

Research



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The youngest South American rhynchocephalian, a survivor of the K/Pg extinction

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Rhynchocephalian lepidosaurs, though once widespread worldwide, are represented today only by the tuatara (*Sphenodon*) of New Zealand. After their apparent early Cretaceous extinction in Laurasia, they survived in southern continents. In South America, they are represented by different lineages of Late Cretaceous eupropalinal forms until their disappearance by the Cretaceous/Palaeogene (K/Pg) boundary. We describe here the only unambiguous Palaeogene rhynchocephalian from South America; this new taxon is a younger species of the otherwise Late Cretaceous genus *Kawasphenodon*. Phylogenetic analysis confirms the allocation of the genus to the clade Opisthodontia. The new form from the Palaeogene of Central Patagonia is much smaller than *Kawasphenodon expectatus* from the Late Cretaceous of Northern Patagonia. The new species shows that at least one group of rhynchocephalians not related to the extant *Sphenodon* survived in South America beyond the K/Pg extinction event. Furthermore, it adds to other trans-K/Pg ectotherm tetrapod taxa, suggesting that the end-Cretaceous extinction affected Patagonia more benignly than the Laurasian landmasses.

1. Introduction

Rhynchocephalia, a clade of lepidosaurs solely represented today by the genus *Sphenodon*, survived in southern continents much beyond their extinction in Laurasia (e.g. [1,2]), where the diversification of lizards and competition has been proposed to have driven them to near extinction after the Early Cretaceous [3]. The Late Cretaceous survivors of the clade comprised a diversified group of derived forms with advanced pro-oral jaw motion, mainly restricted to southern continents, which confronted a second extinction event at the Cretaceous/Palaeogene (K/Pg) boundary [4].

In South America, the record of Late Cretaceous rhynchocephalians was substantially increased with the discovery of an unexpected abundance of eupropalinal forms belonging to different lineages. On one hand, the eilenodontine radiation was recognized for Cenomanian–Coniacian times both in northern and central Patagonia (e.g. [1,5,6]). On the other hand, other lineages, sphenodontines and non-eilenodontine opisthodontians appeared in rocks belonging to the Campanian–Maastrichtian stage, both in the Allen and Los Alamos formations (e.g. [2,4,7]). All this material supports the claim that rhynchocephalians survived in South America at least until the very end of the Cretaceous.

New remains belonging to a rhynchocephalian from Lower Tertiary rocks of Chubut Province, central Patagonia, Argentina, provide evidence that at least one group of rhynchocephalians not related to the extant *Sphenodon*, but with deep roots in the Mesozoic radiation of sphenodontians survived in South America beyond the K/Pg extinction event.

