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C. R. Palevol 4 (2005) 663–669
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Systematic Paleontology (Vertebrate Paleontology)

# A Late Campanian sphenodontid (Reptilia, Diapsida) from northern Patagonia

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Received 11 October 2004; accepted 7 June 2005

Available online 28 July 2005

Presented by Philippe Taquet

**Abstract**

The fossil record of sphenodontids in the Southern Hemisphere is much longer than in Laurasia, where they became extinct after Early Cretaceous times. Recent works demonstrated the persistence of at least eilenodontine sphenodontids until the 'mid'-Cretaceous of Patagonia. Focused examination of the Los Alamitos Formation collections provided remains of Late Campanian sphenodontids. Although the phylogenetic position of these remains is still uncertain, they belong to a new, unrecorded species of sphenodontid perhaps related to opisthodontians or primitive, toothed sapheosaurs. ***To cite this article: S. Apesteguía, C. R. Palevol 4 (2005)***.


**Résumé**

**Un sphénodontide (Reptilien, Diaprida) de la fin du Campanien du Nord de la Patagonie**. L'enregistrement de fossiles de sphénodontides est beaucoup plus important dans l'hémisphère sud qu'en Laurasie, où l'on note leur extinction après le Crétacé inférieur. De récents travaux démontrent que des sphénodontides eilénodontides, au moins, ont survécu en Patagonie jusqu'au milieu du Crétacé. L'examen détaillé des échantillons récoltés dans la formation de Los Alamitos a fourni des restes de sphénodontides datant du Campanien supérieur. Bien que la position phylogénétique de ces restes soit encore incertaine, ceux-ci appartiennent à une nouvelle espèce de sphénodontides non répertoriée, peut-être en relation avec les opisthodontes ou des saphéosaures dentés primitifs. ***Pour citer cet article : S. Apesteguía, C. R. Palevol 4 (2005)***.


*Keywords:* Late Cretaceous; Sphenodontid; Gondwana; Patagonia

*Mots clés :* Crétacé supérieur ; Sphénodontide ; Gondwana ; Patagonie

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doi:10.1016/j.crpv.2005.06.003

## 1. Introduction

As evidenced by their fossil record, sphenodontids survived in southern continents much beyond their proposed extinction in Laurasia [2], where the diversification of lizards probably restricted their adaptive zones and drove them to extinction after Early Cretaceous times [7].

The presence of extant sphenodontines in New Zealand predicted the survival of this group in at least some regions of Greater Gondwana [1] through most of the Late Cretaceous. This was corroborated by *Priosphenodon*, which shows not only the survival of sphenodontids into the 'mid'-Cretaceous, but also the presence of a different lineage from that including the extant *Sphenodon*. Eilenodontine sphenodontids survived in Patagonia until 'mid'-Cretaceous times, at least [2]. However, no other lineages, including the sphenodontines, have been recorded up to now in younger Cretaceous strata.

The Late Campanian Los Alamitos Formation yielded an abundant fossil collection housed in the Museo Argentino de Ciencias Naturales, resulting from the collection trips of Jose F. Bonaparte during the years 1980–1990 [3–6]. Careful examination of these abundant remains, focused on lepidosaurian remains, yielded fragmentary sphenodontid material, including a rather well-preserved lower jaw and other fragments belonging to species unknown until then.

## 2. Systematic palaeontology

Lepidosauria Haeckel 1866
Rhynchocephalia Günther, 1867
Sphenodontia Williston, 1925
Sphenodontidae Cope, 1869
*Kawasphenodon expectatus* gen et. sp. nov.

### *Holotype*

MACN Pv RN1098 (Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires, Argentina), consisting of an incomplete adult left lower jaw (Figs. 2 and 3a).

### *Etymology*

From Tehuelchean *Kawas*, god of the seas; *sphenos*, wedged; *odontos,* tooth, in reference to the littoral sediments where it was found; and *expectatus* because, as living today in New Zealand, sphenodontids were expected to occur in Patagonia throughout the Cretaceous, and this fact prompted the re-examination of the fossil collections focusing on sphenodontids.

