alveolar row, it seems that at least a short maxillary infraorbital plate was present (c.60[1]). In posteroventral view, the ventral infraorbital foramen has an oval outline (~12 mm wide by 9 mm high); its dorsolateral edge is formed by the maxilla, dorsomedially by the frontal, and ventrally and ventromedially by the maxilla (c.58[0], [59[0]).

In dorsal view, the rostrum seems to have been fairly wide (c.7[1]; Fig. 15). At the base of the rostrum, the maxillary surface faces dorsolaterally, and is shallowly convex to flat as it ascends over the supraorbital processes of the frontal~~,~~ thus as in other species of *Olympicetus*, it lacks a rostral basin (c.66[0]; Fig. 15). At the base of the rostrum, there are at least three anterior dorsal infraorbital foramina ranging in diameter between 2-5 mm, with a fourth, more posterior foramen, dorsomedial to the antorbital notch (c.65[3]; Figs. 16, 17). The maxillae are eroded at the level of the antorbital notch, so it is uncertain if these formed part of the posterior wall of the notch as in *Olympicetus avitus*. The ascending process of the maxilla~~e~~ partially covers the supraorbital process~~es~~ of the frontal, extending posteriorly beyond the anterior half of the process~~es~~, and posteromedially, coming into contact with the frontal~~s~~ and forming a gently sloping surface towards the edge of the orbit~~s~~, but not reaching its border~~s~~ (c.49[0], 77[1], 78[2], 79[0], 80[0], 130[0], 308[1]; Fig. 15).

Vomer—The vomer is mostly missing anterior to the antorbital notches and eroded anteroventrally, nevertheless, it is evident that it formed the lateral and ventral surfaces of the mesorostral fossa. Ventrally, the vomer likely was exposed through a diamond-shaped window towards the posterior end of the palate as in other simocetids (Fig. 16). Dorsal and posterodorsal

to this point the vomer forms the nasal septum, forming the medial walls of the choanae. From the posterior palatal exposure, the vomer gently slopes posterodorsally, to form a triangular, horizontal plate extending over the still open, basisphenoid-presphenoid contact, but not reaching as far posterior as the fused basisphenoid/basioccipital contact (c.191[0]; Fig. 16). The horizontal plate of the vomer has a triangular outline, contacting the dorsal laminae of the pterygoids along its anterolateral end (Figs. 16-17).

Palatine—Only some very small fragments of the right palatine are preserved. The contact between the palatines and maxilla seems to have been bowed anteriorly (c.20[?0], 21[1]; Figs. 16-17). Posterodorsally, a fragment of the orbital lamina of the palatine reaches the frontal, forming part of the infundibulum for the sphenopalatine and infraorbital foramen, as well as the posterior border of a round (~5 mm diameter) sphenopalatine foramen (Fig. 17). The infundibulum has an oval outline, being broader than high (20 mm x 10 mm), and is bounded dorsally by the frontal and lacrimal, and the maxilla ventrally and ventrolaterally (Fig. 17).

Nasal—Although incompletely preserved, the nasals seem to have been the highest point of the vertex, were longer than wide and dorsoventrally thin, as in other simocetids (c.114[0], 116[0], 118[?0], 124[0], 125[0], 312[0]; Fig. 15). Along their posterior border, they are separated by the narrow, narial process of the frontal (Fig. 15). The anterior edge of the~~n~~ nasals is incompletely preserved, but extended far forward of the anterior edge of the supraorbital processes, while posteriorly they reach a level in line with midpoint of the supraorbital processes (c.81[3], 123[1]; Fig. 15).

Frontal—As in other *Olympicetus*, there is a wedge-shaped exposure of the frontal along the midline, surrounded by the maxilla laterally and nasals anteriorly, although poor preservation of the surrounding bones does not allow precise determination of size relative to the nasals (Fig. 15). Along the midline, the bone is poorly preserved, although it does seem like the frontal are lower than the nasals, preserving the saddle-like profile (in lateral view) seen in other species of *Olympicetus*. Posteriorly, the frontal-parietal suture seems to have been broadly V-shaped dorsally, and sinusoidal in the temporal region, with no intervention of the parietals into the supraorbital processes. Laterally, the supraorbital processes slope very gently ventrolaterally (c.47[?0]). Dorsally, the maxillae only cover the supraorbital processes to a point beyond their mid-point, but do not extend laterally over the orbit (c.78[2]), leaving the preorbital and postorbital processes broadly exposed dorsally (Fig. 15). Anteroventrally, the preorbital process~~es~~ contact the lacrimal. The postorbital processes are incompletely preserved, but seem to have been relatively short, robust, and oriented posteroventrolaterally (Fig. 15). In lateral view the dorsal edge of the orbit is highly arched, but positioned at a lower position (c.48[1]), relative to the lateral edge of the rostrum, than is observed in *Olympicetus avitus* or *O. thalassodon*. A low, sharp temporal crest extends anterolaterally from near the frontal/parietal suture and into the posterodorsal and dorsal surface of the supraorbital process (c.132[2]; Fig. 15), differing from the condition in other *Olympicetus*.

Ventrally, the frontal contact the lacrimal anteroventrally, and the maxilla and/or palatine more medially, resulting in the frontal forming part of the posterodorsal edge of the infundibulum for

the ventral infraorbital and sphenopalatine foramina (Figs. 16-17). The optic foramen is partially covered by sediment, its general orientation seems to be anterolateral, with its posterior border being defined by a low, but sharp infratemporal crest (c.63[0]). Similar to other simocetids, a small (~3 mm diameter) ethmoid foramen is anterolateral to the optic foramen, and is accompanied by four to five smaller (1-2 mm) foramina located along the dorsolateral roof of the orbit (Figs. 16-17).

Lacrimal + Jugal—Only a small portion of the jugal is preserved, but it is evident that it was not fused with the lacrimal (c.54[0], 55[0]; Fig. 17). The portion of the jugal that is preserved is stout and cylindrical, tapering medially, and wedged between the lacrimal and maxilla, which excludes it from forming part of the ventral infraorbital foramen (Fig. 17). The lacrimals are large, and rod-like, but with a relatively small ventral exposure (c.51[1], 56[0]). It contacts the preorbital process of the frontal anteroventrally, tapering medially, and seems to have been exposed anteriorly, forming part of the posterior wall of the antorbital notch, but not extending dorsally onto the supraorbital process (c.52[0]; Fig. 15, 17).

Parietal—the parietals are exposed dorsally, but badly eroded (c.135[0], 136[?]; Fig. 15). The parietals contact the frontal along a broad, V-shaped suture, but differ from other species of *Olympicetus* in that they do not extend into the base of the supraorbital processes. In cross section through the intertemporal region, the parietals seem to have an ovoid outline (c.137[?1]), resembling the condition in other *Olympicetus*. Along the temporal surface the parietal has a sinuous suture with the frontals anteriorly, and the temporal surface becomes more inflated posteriorly towards its contact with the squamosal and alisphenoid (Fig. 17). Ventrally, the parietal has an internal projection that contacts the squamosal medial to the periotic fossa, constricting the cranial hiatus as in other simocetids (c.184[2]; Fig. 16).

Supraoccipital—The supraoccipital is only partially preserved, with the exception of its dorsolateral borders. The lambdoidal crests are sharp, directed dorsolaterally and only slightly overhanging the temporal fossa (c.154[1]; Fig. 15), curving posteroventrally to join the supramastoid crest of the squamosal.

Exoccipital—Generally poorly preserved. Dorsal to the remaining parts of the right occipital condyle, there is what seems to be a shallow dorsal condyloid fossa (c.157[?1]). The surface lateral to the condyles is flat to shallowly convex.

Basioccipital—As preserved, the basioccipital crests seem to have been relatively thick transversely (c.192[?1]) and oriented posterolaterally, at about an angle of 45 degrees (c.195[3]; Fig. 16). The rest of the ventral surface is incompletely preserved.

Squamosal—The zygomatic processes are incompletely preserved. Posteromedially, the sternomastoid fossa forms a distinct emargination that is overhung dorsally by the supramastoid crest much more than in *Olympicetus avitus* (c.145[1]; Fig. 15). The supramastoid crest seems to have been continuous with the lamboidal crest (c.150[0]). The squamous portion contacts the parietal along an anteroventrally sloping interdigitated suture, meeting the alisphenoid to form part of the subtemporal crest. Ventrally, the squamosal is heavily eroded, and only a small

portion of the periotic fossa is preserved, where it contacts the medial extension of the parietal (Fig. 16).

Pterygoid—Most of the pterygoid is missing on both sides of the skull. A portion of the dorsal lamina extends posterodorsally towards the parietal and contributes to the posteroventral edge of the optic infundibulum as in *Olympicetus avitus* (Fig. 17). As preserved, the pterygoid sinus fossa is anteroposteriorly longer than wide, and is located entirely anterior to the foramen ovale (c.164[2], 169[0]; Figs. 16-17).

Alisphenoid—As in *Olympicetus avitus*, the alisphenoid forms the posterodorsal surface of the pterygoid sinus fossa (Figs. 16-17). The medial and posterior ends of the bone are incompletely preserved or eroded on both sides, making it difficult to determine the position of the alisphenoid squamosal suture or the path of the mandibular nerve (V3). On the temporal wall, the exposure of the alisphenoid is limited to a small sliver, as it is mostly overlapped by the parietal and the squamosal (c.142[1]; Fig. 17).

Basisphenoid—Posteriorly the basisphenoid is fused with the basioccipital, while anteriorly its contact to the presphenoid (sphenoidal synchondrosis) is still open, resembling the growth stage of the type of *Olympicetus avitus* (Velez-Juarbe, 2017). The ventral surface is flat, and covered by the horizontal plate of the vomer (Fig. 16).

Optic Infundibulum—The optic infundibulum is a slightly sinusoidal opening bounded by the frontal anteriorly and dorsally, parietal posteriorly, pterygoid ventrally and anteroventrally (Fig. 17). The optic foramen, orbital fissure and foramen rotundum are still partly covered by sediment. The frontal forms most of the borders of the optic foramen anterodorsally, while posteroventrally the foramen rotundum was bounded laterally by the parietal~~s~~ and floored by the pterygoid. The anteroventral edge of the parietal~~s~~ that forms part of the infundibulum, has a narrow groove that trends anterodorsally, and would have carried the ophthalmic artery, resembling the condition in *Simocetus rayi* and *Olympicetus avitus* (Fig. 17; Fordyce, 2002; Velez-Juarbe, 2017). While along the ventral edge of the infundibulum, the pterygoid has a distinct, but shallow groove, that would have presumably carried the maxillary nerve (V2), extending along its dorsolateral surface and diverging slightly over its lateral surface anteriorly (Fig. 17).

Malleus—The left malleus is still articulated with the corresponding tympanic (Fig. 18). The head has a semicircular outline, with paired facets for articulation with the incus~~,~~ that are oriented at about 90 degrees to each other; the more anterior facet is about ~~as~~ twice as large as the posterior one as in *Olympicetus avitus* (Fig. 18; Velez-Juarbe, 2017). The tubercle is relatively large, nearly as long as the head (c.199[0]; Fig. 18). The manubrium is prominent and slightly recurved posteroventrally (Fig. 18). The anterior process is fused laterally to the tympanic, dorsally forming a continuous surface with the mallear ridge, while its ventral edge is shelf-like, together forming a deep, narrow sulcus for the chorda tympani (Fig. 18A, C, E).

Tympanic Bulla—Only the left tympanic bulla is preserved (Fig. 18), but missing its posterior process~~,~~ overall it closely resembles in size and morphology that of *Olympicetus avitus* (Velez-Juarbe, 2017). In dorsal or ventral view, the bulla has a heart-shaped outline, being relatively

short and wide (c.252[1]), unlike the larger and transversely narrower bulla of *Olympicetus thalassodon* (Figs. 10, 18). The lateral surface is broadly convex, while ~~medially it~~ is straight; the posterior prominences give~~s~~ the bulla a bilobed outline posteriorly while anteriorly, the lateral surface converges medially more steeply than the medial surface along a smooth curve, ~~t~~there is no indication of the presence of an anterior spine (c.251[0]). Posteriorly, a broad interprominential notch extends from the level below the elliptical foramen, continuing along the ventral surface of the bulla for only about a third of its length (c.267[0]). The interprominential notch is divided by a transverse ridge (c.268[0]; Fig. 18D), resembling the condition observed in *Olympicetus thalassodon*, differing from that of *O. avitus*, which does not have an interprominential ridge. The inner and outer prominences extend posteriorly to nearly the same level (c.270[0]). The ventromedial keel is poorly defined, forming a smooth curve around the posterior part of the involucrum, its posteromedial surface just slightly bulging farther medially than the rest of the involucrum (c.253[0], 274[2], 275[0], 276[0]). The elliptical foramen seems to have been narrow, and nearly vertical (c.262[0]).

In lateral view, the ventral edge of the bulla is nearly flat (c.269[0]), differing from the more broadly concave ventral margin observed in some xenorophids, like *Albertocetus meffordorum* (Uhen, 2008). The ventrolateral keel forms a blunt ridge that descends ventrolaterally from the conical pyramidal process. The lateral furrow is nearly vertical, forming a relatively broad sulcus (c.257[0], 258[0]; Fig. 18B). Dorsally, the sigmoid process is vertical and perpendicular to the long axis of the bulla (c.259[0]), with its posterior edge curving anteriorly along a smooth curve (c.260[0]). The mallear ridge extends obliquely from the anteromedial base of the sigmoid process towards the dorsalmost extension of the lateral furrow. A narrow, dorsally open sulcus for the chorda tympani extends anteriorly for a length of 17 mm along the dorsomedial edge of the outer lip, originating at the junction between the anterior process of the malleus and the mallear ridge (Fig. 18A, C, E). The anterodorsal crest descends steeply towards the anterior edge of the bulla.

In medial view the dorsal and ventral edges of the involucrum gradually converge towards the anterior end of the bulla (c.271[0]; Fig. 18A). The involucrum has numerous, faint vertical ridges (c.272[1]), differing from the deeper grooves observed in xenorophids, like *Albertocetus meffordorum* (Uhen, 2008).

Periotic—Only the right periotic is preserved (Fig. 19A-H) and is overall very similar to that of CCNHM 1000 described by Racicot et al. (2019). The anterior process is oriented anteriorly and short relative to the length of the cochlea, with its anteroventral and anterodorsal ends being bluntly pointed, ~~that~~ together give~~s~~ it a nearly squared-off outline (c.201[0], 202[0], 204[2]; Fig. 19C-D). In medial view, the apex of the anterior process is slightly deflected ventrally, forming a slightly convex to flat surface (c.203[1], 205[0]; Fig. 19C-D). In lateral view, at the base of the anterior process there is a shallow, C-shaped sulcus that begins near the anterodorsal edge, curves posteroventrally towards the lateral tuberosity, then curv~~ing~~ anterodorsally~~, that~~ is interpreted as a combined anteroexternal+parabullary sulcus (sensu Tanaka and Fordyce, 2014; Fig. 19G-H). This condition resembles that of other early odontocetes such as *Waipatia*

maerewhenua Fordyce, 1994, *Papahu taitapu* Aguirre-Fernández and Fordyce, 2014, and *Notocetus vanbenedeni* Moreno, 1892, but differs from others like *Otekaikea marplesi* (Dickson, 1964) where these sulci are separate, and from the much deeper sulcus in *P. taitapu* (Tanaka and Fordyce, 2014; Viglino et al., 2022). In cross-section, the anterior process is ovoid, being taller (~14 mm) than wide (~9 mm) (c.209[1]). The anteroventral surface of the anterior process has as well-defined anterior bullar facet (c.210[3]; Fig. 19E-F). Posterior to the anterior bullar facet, the fovea epitubaria forms a smooth curve that is interrupted by a prominent lateral (ventrolateral) tuberosity (c.212[1]). The lateral ~~process~~ has a triangular outline in ventral view, but does not extend as far laterally as in other stem odontocetes such as *Cotylocara macei* (Geisler et al., 2014), being instead barely visible in dorsal view. A similarly, broadly arched epitympanic hiatus lies posterior to the lateral tuberosity and anterior to the base of the posterior process (c.213[1]). Posteromedial to the epitympanic hiatus, is a small (diameter: ~2 mm) rounded fossa incudis, while anterior to it and medial to the lateral tuberosity is a broad (diameter: ~6 mm), circular mallear fossa (c.214[1], 215[0]; Fig. 19E-F). The lateral surface of the periotic is generally smooth with the exception of the posterior process, whose lateral surface is rugose (c.217[2]; Fig. 19G-H). Medially, the anterior process is separated from the cochlea by a well-defined groove (anterior incisure, *sensu* Mead and Fordyce, 2009) that extends anterodorsally, and marks the origin for the tensor tympani muscle (c.218[1]).

