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ARTICLE

CRANIAL ANATOMY OF *MORTURNERIA SEYMOURENSIS* FROM ANTARCTICA, AND THE EVOLUTION OF FILTER FEEDING IN PLESIOSAURS OF THE AUSTRAL LATE CRETACEOUS

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ABSTRACT—This paper redescribes the holotype skull of the aristonectine elasmosaur *Morturneria seymourensis* from the upper Maastrichtian of Seymour Island, Antarctica. This description supports the validity of the genus *Morturneria*, distinct from the genus *Aristonectes* from Chile and Argentina. The paroccipital process of *Morturneria* is plesiomorphic, similar to *Alexandronectes* and unlike the autapomorphic occiput of *Aristonectes*. The palate of *Morturneria* is autapomorphic in possessing a strongly developed midline keel. The cranium of *Morturneria* is about 60% complete and preserves the anterior skull roof and palate; both regions were previously unknown in any aristonectine. The combination of the *Morturneria* holotype and recent research on other aristonectines allows the first confident cranial reconstruction of an aristonectine elasmosaur. The cranial anatomy of both *Morturneria* and its close relatives is derived relative to all other plesiosaurs, possessing a novel suite of dental and oral cavity adaptions. The suspensorium extends far behind the occipital condyle, and the jaw is long and hoop-like; together these features allowed a large gape and oral cavity volume. The palate of *Morturneria* is strongly keeled, forming arched lateral oral chambers that further increased oral cavity volume. The dentition of *Morturneria* is similar to that of *Aristonectes*, and all share autapomorphic interlocking combs of needle-like teeth that occluded outside the mouth and did not meet tip to tip. The upper and lower dentition formed an oral battery that may have functioned like a sieve in straining food particles from substrate ejected from the oral cavity. We theorize that this highly derived suite of adaptations is convergent with extant gray whales and archaic mysticetes and hypothesize that it functioned similarly in sieve feeding following suction. This is the first identification of whale-like filter feeding in any marine reptile, a condition once claimed to be anatomically impossible.

INTRODUCTION

The enigmatic aristonectine plesiosaurs of the Austral Late Cretaceous have puzzled paleontologists since their discovery in Patagonia during the Second World War (Cabrera, 1941). The cranial morphology of these animals is both derived and poorly known, and although recent discoveries from Chile have established beyond doubt that the aristonectines are a clade of highly derived elasmosaurid plesiosaurs (Gasparini et al., 2003; Benson and Druckenmiller, 2014; Otero et al., 2014, 2016; O'Gorman, 2016), their detailed anatomy and life habits have defied elucidation. The fragmentary known material possessed numerous gracile teeth and robust, hoop-shaped mandibles, leading to tentative suggestions of filter feeding for the clade. The degree of adaptation to this feeding strategy was thought to be modest, however, similar to that seen in crabeater seals (Chatterjee and Small, 1989). However, the lack of a complete cranium has prevented

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an understanding of the basic anatomy and even shape of the aristonectine skull, severely limiting inferences of feeding behavior.

In this paper, we redescribe the cranial anatomy of the aristonectine '*Morturneria*' *seymourensis* based on the partial skull of the holotype, found several meters below the K/Pg boundary on Seymour Island, Antarctica, by teams from Texas Tech University in the early 1980s. This skull is about 60% complete but largely disarticulated, and its incompleteness and odd morphology have defied reconstruction until now. However, the recent description of the partial skull of *Aristonectes quiriquinensis* from Chile (Otero et al., 2014) provides the context necessary for the first confident cranial reconstruction of '*Morturneria*' and thereby enables study of the complete aristonectine skull.

'*Morturneria*' displays a highly derived suite of oral cavity adaptations, including gracile tooth combs that project laterally from the jaws and intersect outside the mouth. The extreme posterior position of the jaw articulation, arched palate, and large hooped mandible create a large oral cavity volume. '*Morturneria*' shares many of these oral specializations with *Aristonectes* and the two taxa are closely related, but the hypothesis

that '*Morturneria*' is a juvenile *Aristonectes* (Gasparini et al., 2003) can be confidently rejected. '*Morturneria*' is a valid genus that is plesiomorphic in several characters. Elasmosaur ingroup relationships have received a recent, exhaustive treatment (O'Gorman et al., 2015; Otero, 2016), and we do not repeat the phylogenetic analysis here; the aristonectines are nested high within Elasmosauridae.

The most autapomorphic aristonectine cranial feature is the long and robust posterior extension of the quadrate flange of the pterygoid. In most plesiosaurs, this is a short, laterally directed process that joins the quadrate to the basicranium (O'Keefe, 2001; Otero et al., 2016). In aristonectines, the quadrate flange of the pterygoid is greatly elongated, displacing the jaw articulation far behind the basicranium (Fig. 1). Hence, the occipital condyle resides in a deep embayment in the back of the skull, with the suspensorium enveloping the atlas/axis complex and the subsequent one or two cervicals (Otero et al., 2014; Fig. 1). The dorsal surface of the pterygoid also possesses a long, neomorphic contact with the inner face of the squamosal arch. A small contact between the squamosal and pterygoid is present in more basal elasmosaurs, but its expansion into a long suture, and the development of a deep adductor chamber in the squamosal, is autapomorphic for aristonectines (Otero, 2016; Otero et al., 2016). The posterior displacement of the jaw articulation results in great elongation of the temporal region and restriction of the orbits, external nares, and dentition to the anterior half of the platycephalic skull. The relatively small and anteriorly located face relative to the long jaws yields an overall head shape resembling a gulper eel (Fig. 1). This head shape is unique to '*Morturneria*' and its close relatives and enables an increase in oral cavity volume relative to more basal elasmosaurs.

Suspension feeding, or the bulk processing of water or other substrate to collect multiple, usually small, food items, is a common feeding strategy among vertebrates. Suspension feeding has evolved multiple times in elasmobranchs, osteichthyan fish, and in tetrapod clades ranging from birds to pterosaurs to mammals (Sanderson and Wassersug, 1993). However, adaptations to filter feeding are rare in Mesozoic marine reptiles. The two best-known marine reptiles thought to filter feed in some manner are both Triassic. One is a sauropterygian, the derived German placodont *Henodus* (Reif and Stein, 1999). The other is *Atopodentatus*, a bizarre basal diapsid from China (Chun et al., 2016). Both animals have straight, transverse batteries of fine teeth at the front of the mouth and are postulated to have scraped (possibly plant) food from the substrate, ingested it via suction, and then ejected excess water through the sieving tooth batteries at the front of the jaw (Chun et al., 2016). Although both taxa are highly autapomorphic, neither has a modern analog and neither survived into the Jurassic. Among subsequent marine reptile clades throughout the Jurassic and Cretaceous, only the Late Jurassic cryptoclidids have been hypothesized to filter feed (Brown and Cruickshank, 1994). The cranial anatomy of these animals is poorly known; however, convergences between cryptoclidids and aristonectines misled taxonomists concerning the affinities of '*Morturneria*' for many years (e.g., Chatterjee and Small, 1989; O'Keefe, 2001, 2004). Yet the cryptoclidid skull is not as derived as that of aristonectines, and no clade of marine reptile appears to have evolved filter feeding to the degree we postulate below for aristonectines (for discussion, see Deméré et al., 2008; Goldbogen et al., 2012; Pyenson et al., 2014). The evolution of whale-like filter feeding has been hypothesized to be anatomically impossible in plesiosaurs and other marine reptiles due to the lack of a secondary palate in these clades (Sanderson and Wassersug, 1993; Collin and Janis, 1997). However, the extensive suite of adaptations documented here suggest that aristonectines may have been filter feeders that utilized benthic suction and sieving, a feeding style considered symplesiomorphic for mysticete cetaceans and still used by modern gray whales (Marx et al., 2016).

MATERIALS AND METHODS

The material described here is a well-preserved partial skull (TTU P 9219) from the upper Maastrichtian Lopez de Bertodano Formation, exposed on Seymour (Marambio) Island east of the Antarctic Peninsula. The specimen also includes the atlas/axis complex and other cervical vertebrae that are not redescribed here (see Chatterjee and Small, 1989). The locality is in the upper, molluscan units of the formation, close to the K/Pg boundary (Huber, 1985; Chatterjee and Small, 1989). The material was collected and acid/mechanically prepared in the 1980s by teams from Texas Tech University, with an initial description by Chatterjee and Small (1989). Those authors made TTU P 9219 the holotype of the new cryptoclidid genus '*Turneria seymourensis*,' amended to '*Morturneria*' due to preoccupation (Chatterjee and Creisler, 1994). O'Keefe's (2001, 2004) original analyses of plesiosaur relationships recovered '*Morturneria*' as a cryptoclidid. However, the taxon was declared a junior synonym of the large-bodied taxon *Aristonectes parvidens* Cabrera, 1941, by Gasparini et al. (2003), and *Aristonectes* was further assigned to Elasmosauridae by those authors. Later phylogenetic analyses have agreed with this placement, and a host of recently discovered postcranial synapomorphies place the aristonectines firmly in Elasmosauridae. However, we demonstrate here that '*Morturneria*' is a valid elasmosaur genus. The validity of '*Morturneria*' has also been supported in recent analyses of elasmosaurid ingroup relationships (Otero, 2016; Otero et al., 2016).

