

The synonymy of the Late Cretaceous mosasaur (Squamata) genus *Lakumasaurus* from Antarctica with *Taniwhasaurus* from New Zealand and its bearing upon faunal similarity within the Weddellian Province

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Novas *et al.* (2002, *Ameghiniana* 39:245–249) described and named a new mosasaur as *Lakumasaurus antarcticus* from the Late Cretaceous marine deposits of the Antarctic Peninsula. The specimen was recovered from the late Campanian Santa Marta Formation on James Ross Island. A number of characters indicate the affinities of *Lakumasaurus* with the Tylosaurinae. However, other characters of *Lakumasaurus* are unusual among tylosaurines, particularly the dentition bearing fine striae, teeth with non-serrated anterior carinae, anterior teeth without posterior carinae, relatively straight lateral margins on frontal and relatively small size. Investigation of mosasaurs from New Zealand confirms that these characters occur in the type specimen of *Taniwhasaurus oweni* Hector 1874, collected from the late Campanian Conway Formation of Haumuri Bluff. Size and similar morphological characters indicate the synonymy of *Lakumasaurus* with *Taniwhasaurus*.

The synonymy of *Lakumasaurus* with *Taniwhasaurus* adds significantly to the evidence of endemism among marine reptiles in Antarctica, New Zealand and Patagonia (Weddellian Province) during the Late Cretaceous. *Taniwhasaurus* along with the possible co-occurrence of *Moanasaurus* are the first mosasaurs at a generic level to indicate Gondwanan endemism. The mosasaur evidence is complemented by the plesiosaur *Aristonectes*, which occurs in the Maastrichtian of Argentina and Antarctica and appears similar to *Kaiwhekea* from the Maastrichtian of New Zealand, and by *Mauisaurus*, an elasmosaurid which occurs in the Maastrichtian of Antarctica and medial Campanian-Maastrichtian of New Zealand. Copyright © 2007 John Wiley & Sons, Ltd.

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1. INTRODUCTION

Some of the first mosasaurs from the Southern Hemisphere were described from the South Island of New Zealand during the nineteenth century (e.g. Hood 1870; Hector 1874). These vertebrates were carnivorous marine reptiles that evolved and diversified in the Late Cretaceous to become worldwide in distribution before their demise at the Cretaceous-Tertiary boundary. Much of the early research concerning the Mosasauridae occurred in North America and Europe, and the last continent upon which these marine reptiles were identified is Antarctica (Gasparini and del Valle 1981). The mosasaur genera under consideration here were both found in the Southern Hemisphere, *Taniwhasaurus* from New Zealand (Figure 1A) and *Lakumasaurus* from Antarctica (Figure 1F).