In dorsal view, a low crest delimits the dorsolateral surface of the periotic, it extends from the low pyramidal process towards the anterodorsal spine of the anterior process (Fig. 19A-B). Medial to this crest is an elongated depression, the suprameatal fossa, which is about 13.5 mm long by 7 mm wide, and around 1.5 mm deep (Fig. 19A-B). The fundus of the internal acoustic meatus is funnel-shaped, with an oval outline, delimited by a low ridge (c.235[0]; 236[0]). The area cribosa media and the spiral cribiform tract are separated by a very low ridge, these two are in turn separated from the superior vestibular area (previously called the foramen singulare; Ichishima et al., 2021) by a low transverse crest that lies about 3 mm below the upraised rim of the internal acoustic meatus, while its separation from the dorsal opening of the facial canal by a ridge that is slightly lower (~4 mm from the edge of the rim) (c.237[2]; Fig. 19A-B). The proximal opening of the facial canal has an oval outline and located anterolateral to the spiral cribriform tract (c.238[0], 239[1]); anterodorsally it is bridged, forming a "second" foramen, which is smaller and rounded (Fig. 19A-D), resembling the condition observed in other early odontocetes, such as *Waipatia maerewhenua*, and similarly, it is interpreted as the foramen for the greater petrosal nerve (Fordyce, 1994). The endolymphatic duct (vestibular aqueduct) is slit-like (~4 mm long by 1 mm wide), and located posterolateral to the internal acoustic meatus, just below the more vertical posterior surface of the pyramidal process, and separated from the fenestra rotunda by a very wide distance (c.230[3]; Fig. 19A-D). In contrast, the perilymphatic duct (cochlear aqueduct) is rounded (diameter = 3mm) and located posteromedial to the internal acoustic meatus and medial to the endolymphatic duct, and broadly separated from the fenestra rotunda (c.228[1], 229[2]). A small, curved depression posteroventral to the endolymphatic duct is interpreted as a shallow stylomastoid fossa (c.225[1]). The dorsomedial surface of the cochlear

portion has a shallow depression that accentuates the raised medial rim of the internal acoustic meatus. In medial view, the cochlea is relatively flat (maximum height ~11 mm), its ventromedial surface is anteroposteriorly convex and a low, faint ridge extends along its ventrolateral end (c.221[0]; Fig. 19C-F). In ventral view, the cochlear portion has a subrectangular outline (c.219[1], 220[1], 222[1]). Posteriorly, the fenestra rotunda is located towards the lower half of the posterior surface, and it is wider than high (4 x 2 mm), with a kidney-shaped outline (c.223[0]). Posterolateral to the fenestra rotunda, the caudal tympanic process projects farther posteriorly than the rest of the posterior surface of the cochlea, although it is not as prominent as that of other simocetids (i.e. CCNHM 1000; Racicot et al., 2019), and its ventral and posterior borders intersect along a curved edge (c.226[1]; Fig. 19C-F). Ventrally, the foramen ovale is longer than wide (4 x 3 mm), and located towards the posterior half of the cochlea. The ventral opening of the facial canal (~2 mm in diameter) is lateral to the foramen ovale, and are separated by a sharp crest. The facial canal opens posteroventrally, and continues as a groove that merges with the stapedial muscle fossa at the base of the posterior process; the fossa is deep and rounded, with its posterodorsal edge nearly in line with the fenestra rotunda (c.224[0]).

The posterior process is short and robust, with its long axis ~~is~~ oriented posterolaterally (c.246[1], 247[1], 249[0]; Fig. 19A-B, E-F). Proximally, the lateral surface of the posterior process is rough, with an irregular, near vertical ridge interpreted here as a poorly-developed articular rim (c.240[1]), resembling the condition in other simocetids (i.e. CCNHM 1000) and early odontocetes like *Notocetus vanbenedeni*, and differing from the more prominent articular rim observed in platanistids (Muizon, 1987; Racicot et al., 2019; Viglino et al., 2022; Fig. 19A-B). the dorsal edge of the posterior process forms a straight line (c.248[0]). The posterior bullar facet has a kite-shaped outline, its surface is smooth and shallowly concave transversely (c.242[0], 243[0]); the edges of the facet are sharp, with the exception of the posteromedial edge which is rounder (c.244[0]).

Dentition—Only two, incompletely preserved teeth are associated with LACM 124105 (Fig. 19I-L). Both are postcanine teeth, with striated enamel and ecto- and entocingula and denticles (c.27[1], 32[1] 33[0], 35[?1]). As in other simocetids, the buccal surface of the crowns are more concave. The roots are long and conical, becoming fused proximally. Tooth PCa (Fig. 19I, K) measures 12 mm long by 6 mm wide, while tooth PCb (Fig. 19J, L) measures 9 mm high and 6 mm wide.

Remarks—LACM 124105 shows multiple diagnostic features with the other named species of *Olympicetus*, such as having a broadly open temporal fossa, unfused lacrimal/jugal (c.54[0]), lacking a maxillary foramen (c.76[0]), and maxilla covering only about the anterior half of the supraorbital process (c.77[1]). However, it does differ by having a more sharply defined infratemporal crest, orbit at a lower position relative to the edge of the rostrum (c.48[1]), dorsolateral edge of ventral infraorbital foramen formed by the maxilla (c.58[0]), and more notably, the lateral end of the temporal crest extend~~s~~ along the posterodorsal surface of the supraorbital process of the frontal (c.132[2]; Fig. 15). These differences are considered to be

species-related, and not the result of ontogenetic change as this specimen shows a similar growth stage as the type of *Olympicetus avitus* (LACM 149156; Vélez-Juarbe, 2017). Nevertheless, because of its incomplete preservation, it is preferably left in open nomenclature until better material belonging to this taxon is identified.

Discussion

While particular attention has been paid to Oligocene mysticetes from the North Pacific over the last few decades (e.g. Barnes et al., 1995; Okazaki, 2012; Marx et al., 2015; Peredo et al., 2018; Solis-Añorve et al., 2019; Hernández-Cisneros, 2022; Hernández-Cisneros and Nava-Sánchez, 2022), the same cannot be said with regards to the odontocetes. Oligocene odontocetes from around the North Pacific are not entirely missing from the scientific literature and have been mentioned multiple times, often identified informally as "non-squalodontid odontocetes", "agorophiid" or "*Agorophius*-like" (see Whitmore and Sanders, 1977; Goedert et al., 1995; Barnes, 1998; Barnes et al., 2001; Fordyce, 2002; Hernández Cisneros et al., 2017). However, given their importance, most of these have yet to be properly described and our understanding of species richness and relationships between Oligocene odontocetes from the North Pacific is not fully understood.

The first of these taxa to be described was *Simocetus rayi* from the early Oligocene Alsea Fm. of Oregon which was placed in its own family, Simocetidae (Fordyce, 2002). Since then, only two other North Pacific Oligocene odontocetes had been named, specifically, the platanistoid *Arktocara yakataga* from the Oligocene Poul Creek Fm. in Alaska, which is likely one of the earliest crown odontocetes, and the stem odontocete *Olympicetus avitus* from the Pysht Fm. in Washington (Boersma and Pyenson, 2016; Vélez-Juarbe, 2017). More recently, Racicot et al. (2019) described a neonatal skull (CCNHM 1000) from the Pysht Fm. in Washington, that closely resembles *Olympicetus avitus*, but did not group with *Simocetus rayi* nor with *O. avitus*, and instead all three taxa occupied different positions outside of crown odontocetes (Racicot et al., 2019).

Herein, the description of three additional specimens from the mid-Oligocene Pysht Formation in Washington have potentially clarified the relationship between stem odontocetes from the North Pacific. The phylogenetic analysis including these new specimens, resulted in 36 most parsimonious trees 3649 steps long, with retention index (RI) = 0.520 and consistency index (CI) = 0.182. Other statistical values are shown in the strict consensus tree (Fig. 20). Based on these results, Simocetidae now seem to form a monophyletic group that includes *S. rayi*, CCNHM 1000, *Olympicetus* spp. and a large unnamed simocetid (Fig. 20). Furthermore, the phylogenetic analysis recovered CCNHM 1000 as part of the Simocetidae, differing from the analysis of Racicot et al. (2019) where it was recovered at the base of a clade including all odontocetes, with the exception of Xenorophidae. As discussed by Racicot et al. (2019) CCNHM 1000 does resemble *Olympicetus avitus*, more specifically, based on the new specimens described here, it shares with *Olympicetus* spp. having closely-spaced posterior buccal teeth (c.26[0]), buccal teeth with ecto- and entocingula (c.32[1], 33[0]), presence of a small maxillary infraorbital plate

(c.60[1]), and the presence of a transverse cleft on the apex of the zygomatic process (c.335[1]), amongst others. However, CCNHM 1000, does show some dental characteristics that sets it apart from *O. avitus* as discussed by Racicot et al. (2019), and others that differentiates it from other specimens of *Olympicetus*, such as having a relatively lower position of the orbit (c.48[1]; shared with *S. rayi* and *Olympicetus* sp.), 63[1], presence of an interparietal (c.136[0]), a more anterior position of the apex of the supraoccipital (c.140[1]), and a very low lambdoidal crest (c.154[2]). Some of these characters, such as the position of the apex of the supraoccipital and the morphology of the lambdoidal crest are also observed in the neonate skull referred to *O. avitus*, suggesting that these characters change ontogenetically, with neonatal individuals displaying more plesiomorphic conditions. Along these same lines, the presence of a distinct interparietal in CCNHM 1000 is considered as another plesiomorphic character, ~~that~~ when combined with the other characters mentioned previously, ~~it is suggestive that this~~ may account for the more basal position of CCNHM 1000 in the phylogenetic analysis (Fig. 20). Besides this, it seems clear that CCNHM 1000 should be regarded as a neonate of *Olympicetus* sp.

The inclusion of CCNHM 1000 has some interesting implications for Simocetidae. Racicot et al. (2019) described the inner ear morphology of CCNHM 1000 showing that it does not have the capability of ultrasonic hearing, which is suggestive that other taxa within this clade are also non-echolocating odontocetes and may be a characteristic unique to this family. Future studies on the inner ear morphology of the periotics of other simocetids, such as *Simocetus rayi*, *Olympicetus* sp. 1 (LACM 124105), will likely provide more information to this regard.

Stem Odontocetes from the North Pacific

The early odontocete clade Simocetidae now includes six OTUs: *Simocetus rayi*, *Olympicetus avitus*, *Olympicetus* sp. (LACM 124105), *O. thalassodon* (LACM 158720), an unnamed large simocetid (LACM 124104) and CCNHM 1000 (Fig. 20). All specimens, with the exception of *S. rayi*, are from the Pysht Fm., with four of them: LACM 124104, LACM 124105, LACM 158720 and CCNHM 1000, coming from the same general area (LACM Loc. 5123). The results of the phylogenetic analysis resemble those of an earlier, preliminary study that also recovered a monophyletic Simicetidae composed of most of the OTU~~'~~s used here as well as a few other~~s~~ undescribed specimens from the eastern North Pacific, but that also recovered *Ashleycetus planicapitis*, from the early Oligocene of South Carolina, as part of that clade (Velez-Juarbe, 2015). In contrast, the results of the present work suggest that Simocetidae represents an endemic radiation of North Pacific stem odontocetes, that parallels that of the Aetiocetidae in the same region (Hernández Cisneros and Velez-Juarbe, 2021), and the Xenorophidae (here considered to include Ashleycetidae and Mirocetidae; Fig. 20) in the North Atlantic and Para-Tethys (Marx et al., 2016a). The occurrence of crown (i.e. *Arktocara yakataga*) as well as stem (Simocetidae) odontocetes in the Oligocene of the North Pacific suggest that the initial diversification of crown odontocetes must have occurred during the latest Eocene to earliest Oligocene (Boersma and Pyenson, 2016). This highlights the importance of the fossil record of the North Pacific towards further understanding the early history and radiation of odontocetes.

At present, there are no published accounts of simocetids from the western North Pacific, although these are expected to be present based on the occurrence of closely-related marine tetrapods in Oligocene deposits on both sides of the basin (e.g., plotopterids, desmostylians, aetiocetids; Olson, 1980; Domning et al., 1986; Ray et al., 1994; Olson and Hasegawa, 1996; Inuzuka, 2000; Barnes and Goedert, 2001; Sakurai et al., 2008; Ohashi and Hasegawa, 2020; Mayr and Goedert, 2016, 2022; Mori and Miyata, 2021; Hernández-Cisneros and Vélez-Juarbe, 2021), which makes this apparent absence an interesting question. However, some records from Japan bear close resemblance to simocetids and should be analyzed further. These include a mandible with two cheek teeth (KMNH VP 000011) and an isolated tooth (KMNH VP 000012) referred by Okazaki (1988) to *Squalodon* sp. from the Oligocene Waita Formation of the Ashiya Group. The general morphology of the mandible (KMNH VP 000011) resembles *Olympicetus thalassodon* and other basal odontocetes with multi-cusped cheek teeth, such as *Prosqualodon davidis* Flynn, 1947, and *Waipatia maerewhenua*, where the dorsal surface of the condyle is at about the same level as the horizontal ramus and the ventral border is relatively straight (Flynn, 1947; Fordyce, 1994). Furthermore, the two cheek teeth preserved with KMNH VP 000011 are much more like those of *Olympicetus* with the more anterior tooth (B3 in Okazaki, 1988) having only a small accessory denticle along the base of the mesial edge, while three larger ~~ones~~ distally, that increase in size apically, greatly resembling the premolars of *O. thalassodon* (Figs. 11A, C, 12G). Meanwhile, the second tooth (B7 in Okazaki, 1988) resembles the m3 of *Olympicetus thalassodon*, by being smaller than the more anterior teeth, and having three accessory denticles along the distal edge that diminish in size towards the base of the crown, lacking accessory denticles along the mesial carina, and little to no ornamentation on the buccal side. The isolated tooth (KMNH VP 000012) resembles cheek tooth 'pp4' of *Olympicetus avitus*, as they are relatively low and long, with multiple accessory denticles along the mesial and distal edges, as well as having lingual and buccal cingula (Okazaki, 1988; Vélez-Juarbe, 2017). One distinguishing character is that the accessory denticles of *Olympicetus* spp. and the Waita Fm. odontocetes are closer in size to the main cusp than those of other basal odontocetes with multi-cusped cheek teeth. For example, lower cheek teeth of *Squalodon calvertensis*, *Prosqualodon davidis*, *P. australis* Lydekker, 1894, *Phoberodon arctirostris* Cabrera, 1926, and *Waipatia* spp. do have accessory denticles along their distal edges, but are ~~obviously~~ much smaller than the main cusp (Kellogg, 1923; Flynn, 1947; Fordyce, 1994; Tanaka and Fordyce, 2015; Gaetan et al., 2019; Viglino et al., 2019). The combination of these morphological features suggest that the specimens described by Okazaki (1988)~~,~~ could be considered as aff. *Olympicetus* sp., although this needs to be confirmed by direct observation of the specimens. Other cetaceans from the Ashiya Group include a toothed mysticete from the Waita Fm., originally assigned to *Metasqualodon symmetricus*, but now considered to represent an aetiocetid, and the eomysticetid *Yamatocetus caniliculatus* from the Jinnobaru Fm. (Okazaki, 1987, 2012; Fitzgerald, 2010). Similarly, other potential records of simocetids are found in the late Oligocene El Cien Formation of Baja California Sur. Hernández-Cisneros et al. (2017) briefly discussed two skulls from the El Cien Fm., comparing one with *Simocetus rayi* and the other with an undescribed

skull (USNM 205491) from the Alsea Fm.~~,~~ ~~and~~ may represent other undescribed simocetids. These odontocetes from El Cien Fm. are currently under study (A. E. Hernández-Cisneros, pers. comm.), and other described taxa from this formation include kekenodontids, aetiocetids, eomysticetids and other stem mysticetes (Hernández-Cisneros and Tsai, 2016; Hernández-Cisneros et al., 2017; Solis-Añorve et al., 2019; Hernández-Cisneros, 2022; Hernández-Cisneros and Nava-Sánchez, 2022). These records from the Jinnobaru Fm.~~,~~ and El Cien Fm., resemble the odontocete assemblage of the Pysht Fm, which includes simocetids, aetiocetids and other early mysticetes, and is therefore likely that simocetids ~~are~~ would be present in these units as well (Barnes et al., 1995; Peredo and Uhen, 2016; Vélez-Juarbe, 2017; Shipps et al., 2019; Hernández Cisneros and Vélez-Juarbe, 2021; this work).

Dentition and Feeding in Simocetids

As in most other groups of stem odontocetes (e.g. xenorophids, agorophiids), simocetids have heterodont dentition, but do seem to have a more conservative tooth count, closer to that of basilosaurids such as *Cynthiacetus peruvianus* (Martínez-Cáceres and Muizon, 2011), which consists of three incisors, one canine, four premolars, two upper and three lower molars, a pattern that is also observed in early mysticetes like *Janjucetus hunderi* Fitzgerald, 2006, and *Mystacodon selenensis* (Fitzgerald, 2010; Lambert et al., 2017). While the tooth count of some simocetids is hard to interpret (e.g. *Olympicetus avitus*; Vélez-Juarbe, 2017), others such as *Simocetus rayi* and *Olympicetus thalassodon* offer more definite clues with regards to their dentition. In the case of *Simocetus rayi*, its tooth count seems to be secondarily reduced from the plesiomorphic condition through the loss of the upper incisors, while the lower ones are retained (Fordyce, 2002). Although mostly missing, the teeth of *S. rayi* were widely separated and ~~comparatively~~ small (when compared to those of *Olympicetus*). In contrast, the teeth of *Olympicetus thalassodon* are closely spaced and based on the preserved teeth and alveoli, its dental formula is tentatively interpreted as ?I3, C, P4, M2/?i3, c, p4, m3. If these interpretations are correct, then the dentition of simocetids is the most plesiomorphic amongst odontocetes, paralleling that of basal mysticetes. This would contrast with xenorophids which seem to have polydont dentition~~,~~ for example, *Xenorophus sloanii* and *Echovenator sandersi*~~,~~ both have significantly higher count of postcanine teeth (Sanders and Geisler, 2015; Churchill et al., 2016). Nevertheless, the dentition of many xenorophids is still unknown, including key taxa, such as *Archaeodelphis patrius*, which may offer additional insight into early odontocete dental evolution.