### *Locality and horizon*

Mid layers of the Los Alamitos Formation (Late Campanian–Early Maastrichtian) at the Estancia 'Los Alamitos', Río Negro Province, northwestern Patagonia, Argentina (Fig. 1). The specimen was found in fluvial mudstones and sandstones, in association with snakes, turtles, crocodyliforms, theropod and sauropod dinosaurs, mammals and dipnoan fishes.

### *Additional material*

Four isolated additional fragments were also found in the same area. From these, only two (MACN Pv RN1099a–b) constitute the hypodigm of this new species. On the other side, MACN Pv RN1099c and MACN Pv RN1100, Fig. 4) are here considered as Sphenodontidae indet., because they cannot be confidently referred to *K. expectatus*.

### *Diagnosis*

*Kawasphenodon* differs from other sphenodontians in having a distinct, deep and single groove on the pos-

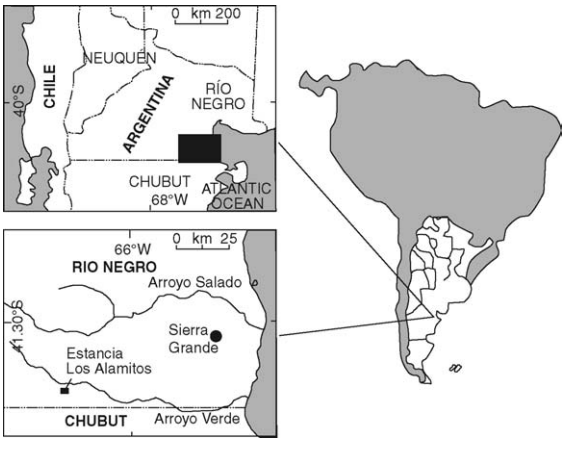


Fig. 1. Map of South America showing the Los Alamitos fossil locality (modified from [4]).
Fig. 1. Carte d'Amérique du Sud montrant la localité fossilifère de Los Alamitos (modifiée d'après [4]).