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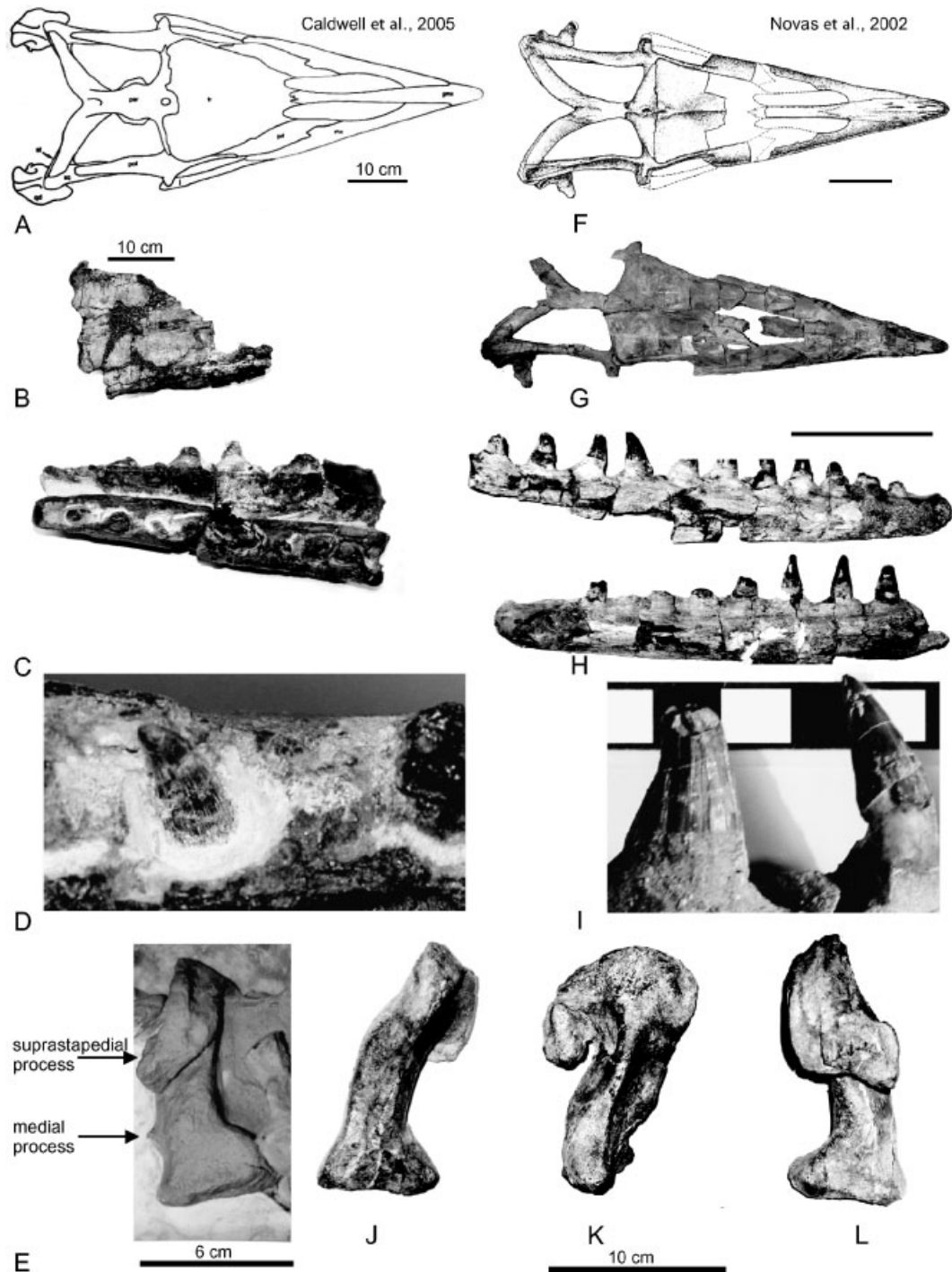


Figure 1. *Taniwhasaurus oweni*, KHM N99-1014: (A) Cranial reconstruction, dorsal view, from Caldwell *et al.* (2005). *T. oweni*, NZNM R1536: (B) Cranial roof, dorsal view; (C) Lower jaws, dorsolateral view; (D) Close-up of erupting tooth. *T. oweni*, KHM N99-1014: (E) Quadrate cast, posterior view. *Taniwhasaurus antarcticus*, IAA 2000-JR-FSM-1: (F) Cranial reconstruction, dorsal view, from Novas *et al.* (2002); (G) Cranium, dorsal view; (H) Lower jaws, lateral view; (I) Close-up of teeth; (J) Quadrate, anterior view; (K) Quadrate, medial view; (L) Quadrate, posterior view. Scales in cm. Scale of B applies also to G; H applies also to C; I applies also to D, and K applies also to J and L.

The discovery and recognition of the mosasaurs in Europe, first represented by *Mosasaurus hoffmanni*, has become legendary (e.g. Russell 1967; Bardet and Jagt 1996), and once their relationships became better understood, researchers recognized these marine creatures in the Late Cretaceous of New Zealand. The first mosasaur appears to have been collected in 1869 by Thomas Hood Cockburn Hood from the Waipara River drainage on the South Island of New Zealand (Hood 1870). Hood communicated with both Julius Haast, who founded the Canterbury Museum in Christchurch, and Richard Owen, the renowned English anatomist. Owen previously described plesiosaurs that had been collected and shipped to him by Hood. In similar fashion, the mosasaur specimens from the Waipara River area were inspected by Haast, who had a drawing made of the largest (78 cm) and most complete specimen (Welles and Gregg 1971, p. 11), and shipped to Owen in England via the *Matoaka*. However, the specimens did not arrive at their destination because the *Matoaka* was apparently lost at sea. Therefore, only the 1:1 drawing remains of the lower jaws and maxilla of this specimen.