Although simocetids seem to share similar conservative tooth counts and generalized features of their teeth, there are some interesting differences between some of the species. One conspicuous difference between the dentition of *Olympicetus avitus* and *O. thalassodon* is the presence of a "carnassial"-like tooth in the former (tooth 'mo3' in Velez-Juarbe, 2017:fig.7O,Bb). This tooth is distinguished from all other postcanine teeth by having a ridge with accessory denticles that descends lingually from the apex, while its root is expanded lingually, giving the impression of the presence of three roots (mesial, distal and lingual), rather than two (mesial and distal) as in

the other postcanine teeth. Meanwhile, a third, lingual root seems to be present in the P4 of *Simocetus rayi* (Fordyce, 2002), as well as in an unnamed *Simocetus*-like taxon from the Lincoln Creek Fm. (Barnes et al., 2001), and could be a character that is shared among some simocetids, although better preserved specimens are needed to corroborate this. Interestingly, tooth B7 (*sensu* Sanders and Geisler, 2015) of *Xenorophus sloani* seems to present a more inconspicuous version of the "carnassial" tooth of simocetids~~,~~ this tooth occupies a ~~similar~~ position ~~of~~ that of P4 ~~of~~ *Simocetus rayi*, and ~~is likely a~~ character ~~that~~ should be explore further as more specimens become available.

Some of the morphological characters observed in described simocetids, such as the arched palate, short and broad rostrum, smaller and widely-spaced teeth, as in *Simocetus rayi*, ~~are~~ interpreted as features of a bottom suction feeder (Fordyce, 2002; Werth, 2006; Johnston and Berta, 2011). Some of these features, such as the arched palate are also present in *Olympicetus*, however, *O. thalassodon*, has closely spaced, larger teeth, as well as a relatively gracile, unfused hyoid apparatus (Figs. 11-13A-C; Johnston and Berta, 2011; Viglino et al., 2021), which suggest that this taxon was instead a raptorial or combined feeder. Taking this into account, it is likely that simocetids employed different methods of prey acquisition, likely akin to the amount of variation observed in other contemporaneous groups, such as xenorophi~~i~~ds, which include taxa with long narrow rostra (e.g. *Cotylocara macei*; Geisler et al., 2014) that can be interpreted as raptorial feeders, as well as brevirostrine suction feeding tax~~a~~ (i.e. *Inermorostrum xenops*; Boessenecker et al., 2017). Thus it seems that multiple methods of prey acquisition evolved iteratively across different groups of odontocetes soon after their initial radiation.

Conclusions

Three new specimens of odontocetes from the middle Oligocene Pysht Formation were described herein further increasing our understanding of richness and diversity of early odontocetes, specially for the North Pacific region. Inclusion of this new material in a phylogenetic analysis showed that Simocetidae is a much more inclusive clade, ~~that,~~ besides *Simocetus rayi*, ~~it~~ now includes *Olympicetus avitus*, *O. thalassodon* sp. nov., *Olympicetus* sp. 1, and a large unnamed taxon. Of these, *Olympicetus thalassodon* is ~~the~~ one of the most completely known simocetids, offering new information on the morphology of early odontocetes, while the inclusion of CCNHM 1000 within this clade suggest that simocetids may represent a clade of non-echolocating odontocetes. This shows that some morphological features that have been correlated with the capacity to echolocate, such as an enlarged attachment area for the maxillonasolabialis muscle, and presence of a premaxillary sac fossae (Fordyce, 2002; Geisler et al., 2014), appeared before the acquisition of ultrasonic hearing. Furthermore, the dentition of simocetids, as interpreted here, seems to be the most plesiomorphic amongst odontocetes, while other craniodental features within members of this clade suggests various forms of prey acquisition, including raptorial or combined in *Olympicetus* spp., and suction feeding in *Simocetus* (as suggested by Fordyce, 2002). Meanwhile, body size estimates for simocetids show that small to moderately large taxa are present in the group, ~~with~~ the largest taxon represented by

LACM 124104 with an estimated body length of 3 meters~~, which~~ plac~~es it as the largest known simocetid, and~~ amongst the largest Oligocene odontocetes, only surpassed in bizygomatic width (and therefore estimated body length) by the xenorophids *Mirocetus riabinini* and *Ankylorhiza tiedemani* (Boessenecker et al., 2020; Sander et al., 2021). Finally, the new specimens described here add to a growing list of Oligocene marine tetrapods from the North Pacific, further facilitating faunistic comparisons ~~across~~ other contemporaneous and younger assemblages, thus improving our understanding of the evolution of marine faunas in the region.

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Figure 1

Dorsal view of skull of Simocetidae gen. et sp. A (LACM 124104).

Unlabeled (A) and labeled (B) skull in dorsal view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: as, alisphenoid; cp, coronoid process; eo, exoccipital; f, frontal; oc, occipital condyle; oi, optic infundibulum; pa, parietal; pp, paroccipital process; pt, pterygoid; smf, sternomastoid fossa; so, supraoccipital; sq, squamosal; zps, zygomatic process of squamosal.

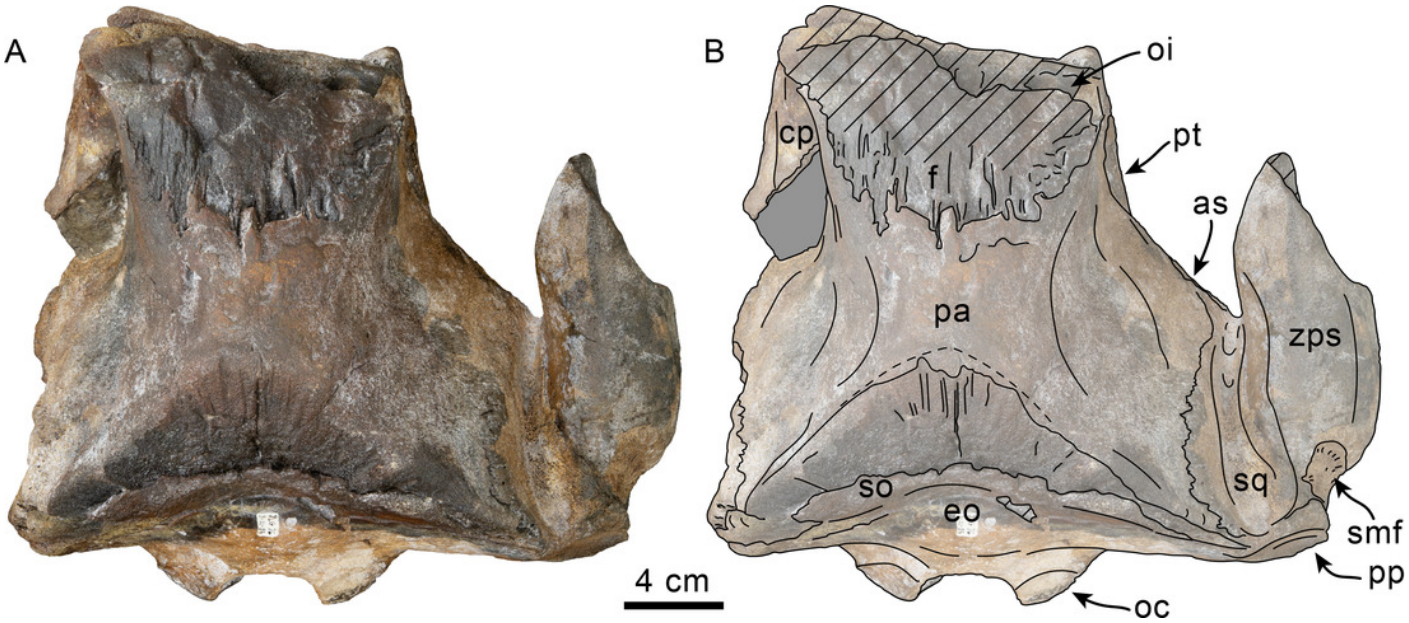


Figure 2

Posterior and ventral views of skull of Simocetidae gen. et sp. A (LACM 124104).

Unlabeled (A) and labeled (B) skull in posterior view; unlabeled (C) and labeled (D) skull in ventral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: as, alisphenoid; bo, basioccipital; bo, basioccipital crest; cp, coronoid process; eo, exoccipital; fm, foramen magnum; fs, foramen spinosum; g, glenoid; hf, hypoglossal foramen; jn, jugular notch; oc, occipital condyle; pa, parietal; pe, periotic; pgp, postglenoid process; ph, pterygoid hamulus; pl, palatine; pll, pterygoid lateral lamina; pml, pterygoid medial lamina; pp, paroccipital process; psf, pterygoid sinus fossa; pt, pterygoid; scf, supracondylar fossa; smf, sternomastoid fossa; so, supraoccipital; sq, squamosal; tr, tympanosquamosal recess; V3, groove and path of mandibular branch of trigeminal nerve; vo, vomer; zps, zygomatic process of squamosal.

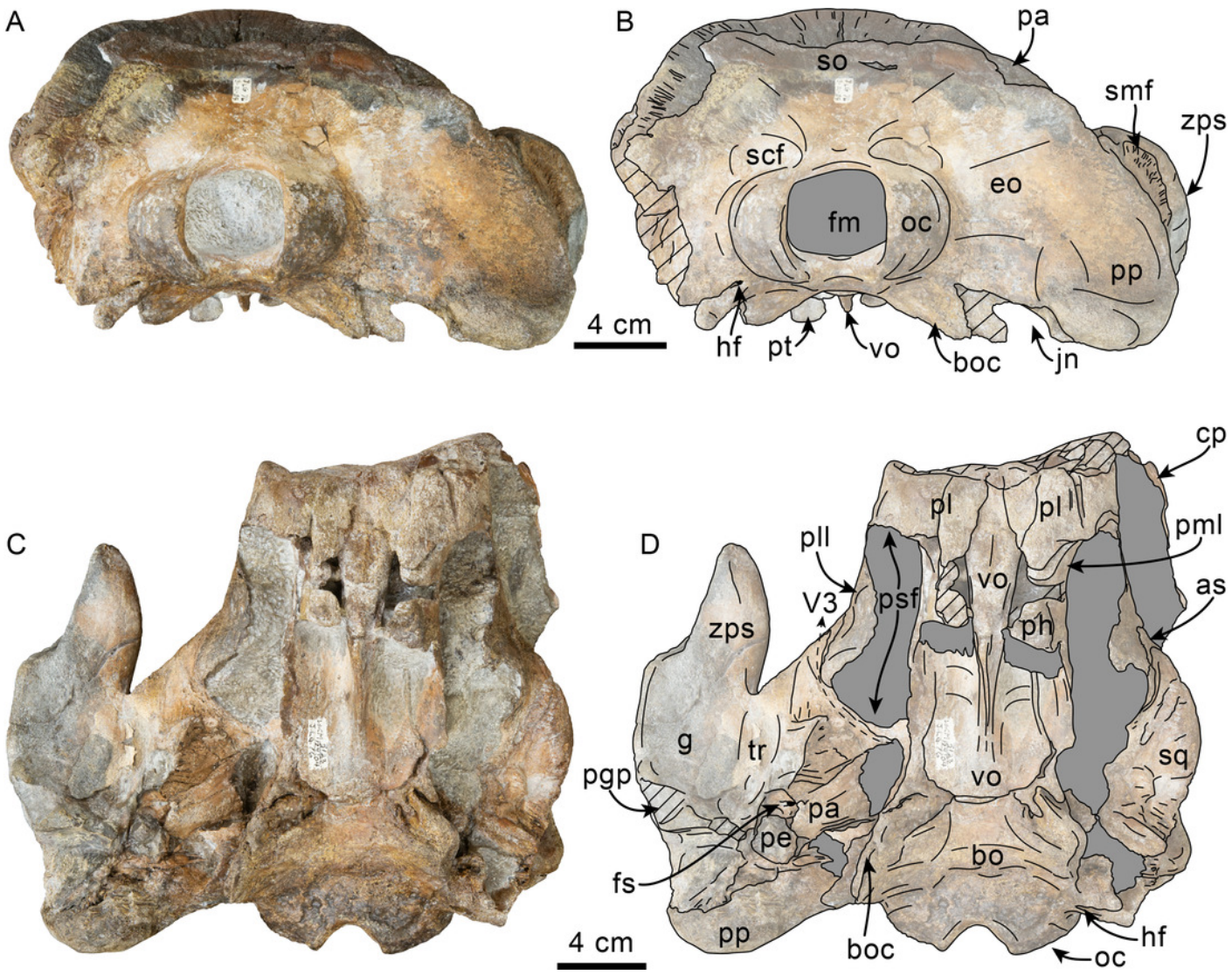

A
B
pa
so
smf
zps
scf
eo
fm
oc
pp
4 cm
hf
pt
vo
boc
jn
C
D
cp
pl
pl
pll
pml
V3
psf
vo
as
zps
ph
g
tr
sq
pgp
vo
pa
pe
bo
fs
pp
boc
hf
oc
4 cm

Figure 3

Lateral view of skull of Simocetidae gen. et sp. A (LACM 124104).

Unlabeled (A) and labeled (B) skull in right lateral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: as, alisphenoid; boc, basioccipital crest; eo, exoccipital; f, frontal; fp, falciform process; oc, occipital condyle; oi, optic infundibulum; pa, parietal; ph, pterygoid hamulus; pl, palatine; pll, pterygoid lateral lamina; pml, pterygoid medial lamina; pp, paroccipital process; psf, pterygoid sinus fossa; smf, sternomastoid fossa; sq, squamosal; vo, vomer; zps, zygomatic process of squamosal.

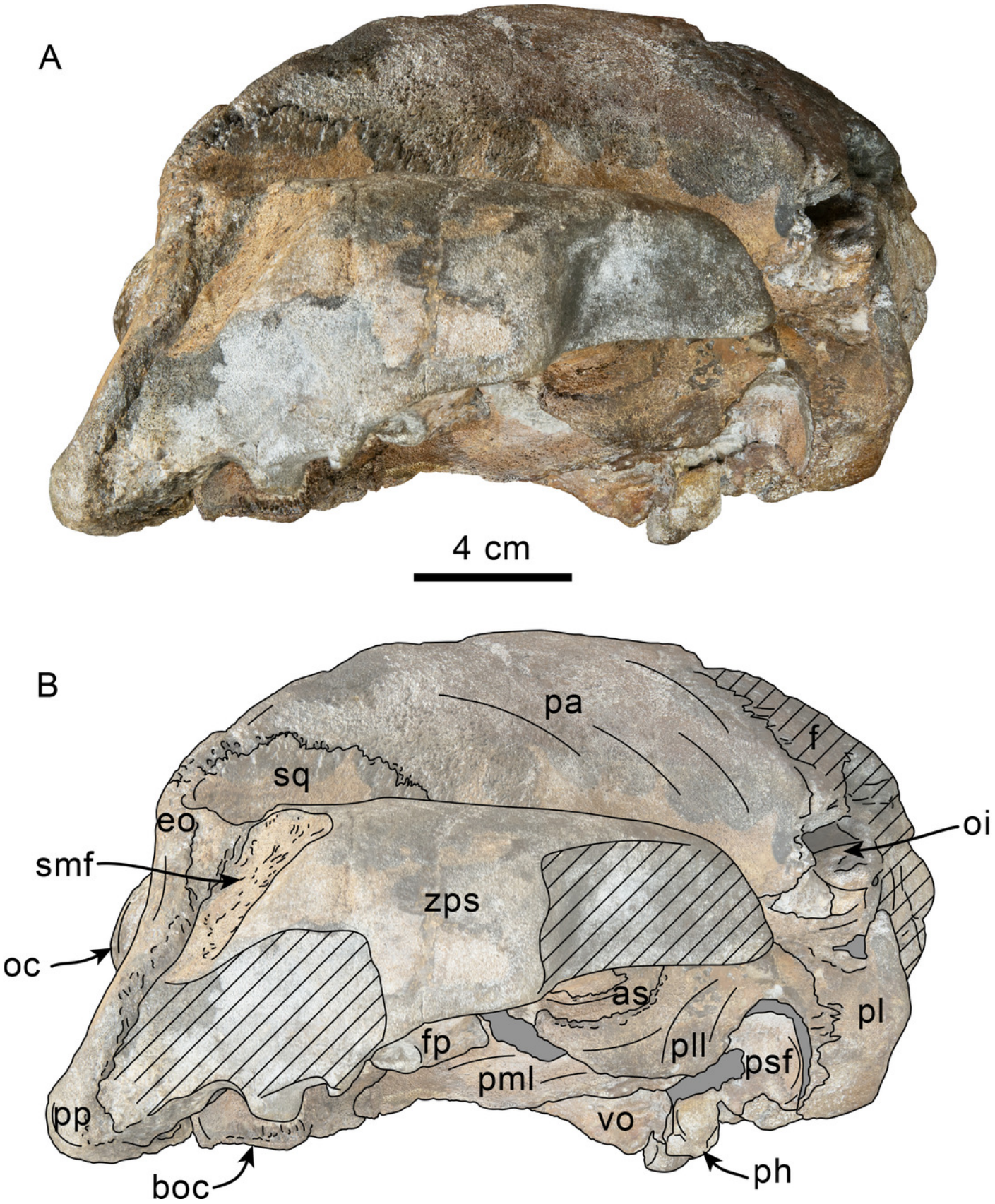

A
4 cm
B
pa
f
sq
eo
oi
smf
zps
oc
as
pl
fp
pll
psf
pml
pp
vo
ph
boc

Figure 4

Ventrolateral view of skull of Simocetidae gen. et sp. A (LACM 124104).

Unlabeled (A) and labeled (B) skull in right ventrolateral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: as, alisphenoid; boc, basioccipital crest; f, frontal; fp, falciform process; g, glenoid; oi, optic infundibulum; pa, parietal; pe, periotic; pgp, postglenoid process; ph, pterygoid hamulus; pl, palatine; pll, pterygoid lateral lamina; pml, pterygoid medial lamina; pp, paroccipital process; psf, pterygoid sinus fossa; smf, sternomastoid fossa; sq, squamosal; tr, tympanosquamosal recess; vo, vomer; zps, zygomatic process of squamosal.