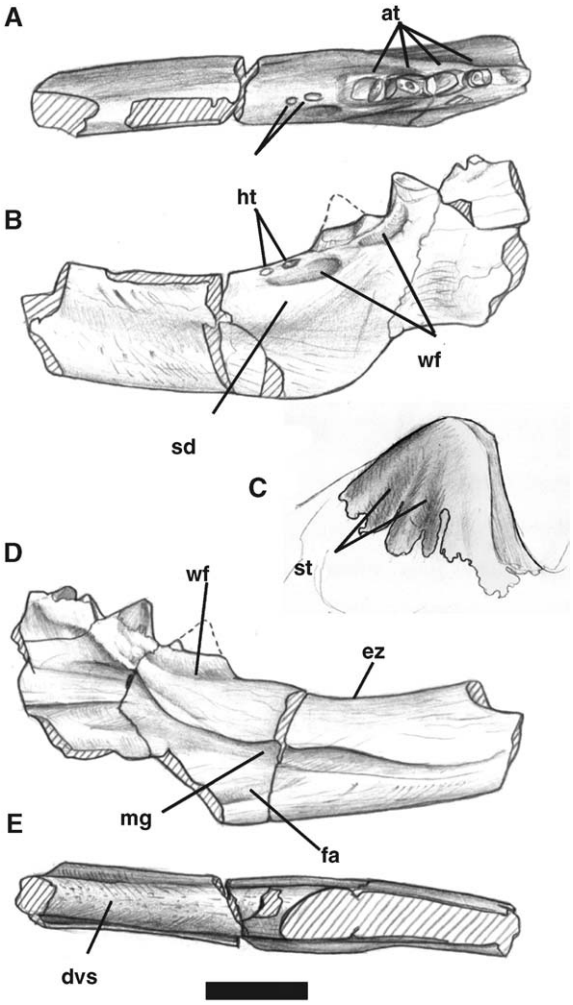


Fig. 2. MACN Pv RN1098. *Kawasphenodon expectatus* nov. gen. et sp. Left lower jaw in occlusal (**A**), labial (**B**), lingual (**D**) and ventral (**E**) views. **C** shows a detail of a tooth in lingual view. Abbreviations: **at**, additional teeth; **dvs**, dentary ventral sculpture; **ez**, edentulous zone; **fa**, facet for angular; **ht**, hatching teeth; **mg**, Meckelian groove; **sd**, secondary dentine; **st**, striae; **wf**, wear facets. Scale bar: 10 mm.
Fig. 2. MACN Pv RN1098. *Kawasphenodon expectatus* nov. gen. et sp. Mâchoire inférieure gauche en vues occlusale (**A**), labiale (**B**), linguale (**D**) et ventrale (**E**). **C** représente un détail de dent en vue linguale. Abréviations : **at**, dents additionnelles ; **dvs**, sculpture dentaire ventrale ; **ez**, zone sans dent ; **fa**, facette pour l'angulaire ; **ht**, dents de remplacement ; **mg**, canal de Meckel ; **sd**, dentine secondaire ; **st**, stries ; **wf**, facettes d'usure. Barre d'échelle : 10 mm

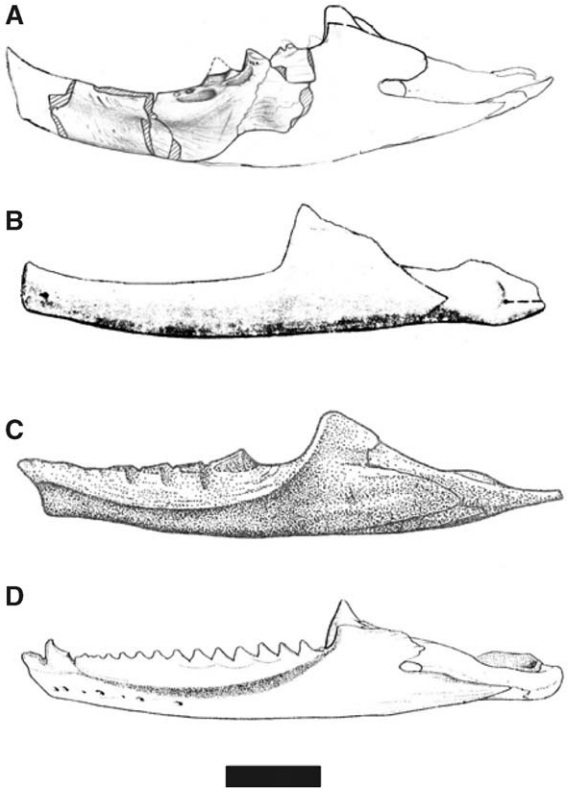


Fig. 3. MACN Pv RN1098. Reconstructed left lower jaw of *Kawasphenodon* (**A**), *Sapheosaurus* (**B**), *Clevosaurus* (**C**), and *Sphenodon* (**D**). Scale bar: 20 mm for **A**; 7 mm for **B** and **C**; 10 mm for **D**. **B** from [8]; **C** from [10]; **D** from [14].
Fig. 3. MACN Pv RN1098. Reconstitution de la mâchoire inférieure gauche de *Kawasphenodon* (**A**), *Sapheosaurus* (**B**), *Clevosaurus* (**C**), et *Sphenodon* (**D**). Barre d'échelle : 20 mm pour **A** ; 7 mm pour **B** et **C** ; 10 mm pour **D**. **B** selon [8] ; **C** selon [10] ; **D** selon [14].

terior side of the adult or additional teeth. Additionally, it bears the following unique combination of features: large size; robust, strongly curved, lower jaw, with sculptured ventral and labial aspects; jaw depth larger in the posterior region and much lower in the edentulous anterior region; teeth restricted in the adult forms to the last part of the jaw, with an extensive edentulous mid and anterior region; lower jaw teeth out of the midline; square-based additional teeth; antero-labial flanges subequal or slightly larger than antero-lingual ones; teeth with few, mostly two deep and wide lingual grooves and, when present, fine, dense labial grooves; strongly concave anterior side of the additional teeth, going the tip beyond the base of the tooth in new, unworn teeth.

