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A Late Campanian Sphenodontid Maxilla from Northern Patagonia

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ABSTRACT

At the end of the Early Cretaceous the once abundant sphenodontians vanished from the Laurasian record and were thought to have become virtually extinct, with the sole exception of *Sphenodon*, the living tuatara. Recent findings of large and abundant eilenodontine sphenodontids in the Early Late Cretaceous (Cenomanian-Turonian) and fragmentary material from other lineages from Late Campanian outcrops of Patagonia, Argentina, have demonstrated that sphenodontids constituted an important component of the Late Cretaceous terrestrial ecosystems in South America and possibly Gondwana. Although eilenodontine and possibly sphenodontine sphenodontids are present in the Late Cretaceous of Gondwana, they were only part of an unknown southern radiation. We report here on a new sphenodontid, *Lamarquesaurus cabazai*, n. gen. et sp., which is represented by an incomplete right maxilla that represents a previously unknown non-eilenodontine lineage and illustrates the diversity and role of sphenodontians in the tetrapod communities of the Late Mesozoic of South America.

INTRODUCTION

Sphenodontids are today a relictual group of lepidosaurs represented by two species of *Sphenodon* living on a few inaccessible islands off the coast of New Zealand (Daugherty et al., 1990). Until recently, their fossil record was limited to Triassic through Early Cretaceous occurrences (Gilmore, 1909;

Huene, 1910; Simpson, 1926; Cocude-Michel, 1973; Fabre, 1973, 1974; Throckmorton et al., 1981; 1988; Rasmussen and Callison, 1981; Fraser, 1982, 1986, 1988; Carroll, 1985; Whiteside, 1986; Fraser and Benton, 1989; Evans, 1992; Sues and Baird, 1993; Sues et al., 1994; Wu, 1994; Reynoso, 1996, 1997, 2000, 2005). However, the survival and proliferation of sphenodontids into the Late Cretaceous of

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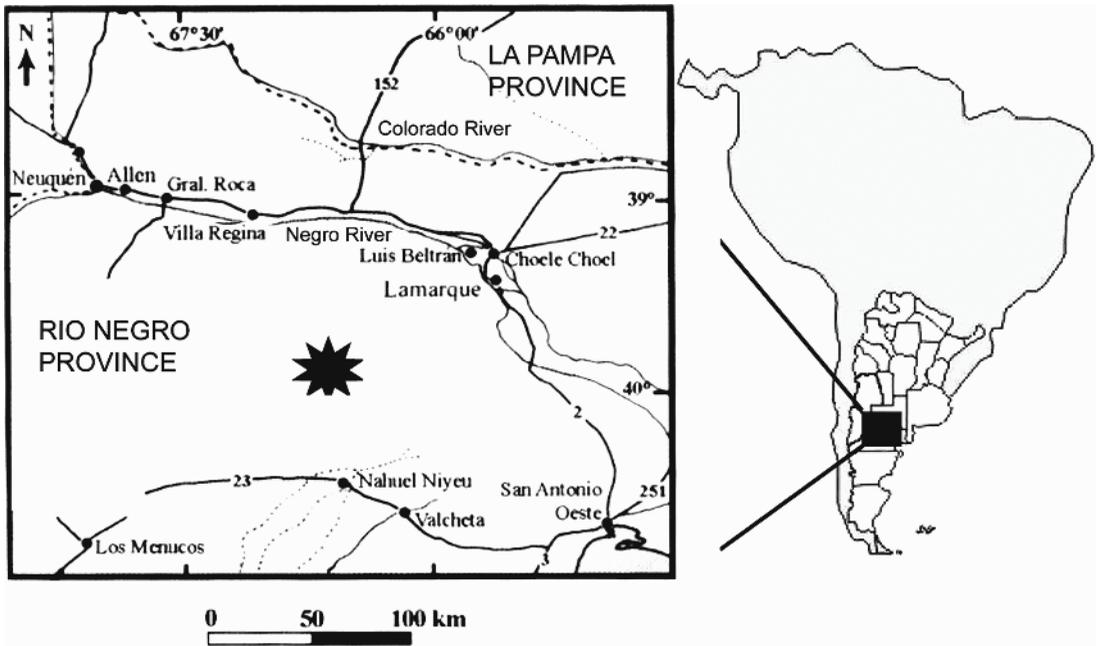