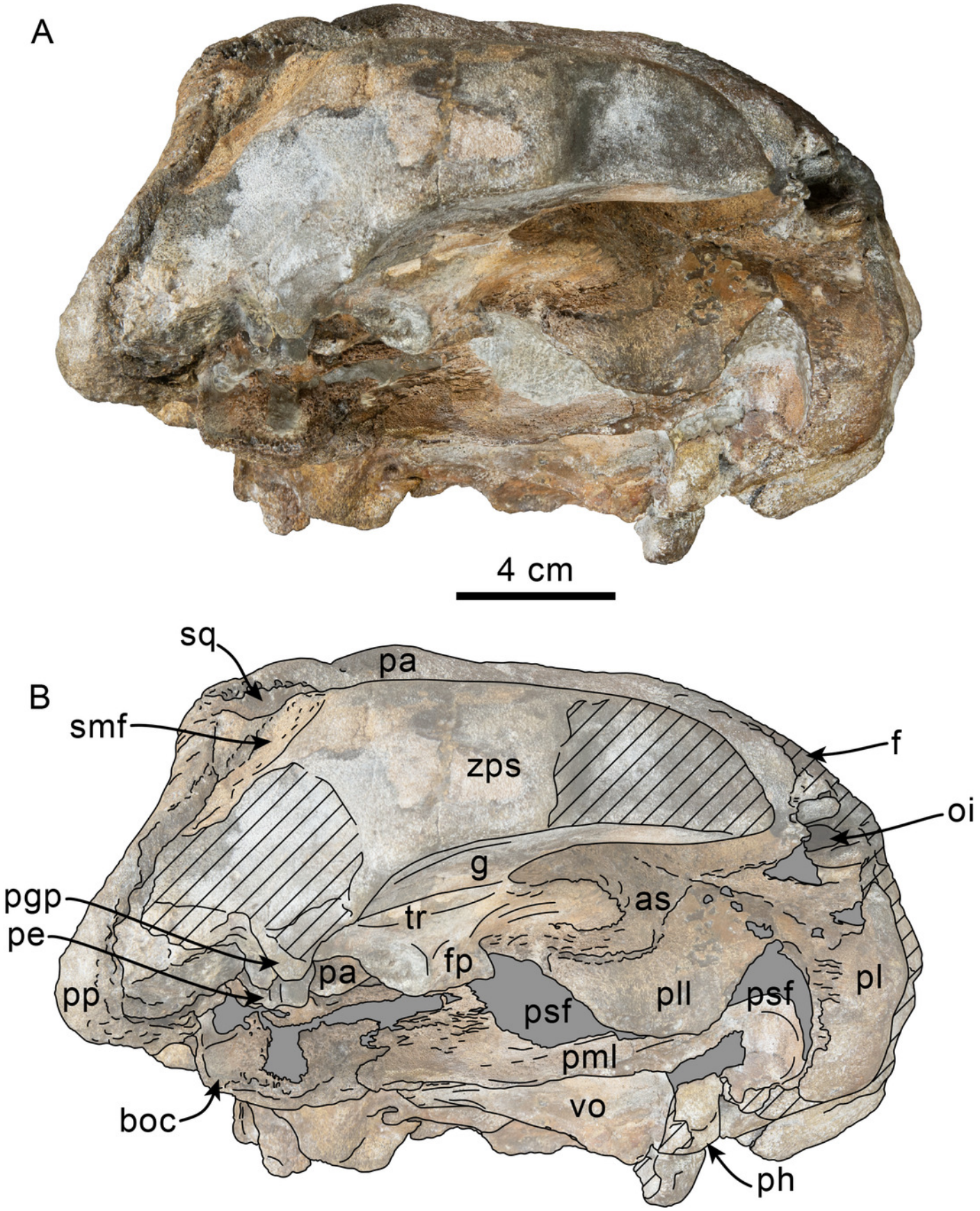

A
4 cm
B
sq
pa
smf
f
zps
oi
g
pgp
as
tr
pe
fp
pa
pp
pll
psf
pl
psf
pml
vo
boc
ph

Figure 5

Tooth and vertebrae of Simocetidae gen. et sp. A (LACM 124104).

Upper postcanine tooth in buccal (A), lingual (B) and occlusal (C) views. Atlas (D, E), axis (F, G) and third cervical (H, I) vertebrae in anterior (D, F, H) and posterior (E, G, I) views. Abbreviations: aa, anterior articular facet; ad, accessory denticles; c, centrum; lc, lingual cingulum; fop, facet for odontoid process; md, main denticle; op, odontoid process; przp, prezygapophysis; tf, transverse foramen; tp, transverse process; va, ventral arch.

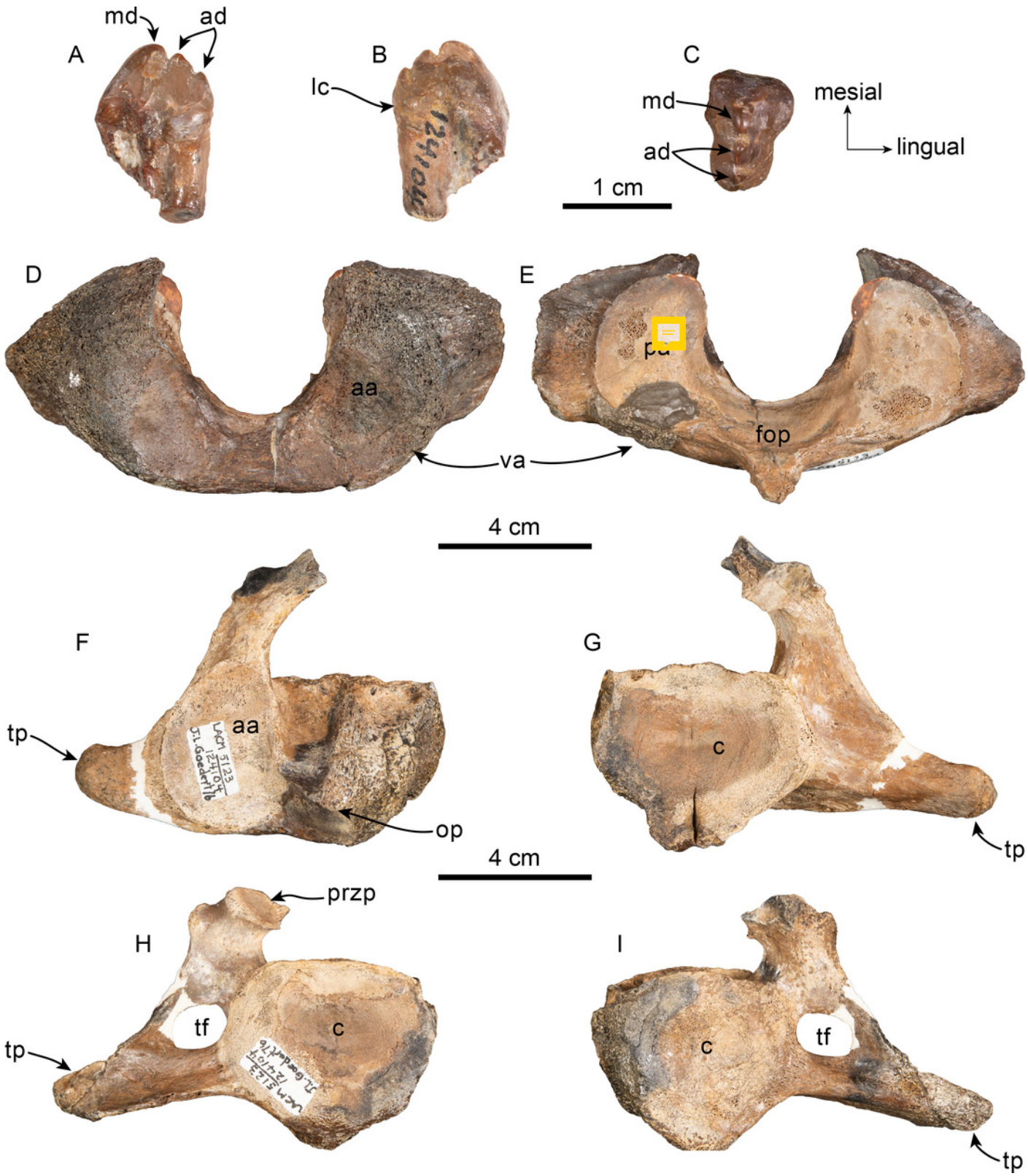

A
md
ad
B
lc
C
md
ad
mesial
lingual
1 cm
D
aa
E
pa
fop
va
4 cm
F
aa
tp
op
G
c
tp
4 cm
H
przp
tf
c
tp
I
c
tf
tp

Figure 6

Dorsal view of skull of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Unlabeled (A) and labeled (B) skull in dorsal view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: anterior dorsal infraorbital foramina; aon, antorbital notch; ascending process of maxilla; appx, ascending process of premaxilla; as, alisphenoid; eo, exoccipital; f, frontal; la, lacrimal; n, nasal; oc, occipital condyle; P2, second upper premolar; pa, parietal; pf, premaxillary foramen; pls, posterolateral sulcus; pms, posteromedial sulcus; pmx, premaxilla; pop, postorbital process; pp, paroccipital process; psf, premaxillary sac fossa; so, supraoccipital; sop, supraorbital process; sq, squamosal; vo, vomer; zps, zygomatic process of squamosal.

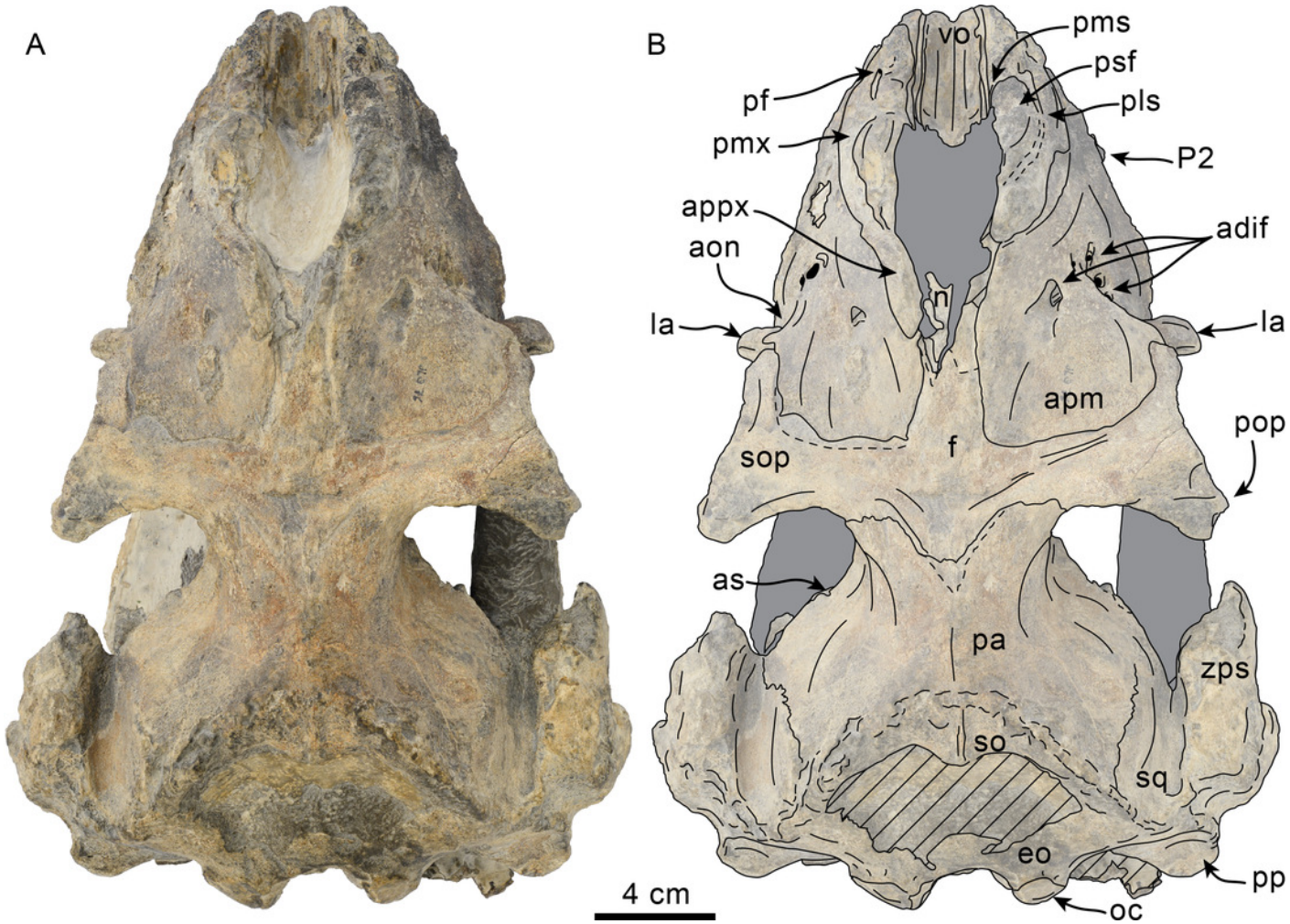

A
B
vo
pms
psf
pf
pls
pmx
P2
appx
adif
aon
n
la
la
apm
pop
sop
f
as
pa
zps
so
sq
eo
pp
oc
4 cm

Figure 7

Posterior and ventral views of skull of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Unlabeled (A) and labeled (B) skull in ~~ventral~~ view; (C) unlabeled and labeled skull in ~~right lateral~~ view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: at, atlas; bo, basioccipital; boc, basioccipital crest; eam, external auditory meatus; ef, ethmoid foramen; la, lacrimal; m1, first lower molar; ma, mandible; mx, maxilla; p3–4, third and fourth lower premolars; pc, palatal crest; pc?, postcanine teeth of unknown placement; pf, palatine foramen; pgp, postglenoid process; ph, pterygoid hamulus; pl, palatine; pmx, premaxilla; pop, postorbital process; pp, paroccipital process; ppt, posterior process of tympanic; psf, pterygoid sinus fossa; pt, pterygoid; sth, stylohyal; trh, thyrohyal; ty, tympanic; vo, vomer; zps, zygomatic process of squamosal.

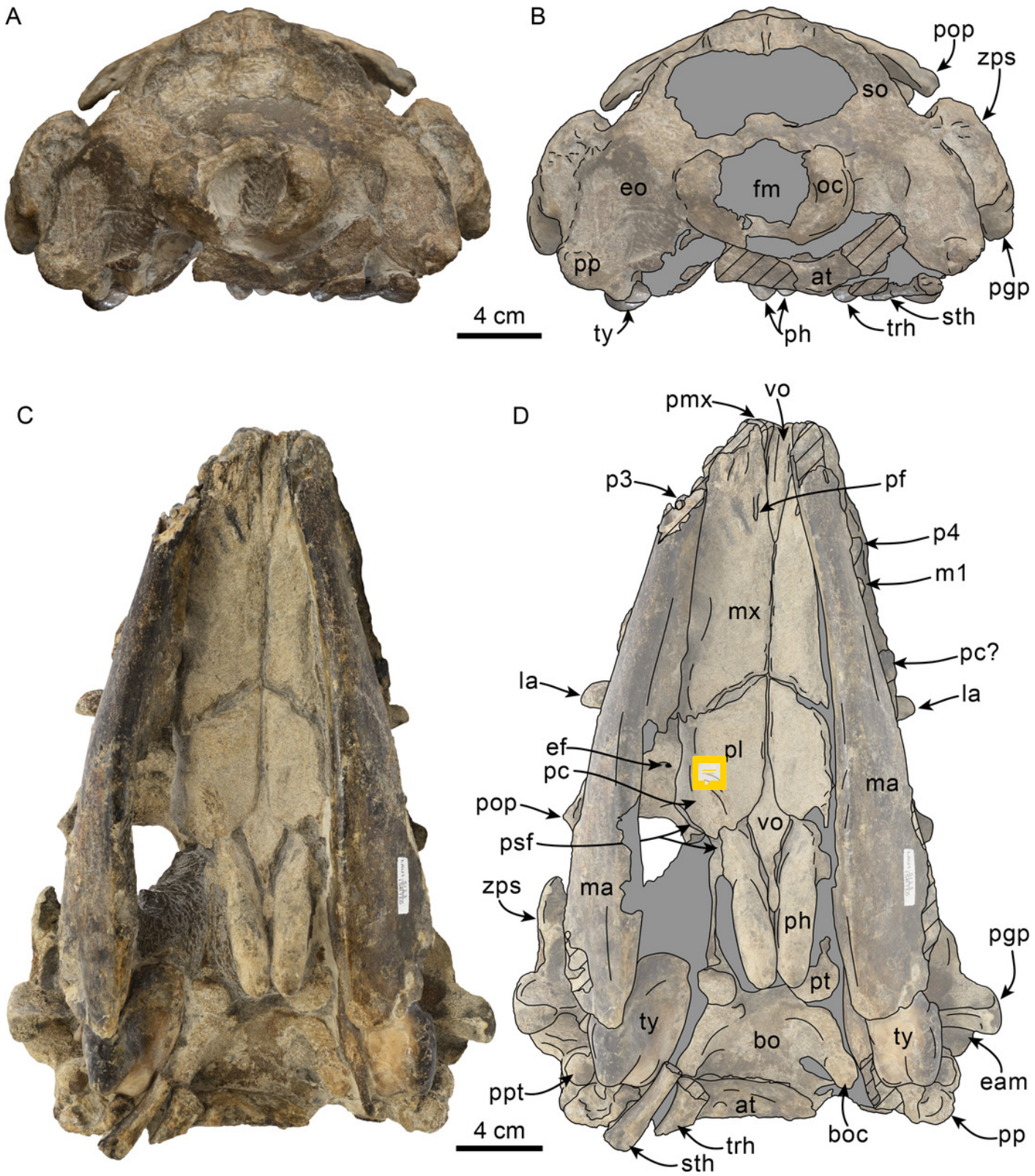

A
B
pop
zps
so
eo
fm
oc
pp
at
pgp
ty
ph
trh
sth
4 cm
C
D
pmx
vo
p3
pf
p4
m1
mx
pc?
la
la
ef
pl
pc
ma
pop
vo
psf
zps
ma
ph
pgp
pt
ty
bo
ty
eam
ppt
at
boc
pp
trh
sth
4 cm

Figure 8

Lateral view of skull of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Unlabeled (A) and labeled (B) skull in right lateral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: a.C, alveolus for upper canine; a.P1, alveoli for upper premolar ~~one~~; adif, anterior dorsal infraorbital foramina; apm, ascending process of maxilla; eam, external auditory meatus; f, frontal; j, jugal; la, lacrimal; m1–3, lower molars ~~one~~, ~~two~~ and ~~three;~~ ma, mandible; mc, mandibular condyle; mip, maxillary infraorbital process; mf, mental foramina; mx, maxilla; n, nasal; nc, nuchal crest; oc, occipital condyle; p3, lower third premolar; P4, upper fourth premolar; pa, parietal; pgp, postglenoid process; pl, palatine; pls, posterolateral sulcus; pop, postorbital process; pp, paroccipital process; psf, pterygoid sinus fossa; ptp, posttympanic process; spf, sphenopalatine foramen; sq, squamosal; sth, stylohyoid; ty~~m~~ tympanic; viof, ventral infraorbital foramen; zc, zygomatic cleft; zps, zygomatic process of squamosal.