## 3. Description

The most conspicuous specimen, and thus the holotype, is a large left lower jaw, preserving the central

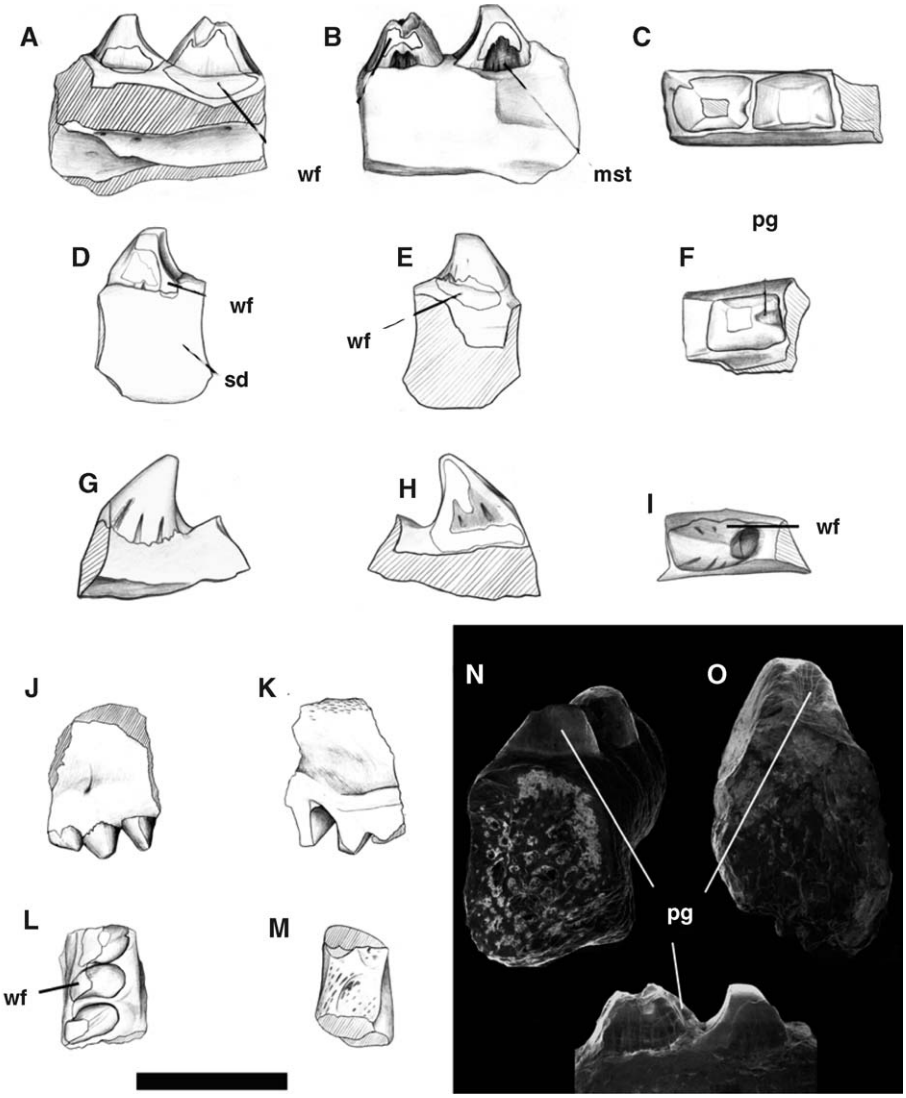


Fig. 4. MACN Pv RN1099a (**A**–**C**). *Kawasphenodon expectatus* nov. gen. et sp. ?Left lower jaw in lingual (**A**), labial (**B**), and occlusal (**C**) views. MACN Pv RN1099b (**D**–**F**). *Kawasphenodon expectatus* nov. gen. et sp. Fragment of ?right lower jaw, with tooth in occlusal (**D**), labial (**E**), and lingual (**F**) views. MACN Pv RN1099c. Sphenodontidae indet. Right lower jaw in lingual (**G**), labial (**H**), and occlusal (**I**) views. MACN Pv RN1100. Sphenodontidae indet. Right palatine in lingual (**J**), labial (**K**), ventral (**L**), and dorsal (**M**) views. SEM images of *Kawasphenodon expectatus* nov. gen. et sp. in posterior views (N, MACN Pv RN1099a and O, MACN Pv RN1099b), and in labial view (P, MACN Pv RN1099a), showing the posterior grooves. Abbreviations: **mst**, microstriations; **pg**, posterior groove; **prf**, prefrontal facet; **sd**, secondary dentine; **wf**, wear facet. Scale bar: 10 mm.

Fig. 4. MACN Pv RN1099a (**A**–**C**). *Kawasphenodon expectatus* nov. gen. et sp.? Mâchoire inférieure gauche en vues linguale (**A**), labiale (**B**) et occlusale (**C**). MACN Pv RN1009b (**D**–**F**). *Kawasphenodon expectatus* nov. gen. et sp. Fragment (?) de mâchoire droite inférieure, avec dent en vues occlusale (**D**), labiale (**E**) et linguale (**F**). MACN Pv RN1099c. Sphenodontidae indet. Mâchoire inférieure droite en vues linguale (**G**), labiale (**H**) et occlusale (**I**). MACN Pv RN1100. Sphenodontidae indet. Palatin droit en vues linguale (**J**), labiale (**K**), ventrale (**L**) et dorsale (**M**). Images MES de *Kawasphenodon expectatus* nov. gen. et sp. en vues postérieures (N, MACN Pv RN1099a et O, MACN Pv RN1099b) ; et labiale (P, MACN Pv RN1099a), montrant les canaux postérieurs. Abréviations : **mst**, micro-striations ; **pg**, rainure postérieure ; **prf**, facette préfrontale ; **sd**, dentine secondaire ; **wf**, facette d'usure.

region, but lacking both symphysial and coronoid regions (Figs. 2 and 3).