Institutional Abbreviations—**MLP**, Museo de la Plata, La Plata, Argentina; **OU**, Geology Museum, University of Otago, Dunedin, New Zealand; **SGO.PV**, Área Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; **TTU**, Museum of Texas Tech University, Lubbock, Texas, U.S.A.

Anatomical Abbreviations—**bo**, basioccipital; **bot**, basioccipital tuber; **bptp**, basipterygoid process; **bs**, basisphenoid; **cp**, clinoid process; **cpr**, coronoid process; **d**, dentary; **en**, external naris; **exo**, exoccipital; **f**, frontal; **hsc**, horizontal semicircular canal; **ic**, groove for internal carotid; **in**, internal naris; **jf**, jugular foramen; **m**, maxilla; **mf**, maxillary fragment; **mof**, metotic fissure; **ncp**, notochordal pit; **oc**, occipital condyle; **ocl**, occlusal lamina; **p**, parietal; **pbs**, parabasisphenoid; **pf**, prefrontal; **pl**, palatine; **pm**, premaxilla; **pop**, paroccipital process; **prof**, facet for prootic; **ps**, parasphenoid; **psc**, posterior semicircular canal; **pt**, pterygoid; **ptf**, postfrontal; **q**, quadrate; **sof**, facet for supraoccipital; **sq**, squamosal; **st**, sella turcica; **ut/sac**, chamber for utriculus and sacculus; **v**, vomer; **VI**, abducent nerve foramen.

SYSTEMATIC PALEONTOLOGY

Order PLESIOSAURIA de Blainville, 1835
Family ELASMOSAURIDAE Cope, 1869
Subfamily ARISTONECTINAE O'Keefe and Street, 2009
(sensu Otero, Soto-Acuña, and Rubilar-Rogers, 2012)
Genus *Morturneria* (Chatterjee and Small, 1989)

Type Species—*Morturneria seymourensis* (Chatterjee and Small, 1989).
Generic Diagnosis—As for species (monotypic), below.

MORTURNERIA SEYMOURENSIS (Chatterjee and Small, 1989)

Turneria seymourensis: Chatterjee and Small, 1989.
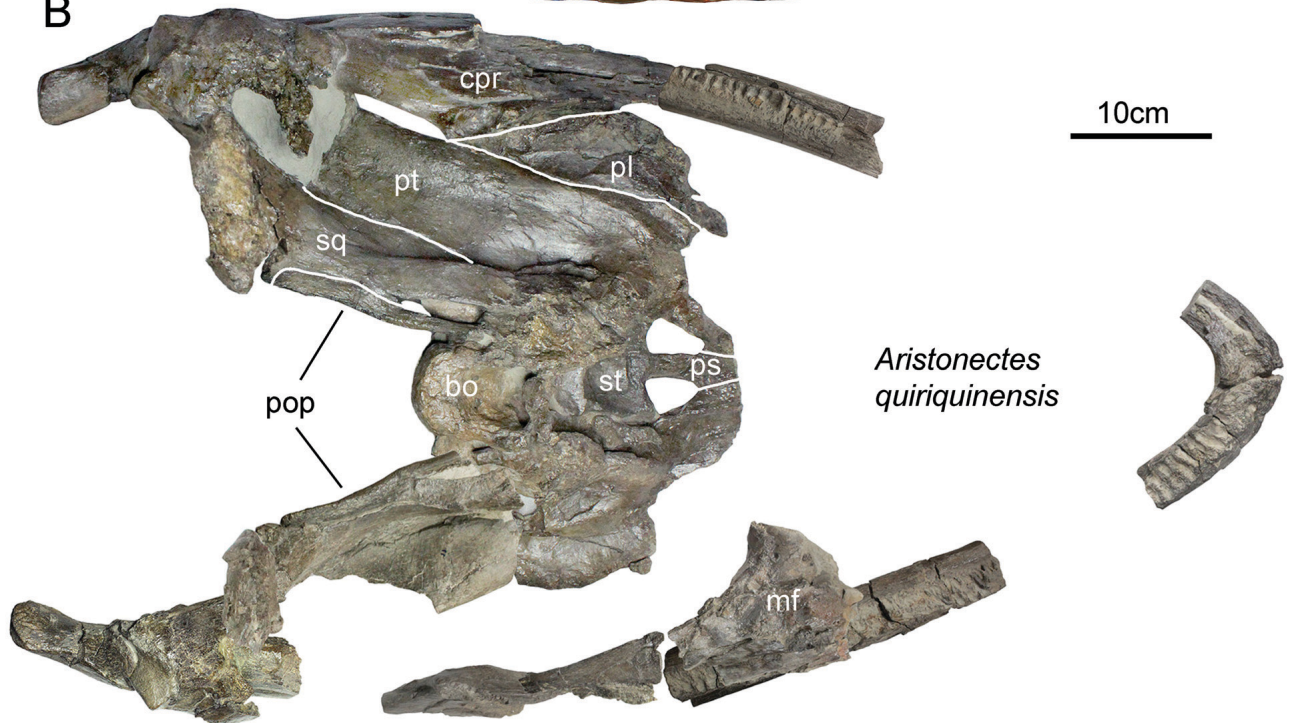*Morturneria seymourensis:* Chatterjee and Creisler, 1994.
Aristonectes parvidens: Gasparini et al., 2003.

Holotype—TTU P 9219, partial skull including premaxilla, maxilla, anterior and medial palate, skull roof, partial

A — *Kaiwhekea katiki*

B — *Aristonectes quiriquinensis*

cpr, pl, pt, sq, pop, bo, st, ps, mf

C — *Aristonectes parvidens*

40·XI·14·6

10cm

10 cm

suspensorium, braincase, and parts of left and right dentaries; atlas/axis complex; mid-cervical vertebrae.

Locality Horizon and Age—Seymour (Marambio) Island, Antarctica. Higher, 'molluscan' units (Klb9) of the López de Bertodano Formation, upper Maastrichtian (Late Cretaceous).

Revised Diagnosis—Autapomorphic traits include palatal surface unique among elasmosaurids (and likely among known plesiosaurians) in having a deeply arched palate with a ventral keel formed anteriorly by a ventral projection of the vomer; posterolateral vomerine process partially covers obliquely oriented internal naris; dentary teeth with procumbent alveoli recurving ventrally; enlarged anterior maxillary teeth, with larger ones interlocking with diastema on dentary; maxillary alveoli confluent; lateral border of internal naris formed by palatine; discrete, round facet for articulation of flared end of paroccipital process on squamosal only; parabasisphenoid complex relatively long and lacking ventral keel; and relatively long posterior interpterygoid vacuities. Additional informative characters of *Morturneria* include a skull that is relatively narrow mediolaterally, less derived than the platycephalic *Aristonectes*; eight or nine premaxillary teeth; at least 38 maxillary teeth; and at least 46 dentary teeth. *Morturneria* shares with *Aristonectes quiriquinensis*, *Alexandronectes zealandiensis*, and *Kaiwhekea katiki* the presence of a posterior extension of the pterygoids far beyond the occipital condyle; however, it differs from *Ar. quiriquinensis* in having a different pterygoid outline and in lacking a long contact with the paroccipital processes. The pterygoid of *Morturneria* is more similar to that of *Al. zealandiensis*, but the former differs in having a laterally expanded posterior pterygoid, unlike the plesiomorphic *Al. zealandiensis*; *Morturneria* also differs from *Aristonectes* spp. in possessing a smaller skull (ca. 60 cm, contrary to the ca. 80 of *Ar. parvidens* and *Ar. quiriquinensis*) and in possessing a dentary with a ventral keel, contrary to the dentary of *Aristonectes* spp., which are ventrally rounded (a dentary with ventral keel is also present in *K. katiki* and likely in *Al. zealandiensis*). *Morturneria* has a long and slender paroccipital process, unlike that of *Al. zealandiensis*, which is comparatively much shorter, thicker, and distally expanded. It also differs from the paroccipital process of *Ar. quiriquinensis*, where the process is quite long but fused to the posterior pterygoid along its distal half. Finally, *Morturneria* differs from *K. katiki* in the lateral orientation of the dentary teeth (dorsally oriented in *K. katiki*).

DESCRIPTION

Skull Roof

The anterior skull roof of *Morturneria* is preserved as a large midline fragment comprising the anterior parietals and their clear articulation with the dorsal premaxillary processes (Fig. 2). There is no obvious pineal foramen between the parietals; the premaxillary processes have separated on the midline due to postmortem deformation, but this is not a pineal foramen (contra Benson and Druckenmiller, 2014). The complete left medial and right lateral orbital margins are preserved, allowing reconstruction of the entire orbit except for the postorbital bar. A suture and fragment of the postfrontal is present behind the frontal on the anatomically left side. The dorsal orbital margin is formed by the frontal, and the anterodorsal margin is formed by the frontal and prefrontal. The frontal is deeply creased anteroposteriorly, first descending from the midline ridge by the premaxillary process, then flaring out in a palpebral-like expansion. Similar expansions are also present in polycotylid plesiosaurs (O'Keefe, 2008) and may have protected a prominent eyeball. The deep

groove between the frontal eminence and the midline ridge also contains the posterior margin of the external naris (Fig. 3). We speculate that this groove may have channeled bubbles from the naris around the eye when moving forward. The posterior margin of the external naris is bordered by the frontal. The small prefrontal is complete on the left side and contributes the lateral wall of the naris; however, the frontal-prefrontal suture on the left side could not be identified. It is present on the less-complete right side. The medial border of the naris is formed by the dorsal premaxillary process; the body of the premaxilla borders most of the anterior rim, and the maxilla completes the anterior and lateral margins (Fig. 3). A clear suture between the premaxilla and maxilla traverses the alveolar row and then trends medially and dorsally to the margin of the external naris. The orbital margin of the maxilla bears a shallow depression anteriorly that blends into a raised eminence posteriorly. This eminence creates a convex lateral orbital margin, a feature shared with *Kaiwhekea* (Fig. 1). The lateral, rather than ventral, margin of the maxilla carries the alveolar row.