Fig. 1. Map of the Bajo de Santa Rosa area, Río Negro Province, Argentina. The star indicates the fossil quarry (modified from Martinelli and Forasiepi, 2004).

South America has led to a reappraisal of the role played by sphenodontids in terrestrial Mesozoic communities (Novas et al., 1999; Apesteguía and Novas, 2003; Simón and Kellner, 2003). The abundant Cenomanian-Turonian sphenodontids described from the Candeleros Formation at La Buitrera (i.e., *Priosphenodon avelasi*) and El Chocón (i.e., *Kaikaiifilusaurus calvoi*) show the survival of the herbivorous eilenodontines in the early Late Cretaceous. Recent fragmentary findings from the latest Cretaceous described from the Bajo de Santa Rosa (Martinelli and Forasiepi, 2004) and Los Alamitos fossil quarries (i.e., *Kawasphenodon expectatus* Apesteguía, 2005) dramatically improved knowledge of the hidden diversity of Late Cretaceous sphenodontids in Patagonia (fig. 1). However, these latest Cretaceous remains are scarce and their phylogenetic position is far from understood. Additionally, no indisputable remains of sphenodontine sphenodontids (the only group with living relatives) have yet been found in southern continents; they have, however, an

important record in the Jurassic and Early Cretaceous of England (Evans, 1992) and Mexico (e.g., Reynoso, 1996, 1997).

Early in 2003, an expedition led by G.W.R. to Late Campanian outcrops of northern Patagonia resulted in recovery of a rich fauna of microvertebrates that included disarticulated elements of snakes, turtles, dinosaurs, mammals, frogs, and fishes. Among these fossils a right maxilla of a large sphenodontid was recovered. The fossil concentrate collected is still being processed and will likely result in the discovery of additional sphenodontian elements. The new specimen is diagnostic, well preserved, and warrants recognition of a new taxon, which is preliminarily described herein. This maxilla, together with isolated fragments of lower jaws referred as possible sapsheosaurine sphenodontids from other Late Campanian localities (Apesteguía, 2005) and indetermined sphenodontids from the Bajo de Santa Rosa (Martinelli and Forasiepi, 2004), illuminates the poorly known radiation of sphenodontids in the southern hemisphere.

SYSTEMATIC PALEONTOLOGY

LOCALITY AND HORIZON

Fossils were collected in the “Cerro Tortuga” locality, part of the Bajo de Santa Rosa area, about 30 km from the locality of Lamarque, Río Negro. The material was obtained by screenwashing a particularly rich layer of friable yellowish sandstone about mid-level of the Allen Formation (Upper Campanian). The deposits of the Allen Formation comprise siltstones and sandstones that show evidence of an old lacustrine environment with fluvial influence particularly evident in the basal portion of the formation (Casadío, 1994). These fluvial channels contain abundant remnants of freshwater mollusks and terrestrial vertebrates (Hugo and Leanza, 2001b). The Allen Formation forms the early stages of the transgression that flooded northern Patagonia during the Early Maastrichtian (Jagüel and Roca formations), forming the epeiric Kawas Sea (Rocanense Sea). The Kawas Sea occupied more than 500,000 km² (Malumian and Caramés, 1995) and extended as a westward seaway surrounding the archipelago, large islands, and emerged zones of the Somuncurá Massif (Yrigoyen, 1969; Riccardi, 1987). The sea-level change and the subsidence of the Atlantic margin was responsible for the deposition of several, roughly equivalent, littoral or epeiric units including the Allen, Los Alamitos, La Colonia, Angostura Colorada, Loncoche, and Paso del Sapo formations (Wichmann, 1924; Volkheimer, 1973; Uliana and Dellapé, 1981; Andreis, 1987; Andreis et al., 1990; Hugo and Leanza, 2001a). These sediments were generally named since the beginning of the 20th Century as the “Lacustrine Senonian” and bear the bulk of the known latest Cretaceous microvertebrates in South America.