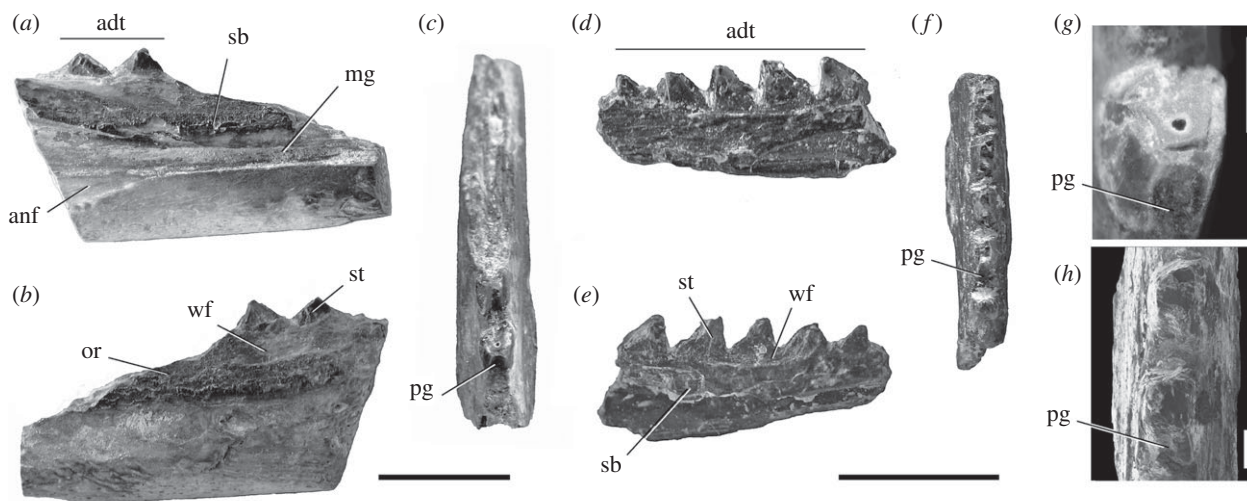


Figure 1. *Kawasphenodon peligrensis* sp. nov. (a–c) Holotype MPEF PV 1989. Left lower jaw in lingual (a), labial (b) and occlusal (c) views. (d–f) Paratype MPEF PV 1990. Right lower jaw in lingual (d), labial (e) and occlusal (f) views. (g) Close-up of additional tooth in occlusal view of MPEF PV 1989. (h) Close-up of additional tooth in occlusal view of MPEF PV 1990. adt, additional teeth; anf, angular facet; mg, meckelian groove; or, ornamentation; pg, posterior groove; sb, secondary bone; st, striae; wf, wear facet. Scale bars: (a–c,d–f) 5 mm; (g,h) 1 mm.

2. Systematic palaeontology

Rhynchocephalia [8]
 Opisthodontia [1]
 Genus *Kawasphenodon* [9]
 Type species: *K. expectatus* [9]

(a) Emended diagnosis

Kawasphenodon differs from other rhynchocephalians in the following unique traits (see the electronic supplementary material): groove on the posterior side of additional teeth (ch. 72:2, synapomorphy); medial ridge on the anterior side of additional teeth (a putative synapomorphy). Additionally, it differs from all other opisthodontians in the presence of deep labial wear marks on the secondary bone (about one and a half tooth lengths) on the posterior half of the dentary (longer than in *Opisthias* and shorter than in eilenodontines).

Kawasphenodon peligrensis sp. nov.

(b) Etymology

The species name is after the locality where the specimens were found, Punta Peligro, Chubut Province, Argentina.

(c) Material

Museo Palaeontológico Egidio Feruglio (MPEF) PV 1989 (holotype, figure 1) consists of an incomplete left lower jaw preserving two teeth.

MPEF PV 1990 (paratype, figure 1) consists of an incomplete right lower jaw preserving four teeth.

(d) Type locality and horizon

Punta Peligro locality, nearly 27 km north of Comodoro Rivadavia, Chubut province, Argentina (see the electronic supplementary material). ‘Banco Negro Inferior’ (BNI), Upper part of the Hansen Member of the Salamanca Formation [10], Peligran South American Land Mammal Age [11], early Palaeocene [12–14].

(e) Differential diagnosis

Kawasphenodon peligrensis differs from the only known other species of the genus, *Kawasphenodon expectatus*, and from all other rhynchocephalians in the following unique combination of features: small size (about one-third the size of *K. expectatus*), a straight ventral dentary border (vs. curved in *K. expectatus*), region ventral to the Meckelian groove deep throughout (vs. strongly tapering anteriorly in *K. expectatus*), sculptured secondary bone on the dentary surface (vs. smooth surface in *K. expectatus*), the presence of at least five additional teeth on the jaw (vs. maximum four in *K. expectatus*), additional dentition present at the level of the anterior tip of the angular facet (vs. additionals well posterior to this level in *K. expectatus*) and additional teeth posterior fossa devoided of ridges (vs. ridged in *K. expectatus*).

3. Description

The holotype (MPEF PV 1989) preserves the mid to posterior part of the dentary of a young adult rhynchocephalian, lacking both symphyseal and coronoid regions (figure 1). The jaw is relatively high posteriorly, in particular close to the coronoid region. The anterior half is incomplete, lacking the tooth-bearing portion. The complete jaw would have been about 38 mm if using *Sphenodon* as a model; thus being much smaller than the dentary of the adult *K. expectatus* specimen (around 110 mm in length) and with its ventral margin clearly not curved as in the latter ([9]; see the electronic supplementary material). Both sides of the jaw are rather vertical, the labial side being only slightly laterally convex. The lower half of the labial side bears oblique striae and foramina related to the attachment of skin. Particularly, two conspicuous foramina suggest that the specimen, despite its high number of additionals, might represent a young adult (see [6]: fig. 3M). The ventral surface, as in other opisthodontians, bears long and conspicuous oblique striae.

The ventral half is separated from the upper one by a strong shelf of unworn secondary bone, less than one-fifth of the jaw in height, similar in texture to that present in the maxilla of *Lamarquesaurus* [4]. The secondary bone of

the shelf is dorsally limited by three long, shallow, curved marks made by the upper dentition (figure 1; see the electronic supplementary material). These marks overlap each other, suggesting a moderate pro-oral movement of the jaw, each mark involving an approximate length of about two teeth, an extension that is longer than in *Opisthias* but shorter than in eilenodontines, in which the wearing is continuous. The upper part of the dentary shows a smooth surface formed by a thick layer of secondary bone that frames and covers the base of the teeth.