The dorsal surfaces of both the maxilla and premaxilla are deeply pitted and lined with neurovascular foramina. The premaxilla contains poorly delineated alveoli for at least eight teeth. This increase over the plesiomorphic number of five (Cabrera, 1941; Gasparini et al., 2003) was once thought synapomorphic for derived cryptoclidids (O'Keefe, 2001) but is now known to be convergent (Otero, 2016). The maxilla and premaxilla were significantly arched in life, contributing to a large oral chamber (Fig. 4). However, postmortem deformation has slightly flattened this portion of the skull (Fig. 5A). The anterior five alveoli are well delineated; the first two are relatively small, the next three are larger. The rest of the alveolar row comprises a shallow groove of poorly ossified bone along the edge of the maxilla. Septa between alveoli are subtle or absent. Only the roots of three adult teeth, and three replacement teeth, are preserved (Fig. 5B). The dentition was laterally rather than ventrally directed, and interdigitated laterally with the mandibular teeth.

Palate

The palate of *Morturneria* is deeply arched laterally, beginning at the alveolar margin of the premaxilla and maxilla and extending back to the massive and highly vaulted pterygoid quadrate flanges. The resulting large oral chambers are separated on the midline by a deep keel. The keel is triangular in ventral view, narrow at the premaxilla and broadening back to the basiocciput (Figs. 2, 4). Anteriorly, the keel begins as a boss on the premaxilla, articulating in a clear transverse suture with the paired vomers. The vomer forms the midline keel to the level of the internal naris where it articulates with the pterygoid. The triangular anterior processes of the paired pterygoids comprise the midline keel for the rest of its length. Most of the palatine is not preserved; this element was delicate, arching from a longitudinal medial suture with the pterygoid to a lateral one with the maxilla (Fig. 4). A small fragment of the palatine is preserved attached to the maxilla. A larger piece is preserved anteriorly, in articulation between the maxilla and premaxilla. The palatine bears the entire lateral border of the internal naris and sends an anterior process almost to the alveolar margin. This condition is derived relative to more basal elasmosaurs, which lack a vomerine anterior process (Carpenter, 1997). Only *Aristonectes* has a similar process, although it is shorter and may not contribute to the border of the internal naris. The vomer forms the entire border of this opening in *Morturneria*, similar to more basal elasmosaurs and probably differing from *Aristonectes*, whose narial morphology is both

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←FIGURE 1. Holotype cranial material of **A**, *Kaiwhekea katiki* (OU 12649) in lateral view; **B**, *Aristonectes quiriquinensis* (SGO.PV.957) in dorsal view; and **C**, *Aristonectes parvidens* (MLP 40-XI-14-6) in lateral view. The two skulls in **A** and **B** were used to reconstruct the missing areas of *Morturneria*. **C** shows a detail of the alveolar margins from *Ar. parvidens*, demonstrating lateral orientation of the teeth. For abbreviations, see text.
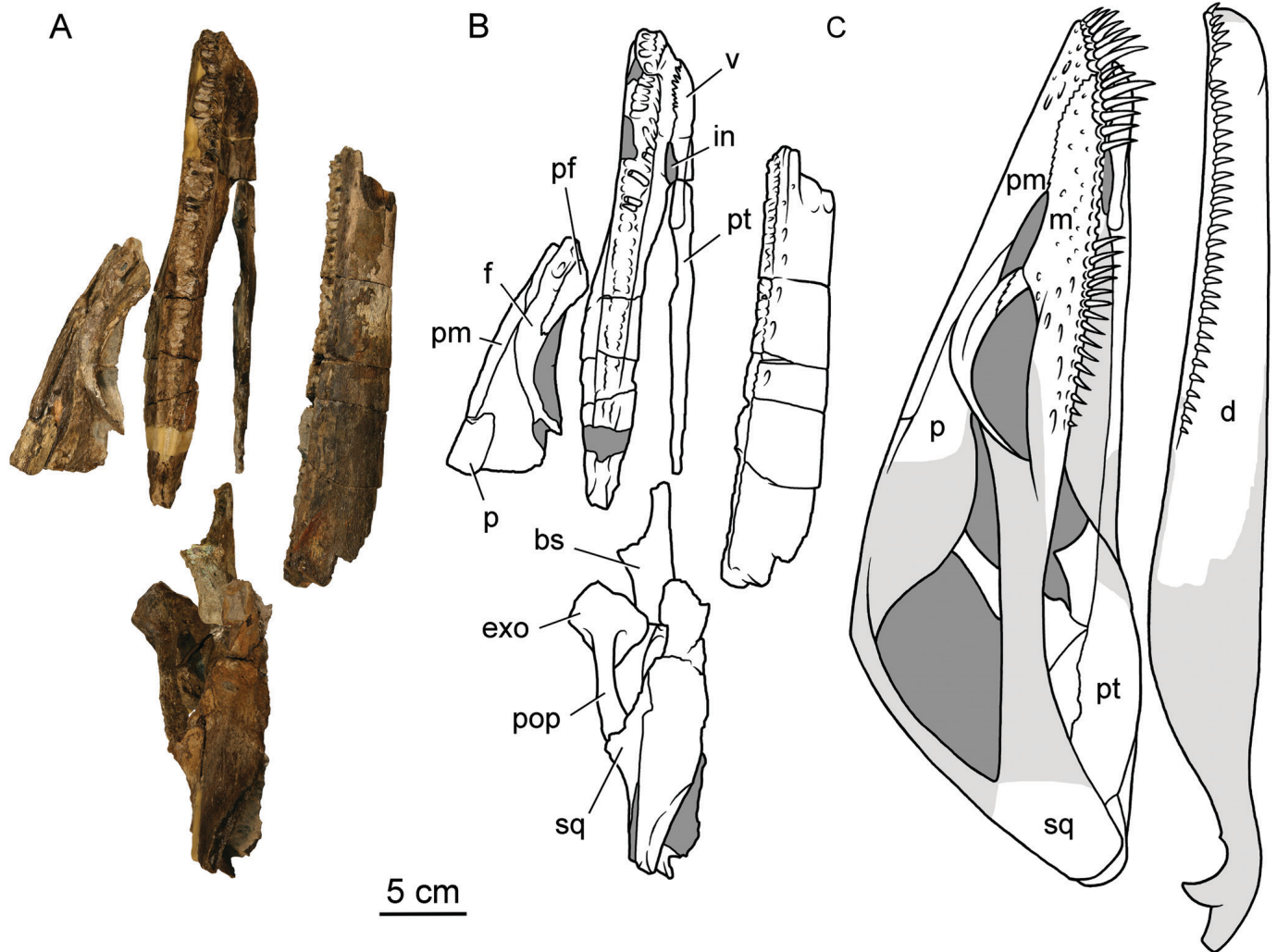
FIGURE 2. Preserved cranial elements (**A**), interpretation (**B**), and reconstruction (**C**) of the holotype of *Morturneria seymourensis* (TTU P 9219) in lateral view. Some maxillary teeth have been omitted from **C** to allow depiction of the palatal keel, lateral orientation of the internal naris, and posterior vomerine flange. The dark gray shading indicates matrix and bone deep to fenestra margins in the interpretation and indicates fenestrae in the skull in the reconstruction. For abbreviations, see text.

autapomorphic and poorly understood (O'Gorman, 2016). A significant portion of the internal naris is directed laterally in *Morturneria* because it is located on the lateral face of the keeled vomer; the vomer continues as a distinct flange projecting posterolaterally from the keel behind the internal naris (Figs. 3, 5). This condition is unique among known plesiosaurs.

The paired pterygoids are preserved on a separate fragment from the more anterior palatal structures. This fragment also carries the posterior end of the right vomer and articulates with the rest of the vomer on the portion comprising the maxilla and premaxilla (Fig. 3). The pterygoids are shown articulated to the anterior fragment in Figure 2, but the two pieces are not preserved in life position; the skull roof is crushed down and rotated into the area that presumably held the sphenethmoid cartilage. These two areas are depicted as disarticulated and in life position in Figures 2 and 3. Near the center of the palate, the pterygoids separate on the midline, creating a triangular space filled by the anterior process of the parasphenoid rostrum. The pterygoids and parasphenoid end posteriorly at a diagonal break. This break does not articulate with the rest of the parabasisphenoid complex (Fig. 6), and the length of the missing portion is ambiguous (Fig. 4). Between the anterior end of this element and the

posterior end of the parasphenoid rostrum is the only place in the skull lacking a clear articulation, breaking the skull into front and back halves. We have reconstructed the skull with the minimum amount of space between the back and front halves, but the skull may have been longer than shown here. As reconstructed, the skull is much narrower (and plesiomorphic) than that of *Aristonectes* (Fig. 1) and would be still narrower if a significant portion of the parasphenoid rostrum were missing (cf. *Aristonectes*; Fig. 1). There is no keel on the preserved portion of the parasphenoid rostrum.