The jaw is very high at the posteriormost region, close to the coronoid, and becomes low in the anterior part, edentulous in the adult, where it tapers (Figs. 2 and 3a,b). This jaw configuration resembles that of the sapheosaur *Ankylosphenodon* [11 (Fig. 2)], but the curvature of the bone suggests that the coronoid process, probably low, should have been in a high location, resembling *Sphenodon*. The complete jaw must have measured about 11 cm and the dentary is curved, especially in the dorsal border, as in *Clevosaurus* (Fig. 3e,f) and *Sapheosaurus* (Fig. 3c,d). In both of them, as in *Kawasphenodon*, the process of tooth reduction is advanced, the teeth being restricted to the back of the jaw, with a long completely edentulous mid and anterior region of adult specimens, also present in some *Opisthias* specimens (LACM 120467, 120542) and extreme in *Sapheosaurus* [8]. However, the toothed sapheosaur *Ankylosphenodon* shows that sapheosaur tooth implantation was different from that of known sphenodontids (i.e. ankylotecodonty *sensu* Reynoso 2000 [12]), or at least extremely variable.

In medial view, the preserved region of the mandible shows the anterior end of the facet for the angular, but the preserved part is too anterior to show parts of the coronoid or pre-articular regions. No tooth remains are evident anterior to the angular facet level.

As in *Sphenodon*, the Meckelian groove narrows in the same region in which the angular facet disappears. The lateral region of the jaw, under the secondary dentine growth that forms the labial border, shows narrow, long grooves and pits that are evidence of vascularization and nerves. However, because of the still posterior position of the preserved part of the jaw, there are no preserved mental foramina. The very-well-developed secondary dentine shelf, as in most sphenodontids (e.g., *Cynosphenodon*, *Sphenodon*, *Priosphenodon*, *Clevosaurus*) commonly suffers bone erosion by the maxillary teeth. These wear facets can be precise and triangular in non-propalinal taxa, but in propalinal sphenodontids become long, anteroposteriorly directed grooves or even a continuous abraded region in advanced, eupropalinal sphenodontids (sphenodontines and eilenodontines). The wear facets present in *Kawasphenodon* are not precise, but elongated, thus demonstrating relatively long propalinal movements.