Three other workers were to become central figures in the early discovery of New Zealand mosasaurs. James Hector established the Colonial Museum in Wellington 4 years after Haast became director of the Canterbury Museum. William Thomas Locke Travers collected for the Colonial Museum, and both directors hired Alexander McKay to collect for their respective institutions during the ensuing two decades.

Another locality had been discovered nearly 100 km north of the Waipara River area near Haumuri Bluff. Haast, Hector, Travers and McKay all contributed to the knowledge of the marine reptile assemblage at Haumuri Bluff. One of the pivotal works in the understanding of this assemblage was that of Hector (1874), who described eight new marine reptiles, including two mosasaurs from Haumuri Bluff. These included a medium-sized mosasaur, *Taniwhasaurus oweni* collected by Travers and a large taxon usually considered *Tylosaurus haumuriensis* (e.g. Welles and Gregg 1971) collected by McKay. The former species exhibits a number of characters taken together that diagnose a distinct tylosaurine taxon, including fine striae on the teeth, dentition bearing non-serrated anterior carinae, anterior dentition without posterior carinae, relatively straight lateral margins on the fused frontal shield and relatively small size for a tylosaurine.

Only the lectotype specimen of *T. oweni*, NMNZ R1536, housed at the Museum of New Zealand Te Papa Tongarewa in Wellington, was known from the 1800s until recently, and that specimen included only a partial cranial table and the anterior portions of both dentaries (Figure 1B,C). Recently, a second specimen was recovered in the Haumuri Bluff area on the South Island of New Zealand. The second specimen, KHM N99–1014, reposed at the Kaikoura Historical Museum, is more complete than the lectotype, consisting of a partial skull including the quadrate (Figure 1E) and portions of both lower jaws (Caldwell *et al.* 2005).

The stratigraphic source of these two specimens is important in their comparison to *Lakumasaurus* from Antarctica. Recent investigations (Wilson *et al.* 2005) utilizing the biostratigraphy of dinoflagellates from Late Cretaceous sections have allowed greater resolution of the stratigraphic sources of the marine reptiles from New Zealand. Both specimens were collected from the Conway Formation in the Haumuri Bluff area. By comparing the dinoflagellate cysts associated with the lectotype of *T. oweni*, a late Campanian age was established for the specimen. The recently discovered referred specimen of *T. oweni* was collected from lower in the section at Haumuri Bluff from middle Campanian sediments (Wilson *et al.* 2005).

The second taxon under consideration is the holotype specimen of *Lakumasaurus antarcticus*, described from James Ross Island, east of the Antarctic Peninsula (Novas *et al.* 2002). The previously known mosasaur specimens from Antarctica were poorly preserved, consisting mostly of isolated fragmentary teeth (Martin *et al.* 2002). Two partial jaws of *Leiodon* and fragmentary cranial elements of a specimen tentatively assigned to *Moanasaurus* were described, but the remaining specimens were mostly isolated teeth assigned to mosasaurines and plioplatecarpines. The latter teeth were assigned to the Plioplatecarpinae based upon small teeth with distinct striations. The holotype of *L. antarcticus* was the first relatively well-preserved skull (Figure 1G) from Antarctica, and significantly, was also collected from the late Campanian portion of the Late Cretaceous (Martin 2006). The specimen consists of a partial cranium with quadrates, lower jaws and numerous vertebrae.

Both *Taniwhasaurus* and *Lakumasaurus* were derived from the Weddellian faunal province (Zinsmeister 1979, 1982) that includes Patagonia, New Zealand, Antarctica and eastern Australia. Both genera were also collected from middle to upper Campanian deposits. Therefore, the geographic and stratigraphic positions are both similar.