The articulated braincase (described below) allows accurate placement and reconstruction of the posterior elements of the cranium. The back of the skull is preserved as matching left and right fragments, the right one more complete. This fragment is mostly right pterygoid, with a dish-shaped fossa anterodorsally for articulation with the basioccipital tuber. This area resembles *Aristonectes*, although the fossa is much larger than the corresponding tuber on the basioccipital in *Morturneria*. We believe that this reflects lack of ossification of the endochondral basioccipital tuber, indicating that the skull belonged to a juvenile, and hence the character is not taxonomically informative. Posterior to the articulation with the basioccipital tuber, the pterygoid
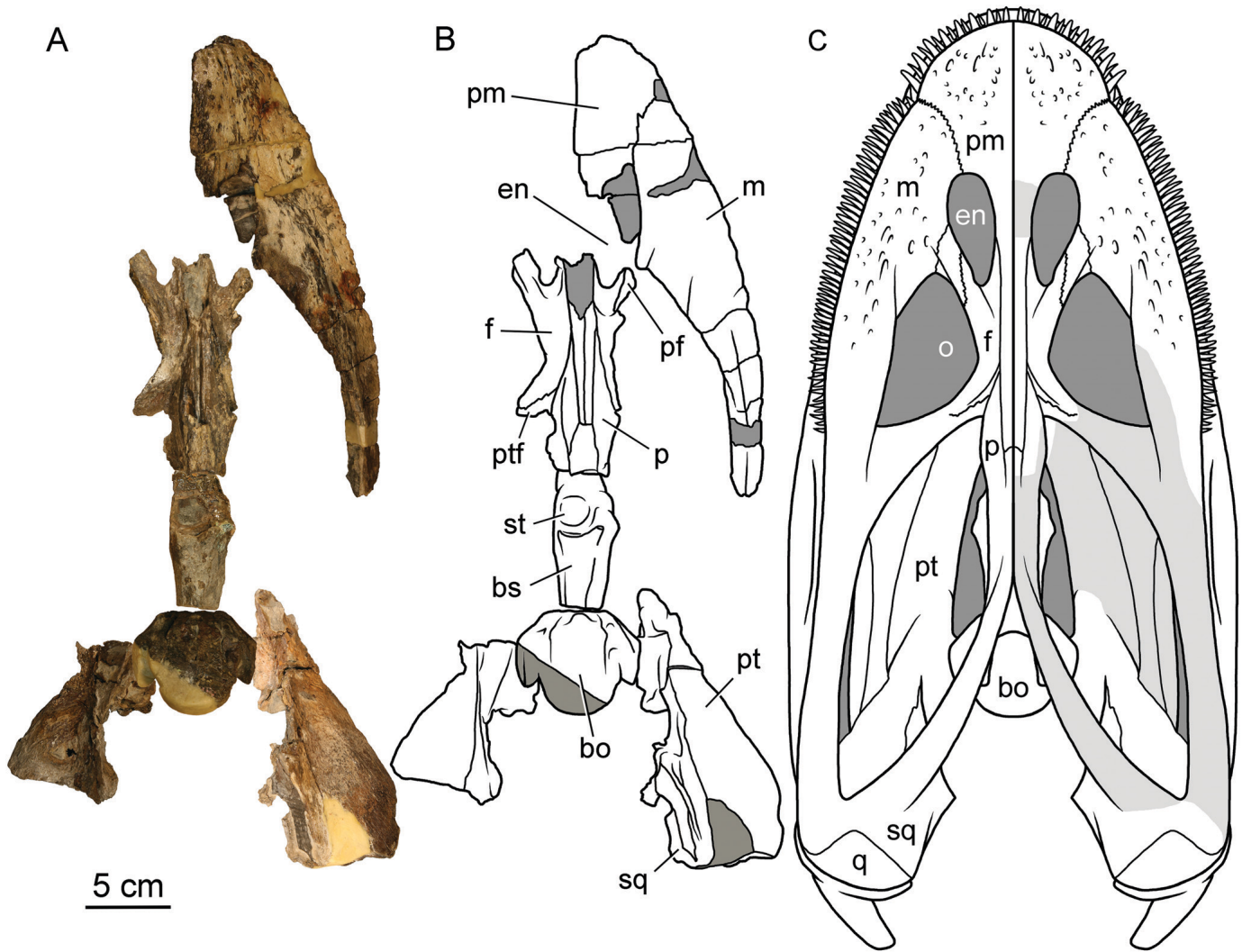
FIGURE 3. Preserved cranial elements (**A**), interpretation (**B**), and reconstruction (**C**) of the holotype of *Morturneria seymourensis* (TTU P 9219) in dorsal view. Missing elements are shaded light gray on the anatomically right side. The dark gray shading indicates matrix and bone deep to fenestra margins in the interpretation and indicates fenestrae in the skull in the reconstruction. For abbreviations, see text.

expands into a robust, arched process extending far behind the occipital condyle. This hypertrophy of the quadrate flange of the pterygoid is shared only by *Aristonectes* (Fig. 1), although it is more arched in *Morturneria*. The posterior end of the pterygoid ends in a shallow socket for articulation with the quadrate. The quadrate seems to have projected more posteriorly than ventrally; an element we believe is the left quadrate is preserved with the skull, but we do not show it articulated because we are unsure of its placement and orientation. We depict the quadrate in the reconstruction.

The right posterior skull fragment also preserves the base of the right squamosal. This is apomorphic in the possession of an elaborate medial process; the squamosal is a dermatocranial element and therefore lateral plesiomorphically to the quadrate (Romer, 1956). In *Morturneria*, the squamosal sends a large process anteriorly almost to the basioccipital tuber. This process articulates ventrally with the pteryoid, and a clear suture is visible in lateral view (Fig. 3). Medially, the squamosal extends ventrally as a thin sheet, covering the medial edge of the pterygoid (Figs. 2, 4). This anterior medial process of the squamosal, and its long suture with a hypertrophied quadrate flange of the pterygoid, is shared only

with *Aristonectes* (Fig. 1; the condition in *Kaiwhekea* is unknown). The left posterior portion of the skull consists of an incomplete pterygoid. This element is not complete posteriorly but does preserve a facet for articulation with the anterior medial process of the squamosal, and with a small fragment of that bone. The fossa for the articulation with the basioccipital process is present anteriorly. The bone in the region is pathological, bubbly in texture, and hypertrophied (Fig. 4). Both pterygoids are broken just anterior to this region, and the breaks here do not articulate with the more anterior pieces of the pterygoids. The dorsal apices of the preserved portions of both the left and right squamosals bear discreet articulations for the paroccipital processes. These articulations are point contacts, very different from the long suture present in *Aristonectes* (Fig. 1).

Braincase

The braincase of *Morturneria* is well preserved, missing only the prootics and half of the supraoccipital (Fig. 6). The exocipital/opisthotics and supraoccipital are inclined anteriorly at about 45° from the vertical so that the foramen magnum faces
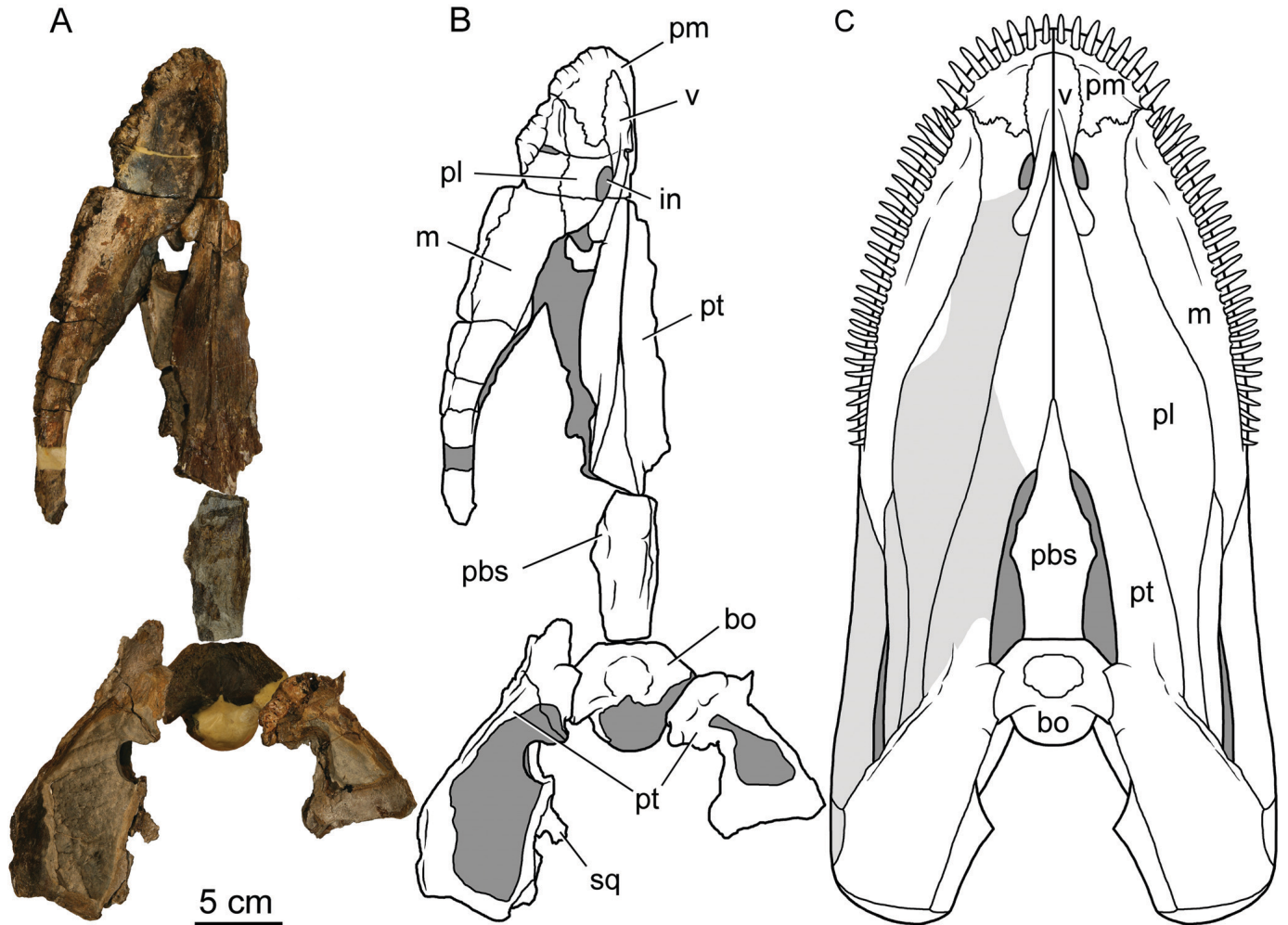
FIGURE 4. Preserved cranial elements (**A**), interpretation (**B**), and reconstruction (**C**) of the holotype of *Morturneria seymourensis* (TTU P 9219) in ventral view. The dark gray shading indicates matrix and bone deep to fenestra margins in the interpretation and indicates fenestrae in the skull in the reconstruction. For abbreviations, see text.