SYSTEMATICS

Lamarquesaurus cabazai, n. gen et sp.

Lepidosauria Haeckel, 1866.
Sphenodontia Williston, 1925.

HOLOTYPE: MML-PV-42. Right maxilla preserving 10 teeth with different degrees of completeness. The fossil material is three-dimensional and tooth enamel and wear facets are well preserved.

ETYMOLOGY: *Lamarque* after the city of Lamarque in Rio Negro province and its inhabitants, who have strongly supported paleontological exploration of northern Patagonia for decades; *saurus*, Greek for “reptile”; and Cabaza, after Tito Cabaza, amateur paleontologist who discovered the Cerro Tortuga locality and called the attention of professional paleontologists to the region.

LOCALITY AND HORIZON: Lower to middle part of Allen Formation, ca. 6 m from the base levels of exposures at the “Cerro Tortuga” locality (39°26′50″S, 67°19′20″W) and ca. 52 m below the K/T (Cretaceous-Tertiary) boundary, recognized in the overlying Jagüel Formation (Gasparini et al., 2003; Casadío, personal commun.) The fossiliferous layer is 60–65 cm thick and is composed of clean, yellowish to light brown, friable medium sandstone. The layer yields a rich collection of disarticulated fossils with a clear bias to small specimens; fish and snake remains are particularly abundant.

DIAGNOSIS: Sphenodontid with the following combination of features: additional teeth separated by wide spaces; strongly concave maxilla; anterolingual flanges and shallow lateral ridges in maxillary teeth; labial border splits in two portions (fig. 2, sdf); antorbital region of the labial border deeply furrowed (fig. 2, rar); and deep concavities in the maxillary dentina over the third and fifth tooth positions (the last three characters are possibly uniquely derived features).

DESCRIPTION: The preserved part of the maxilla of *Lamarquesaurus* is 36 mm long and about 15 mm tall. The complete length is estimated at 45 mm. The ascending and premaxillary processes are broken. It is evident, however, that the former was wide with respect to the total length of the maxilla (fig. 2A) and that the latter was short. The jugal process is tall and not forked. In medial view (fig. 2B), the maxilla is deeply concave, and part of the jugal facet is preserved.

The infraorbital region shows two conspicuous foramina. The first is located right under