1.1. Institutional abbreviations

DM, Dominion Museum, Wellington, New Zealand = NMNZ, IAA, Instituto Antártico Argentino, Buenos Aires, Argentina; KHM, Kaikoura Historical Museum, Kaikoura, New Zealand; MLP, Museo de La Plata, La Plata, Argentina; NMNZ Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.

2. CHARACTERS

The description of *Taniwhasaurus oweni* Hector, 1874 from New Zealand has been presented by Welles and Gregg (1971) and Caldwell *et al.* (2005), so only salient points will be reiterated here. Also, the holotype of *Lakumasaurus antarcticus* is being redescribed by us and incorporated into a phylogenetic analysis of the tylosaurines. In the meantime, important characters that illustrate the similarity of *Lakumasaurus* to *Taniwhasaurus* will be described herein.

T. oweni and *L. antarcticus* are characterized by a long, premental rostrum, anterior premental process on the dentaries and exclusion of the frontal from the margin of the orbit, indicating affinities with the Tylosaurinae (Russell 1967; Bell 1997). Both genera (Figure 1A,F) are relatively short-faced compared to other members of the Tylosaurinae (*Tylosaurus* and *Hainosaurus*), perhaps accounting for the less derived, robust prefrontal that shares a long contact with the maxilla and remains in contact with the posterior margin of the narial opening (see Caldwell *et al.* 2005). However, unlike most members of the Tylosaurinae and more similar to those of the Plioplatecarpinae, *Taniwhasaurus* and *Lakumasaurus* possess a dentition that is characterized by deep, vertical striations on the tooth crowns (Figure 1D,I). Although the lectotype of *T. oweni* is poorly preserved with broken tooth crowns, remnants and an erupting tooth are finely striated and do not exhibit posterior carinae. Only a cast of the referred specimen of *T. oweni* was available for inspection at the Canterbury Museum as the original was on loan and the teeth were not described by Caldwell *et al.* (2005). However, even on the cast, striated teeth were obvious, and no posterior carinae were noted on KHM N99-1014. *L. antarcticus* has distinctly striated teeth with non-serrated anterior carinae and anterior teeth without posterior carinae. The relatively short, fused premaxillary rostrum of both genera has a dorsal ridge, and the frontal too has a sagittal keel. The lateral margins of the frontal of both genera are straight. Even considering ontogeny, the type specimens of both taxa are of the same approximate size with the frontal of *T. oweni* measuring 160 mm across the orbits whereas that of *L. antarcticus* measures 167 mm. Both genera also possess a quadrate whose main vertical shaft is deflected laterally and a pronounced, ventromedially directed process of the suprastapedial (Figure 1E, J–L). These features essentially lock the posterior motion of the jaws at maximum posterior rotation of the quadrate. The suprastapedial is expanded anterodorsally (Figure 1K) providing long curvature of the dorsal margin of the quadrate that also possesses a shallow groove. However, some differences occur between the species. *T. oweni* has a quadrate with long, squared-off ventromedially directed suprastapedial process (Figure 1E), whereas *L. antarcticus* has a shorter, more blunt process (Figure 1L). *T. oweni* exhibits a medial quadrate process (Figure 1E) occurring at a point approximately a quarter of the length up the quadrate shaft, but this process is absent on the quadrate of *L. antarcticus* (Figure 1L). Also, the posterior frontal suture of *T. oweni* is not linear along its contact with the parietal (Figure 1A), whereas the posterior margin of the frontal is straight on that of *L. antarcticus* (Figure 1F). Therefore, these tylosaurine mosasaurs are very similar, differing in relatively few characters; consequently, *T. oweni* and *L. antarcticus* are herewith subsumed in synonymy at the generic level, but retained as separate taxa at the specific level. *T. oweni* has priority, and therefore remains valid with the Antarctic taxon regarded as *Taniwhasaurus antarcticus* (Novas *et al.*) 2002.