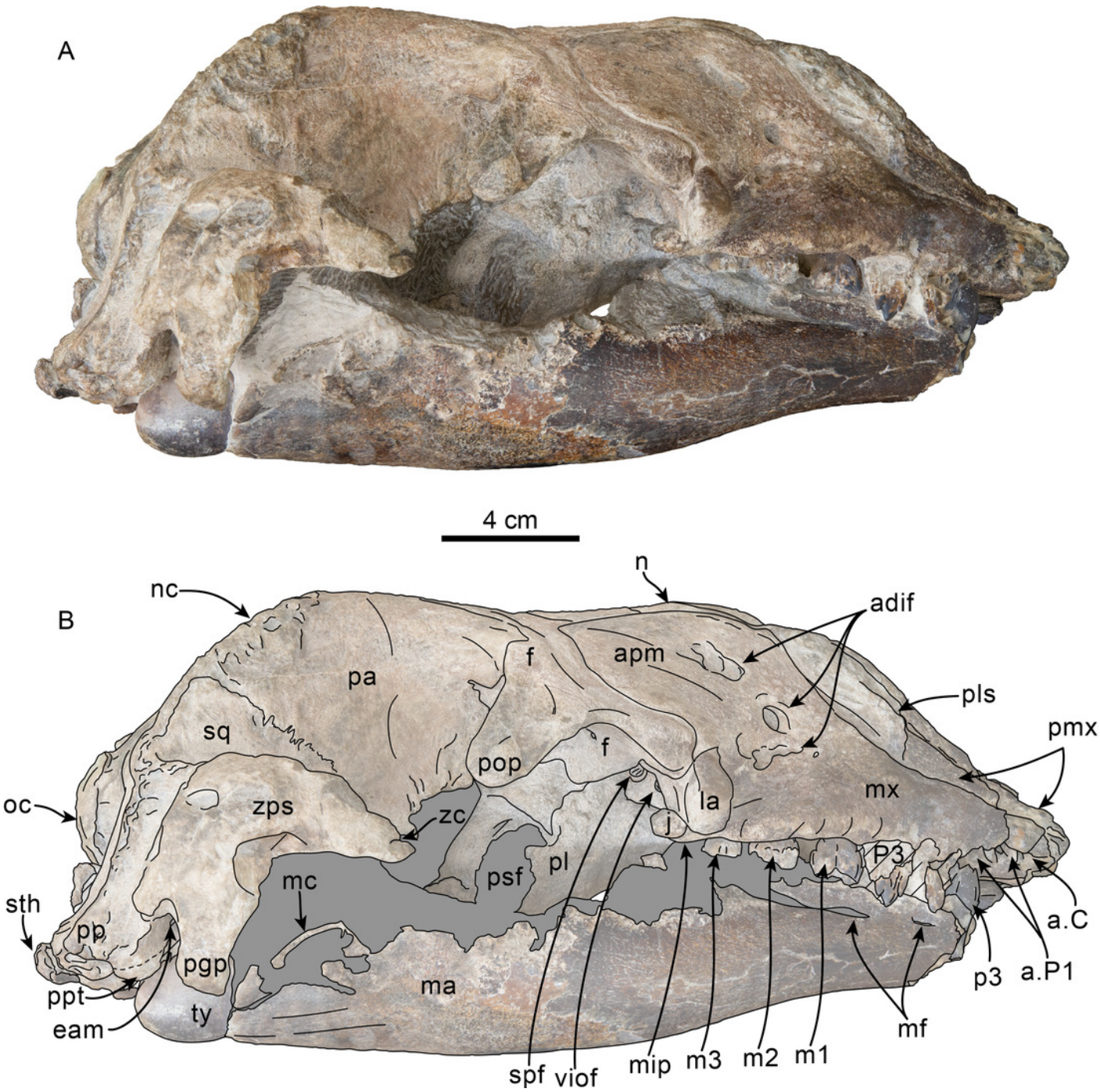

A
4 cm
B
nc
n
adif
apm
f
pa
pls
sq
pmx
f
pop
oc
zps
zc
la
mx
j
P3
psf
pl
mc
sth
pp
a.C
pgp
p3
a.P1
ppt
ma
ty
eam
mf
spf
viof
mip
m3
m2
m1

Figure 9

Orbital region of skull of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Unlabeled (A) and labeled (B) orbital region in right lateral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: adif, anterior dorsal infraorbital foramina; ef, ethmoid foramen; f, frontal; ffdv, foramina for frontal diploic vein; j, jugal; la, lacrimal; m1-3, first through third lower molars; ma, mandible; mip, maxillary infraorbital plate; mx, maxilla; of, optic foramen; P4, fourth upper premolar; pa, parietal; pl, palatine; pls, posterolateral sulcus; pmx, premaxilla; pop, postorbital process; psf, pterygoid sinus fossa; spf, sphenopalatine foramen; viof, ventral infraorbital foramen; zps, zygomatic process of squamosal.

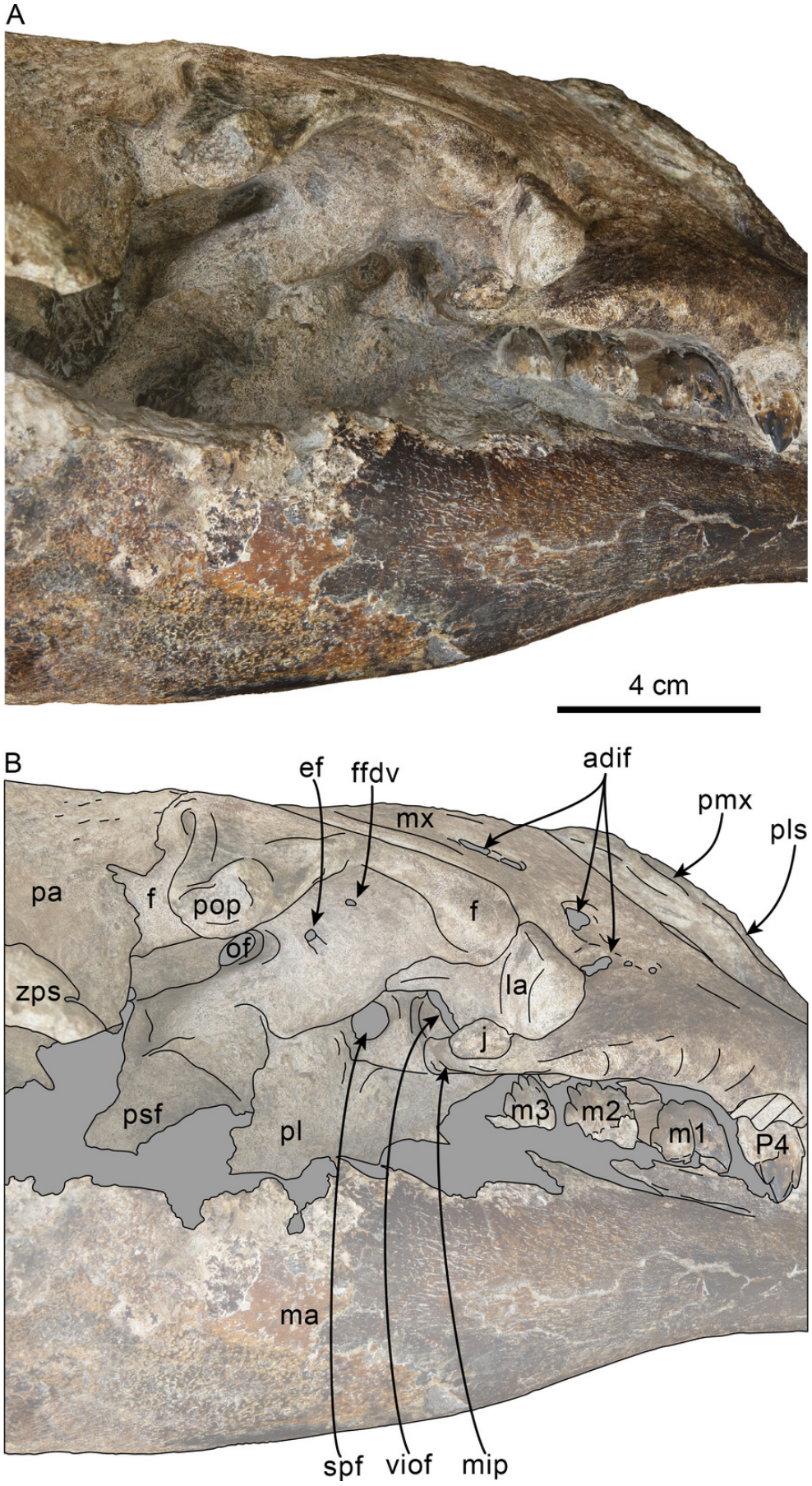

A
4 cm
B
ef
ffdv
adif
pmx
pls
mx
pa
f
pop
f
of
zps
la
j
psf
pl
m3
m2
m1
P4
ma
spf
viof
mip

Figure 10

Tympanic bullae of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Articulated left tympanic bulla in ventral (A) and lateral (B) views; articulated right tympanic bulla in anterolateral (C) view. The bullae have been highlighted to differentiate them from the surrounding bones which obscure some parts. Abbreviations: cp, conical process; fp, falciform process; ipp, inner posterior prominence; lf, lateral furrow; ma, mandible; mr, mallear ridge; opp, outer posterior prominence; pe, periotic; pgp, postglenoid process; pp, posterior process; sp, sigmoid process; sth, stylohyal.

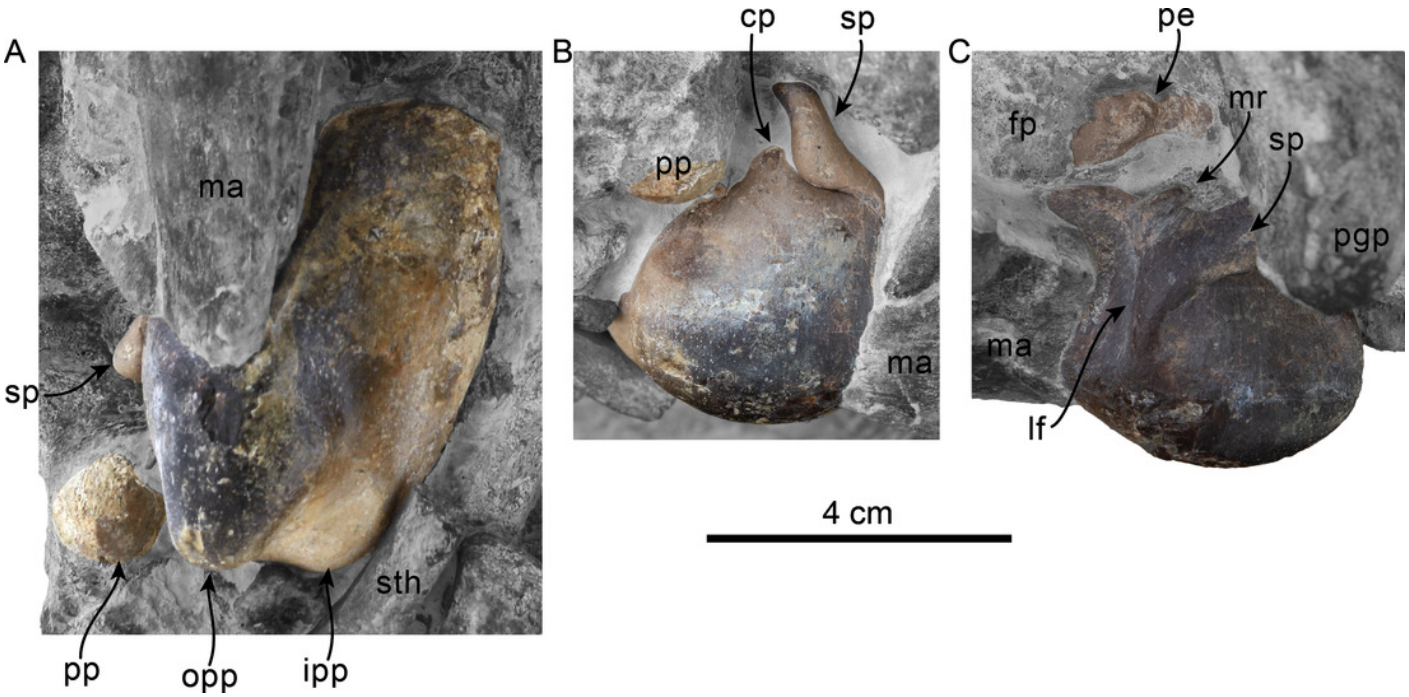


Figure 11

Upper and lower right dentition of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Upper and lower right postcanine teeth in buccal (A-B) views; lower right postcanine teeth (p3-m3) in lingual (C) view; upper right P4-M2 in buccal (D-F) and lingual (G-I) views. Abbreviations: a.P1, alveoli for first upper premolar; M1-2, first and second upper molars; m1-3, first through third lower molars; P2-4, second through fourth upper premolars; p3-4, third and fourth lower premolars.

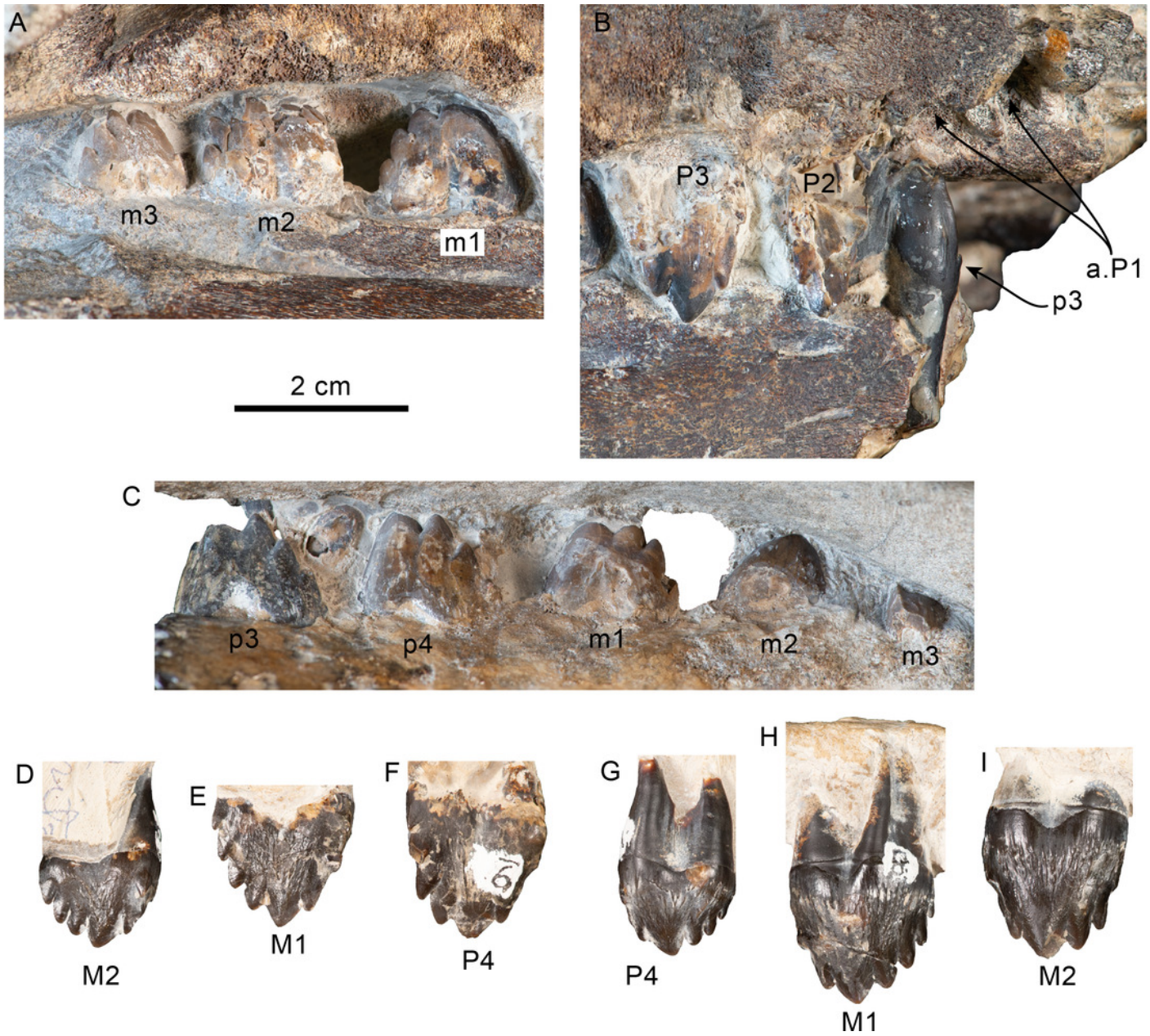

A
m3
m2
m1
2 cm
B
P3
P2
a.P1
p3
C
p3
p4
m1
m2
m3
D
M2
E
M1
F
P4
G
P4
H
M1
I
M2

Figure 12

Upper and lower left dentition of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Upper left P4-M2 in buccal (A-C) and lingual (D-F) views; lower left postcanine teeth (p4-m2) in buccal (G) view; canine or incisor in buccal (H) and mesial (I) views; postcanine tooth in lingual (J) view. Abbreviations: M1-2, first and second upper molars; m1-2, first and second lower molars; P4/p4, upper and lower fourth premolars.