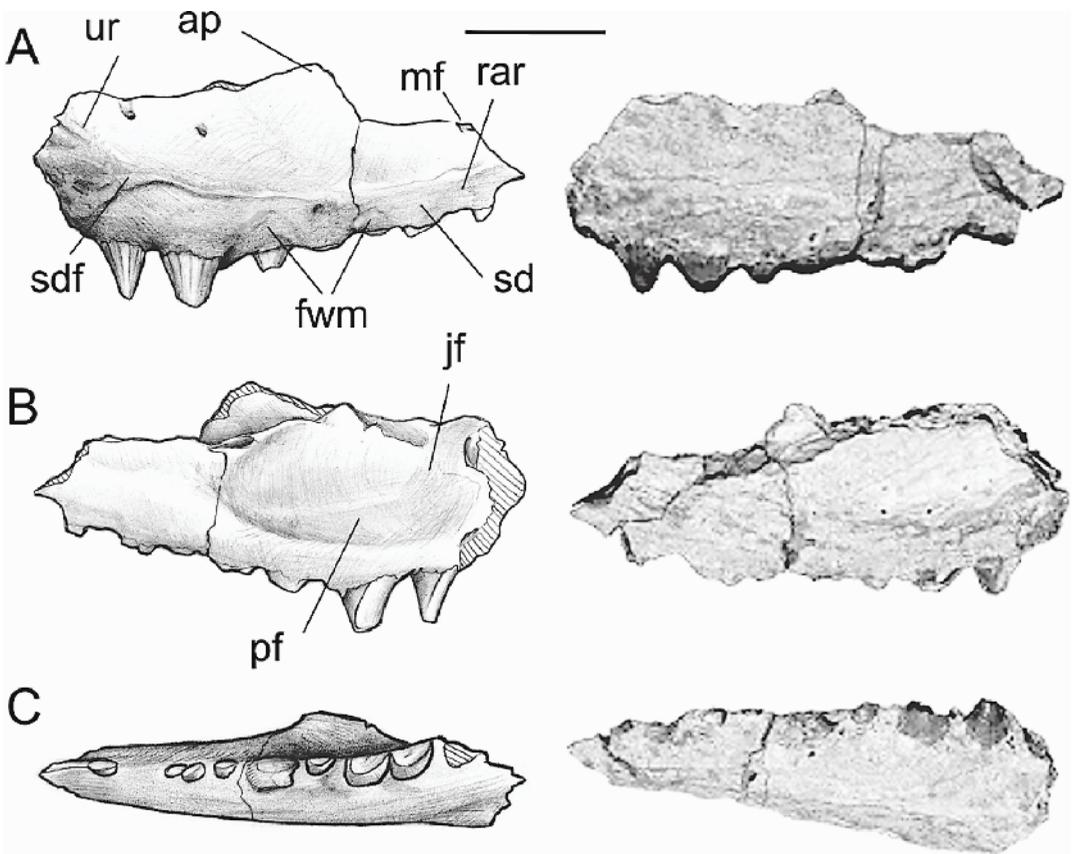


Fig. 2. MML-PV-42. Drawings (left) and pictures (right) of the right maxilla in **A**, lateral view; **B**, medial view; **C**, occlusal view. Abbreviations: ap, ascendent process; fwm, false wear marks; jf, jugal facet; mf, maxillary foramen; pf, palatine facet; rar, rugose anterior region; sd, secondary dentine; sdf, secondary dentine fork point; ur, upper ridge; Scale bar: 10 mm.

the end of the ascending process, and the second is under the mid-length of the orbit, probably reflecting the piercing of the cutaneous branches of the maxillary artery and the maxillary branch of the V (trigeminal) cranial nerve (Oelrich, 1956). Part of the maxillary foramen is present in the broken cranial border. The foramen is visible as a small notch, but the section also shows part of the canal. In lateral view, the ventral edge bears a strong, 5-mm-tall border (fig. 2, sd), dorsally limited by a ridge, whose profuse ornamentation suggest muscle attachments. The ridge splits at the level of the beginning of the orbit. One ridge follows the horizontal, slightly upwardly bent original orientation, while the other runs downward to reach the last pre-

served tooth, as in the eilenodontine *Priosphenodon* (Apesteguía and Novas, 2003).

Toward the cranial region, on the dentine border and over the positions of the third and fifth additionals, there are deep cavities that resemble the common wear marks that sphenodontids with precision bite have in the lower jaw. However, as this is not possible in a maxilla, they are considered here as cavities with unknown function.

Additional teeth are conical in shape, with labial vertical ridges and posterolingual flanges, as in *Tingitana annoulae* (Evans and Sigogneau-Russell, 1997). The additional teeth bear strong medial wear facets that were produced by propalinal movements of the lower jaw. Additional teeth are separated by

wide spaces; probably no more than one or two teeth are missing posteriorly. Although small teeth are present in the antorbital region, they are more probably abraded additional than actual hatchling teeth. A slightly larger tooth is occupying the anteriormost preserved tooth position, so there is no clear evidence to consider it as a successional tooth.