3. SYSTEMATICS

Order SQUAMATA Opperl, 1811
Family Mosasauridae Gervais, 1853
Subfamily Tylosaurinae Williston, 1897
Genus *Taniwhasaurus* Hector, 1874

- 1873 *Taniwhasaurus* Hector, p. 3 (nomen nudum)
 1874 *Taniwhasaurus* Hector, p. 338
 1888 *Platecarpus* Lydekker, p. 270
 2002 *Lakumasaurus* Novas *et al.*, p. 245

Type species. *T. oweni* Hector, 1874

Distribution. Upper Cretaceous of New Zealand and Antarctica

Generic definition. Relatively short-faced tylosaurine mosasaurid with dentition possessing vertical, well-defined non-bifurcating striations that fade near the tooth tips, lack of posterior carinae on anterior teeth, shaft of quadrate strongly deflected laterally, suprastapedial process prominent and ventromedially extended, anterodorsal corner of suprastapedial process expanded resulting in long anteroposterior dorsal surface, premaxillae with dorsal ridge, frontal with straight lateral margins and dorsal keel and pineal opening on raised eminence indicated by raised margin on posterior frontal.

Type species *Taniwhasaurus oweni* Hector, 1874
 (Figure 1A–E)

- 1874 *Taniwhasaurus oweni* Hector, p. 338
 1888 *Platecarpus oweni* (Hector); Lydekker, p. 270

Lectotype: NMNZ, R1536, cranial roof and anterior dentaries.

Referred specimens: KHM N99-1014, partial skull, scapula/coracoid, cervical vertebrae; KHM N99-1015, three caudal vertebrae.

Distribution: Upper Cretaceous (middle to upper Campanian) from the Conway Formation (Wilson *et al.* 2005) on the northern face of Haumuri Bluff south of Kaikoura at Spy Glass Point, South Island, New Zealand.

Diagnosis: A medium-sized tylosaurine mosasaurid having quadrate with long, squared-off ventromedially directed suprastapedial process, quadrate with medial quadrate process occurring at a point approximately a quarter of the length up the shaft, and posterior frontal suture not linear along contact with parietal.

Referred species: *Taniwhasaurus antarcticus* (Novas *et al.*, 2002)
 (Figure 1F–L)

- 2002 *Lakumasaurus antarcticus* Novas *et al.*, p. 245

Holotype: IAA 2000-JR-FSM-1, skull, rib fragments and vertebrae.

Distribution: Upper Cretaceous (upper Campanian) from the Santa Marta Formation from Santa Marta Cove on the northwestern portion of James Ross Island situated east of the Antarctic Peninsula.

Diagnosis: A medium-sized tylosaurine mosasaurid having quadrate shaft without medial quadrate process, relatively short medially flattened suprastapedial process and straight posterior margin of frontal.

4. PALAEOBIOGEOGRAPHY

The synonymy of *Lakumasaurus* with *Taniwhasaurus* is significant in regard to faunal endemism in the Late Cretaceous Weddellian Province (Zinsmeister 1979, 1982) of Antarctica, New Zealand, and Patagonia. *Taniwhasaurus* is the first mosasaur at a generic level to indicate endemism in the Weddellian Province. Martin *et al.* (2002) described fragmentary mosasaur cranial remains collected from Seymour (Marambio) Island from the late Maastrichtian Lopez de Bertodano Formation (Martin 2006) that were compared with *Moanasaurus*, a genus described first from the Mangahouanga Stream on the North Island of New Zealand (Wiffen 1980). Mangahouanga Stream is a tributary of the Te Hoe River occurring in the western Hawke's Bay and contains large boulders from

which the holotype of *Moanasaurus mangahouangae* was collected. These boulders were derived from the Maungataniwha Sandstone of Campanian-Maastrichtian age (Crampton and Moore 1990, p. 333). Therefore, similar age and morphology indicates the probable occurrence of this mosasaur in Antarctica and New Zealand, but not at lower latitudes with our current state of knowledge.