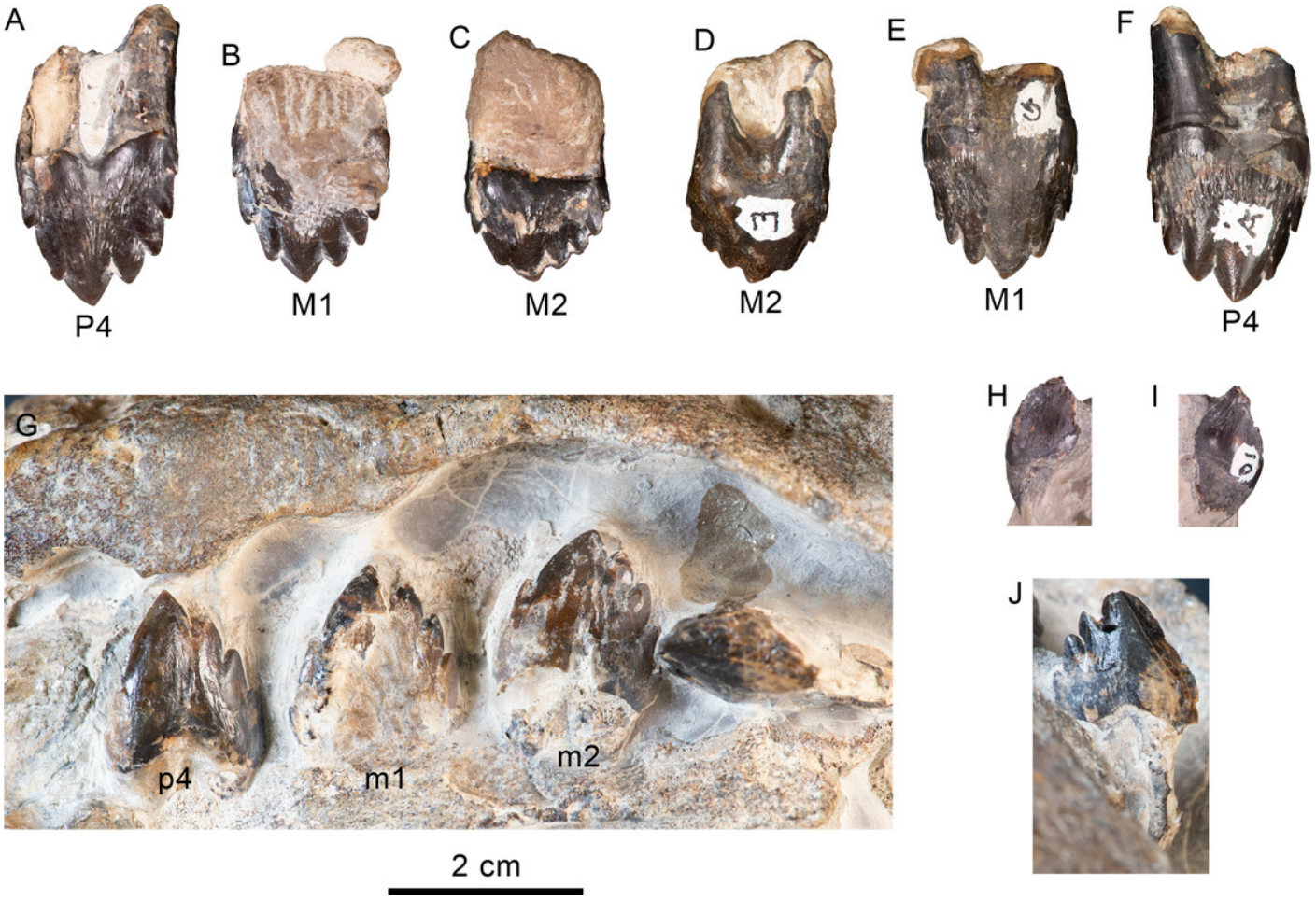


Figure 13

Hyoid elements of *Olympicetus thalassodon* sp. nov. (LACM 158720) and other odontocetes.

(A) Unlabeled and (B) labeled closeup of the right side of the basicranium of *Olympicetus thalassodon* in ventral view. Dorsal views of basihyal and thyrohyals of: (C) *Olympicetus thalassodon* (LACM 158720); (D) *Albireo whistleri* (UCMP 314589); (E) *Phocoenoides dalli* (LACM 43473); (F) *Kogia sima* (LACM 47142); and, (G), *Sagmatias obliquidens* (LACM 27077). Abbreviations: at, atlas; boc, basioccipital crest; bsh, basihyal; eam, external auditory meatus; ma, mandible; mc, mandibular condyle; pgp, postglenoid process; pp, paroccipital process; ppt, posterior process of the tympanic; sth, stylohyal; trh, thyrohyal; ty, tympanic.

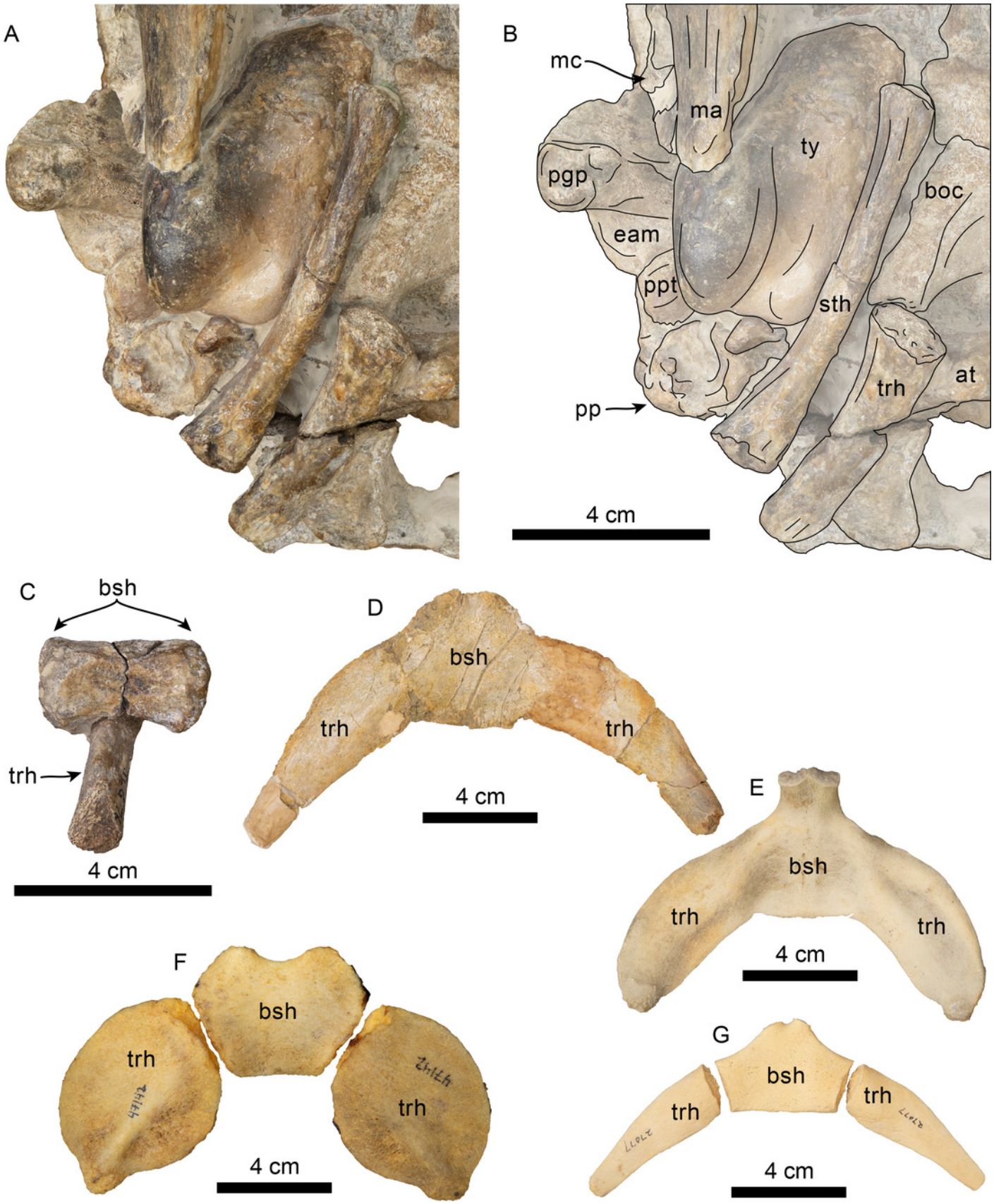

A
B
mc
ma
ty
pgp
boc
eam
ppt
sth
at
trh
pp
4 cm
C
bsh
trh
4 cm
D
bsh
trh
trh
4 cm
E
bsh
trh
trh
4 cm
F
bsh
trh
trh
4 cm
G
bsh
trh
trh
4 cm

Figure 14

Cervical vertebrae of *Olympicetus thalassodon* sp. nov. (LACM 158720).

(A) atlas in posterior view; (B) axis in anterior view; (C) axis and third through seventh cervicals in right lateral view; (D) axis and third through seventh cervicals in dorsal view. Abbreviations: aa, anterior articular surface; ax, axis; c3-7, third through seventh cervical vertebrae; da, dorsal arch; dp, dorsal process; fop, facet for odontoid process; op, odontoid process; pa, posterior articular surface; tp, transverse process; vp, ventral process.

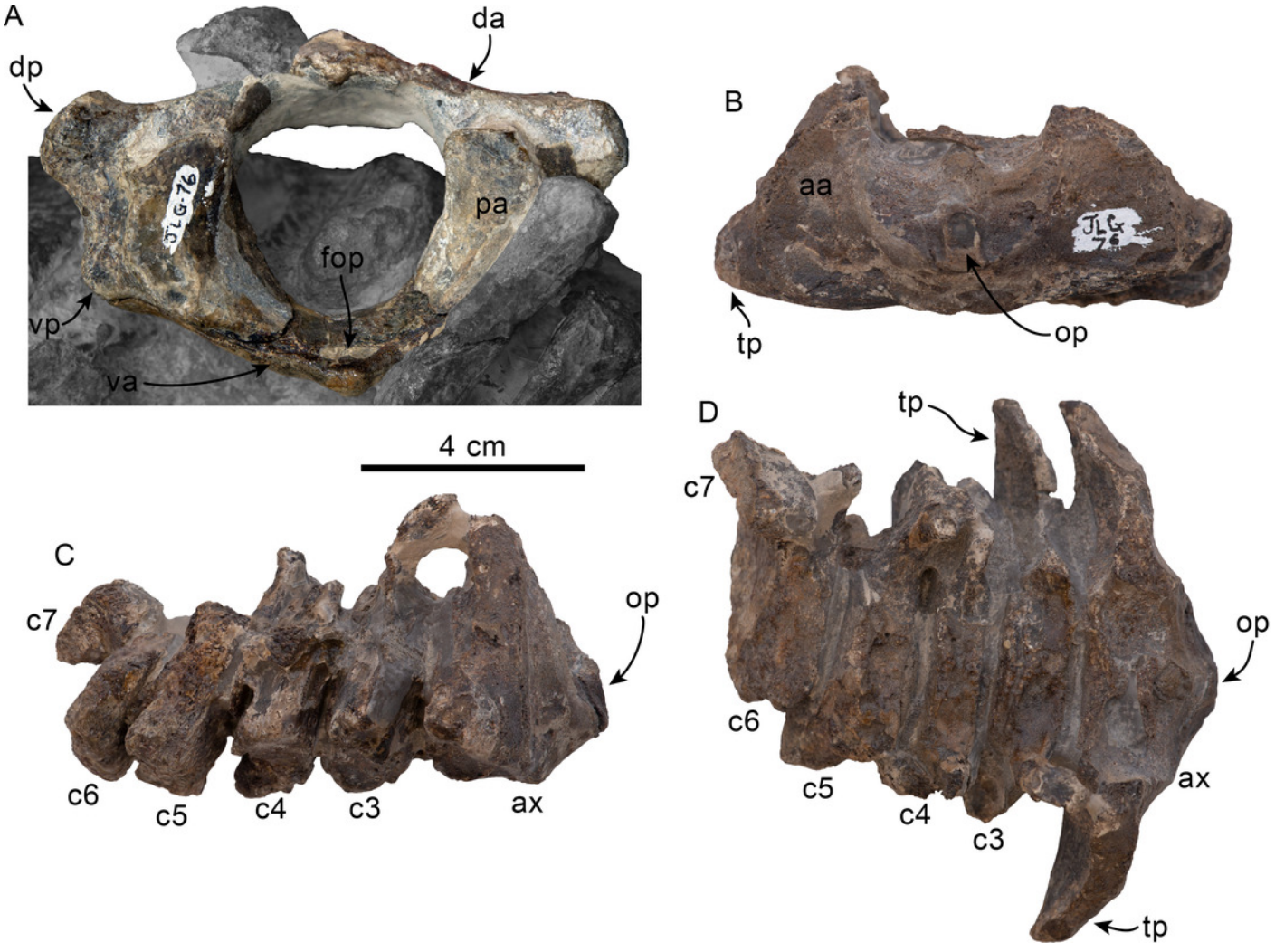


Figure 15

Dorsal view of skull of *Olympicetus* sp. 1 (LACM 124105).

Unlabeled (A) and labeled (B) skull in dorsal view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: adif, anterior dorsal infraorbital foramina; f, frontal; la, lacrimal; mx, maxilla; n, nasals; oc, occipital condyle; pa, parietal; pmx, premaxilla; pop, postorbital process; sop, supraorbital process of frontal; sq, squamosal; tc, temporal crest; vo, vomer; zps, zygomatic process of squamosal.

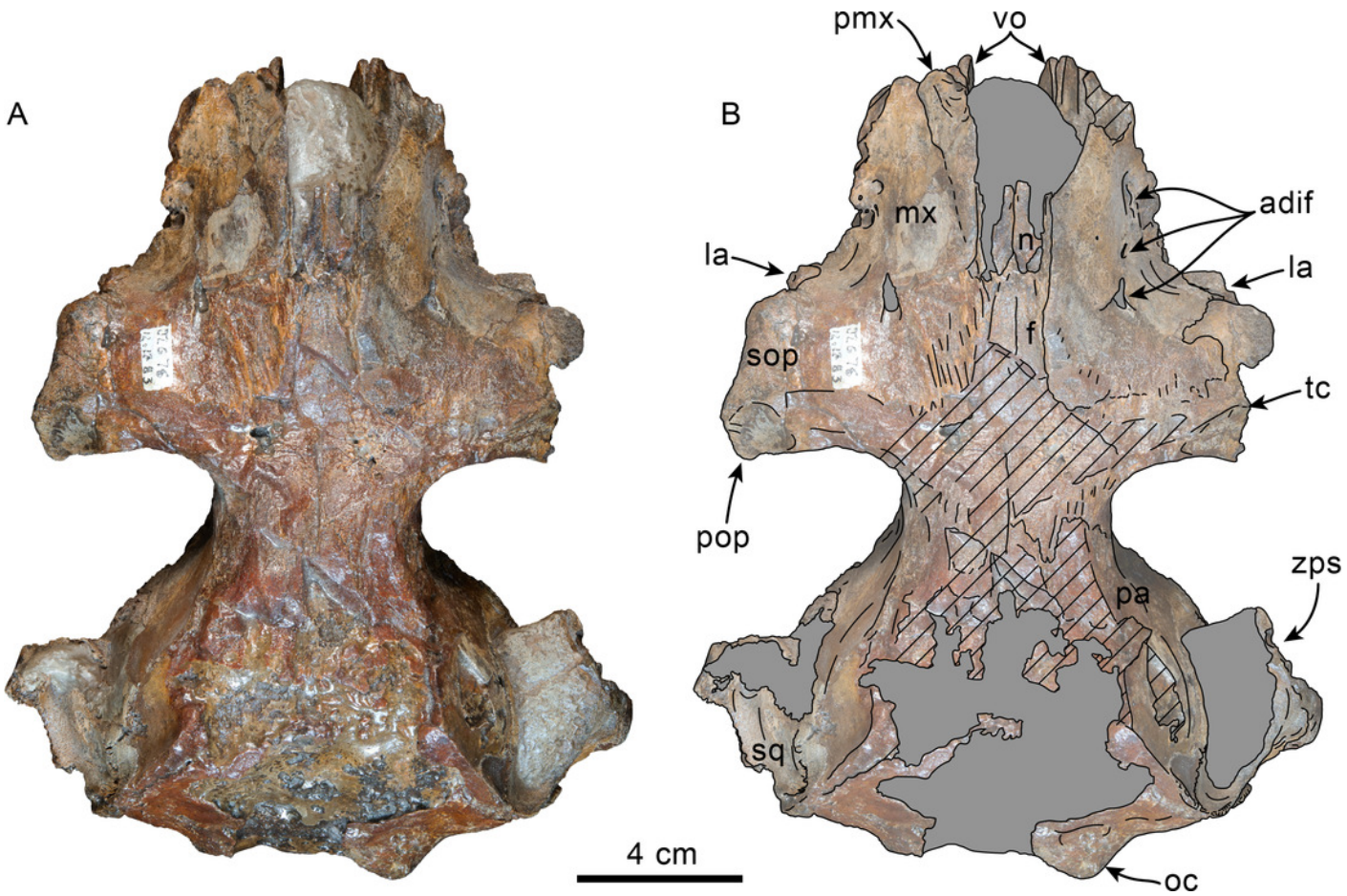


Figure 16

Ventral view of skull of *Olympicetus* sp. 1 (LACM 124105).