both posteriorly and dorsally. The paroccipital process is long and slender, expanding slightly at its tip, where it articulates with the squamosal (Fig. 2). This contact differs from that in *Aristonectes* and is more similar to the plesiomorphic condition in the more basal *Alexandronectes* (Otero et al., 2016). The basioccipital bears well-developed tubers for articulation with the pterygoids, and these present facets for corresponding depressions on the pterygoids, although the size difference between tuber and facet indicates the presence of significant cartilage (Fig. 3). The parabasisphenoid complex has poorly ossified basipterygoid processes; the basal articulation was therefore cartilaginous as well. The dorsum sella and sella turcica are present, and the dorsum sella carries low clinoid processes. Just inferior to these, more apparent on the better-ossified right side, is a deep groove. We believe that this groove carried the internal carotid artery, although it is rather dorsal relative to the plesiomorphic diapsid condition (i.e., *Youngina*; Gardner et al., 2010). The internal carotid foramen is in the same location in *Aristonectes* (Otero et al., 2014). Both sides of the parabasisphenoid carry a small foramen, here interpreted as an opening for the abducent nerve (cranial nerve [CN] VI). The parasphenoid and basisphenoid lack a visible suture, and

there is no parasphenoid keel; the anterior process is the only distinct part of the parasphenoid. This is triangular and resides on the midline between the pterygoids (Fig. 4). Compared with *Aristonectes*, the parabasisphenoid complex and posterior interpterygoid vacuities are relatively long, resembling those of more basal elasmosaurs (Otero, 2016), and particularly the basal aristonectine *Alexandronectes* (Otero et al., 2016). The caudal end of the basisphenoid bears a notochordal pit, and this matches a similar pit on the rostral face of the basioccipital. The caudal end of the basioccipital condyle is missing and with it any notochordal pit that may have been present on the condyle.

Poor ossification of the endochondral braincase elements indicates that the animal was a juvenile, and although the metotic fissure between opisthotic and exoccipital is fused, the suture is obvious on the medial faces of both otic capsules. Both exoccipital-opishotics are well preserved and undistorted. Laterally, the exoccipital bears two foramina for branches of the hypoglossal nerve; the jugular foramen is prominent underneath the root of the paroccipital process. Anteriorly, the opisthotic bears well-demarcated articulations for both the supraoccipital and prootic. These facets form an angle of about 90°. The supraoccipital
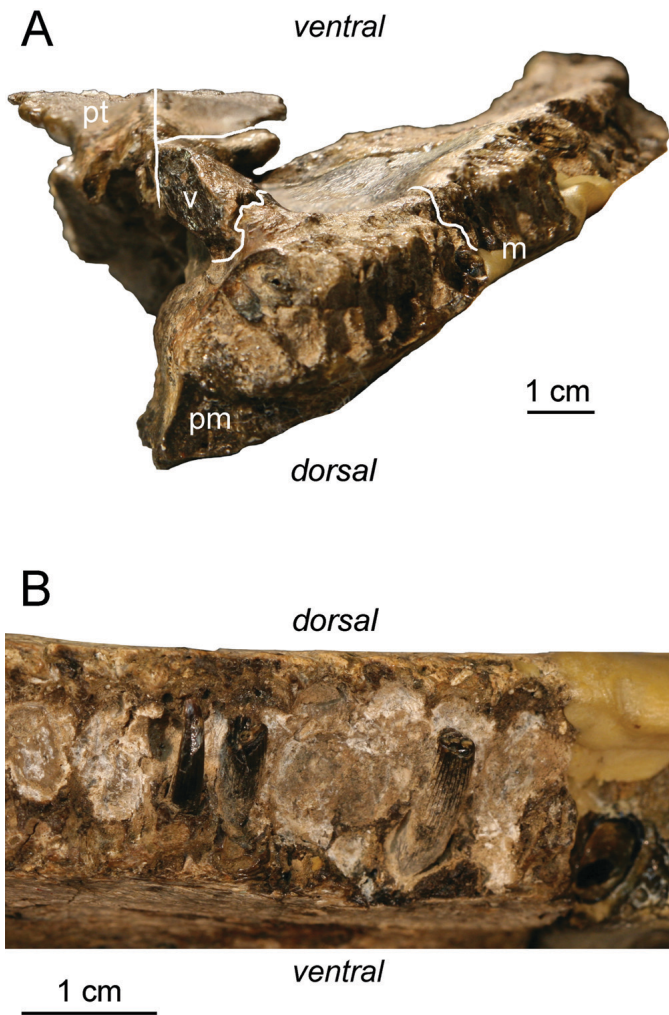
FIGURE 5. Morphological details from the articulated rostral portion of the skull of *Morturneria seymourensis* (TTU P 9219). The photograph in **A** is a composite view taken anteriorly and slightly ventrally, looking down the oral cavity. This shows the keeled palate, the vomer with posterior flange guarding the internal naris, and the arching of the palate generally. The postmortem deformation is visible on the maxilla lateral to the vomer. The photograph in **B** is a detail of the right maxillary alveolar row, showing a functional tooth root, replacement teeth descending into position, and a more posterior tooth that has yet to rotate. For further discussion, see text.

FIGURE 6. Braincase elements of *Morturneria seymourensis* (TTU P 9219). **A**, parabasisphenoid in left lateral (left), dorsal (middle), and ventral (right) views; **B**, **C**, articulated basioccipital and exoccipital/opisthotics in lateral (**B**) and rostral (**C**) views. For abbreviations, see text.

facet bears the ventral half of the posterior semicircular canal; the prootic facet bears the horizontal semicircular canal. Both canals empty into a deep void in the prootic face of the opisthotic. The utriculus and sacculus were presumably housed here following the plesiomorphic diapsid pattern (Gardner et al., 2010). The supraoccipital probably articulated with the parietals on the midline as in other elasmosaurs (Carpenter, 1997), although this area of the skull roof is not preserved in *Morturneria*. We believe that a fragment comprising most of the right half of the supraoccipital is in the holotype material. However, the base of this element is broken and lacks a clear articulation with the opisthotic, and we have not attempted to articulate it in Figure 6. We have reconstructed the temporal fenestra and squamosal arch based on the related taxon *Kaiwhekea*, a more basal aristonectine from New Zealand (Otero et al., 2016; Fig. 1).
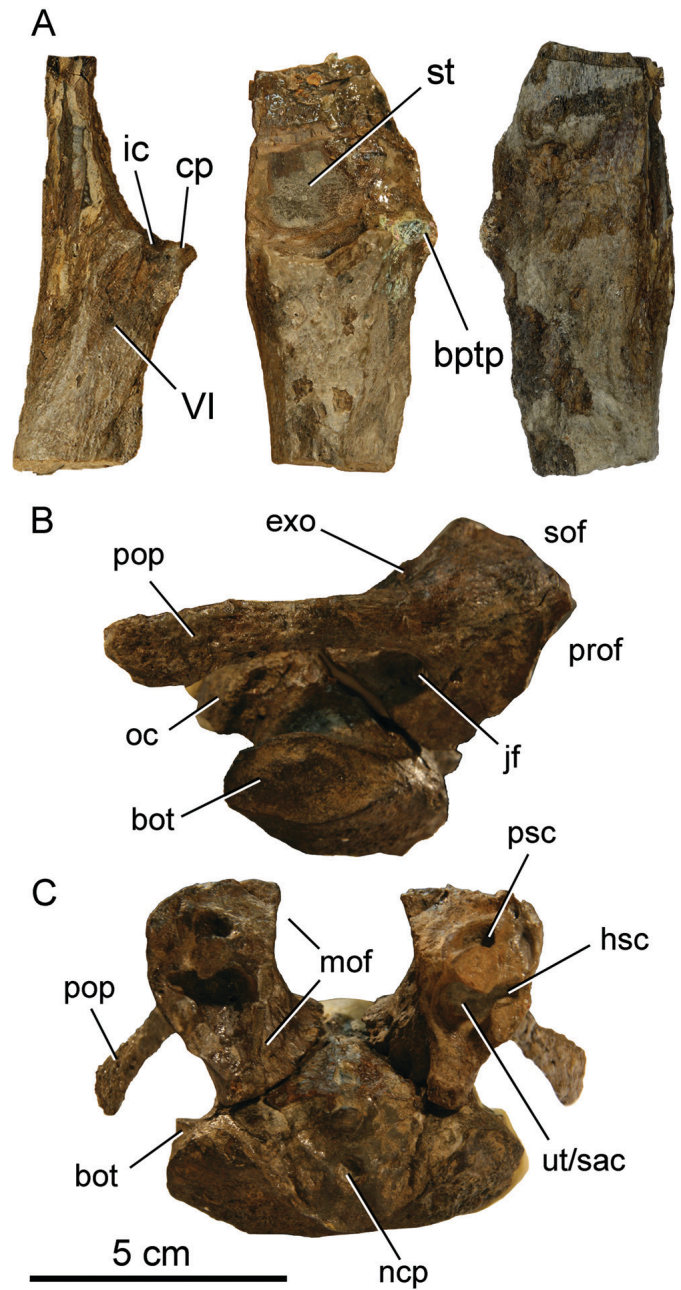
Mandible