DISCUSSION

The maxilla of *Lamarquesaurus* is one of the few described for latest Cretaceous sphenodontids; the relative paucity of sphenodontids in the Cretaceous of South America is probably more artifactual than real, as evidenced by the recent description of other fragmentary remains from the Los Alamitos and the Bajo de Santa Rosa quarries (Martinelli and Forasiepi, 2004; Apesteguía, 2005). Actually, careful inspection of the concentrate collected in Los Alamitos and housed at the Museo Argentino de Ciencias Naturales "B. Rivadavia" revealed the presence of sphenodontid remains misidentified as siluriform fin elements. It is likely that sphenodontid remains are present in the Mesozoic collections of microvertebrates, but they remain largely unrecognized.

Sphenodontids from Los Alamitos, represented mostly by fragmentary jaws and palatines, probably belong to marine sapsaurines (Apesteguía, 2005), a sphenodontian group previously known from Late Jurassic to Early Cretaceous rocks of France (Cocude Michel, 1973) and Mexico (Reynoso, 2000). Differing from the materials from Mexico, which bear a unique ankylotheodont dentition, the materials from Los Alamitos show the same trend to tooth loss present in most aged sphenodontians but developed to an extreme in the sapsaurines (Cocude Michel, 1973).

The peculiar "wear marks" of *Lamarquesaurus* are difficult to explain in a maxilla. Sphenodontids show wear marks only on the lower jaw teeth, because the dentaries are enclosed between the maxillary and palatine tooth rows when the jaw is closed. Those species with a poorly developed propalinity and a strong precision bite show their wear marks in the lower jaw (fig. 3). We have no

functional explanation for wear-like marks in the maxilla; despite their appearance, perhaps they are not wear marks, just concavities not caused by tooth-on-tooth wear.

The relationships between *Lamarquesaurus cabazai* and other sphenodontids are uncertain, mostly due to the fragmentary nature of the specimen. Our new species resembles *Clevosaurus* (Fraser, 1988) in the rounded shape of the teeth, although with much more moderate flanges and striae, just as in *Sphenodon*. It differs from *Kawasphenodon* in the absence of the peculiar deep and single groove on the posterior side of additional teeth that clearly diagnoses the Los Alamitos taxon. However, no maxilla were preserved. Additionally, the rounded teeth of *Lamarquesaurus* differ from the squared or wide teeth characteristic of opisthodontian lineages and also *Kawasphenodon*, which, besides its peculiarities, could also be considered as a rare opisthodontian.

Although the first tooth is wide at its base and slightly more massive than the other, it is not a clear successional one to allow the inclusion of *Lamarquesaurus* into Sphenodontine. However, the general tooth shape resembles the extant *Sphenodon*, providing evidence of a hitherto unknown lineage of sphenodontids in South America probably allied to the Sphenodontine.

CONCLUSIONS

The finding of remains of a new Late Campanian non-eilenodontine sphenodontid in northern Patagonia shows that rhynchocephalians were, as a group, healthy and diverse in South America at least until the very end of the Mesozoic. The phylogenetic position of *Lamarquesaurus* is uncertain, but this find provides evidence of a hitherto unknown lineage of sphenodontids in South America. Although *Lamarquesaurus* is not an eilenodontine because of its low degree of teeth packaging, it could easily be part of an unknown radiation of basal opisthodontians, related to *Opisthias* itself, as suggested by the close similarity with the maxillary teeth of *Opisthias rarus*, or probably allied to the extant *Sphenodon*. In any case, it resembles the morphology of the crown group eupro-