Unlabeled (A) and labeled (B) skull in ventral view. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: a.ps, alveoli for postcanine teeth; as, alisphenoid; bo, basioccipital; boc, basioccipital crest; bs, basisphenoid; ef, ethmoid foramen; ffdv, foramina for frontal diploic veins; insphs, intersphenoidal synchondrosis; j, jugal; la, lacrimal; mx, maxilla; pa, parietal; pf, periotic fossa; pl, palatine; pmx, premaxilla, pop, postorbital process; psf, pterygoid sinus fossa; pt, pterygoid; vo, vomer; zps, zygomatic process of squamosal.

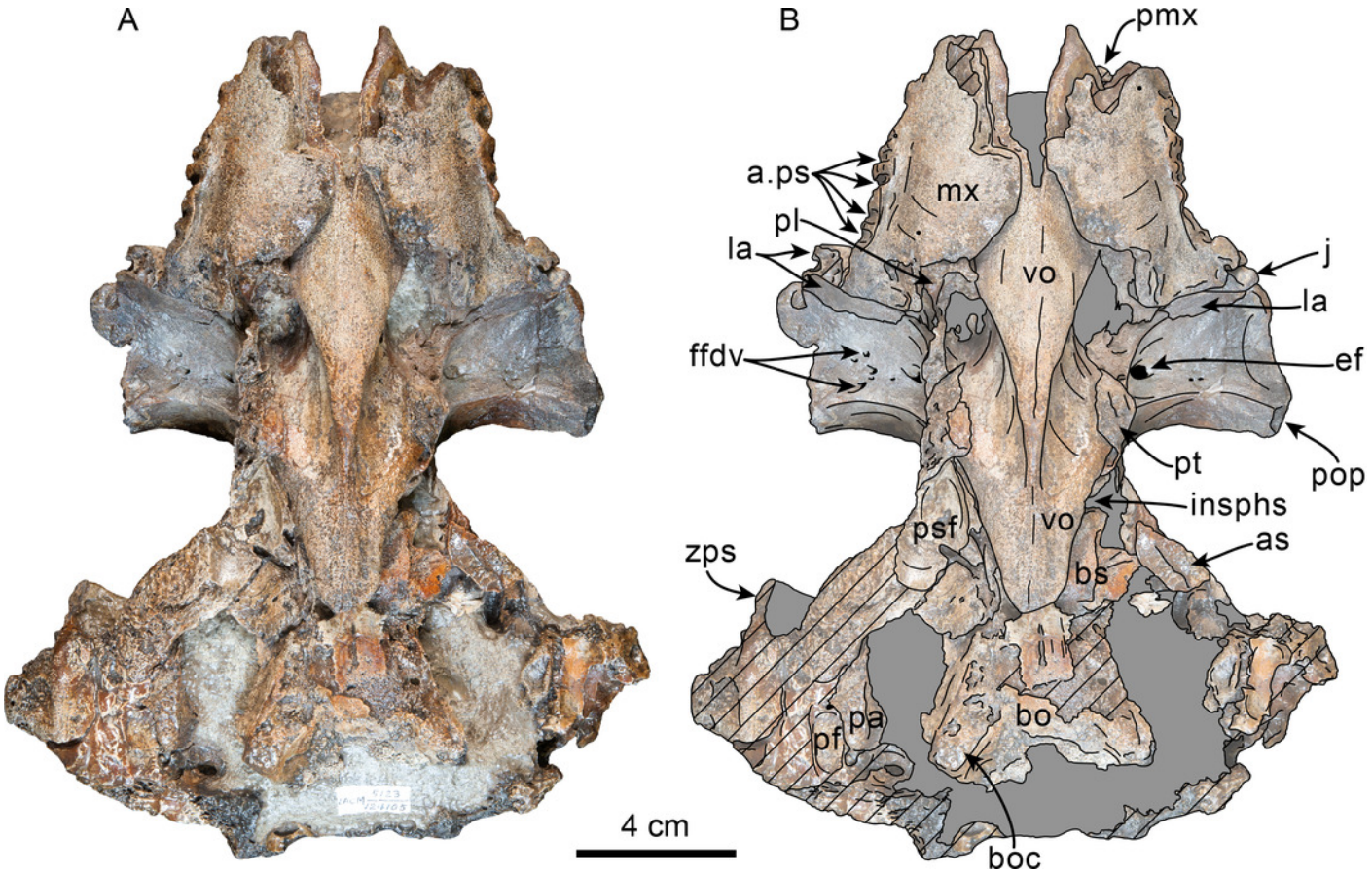


Figure 17

Ventrolateral view of skull of *Olympicetus* sp. 1 (LACM 124105).

Unlabeled (A) and labeled (B) skull in right ventrolateral view focusing on the features of the orbital region. Diagonal lines denote broken surfaces, gray shaded areas are obscured by sediment. Abbreviations: a.ps, alveoli for postcanine teeth; adif, anterior dorsal infraorbital foramina; as, alisphenoid; boc, basioccipital crest; ef, ethmoid foramen; ffdv, foramina for frontal diploic veins; f, frontal; j, jugal; la, lacrimal; mx, maxilla; oa, path for ophthalmic artery; oi, optic infundibulum; pa, parietal; pl, palatine; psf, pterygoid sinus fossa; pt, pterygoid; spf, sphenopalatine foramen; viof, ventral infraorbital foramen; V2, path for maxillary nerve; vo, vomer; zps, zygomatic process of squamosal.

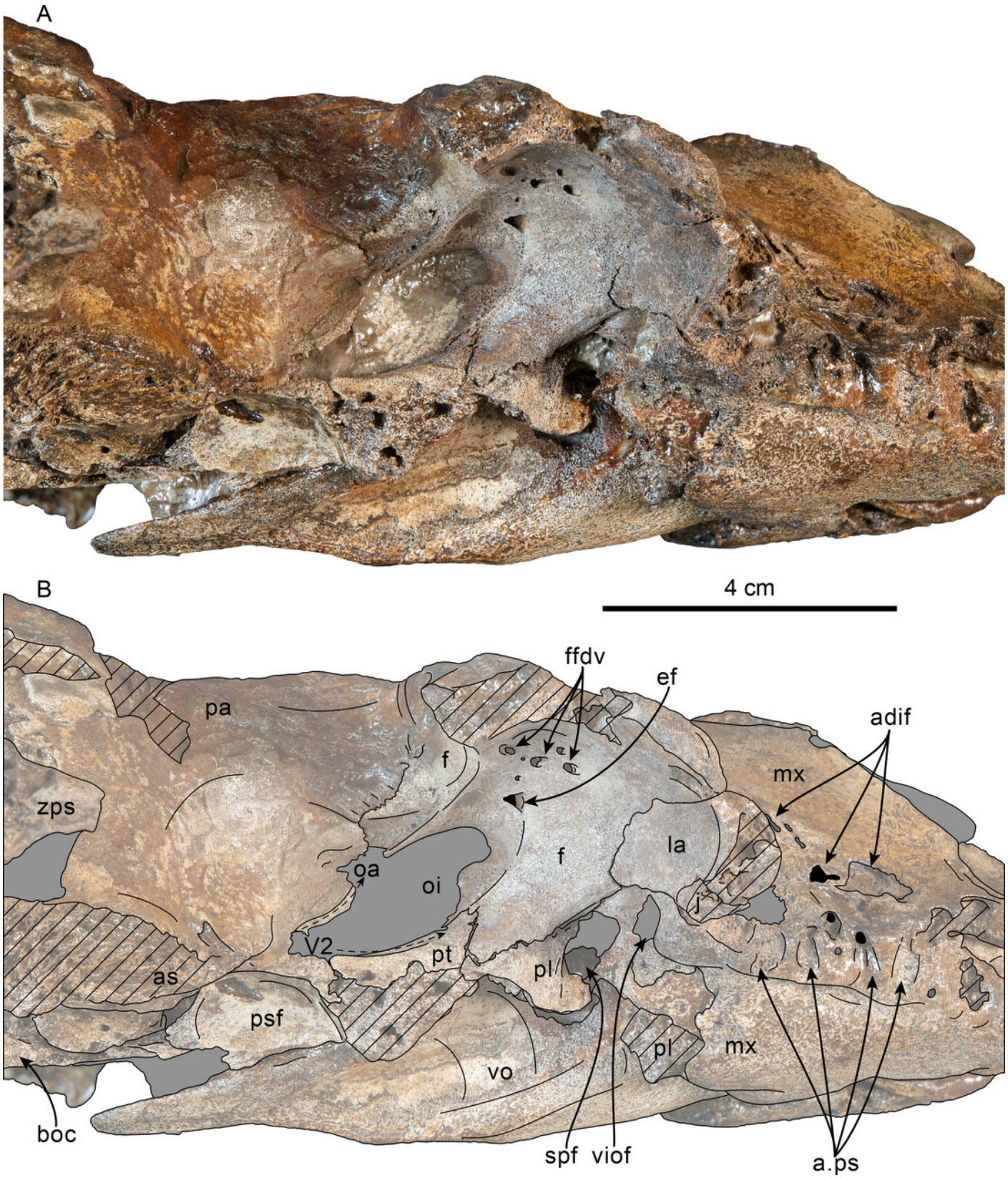
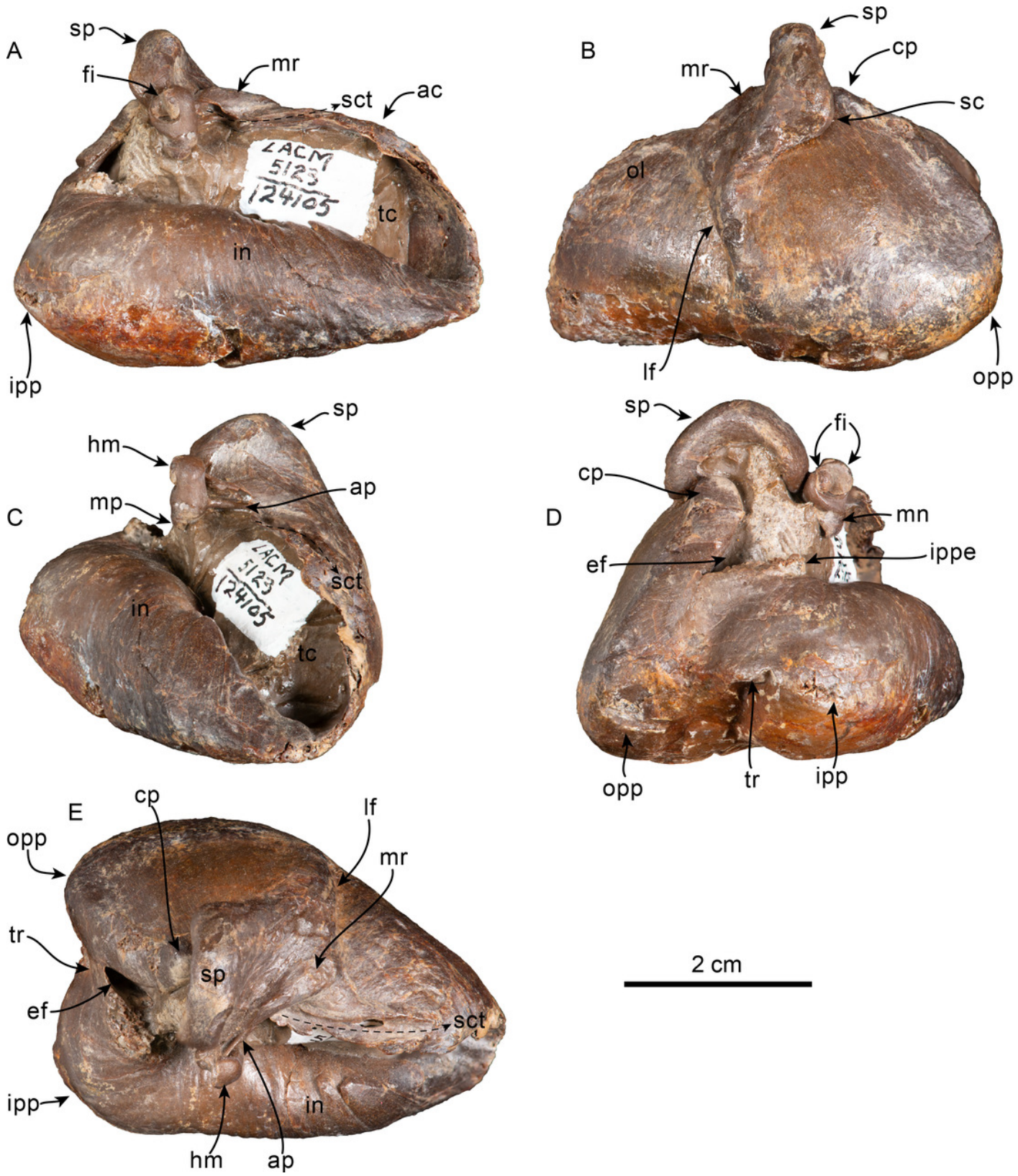

A
B
4 cm
ffdv
ef
adif
pa
f
mx
zps
la
f
oa
oi
j
V2
pt
pl
as
psf
pl
mx
vo
boc
spf
viof
a.ps

Figure 18

Malleus and tympanic bulla of *Olympicetus* sp. 1 (LACM 124105).

Left malleus and tympanic bulla~~e~~ in medial (A), lateral (B), anterior (C), posterior (D), and dorsal (E) views. Abbreviations: ac, anterodorsal crest; ap, anterior process; cp, conical process; ef, elliptical foramen; fi, facet for incus; hm, head of malleus; in, involucrum; ipp, inner posterior prominence; ippe, inner posterior pedicle; lf, lateral furrow; mn, manubrium; mp, muscular process; mr, mallear ridge; ol, outer lip; opp, outer posterior prominence; sc, sigmoid cleft; sct, sulcus for chorda tympani; sp, sigmoid process; tc, tympanic cavity; tr, transverse ridge.


A
sp
fi
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sct
ac
LACM
5123
124105
tc
in
ipp
B
sp
cp
mr
sc
ol
lf
opp
C
sp
hm
ap
mp
sct
in
tc
D
sp
fi
cp
mn
ef
ippe
opp
tr
ipp
E
cp
lf
opp
mr
tr
sp
ef
sct
ipp
in
hm
ap
2 cm

Figure 19

Periotic and teeth of *Olympicetus* sp. 1 (LACM 124105).

Unlabeled and labeled right periotic in dorsal (A-B), medial (C-D), ventral (E-F), and lateral (G-H) views. Postcanine teeth in buccal (I-J) and lingual (K-L) views. Abbreviations: abf, anterior bullar facet; acm, area cribosa media; aepb, anteroexternal+parabullary sulcus; ap, anterior process; ctp, caudal tympanic process; ed, endolymphatic duct; eth, epitympanic hiatus; fc, facial canal; fgp, foramen for greater petrosal nerve; fo, foramen ovale; fr, foramen rotundum; iam, internal acoustic meatus; if, incudal fossa; pbf, posterior bullar facet; pc, pars cochlearis; pd, perilymphatic duct; lt, lateral tuberosity; mf, mallear fossa; pp, posterior process; sct, spiral cribiform tract; sm, stapedial muscle fossa; smf, supramastoid fossa; sva, superior vestibular area; tt, tegmen tympani.