Preserved mandibular elements of *Morturneria* include a portion of the anterior right dentary and a larger portion of the left dentary (Figs. 3, 7). Both mandibular rami bear a deep Meckelian canal on their medial faces that is open ventrally. This gap was filled in life by the splenial, which was probably blocky as in *Aristonectes*. The symphysis is not preserved in *Morturneria* but was clearly gracile. The larger left ramus fragment is bowed outward as in other aristonectines and the curvature matches that of the maxilla, allowing for its positioning anteroposteriorly (Fig. 3). The smaller left ramus fragment overlaps the right and
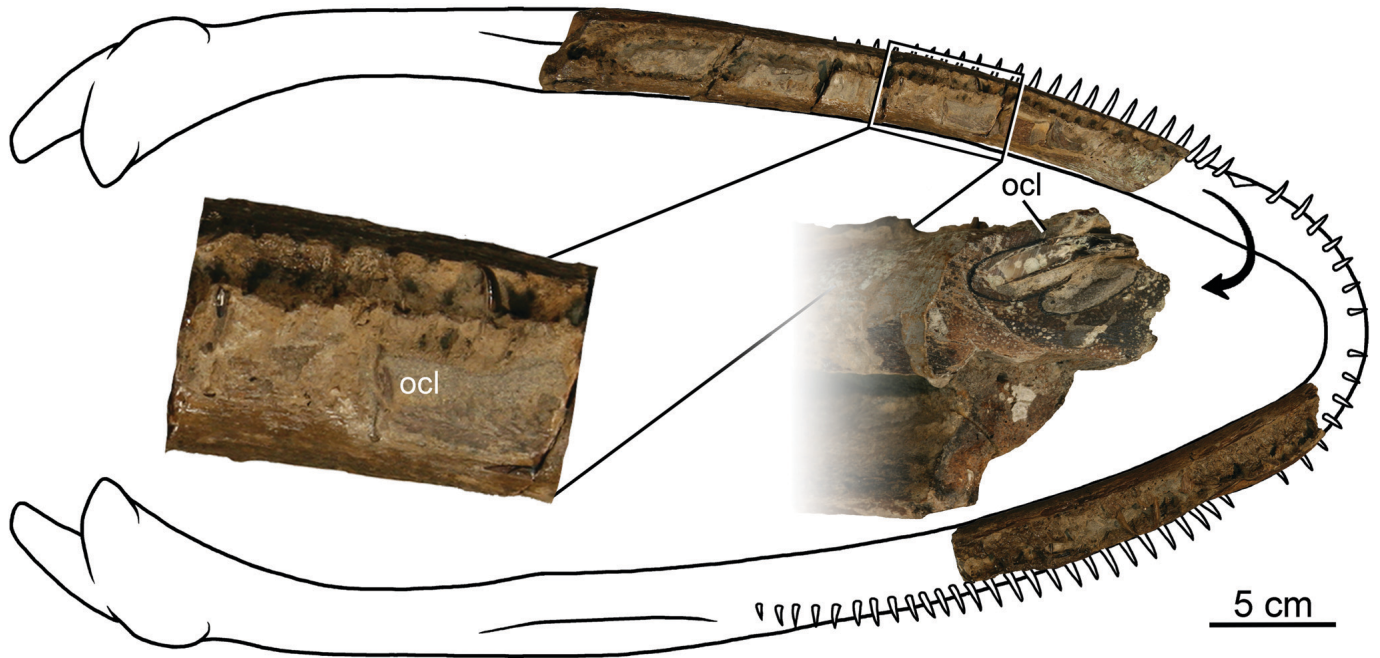
FIGURE 7. Dentary fragments and reconstructed mandible of *Morturneria seymourensis* (TTU P 9219). The left inset is a close-up view of the left dentary as indicated, showing alveoli, the occlusal lamina, and a tooth protruding from underneath it. The right inset is a polished, obliquely sectioned face of the left dentary, showing a replacement tooth emerging from beneath the occlusal lamina dorsal to an older, empty alveolus.

continues anteriorly to near the symphysis, allowing for reconstruction of the mandible from anterior end to coronoid process. The jaw is large and hooped, quadrangular in cross-section with a narrow and gracile symphysis, similar to the condition in *Aristonectes* (Fig. 1C), although relatively longer and narrower. The anterior end of the dentary has a subtle anteroventral expansion as in *Aristonectes*, although there is a diastema in the tooth row at the posterior terminus of this expansion in *Morturneria*. *Morturneria* exhibits unusual specialization of the dentary alveolar margin. The alveoli are directed laterally rather than dorsally and are covered by a delicate sheet of bone on the occlusal surface of the mandible (Fig. 7). This occlusal lamina is a continuous sheet covering the alveolar row, with no indication of individual alveoli. Both the occlusal lamina and the lateral alveolar orientation are shared with both species of *Aristonectes* (O'Gorman, 2016; Fig. 1); these are the only known plesiosaurs, or marine tetrapods, with the condition. The lateral surface of the mandible carries a series of large, posteriorly directed neurovascular foramina about 5 mm below the alveolar row. These foramina are regular in size and orientation and reside in a shallow groove (Fig. 3).

DENTITION

The dentition of *Morturneria* is autapomorphic relative to more basal elasmosaurs (Figs. 3, 7). The teeth are numerous, gracile, and curved, and most are lost due to weak attachment to the cranium and mandible. Loose tooth attachment seems characteristic of aristonectines rather than a juvenile trait of *Morturneria*. The alveoli in both known (adult) *Aristonectes* skulls are better defined, but most teeth are still lost (O'Gorman, 2016; Fig. 1). The number of maxillary and dentary teeth depicted here for *Morturneria* is therefore conjectural, but reasonable based on the preserved tooth roots. The maxilla bears the roots of three functional teeth and two replacement teeth, and a single complete replacement tooth (Fig. 5). This tooth is smaller than the others and was probably still growing. Interestingly, it curves

dorsally rather than ventrally, and its striations are on the concave surface, facing dorsally. The preserved functional tooth roots are oriented so that the striations are ventral, and the tips curved ventrally. The roots of the other two replacement teeth are partially rotated between these two extremes (Fig. 5). Tooth replacement apparently moved in waves down the maxilla from anterior to posterior in the general vertebrate pattern (Romer, 1956), and one of these replacement waves is visible in the right maxilla. The maxillary teeth appear to begin formation out of articulation and then rotate anteroventrally and into functional position when they replace shed teeth. The alveolar row on the premaxilla and maxilla is rotated along the long axis of the mouth, so that it faces laterally rather than ventrally. This may be partially due to postmortem deformation, but we believe that it is largely real. However, the replacement pattern has changed as well, because the more lingual/ventral teeth are functional, and they are replaced from the lateral/dorsal side. The mandibular teeth are also oriented laterally, but their replacement pattern is less derived.

A polished cross-section of the left dentary fragment (Fig. 7) shows a functional tooth. The root of this tooth projects laterally but also dorsally, and the tooth curves so that it projects directly laterally at the border of the occlusal lamina. Continuation of this curvature would yield a tooth crown projecting ventrolaterally. The polished cross-section also reveals an empty alveolus ventral to the functional tooth; we believe that this alveolus held the preceding, shed tooth. In basal elasmosaurs, replacement teeth initially form lingually and then migrate to the mandibular margin (Carpenter, 1997). Replacement of the mandibular teeth in *Morturneria* was similar, but the alveolar row is rotated along the long axis of the mandible, so that it faces laterally rather than dorsally. Replacement teeth would form just ventral to the alveolar bone of the occlusal lamina, and dorsal to the functional teeth. They would then move ventrally to replace shed teeth in the jaw. However, there is no rotation of the teeth as they replace, unlike in the maxilla. In life, the upper and lower teeth projected from the side of the face in regular, mostly homodont,

comb-like rows. The tooth combs interdigitated lateral to the mouth. The upper teeth trended laterally and ventrally, whereas the curvature of the lower teeth resulted in a ventral orientation of their points as well. The tooth crowns were not opposed, and the tooth combs interdigitated at an oblique angle (Fig. 8). All preserved teeth are striated on their ventromedial margin.