The mandible preserves four additional teeth, as well as two small barely eroded anterior teeth, probably corresponding to remains of hatchling teeth. The additional teeth are separated from each other by a narrow space, only as much as necessary to prevent them from being in contact, and the labial and lingual flanges do not overlap the bases of the preceding tooth. The additionals are square-based as in opisthodontians, but are slightly compressed labiolingually. They are striated in the lingual side, with two large dorsally tapering grooves (Fig. 2c) and a large, single posterior groove on the last tooth, which is formed by at least two microstriations. The labial side is too abraded to preserve grooves or striations. The anterior surfaces of the teeth are straight to concave, whereas the posterior sides are long and convex. This way, the tooth points forward and its dorsal tip is located almost at the level of the anterior edge. The anterolingual corner is continued by a slight flange that is better developed than on the labial side.

Four accessory specimens provide information about the details of the dental structure. Two of them can be undoubtedly assigned to the same species because of the similar shape, features, size and quarry.

MACN Pv RN1099a (Fig. 4a–c) is a fragment of lower jaw preserving two additional teeth. The material shows intensive wear on both labial and lingual sides, but this does not mask faint, fine microstriations on the base of the labial side, which form together a large central groove. This situation is the opposite to that of *O. rarus*, in which a large central groove is present on the medial side. The lingual wear, which is more intense, reaches part of the jaw bone ventrally, almost to the beginning of the Meckelian groove; there are no lingual grooves preserved on the tooth surface. Both of the preserved teeth bear anterior flanges on their labial and lingual corners which make the teeth completely square-based. The flanges do not overlap the preceding tooth. The posterior tooth has a deep anterior concavity, which is framed by the anterior flanges. The anterior tooth is basically similar, besides having the tooth tip broken. On the convex, posterior side, there is a vertical groove that constitutes one of the most conspicuous autapomorphic traits of *Kawasphenodon*. This posterior groove is clearly composed of a deep concavity filled with microstriations. The bottom of the Meckelian groove is well preserved and shows a surface pitted by three large foramina.

MACN Pv RN1099b (Fig. 4d–f) consists of a single tooth located over a very abraded piece of a right lower

jaw. Although the jaw bone is broken, it bears well preserved wear facets on both sides. This tooth shows the characteristic square-based structure. A long strip of abraded bone runs along the entire lateral side of the tooth, reaching part of the secondary dentine at its base. On the medial side, the worn region includes only the base of the tooth. Poorly preserved basal grooves, partially filled with dentine overgrowth are present. The *Kawasphenodon* autapomorphic trait, a centered posterior groove, is present on the posterior side of the tooth.

Other sphenodontid remains are MACN Pv RN1099c and MACN Pv RN1100. They could also belong to the same taxon, but MACN Pv RN1099c is too posterior and MACN Pv RN1100 is too small and with more extended flanges. For these reasons, they will be considered here as Sphenodontidae indet.

## 4. Sphenodontidae indet

MACN Pv RN1099c (Fig. 4g–i) is a complete and well-preserved tooth attached to a broken piece of bone. Its sharp profile, eccentric position and slight wear indicate a posterior position. As it is laterally inclined (in both maxillary and dentary posterior fragments, the inclination is always laterally oriented), the wear facet is developed over the inclined lateral surface. This is only possible on a dentary, because a sphenodontid maxillary tooth can only have a medial wear surface; *ergo*, the piece belongs to a right dentary. Its single wear facet does not reach the tip of the tooth. The unworn tip is acute and points forward reaching a level beyond the tooth squared base. The two main lingual grooves are well preserved. One more groove, slightly posterior to the others, is present. Because of its posterior position and its being entirely formed by microstriations in a large groove, it probably represents the posterior groove typical of *Kawasphenodon*. The additional groove is on the postero-lingual side, but much narrower than in MACN Pv RN1099a and b. The lateral side, which shows evidence of at least two strongly worn grooves, is anteriorly extended, forming a large flange.