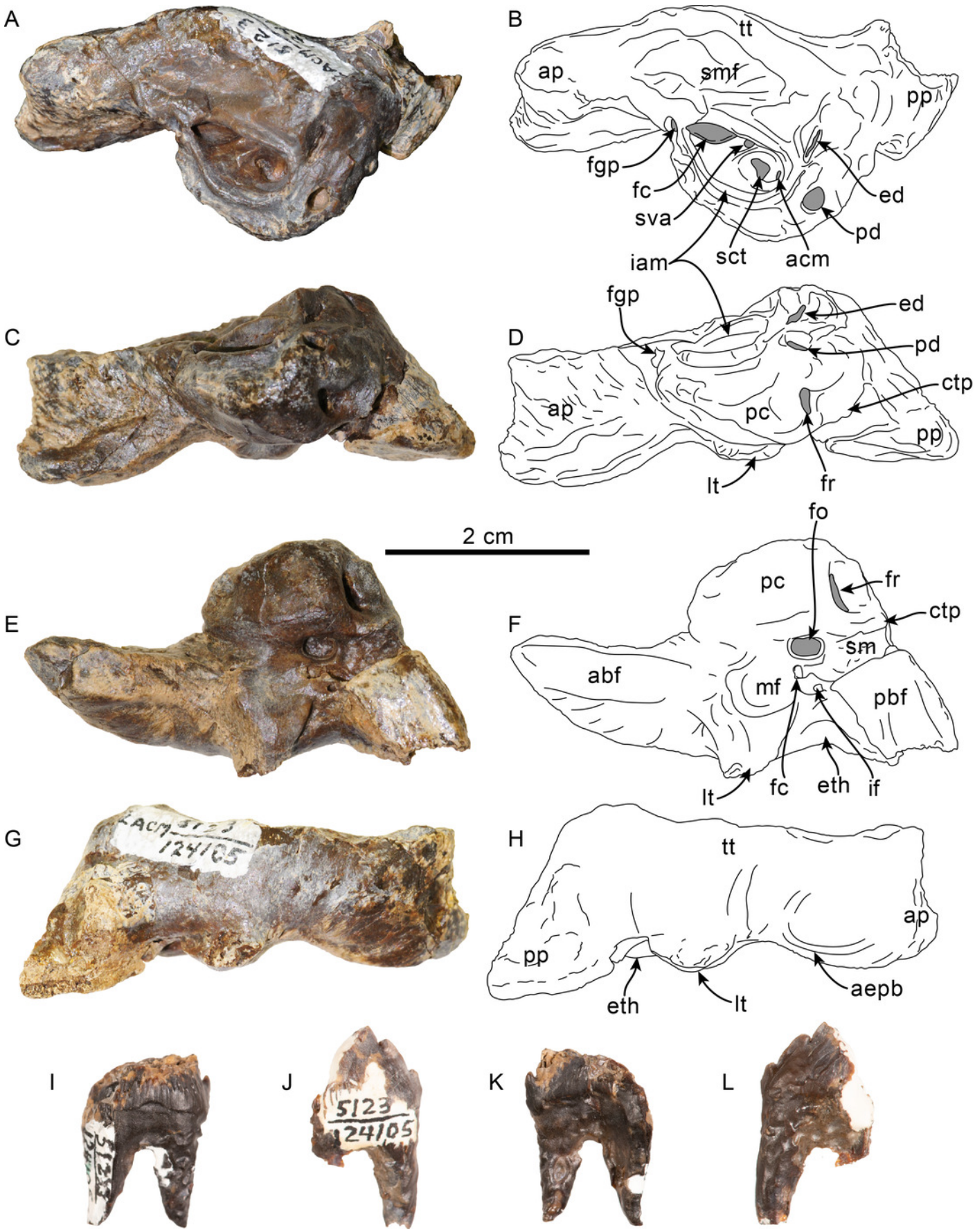
A
B
tt
ap
smf
pp
fgp
fc
sva
iam
sct
acm
ed
pd
C
D
fgp
ed
pd
ctp
ap
pc
pp
lt
fr
2 cm
E
F
fo
pc
fr
ctp
sm
abf
mf
pbf
lt
fc
eth
if
G
H
tt
ap
pp
eth
lt
aepb
I
J
5123
124105
K
L

Figure 20

Time calibrated phylogeny of Cetacea.

Phylogenetic tree showing relationship between Simocetidae with other odontocetes; mysticetes and crown odontocete clades are pruned. Strict consensus tree based on 32 most parsimonious trees of length = 2567, with retention index (RI) = 0.519, and consistency index (CI) = 0.231. Arcs denote **stem-based taxa, while closed circles denote node-based clades; the numbers at the nodes indicate decay indices/bootstrap values. Abbreviations: Aq., Aquitanian; Bar., Bartonian; Burd., Burdigalian; Chatt., Chattian; Holo., Holocene; La., Langhian; M., Messinian; P, Piacenzian; P., Pliocene; Ple., Pleistocene; Priab., Priabonian; Rupel., Rupelian; S., Serravalian; Tort., Tortonian; Z, Zanclean. Time scale based on Cohen et al. (2013); skull outline for *Simocetus rayi* modified from Fordyce (2002).**

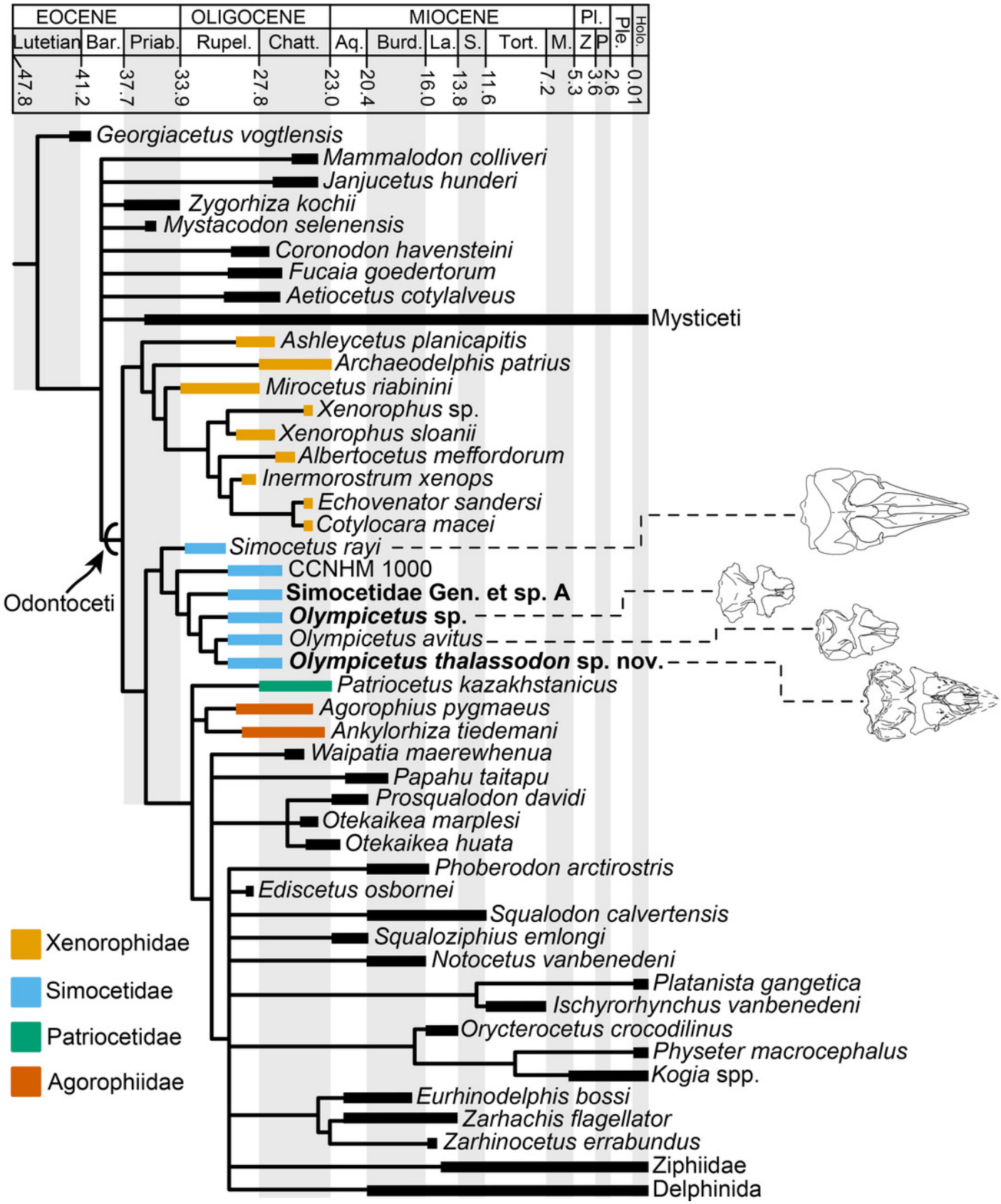
EOCENE
OLIGOCENE
MIOCENE
Pl.
Ple.
Holo.
Lutetian
Bar.
Priab.
Rupel.
Chatt.
Aq.
Burd.
La.
S.
Tort.
M.
Z
P
47.8
41.2
37.7
33.9
27.8
23.0
20.4
16.0
13.8
11.6
7.2
5.3
3.6
2.6
0.01
Georgiacetus vogtlensis
Mammalodon colliveri
Janjucetus hunderi
Zygorhiza kochii
Mystacodon selenensis
Coronodon havensteini
Fucaia goedertorum
Aetiocetus cotylalveus
Mysticeti
Ashleycetus planicapitis
Archaeodelphis patrius
Mirocetus riabinini
Xenorophus sp.
Xenorophus sloanii
Albertocetus meffordorum
Inermorostrum xenops
Echovenator sandersi
Cotylocara macei
Simocetus rayi
CCNHM 1000
Simocetidae Gen. et sp. A
Olympicetus sp.
Olympicetus avitus
Olympicetus thalassodon sp. nov.
Odontoceti
Patriocetus kazakhstanicus
Agorophius pygmaeus
Ankylorhiza tiedemani
Waipatia maerewhenua
Papahu taitapu
Prosqualodon davidi
Otekaikea marplesi
Otekaikea huata
Phoberodon arctirostris
Ediscetus osbornei
Squalodon calvertensis
Squaloziphius emlongi
Notocetus vanbenedeni
Platanista gangetica
Ischyrorhynchus vanbenedeni
Orycterocetus crocodilinus
Physeter macrocephalus
Kogia spp.
Eurhinodelphis bossi
Zarhachis flagellator
Zarhinocetus errabundus
Ziphiidae
Delphinida
Xenorophidae
Simocetidae
Patriocetidae
Agorophiidae

Table 1(on next page)

Measurements of simocetid skulls and mandibles.

Measurements (in mm) of simocetid skulls and mandible, Simocetidae gen. et sp. A (LACM 124104), *Olympicetus thalassodon* gen. et sp. nov. (LACM 158720) and *Olympicetus* sp. 1 (LACM 124105). Modified after Perrin (1975).

TABLE 1. Measurements (in mm) of simocetid skulls and mandible, Simocetidae gen. et sp. A (LACM 124104), *Olympicetus thalassodon* gen. et sp. nov. (LACM 158720) and *Olympicetus* sp. 1 (LACM 124105). Modified after Perrin (1975).

	LACM 124104	LACM 158720	LACM 124105
Width of rostrum at base	-	135	93+
Width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches	-	105	-
Greatest preorbital width (width across preorbital processes)	-	153	136
Greatest postorbital width	-	187	150e
Mid-orbital width	-	151	140e
Maximum width of external nares	-	33	-
Greatest width across zygomatic processes of squamosal	322e	220	186e
Greatest width of premaxillaries	-	83	-
Greatest parietal width within temporal fossae	154	135	100
Vertical external height of braincase from midline of basisphenoid to summit of supraoccipital, but not including external occipital crest	135	112	-
Greatest length of left posttemporal fossa, measured to external margin of raised suture	-	99	-
Greatest width of left posttemporal fossa at right angles to greatest length	-	51	-
Major diameter of left temporal fossa proper	-	111	-

1

TABLE 1. Continued.

Minor diameter of left temporal fossa proper	59	45	-
Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest	-	143e	-
Length of orbit – from apex of preorbital process of frontal to apex of postorbital process	-	55	40+
Length of antorbital process of lacrimal	-	18	12
Greatest length of left pterygoid	132	79	-
Maximum width across occipital condyles	92	78	-
Height of foramen magnum	33	35	-
Width of foramen magnum	39	32	-
Cranial length – antorbital notch to condyles	-	211	165+
Greatest length of left mandibular ramus (as preserved)	-	251+	-
Greatest length of right mandibular ramus (as preserved)	-	244+	-
Maximum height at mandibular condyle	-	54	-

Abbreviations: **e**, estimate; + = measurement on incomplete element.

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Table 2 (on next page)

Measurements of simocetid cervical vertebrae.

Measurements (in mm) of cervical vertebrae of Simocetidae gen. et sp. A (LACM 124104) and *Olympicetus thalassodon* sp. nov. (LACM 158720).

TABLE 2. Measurements (in mm) of cervical vertebrae of Simocetidae gen. et sp. A (LACM 124104) and *Olympicetus thalassodon* sp. nov. (LACM 158720).

	LACM 124105	LACM 158720
Atlas		
Maximum height	-	70
Maximum length	32	27
Width across anterior articular facets	80+	-
Width across posterior articular facets	94	74
Maximum width (across transverse processes)	-	108
Mid-dorsal length	-	24
Mid-ventral length (including odontoid process)	37	22
Neural canal height	-	44
Neural canal width	45	38
Axis		
Maximum height of centrum	46	33
Maximum width of centrum	47	-
Maximum length of centrum	44	30
Width across anterior articular facets	92e	77
Maximum width (across transverse processes)	144e	97
Width of neural canal	46	33
Cervical 3		
Height of centrum	49	34

Width of centrum	53	34
Length of centrum	20	12
Maximum width (across transverse processes)	164e	96e
Width of neural canal	38e	-
Cervical 4		
Height of centrum	-	34
Width of centrum	-	35
Length of centrum	-	12
Cervical 5		
Height of centrum	-	31
Width of centrum	-	32
Length of centrum	-	12
Cervical 6		
Height of centrum	-	27+
Length of centrum	-	10+

Abbreviations: **e** = estimate; + = measurement on incomplete element.

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Table 3 (on next page)

Measurements of simocetid tympanic bullae.

Measurements (in mm) of tympanic bullae of *Olympicetus thalassodon* sp. nov. (LACM 158720), *Olympicetus avitus* (LACM 126010), and *Olympicetus* sp. A (LACM 124105) (modified from Kasuya, 1973, and Geisler et al., 2014).

TABLE 3. Measurements (in mm) of tympanic bullae of *Olympicetus thalassodon* sp. nov. (LACM 158720), *Olympicetus avitus* (LACM 126010), and *Olympicetus* sp. A (LACM 124105) (modified from Kasuya, 1973, and Geisler et al., 2014).

	LACM 158720	LACM 126010	LACM 124105
Maximum length (without posterior process)	65	50	49
Maximum length (including posterior process)	74	54	-
Distance from anterior tip to inner posterior prominence	61	50	48
Maximum width at level of the sigmoid process	40	35	34
Height at sigmoid process	46	37	36
Maximum width of sigmoid process	-	15	15
Maximum length of posterior process	16+	18	-

Abbreviations: +, measurement on incomplete or obscured element.

Table 4 (on next page)

Measurements of simocetid teeth.

Measurements (in mm) of left (l) and right (r) teeth of *Olympicetus thalassodon* sp. nov. (LACM 158720).

TABLE 4. Measurements (in mm) of left (l) and right (r) teeth of *Olympicetus thalassodon* sp. nov. (LACM 158720).

Designation	Length	Width	Height
?Canine	7.4	7.2	7.7
P2 (r)	-	-	15.6
P3 (r)	15.7	-	17.5
P4 (r)	16.5	9.7	17.5
P4 (l)	17.9	9.3	18.3
M1 (r)	16.4	9.4	17.9
M1 (l)	16.5	9.4	16.7
M2 (r)	14.1	8.1	11.9
M2 (l)	14.6	8.4	11.7
p3 (r)	17.1	7.4	14.4+
p4 (r)	15.2	-	13.6+
p4 (l)	16.7	-	18.6
m1 (r)	17.8	6.4	13.9+
m1 (l)	17.6	-	18.3
m2 (r)	16.5	-	13.5+
m2 (l)	17.4	-	17.3
m3 (r)	13.4	-	11.6
Molariform indet.	15.4	9.0	13.5

Abbreviations: +, measurement on incomplete element.

1

Table 5 (on next page)

Measurements of simocetid hyoid elements.

Measurements (in mm) of hyoid elements of *Olympicetus thalassodon* sp. nov. (LACM 158720) (modified after Johnston and Berta, 2011).

TABLE 5. Measurements (in mm) of hyoid elements of *Olympicetus thalassodon* sp. nov. (LACM 158720) (modified after Johnston and Berta, 2011).

Stylohyal (right)	
Maximum length	85
Maximum width of distal articular surface	11
Anteroposterior thickness at mid length	10
Transverse width at mid length	6
Maximum width of proximal articular surface	16
Anteroposterior thickness of proximal articular surface	8
Basihyal	
Maximum length along the midline	14
Maximum depth along the midline	10
Maximum transverse width	33
Length of articular surface	20
Height of articular surface	14
Thyrohyal (right)	
Maximum length	59
Maximum width of distal articular surface	11
Maximum height of distal articular surface	16
Dorsoventral thickness at mid length	7
Transverse width at mid length	11
Maximum width of proximal articular surface	18
Maximum height of proximal articular surface	13

Table 6 (on next page)

Measurement of simocetid periotic.

Measurements (in mm) of periotic of *Olympicetus* sp. 1 (LACM 124105) (modified from Kasuya, 1973, and Racicot et al., 2019).

TABLE 6. Measurements (in mm) of periotic of *Olympicetus* sp. 1 (LACM 124105) (modified from Kasuya, 1973, and Racicot et al., 2019).

Maximum length	43
Proximal dorsoventral thickness of anterior process	12
Length of anterior process	16
Transverse width of anterior process at mid-length	9
Dorsoventral height of anterior process at mid-length	13
Maximum width of periotic	22
Least distance between fundus of internal auditory meatus and aperture for endolymphatic foramen	2
Least distance between fundus of internal auditory meatus and aperture for perilymphatic foramen	3
Least distance between fenestra rotunda and endolymphatic foramen	7
Least distance between fenestra rotunda and perilymphatic foramen	3
Length of articular surface of posterior process	11
Width of articular surface of posterior process	8
Transverse width of cochlear portion	10
Anteroposterior length of cochlear portion	15