DISCUSSION

The holotype skull of *Morturneria* described above supports the validity of the genus *Morturneria*. The poor state of ossification of the endochondral braincase elements and lack of fusion of neural arches and cervical ribs on vertebrae found with the skull (Chatterjee and Small, 1989) indicate that the animal was juvenile when it died, but the hypothesis that *Morturneria* is a juvenile *Aristonectes* can be rejected. Autapomorphies of *Morturneria* include the morphology of the vomer and particularly the keeled palate; only the anterior part of the palate is known in *Aristonectes*, but it lacks a midline keel and the vomer is quite different (O'Gorman, 2016). The nature of the paroccipital process articulation with the squamosal is plesiomorphic in *Morturneria*, as are the skull proportions; both characters are more derived in *Aristonectes*. The latter taxon also lacks diastemata on the maxilla and mandible. Lastly, ontogeny is insufficient to explain the gross size difference between *Morturneria* and *Aristonectes*. Postcranial material in the TTU collection, still under study, demonstrates the presence of a small adult aristonectine on Seymour Island that is certainly not *Aristonectes*. *Morturneria* is a valid taxon that is more plesiomorphic in several characters than the much larger *Aristonectes*. Recent phylogenetic analyses have supported this placement (Otero, 2016; Fig. 9).

The derived aristonectines share a set of extreme adaptions that beg a functional explanation. Because the upper and lower tooth combs interdigitated at an oblique angle, the points of the teeth did not occlude and therefore would be useless in piercing and grasping prey items as did more basal elasmosaurs (Massare, 1987). The weak attachment of the long, gracile teeth, the delicate occlusal lamina on the dentary, and the weak mandibular symphysis probably precluded the jaw from incurring heavy compressive or torsional loads. The posterior distension of the jaw articulation and the hooping of the mandibular rami increase oral volume, as does the arching of the palate (Fig. 8). *Morturneria* had the ability to engulf relatively large volumes of water or other substrate, possibly aided by suction. We speculate that the tooth combs may have been held loosely interdigitated while the substrate was then ejected from the mouth via action of the pharyngeal apparatus. Feeding by suction and sieving requires a strong pharyngeal apparatus; however, no hyoids are currently known from any aristonectine, so we lack data for this region. Robust hyoids are known from other elasmosaurs (Welles, 1950) but are seldom preserved due to lack of bony articulation with the skull. The evolution of mysticete-like filter feeding was long held to be impossible in Mesozoic marine reptiles, constrained by the lack of a secondary palate (Collin and Janis, 1997; Pyenson et al., 2014). However, in *Morturneria*, the external naris is confined medially and anteriorly by the posterior vomerine flange. The addition of a small amount of soft tissue to this flange would create a valve closing off the internal naris, sealing the oral cavity and allowing substrate ejection from the mouth without blowing it out the nose. This sealing of the oral cavity is a necessary precondition for successful suspension feeding (Sanderson and Wassersug, 1993) and is one of a range of adaptations *Morturneria* shares with other tetrapod suspension feeders (including tooth reduction, trapping surfaces on jaw margins, and increased oral cavity volume; Sanderson and Wassersug, 1993).

The overall oral morphology of *Morturneria* and other aristonectines finds its closest modern analog in the gray whale
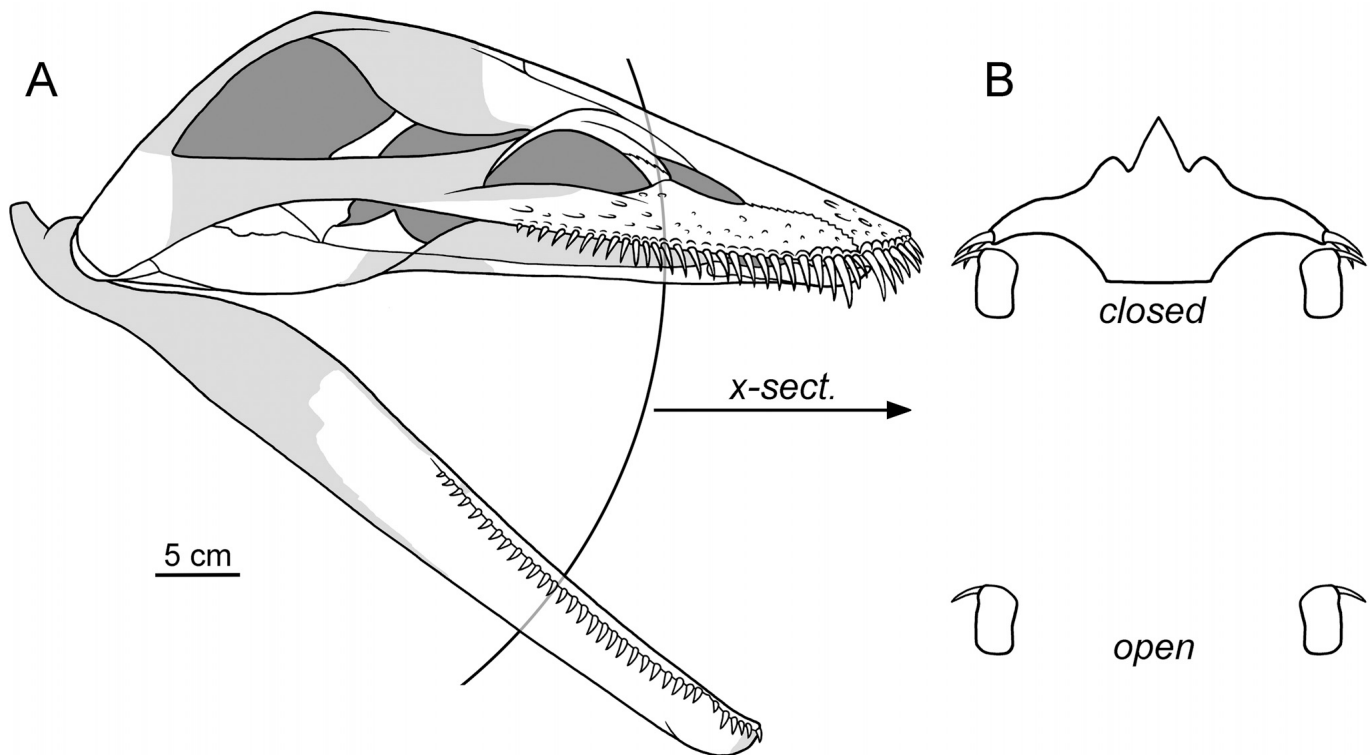

FIGURE 8. Mandibular and oral cavity morphology of *Morturneria*. **A**, the mandible in articulation with mouth open; **B**, a cross-section of the skull along the indicated arc, demonstrating the large volume of the oral cavity, as well as the oblique interdigitation of the tooth combs and the arching of the palate. Dark gray shading indicates skull fenestrae; light gray shading indicates reconstructed portions of the skull.
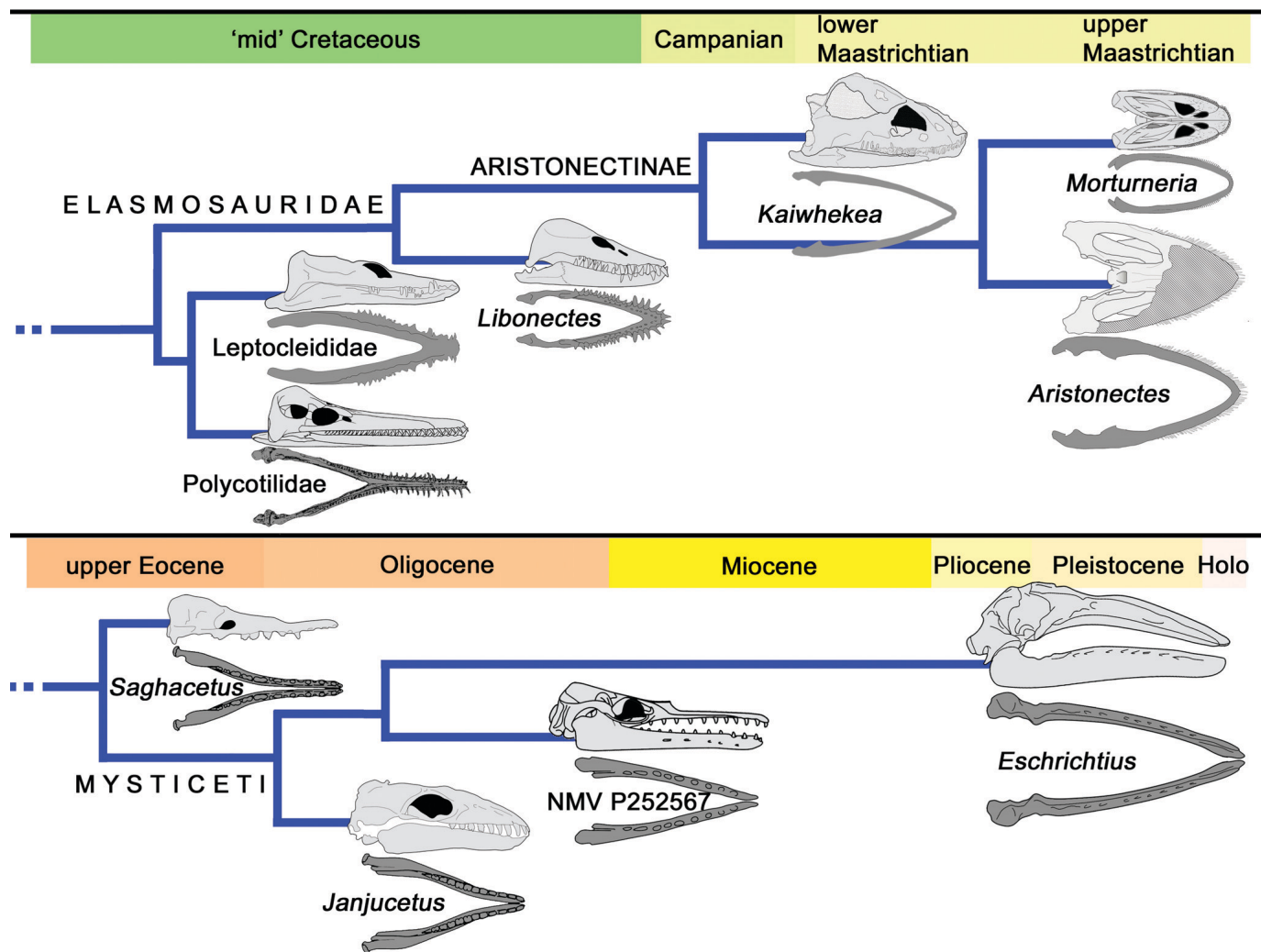
FIGURE 9. Comparative phylogenies of the stepwise evolution of sieve feeding in elasmosaurs (top) and basal mysticete cetaceans (bottom). Phylogeny for elasmosaur relationships is taken from Otero (2016); cetacean phylogeny and reconstruction of feeding mode rely on Marx et al. (2016). Basal members of both clades have large teeth and reinforced mandibular symphyses and probably fed on relatively large, pelagic prey. Both clades then evolve larger mandibles and oral volumes, coupled with decreasing tooth size and gracile symphyses (basal toothed mysticetes in cetaceans, *Kaiwhekea* in aristonectines). Lastly, the most derived members of both clades possess a large oral volume with an arched, keeled palate, massive, bowed mandible, and a specialized sieving battery (interdigitating tooth combs in aristonectines, baleen in cetaceans). Skull outlines not to scale.