MACN Pv RN1100 (Fig. 4j–m) is an incomplete right palatine that preserves part of the tuberose facet for the prefrontal bone, but not the notch for the maxillary nerve. The teeth are smaller, wider, less square-shaped and more closely packed than in other specimens, but this can occur in palatine dentition and it is insufficient evidence on which to propose a further taxon. The main shape of the teeth resembles that of *Opisthias* upper dentition in having a single moderately developed posterolabial flange. The three preserved additional teeth are rather conical, with the tip slightly inclined backwards and the posterior faces slightly concave. They decrease in size anteriorly. The posterolabial flange hides the anterior border of the following tooth, as in opisthodontians. The extensive overgrowth of dentine covering the bases of the third to the second tooth resembles the condition in *Priosphenodon*. The absence of a palatine stabbing tooth precludes its assignation to the Sphenodontinae [2,9].

## 5. Conclusions

The phylogenetic position of *Kawasphenodon* is still uncertain. The general morphology of the lower jaw and the clear trend to an edentulous condition resembles that of the clevosaurs and some sapheosaurs (i.e. *Sapheosaurus*). However, the bizarre sapheosaur *Ankylosphenodon* [12] is not edentulous in the adult specimens.

The square-based teeth and the few precise striae resemble opisthodontians [2]. However, *Kawasphenodon* clearly differs from eilenodontines in having few, large additional teeth when compared to jaw height. As in opisthodontians and *Cynosphenodon* [11], teeth are anteriorly inclined, but no extensive lateral flanges are developed. As in *Opisthias* [13], only the slight posterolabial flange breaks the structure of the mostly conical teeth.

Because of the extreme posterior position of the teeth in the jaw, only a single wear facet is present on one additional lower jaw tooth. However, well-developed double wear, typical in sphenodontids, is clearly present in the more fragmentary jaw specimens.

On the other hand, the labial dorsal part of the secondary dentine bears deep marks from maxillary teeth. These wear facets differ from the precise occlusion from facets of non-propalinal sphenodontians in being anteroposteriorly elongated, thus demonstrating relatively long propalinal movements. The region anterior to the additional teeth, where remains of two small hatchling teeth are preserved, is strongly worn with the loss of all teeth.

A remarkable aspect of *Kawasphenodon* is the long extension of the edentulous region in the adult, as occurs in *Clevosaurus*, some *Opisthias* specimens and the edentulous *Sapheosaurus*. Additionally, the 11-cm estimated length of the *Kawasphenodon* lower jaw makes this taxon one of the largest known sphenodontians, comparable to the sapheosaur *Ankylosphenodon*, which also resembles it in the jaw size and robustness.

The littoral nature of the Los Alamitos Formation, with a mixture of marine and terrestrial taxa, plus the possible relationships of *Kawasphenodon* to aquatic sapheosaurs, suggest the possibility of aquatic sphenodontids populating the littoral lagoons that constituted the depositional environment of the Los Alamitos Formation. However, the fragmentary nature of the remains evidences some degree of transport of the bones.

The presence of a large non-eilenodontine propalinal sphenodontid, perhaps a sapheosaur, in Late Campanian outcrops of northern Patagonia, added to the already-reported eilenodontine from the Cenomanian–Turonian of 'La Buitrera', and the extant sphenodontine *Sphenodon* from New Zealand, provide a very complex panorama for the post-Albian sphenodontid diversity in the Southern Hemisphere. Furthermore, new, unpublished remains of a large sphenodontid left maxilla in outcrops of the Campanian Allen Formation (Apesteguía and Rougier, in prep.) provide additional support for the claim that this group survived to form an important component of the Latest Cretaceous southern terrestrial ecosystems.

## Acknowledgements

I am deeply acknowledged to J.F. Bonaparte who allowed me to study the specimens, the National Geographic Society who granted his fieldtrips, Analía M. Forasiepi who found one of the specimens, and Gabriel Lío for the drawings.

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