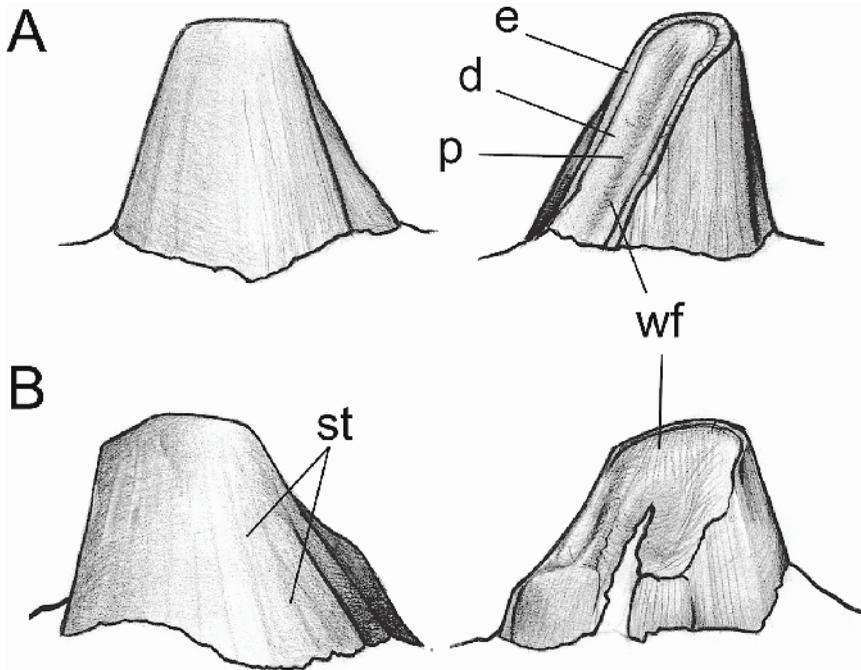


Fig. 3. MML-PV-42. Detail of the ninth (A) and eighth (B) teeth in labial and lingual views showing the wearing marks. Abbreviations: e, enamel; d, dentine; p, pulp; st, striae; wf, wear facet.

palinal sphenodontids (sphenodontines + opisthodontians).

The presence of non-eleiodontine sphenodontids in the Allen Formation (Martinelli and Forasiepi, 2004) and in the approximately coeval Los Alamos Formation (Apesteguía, 2005) points to a relatively wide geographical and stratigraphical distribution of this group during the Late Cretaceous. Furthermore, the large size attained by this specimen shows that they were substantially different from most known non-eleiodontine sphenodontids, of which *Sphenodon* constitutes a proportionately large species. In this regard, *Lamarquesaurus cabazai* resembles the large sphenodontids *Priosphenodon avelasi* (Apesteguía and Novas, 2003), from “La Buitrera”, and *Kawasphenodon*, the “Los Alamos” sphenodontid (Apesteguía, 2005), with skull sizes exceeding 10 cm in both cases.

Sphenodontian lepidosaurs disappeared from most of the world during the Early Cretaceous (Evans, 1992) and were likely replaced by squamates (Carroll, 1988). However, they remained as an important

faunal component in the Late Cretaceous ecosystems of at least South America, showing a moderate taxonomic and ecological diversity, and perhaps extending along all Greater Gondwana (Apesteguía, 2002) including New Zealand, where fragmentary jaws were collected in Miocene sediments (Worthy et al., 1999). There are no records of sphenodontians in the South American Cenozoic, because their disappearance is likely related to the two cardinal Late Cretaceous events: the North America–South America connection, which occurred by the end of the Cretaceous, and the K/T extinction event.

By the latest Cretaceous, several lineages of dinosaurs with a more cosmopolitan or Holarctic distribution entered South America from North America. Other tetrapods also entered with dinosaurs, such as lizards and mammals (Bonaparte, 1986). However, the native assemblages, including the archaic Gondwanan mammals, remained as important components of the mammalian assemblages until at least Paleocene times (Rougier et al., 2000; Gelfo and Pascual, 2001; Rougier

et al., 2003; Rougier and Apesteguía, 2004). It is possible that sphenodontians followed the same fate, especially because the arrival of terrestrial squamates (the aquatic mosasaurs and the snakes are known earlier in the Cretaceous), considered a crucial extinction factor in other places (Carroll, 1988), is not documented until the Paleocene (Baez and Gasparini, 1977; Estes and Báez, 1985). In fact, there is no unambiguous evidence of lizards of Laurasian affinities in South America during the latest Cretaceous. Furthermore, there is clear evidence of Early Cretaceous South American lizards in Brazil (Evans and Yabumoto, 1998), and even pre-Campanian lizards coexisting with successful sphenodontians (e.g., Apesteguía et al., 2005).