(Eschrichtiidae; Bouetel, 2005; Goldbogen et al., 2012; Berta et al., 2015). Both plesiosaur and whale possess deeply arched palates with a midline keel, a posteriorly placed jaw articulation with a hoop-like mandible and poorly reinforced symphysis (Pyenson et al., 2012), and a lateral sieving battery (although comprising teeth rather than baleen in plesiosaurs). We speculate that *Morturneria* may have consumed soft crustaceans or other prey by processing substrate, similar to how modern gray whales consume amphipods (Bouetel, 2005). Small crustacean fossils are abundant in the aristonectine-bearing Lopez de Bertodano Formation of Seymour Island (Chatterjee and Small, 1989) and the Quiriquina Formation of central Chile (Förster and Stinnesbeck, 1987). Baleen whales also have prominent lips lateral to the baleen sieving battery, and it is possible *Morturneria* had lips covering the teeth, nourished and innervated by the large neurovascular foramina present on premaxilla, maxilla, and mandible. However, the presence and function of any labial soft tissue is unknown, and it has been omitted from the reconstruction in Figure 10. The mandibles of baleen whales do carry a row of neurovascular foramina whose size and location resembles that of *Morturneria*.

Recent work on the evolution of cetacean feeding (Marx et al., 2016) documents that feeding modes incorporating suction are widespread in both odontocetes and mysticetes, and that suction feeding is probably plesiomorphic for mysticetes. Marx et al. (2016) further hypothesize that suction-sieve feeding was an intermediate stage in the evolution of the various types of sieve feeding found in derived modern mysticetes, and critically that this feeding mode is not reliant on baleen to function. Some basal mysticetes also had tooth batteries derived for sieve feeding, a remarkable case of convergent evolution (Geisler et al., 2017). The evolution of mysticete-like filter feeding in the aristonectine elasmosaurs of the terminal Cretaceous was the culminating phase of an evolutionary transition that mirrors that of basal mysticetes 30 million years later in the Oligocene (Clementz et al., 2014; Fig. 9). Both basal elasmosaurs and basal mysticetes had robust teeth and heavily reinforced symphyses; the skull of the basal mysticete *Janjucetus*, from the Oligocene of Australia, is remarkably similar to an elasmosaur in overall form. Both clades contain sequentially more derived members with high sagittal crests, gracile symphyses, and reduced
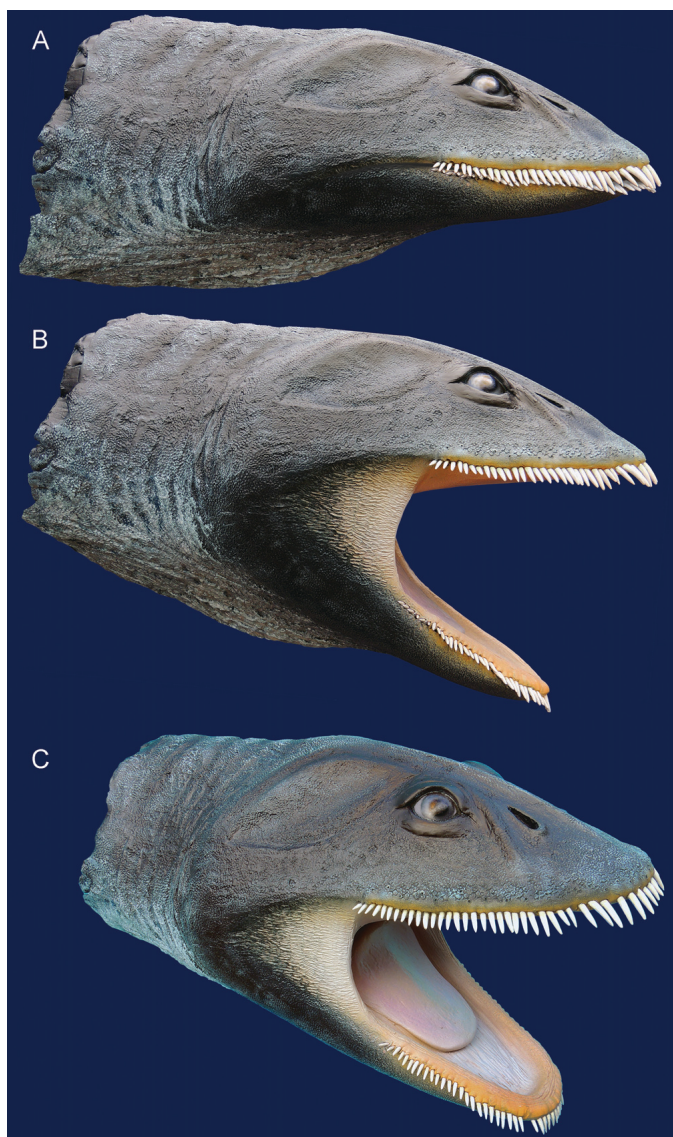
FIGURE 10. Life reconstruction of *Morturneria seymourensis*. Retouched photographs of a model sculpted by S.J.G. **A**, mouth closed; **B**, mouth open; **C**, oblique view with mouth open.

dentition (aetiocetids amongst cetaceans, and *Kaiwhekea* among plesiosaurs), followed by taxa with large, flattened skulls, enlarged oral volume, bowed dentaries, and a sieving battery. This similar sequence of morphological transitions implies that the clades followed similar paths in the evolution of filter feeding. We speculate that aristonectines were suction-sieve feeders, like archaic mysticetes and extant gray whales. Comparison with pinnipeds is also of interest; crabeater seals are known to filter feed and use their very derived teeth and an elongated tooth row to facilitate this (Jones et al., 2013). However, the jaw itself is not derived relative to closely related, raptorial feeders. Aristonectine mandibles are more similar in some ways to those of the extant walrus, sharing a long, 'heavy' ramus and seemingly low bite forces (Jones et al., 2013). Therefore, comparative evidence from both whales and pinnipeds supports an inference of suction-sieve feeding for aristonectines.

Filter feeding is considered a key innovation allowing diversification of mysticete cetaceans (Pyenson et al., 2014) and has been firmly linked to the establishment of the Antarctic Circumpolar Current (ACC) and associated upwelling near the Eocene-Oligocene boundary (circa 34 Ma; Clementz et al., 2014). More generally, changes in ocean circulation and associated primary productivity are a key extrinsic driver of diversification in a range of marine tetrapod clades (Polycn et al., 2014; Pyenson et al., 2014). Here we hypothesize that suction-sieve filter feeding arose in plesiosaurs in the Maastrichtian and hence was not anatomically impossible. Therefore, the general lack of filter feeding in Jurassic and Cretaceous marine tetrapods may have an extrinsic rather than intrinsic cause, and the relatively stagnant ocean conditions prevalent for most of the Mesozoic are an obvious candidate for this (Donnadieu et al., 2016). Recent work has shown that southern ocean circulation reorganized fundamentally in the Late Cretaceous; the inception of Caribbean circulation and the opening of the Drake Passage resulted in better ventilation of the high-latitude southern ocean, with a concomitant increase in upwelling and primary productivity (Clementz et al., 2014). The evolution of plesiosaur filter feeding is coincident with this reorganization. Perhaps whale-like filter feeding did not evolve in plesiosaurs until high-latitude primary productivity increased enough to support it.

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