The mosasaur evidence may be complemented by plesiosaur evidence. *Aristonectes* is a plesiosaur characterized by a short, wide skull with numerous small teeth, indicating this plesiosaur may have strained the waters for small prey (Gasparini *et al.* 2003a). *Aristonectes parvidens* was originally described from the Maastrichtian Lefipan Member of the Paso del Sapo Formation in Chubut Province of southern Argentina (Cabrera 1941). A second specimen was identified from the upper Campanian-lower Maastrichtian Quiriquina Formation from Quiriquina Island, southern Chile (Casamiquela 1969). A juvenile plesiosaur specimen from Antarctica, *Morturneria* (originally described as *Turneria* preoccupied, Chatterjee and Small 1989), was placed in synonymy with *Aristonectes* (Gasparini *et al.* 2003a). This specimen was collected on Seymour (Marambio) Island from the Maastrichtian upper Lopez de Bertodano Formation. Although the specimens from Antarctica and South America were considered conspecific (Gasparini *et al.* 2003a), differences in ontogeny leave some doubt. Some differences between the Antarctic and Argentine specimens such as tooth count are probably due to different ontogenetic stages, but until similar aged specimens are found, the possibility exists that they may be different at a specific level. Nevertheless, this unusual plesiosaur that exhibits lateral ridges on the cervical vertebrae, an elasmosaurid character, occurs in South America and Antarctica, but not at higher latitudes. However, another very similar taxon occurs in New Zealand. *Kaiwhekea* has recently been described from the Maastrichtian Katiki Formation at Shag Point coastal Otago on the South Island of New Zealand (Cruickshank and Fordyce 2002). This taxon is exceedingly similar to *Aristonectes*, but differs significantly in the lack of lateral ridges on the cervical vertebrae. This taxon too appears to have morphologies adapted to strained prey.

Another marine reptile also appears to be confined to the Weddellian Province. When Hector (1874) described *Taniwhasaurus*, he also described a large elasmosaurid, *Mauisaurus haasti*, from a kilometre above the mouth of the Jed River between Haumuri Bluff and the Waipara River area, South Island, New Zealand. The lectotype occurred in the middle Campanian portion of the Conway Formation, and specimens have been found from lower Maastrichtian rocks (Wilson *et al.* 2005). *Mauisaurus* has been characterized by having a circular head on the femur, among other features (Hiller *et al.* 2005), and undescribed specimens collected by parties under the direction of M.O. Woodburne from the Lopez de Bertodano Formation on Seymour Island, Antarctica, preserve the circular head. Also, Gasparini *et al.* (2003b) referred to this taxon a specimen described by Chatterjee and Small (1989) also from the Late Cretaceous Lopez de Bertodano Formation of Seymour Island (Marambio), Antarctica, and Hiller *et al.* (2005) assigned a third elasmosaurid specimen (MLP 82 I 28–1) previously described by Gasparini *et al.* (1984) from the same formation and island to *Mauisaurus*. Another specimen from Seymour Island referred to *Mauisaurus* is a partial skeleton including a femur (Fostowicz-Frelik and Gazdzicki 2001). Therefore, *Mauisaurus* appears relatively common in New Zealand and Antarctica. Patagonia was added to the distribution of elasmosaurids compared to *Mauisaurus* by Gasparini and Salgado (2000) and Gasparini *et al.* (2003b), but Hiller *et al.* (2005) felt these specimens did not preserve diagnostic features to allow assignment to *Mauisaurus*. Perhaps with additional better preserved specimens this taxon will be substantiated to have occurred in Patagonia during the Late Cretaceous. Gasparini *et al.* (2003b) also referred a juvenile specimen from Patagonia as *Tuarangisaurus?* This taxon was originally described from the Mangahouanga Stream area of New Zealand (Wiffen and Molesley 1986). Although this taxon too is uncertain, the overwhelming evidence appears to indicate an endemic Weddellian assemblage of marine reptiles through Campanian-Maastrichtian times.