The K/T extinction certainly affected the South American faunas. However, there seems to be a difference in the severity and timing of the extinctions for different archaic components of the South American biota (Rougier et al., 2003). For example, in the Paleocene locality of Punta Peligro (Salamanca Fm.), at least three Mesozoic mammalian lineages are still present, although they are unknown in the overlying Upper Paleocene Rio Chico Fm.: they are gondawanatheres, mesungulatid/reigitheriid dryolestoids, and monotremes (Pascual et al. 1999, 2001; Rougier et al., 2000, 2002, 2003; Gelfo et al., 2001). The first two groups have an important Mesozoic South American–Gondwanan record. The monotreme Mesozoic record, however, is limited to the Early Cretaceous of Australia (Archer et al., 1985; Rich et al., 2001, 2002, 2004). Other archaic mammalian lineages, such as the Dryolestidae and the Ferugliotheriidae, are not known to extend across the K/T boundary. The driving factors behind the remodeling of the South America fauna during the latest Cretaceous–Early Paleocene are therefore yet unclear, but the drastic change in slope of the southern end of the continent with the establishment of an Atlantic regime (Casamiquela, 1978; Legarreta and Uliana, 1991), the widespread occurrence of epeiric seas (Vergani et al., 1995), and the extraterrestrial perturbances produced by an extraterrestrial event (Álvarez et al., 1980) may all be factors.

The Sphenodontids of the New Zealand archipelago are certainly relictual; that is, they are not only relicts of a once widespread cosmopolitan group, they are truly canopic jars of a Mesozoic radiation now just beginning to be recorded in South America. Considering the increasing record of the group and the archaic nature of some of the faunal elements in the Peligran Paleocene, it is possible that sphenodontines found refuge in Australasia with other taxa (e.g., mammals) during the Early Tertiary. Considering paleogeography, present distribution, and fossil faunal links for the Late Cretaceous–Early Paleocene (Bonaparte, 1986; Pascual et al., 1997; Sampson et al., 2001; Sereno et al., 2004), it is likely that sphenodontines had a more widespread distribution. Australasia, Antarctica, and India are prime candidates to share some of the peculiar taxa presently being discovered in South America.

Although Late Cretaceous Gondwanan sphenodontids belong to advanced eupropalinal lineages (Apesteguía and Novas, 2003), and the apparent precision bite wear marks in the *Lamarquesaurus* maxilla are uncertain, considered altogether the sphenodontid fossil record evidences an important diversity of forms. The presence of sphenodontids themselves is likely to be one more example of the survival of archaic lineages in southern continents (e.g., monotremes and dryolestoid mammals, meiolaniid turtles, lungfishes, pipoid frogs) that survived there long after these groups had disappeared from other land masses after being exposed to interactions with Holartic faunas.

In any event, the arrival of terrestrial lizards and the possible replacement of sphenodontids by lizards are delayed in South America with regard to other continents. The early establishment of an insular regime for New Zealand, which was sporadically separated from Australia by shallow seas at least since the early Cretaceous (Scotese et al., 1999; Vrielynck and Bouysse, 2003; Scotese, 2004), may be another factor that facilitated the survival of sphenodontians. *Sphenodon* is not a forgotten relic on an island but a very advanced eupropalinal taxon with a redeveloped lower bar and important adaptations for living under low-temperature conditions.

Furthermore, sphenodontids remained healthy in New Zealand until approximately the arrival of humans.

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