5. SUMMARY

Both *Taniwhasaurus oweni* and *Lakumasaurus antarcticus* are of similar size and occur in the Campanian deposits of New Zealand and Antarctica, respectively. Both mosasaurs are members of the Tylosaurinae due to possession of an elongate rostrum, shallow dentaries with predental processes and frontal eliminated from orbital margin. Both

genera share the following synapomorphies: relatively short rostrum, striated dentition, premaxillae with dorsal ridge, frontal with dorsal keel and straight lateral sides, quadrate deflected laterally, suprastapedial process of quadrate long and directed ventromedially, and long dorsal margin of quadrate. The retention of the prefrontal forming part of the narial opening is a plesiomorphic character associated with the relatively short snout. Only relatively minor features differ between the two species, and therefore, *Lakumasaurus* from Antarctica is placed in synonymy with *Taniwhasaurus* from New Zealand.

As an aside, *Taniwhasaurus* was named for Taniwha (pronounced Tanifa), the mythical aquatic monster of the native Maori people of New Zealand, and *Lakumasaurus* was named for Lakuma, the mythical sea monster of the Yamana Indians of Tierra del Fuego. Evidently, the synonymy was predestined.

Taniwhasaurus oweni differs from *Taniwhasaurus antarcticus* in possession of a medial quadrate process, long suprastapedial process of quadrate, and non-linear posterior frontal margin.

Caldwell *et al.* (2005) also placed *Tylosaurus haumuriensis* Hector 1874 in synonymy with *Taniwhasaurus*. *T. haumuriensis* is represented only by the holotype cranium and associated jaws, and was collected from the same area as *T. oweni*. However, *Taniwhasaurus oweni* exhibits striated teeth, whereas *T. haumuriensis* possesses smooth-faced enamel; the specimen of the latter taxon also appears significantly larger, particularly when comparing the robust nature of the lower jaws.

Fine vertical striae covering the teeth have long been considered indicative of plioplatecarpine mosasaurs (e.g. Russell 1967), so the occurrence of a tylosaurine mosasaur with prominent striae on the lateral sides of the teeth was somewhat unexpected. However, tylosaurines and plioplatecarpines are closely related in the parafamily Russellosaurina (Polcyn and Bell 2005) and tylosaurines may exhibit striations near the crown base on the internal side, so the occurrence may not be surprising. However, the occurrence of a tylosaurine with this feature casts doubt upon other isolated, totally striated, non-recurved teeth assigned to plioplatecarpines in Gondwana (e.g. Martin *et al.* 2002; Martin 2006; Martin and Crame 2006). Only more complete material from Antarctica and Patagonia will confirm these generic assignments. Of note, among the relatively numerous specimens collected from well over a century in New Zealand, no evidence of a plioplatecarpine has been recovered. One might be tempted to expect that *Plioplatecarpus* was excluded from the Weddellian Province by *Taniwhasaurus*, which also possesses striated teeth. However, tooth shape and the jaw articulation through the quadrate are radically different, indicating much different mosasaurs and presumably different habits.

Late Cretaceous endemism of marine reptiles within the Weddellian faunal province, including Antarctica, New Zealand, and Patagonia, has been proposed previously (e.g. Gasparini *et al.* 2003b). The synonymy of *Lakumasaurus* with *Taniwhasaurus* adds significantly to the evidence of marine reptile endemism. *Taniwhasaurus* along with the possible co-occurrence of *Moanasaurus* are the first mosasaurs at a generic level to indicate endemism. The occurrences of *Taniwhasaurus* and possibly *Moanasaurus* may be coupled with evidence from the Plesiosauroidea. The plesiosaurs *Aristonectes* and *Mauisaurus*, also appear to have inhabited the Weddellian Province. *Aristonectes* occurs in the Maastrichtian of Argentina and Antarctica and appears similar to *Kaiwhekea* from the Maastrichtian of New Zealand, and *Mauisaurus* occurs in the Maastrichtian of Antarctica and medial Campanian-Maastrichtian of New Zealand. Therefore, the marine reptile evidence complements that of the invertebrate assemblages (e.g. Zinsmeister 1982) to indicate endemism during the Late Cretaceous (Campanian-Maastrichtian).

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