The preserved region of the dentary shows the anterior end of the angular facet on the lingual side. The anterior end of the angular facet is at the level of the anteriormost preserved tooth. No part of the coronoid or prearticular regions is preserved. The Meckelian groove is deep, narrowing slightly anteriorly. The ventral region of the jaw under the Meckelian groove is robust and well defined, and it is as high as the dorsal region, a proportion that remains constant along the whole preserved section of the jaw. Whereas the ventral margin of the Meckelian groove is clearly curved in *K. expectatus*, it is straight in *K. peligrensis*.

The complete tooth count is unknown, as only two contiguous additional teeth are preserved. These are only slightly separated; hence, the bases of the teeth are almost in contact, but without overlapping labial or lingual flanges.

The teeth are moderately large, similar in size to the mid-posterior additional teeth of most rhynchocephalians (e.g. *Sphenodon*, *Opisthias*, *Cynosphenodon* and *Kallimodon*), square-based, slightly compressed labiolingually and roughly triangular in lateral view. The lingual side bears two deep, wide grooves. The labial side of the teeth also seems striated by fine and abundant grooves, but its preservation does not allow the description of details. The anterior side of the anteriormost tooth, though badly preserved, shows a straight to concave surface divided by a medial ridge, whereas the posterior side is convex. The tooth points up and forward, but the tip is not preserved well enough to say if it was located at or beyond the level of the anteriormost end of the tooth base. Anterolabial and anterolingual flanges are slightly different from each other, the latter being better developed. The posterior sides of the additional teeth bear a deep, wide, single groove devoid of ridges, which was previously proposed as autapomorphy of *K. expectatus* [9]. The size and morphology of the preserved teeth indicate that they are mid to posterior additional teeth. Furthermore, their position posterior to the anterior tip of the angular facet also supports this interpretation, as mid-posterior additional teeth are those posterior to this level, at least, in eupropalinal rhynchocephalians (e.g. *Sphenodon*, opisthodontians).

The paratype (MPEF PV 1990) is an incomplete right dentary of an individual of approximately the same ontogenetic stage of the holotype, which preserves the mid part of the bone and lacks the ventral border. As in the paratype, the ventral border is lacking, there are no preserved mental foramina. The complete jaw might have been 41 mm in length. Both sides of the jaw are rather vertical.

The lateral aspect of the jaw shows a strengthened area by the positive border of secondary bone, a feature common in most rhynchocephalians (e.g. *Cynosphenodon*, *Sphenodon*, *Priosphenodon* and *Clevosaurus*). At the base of teeth and over the shelf of secondary bone, there are oblique marks made by the maxillary teeth. The first preserved tooth bears a single wear facet, but the following three teeth share a

long, curved facet centred in the third jaw tooth. The last tooth also has its own facet, probably shared with more posterior unpreserved teeth. The medial side is better preserved showing a profusely ornamented bone surface. The upper part of the dentary shows the smooth surface of secondary dentine covering tooth bases. Right at the base of the teeth, a long, continuous mark evidences the wear against the palatine teeth, as in other eupropalinal forms.

The five preserved teeth are mid to posterior additional teeth. They are square-based, slightly compressed labiolingually, triangular and flanged, being the last two preserved teeth particularly similar to those of the holotype. In lateral view, the posterior margin of the teeth is straight to slightly convex, whereas the anterior one is slightly concave or almost vertical. The tip is only preserved in the third and fifth tooth; it points up and forward and does not seem to reach the anteriormost level of the tooth base. The anterolabial flange is better developed than the lingual one. The second, third and fourth teeth are striated on their labial sides, whereas only the third tooth is also striated on the lingual side. In all the observable cases, the striae are arranged in two large, vertical grooves framing a central column of enamel, plus a few shorter and shallower grooves towards anterior and posterior margins.

A medial ridge is present on the concave anterior surface of the second and third teeth. It must be noted that a similar ridge is also evident on the anterior side of the teeth in the specimen MACN PV 1099a of *K. expectatus*, as well as on the posterior groove (S. Apesteguía and R. O. Gómez 2013, personal observation). This latter ridge is absent on the posterior groove of *K. peligrensis*. This deep, wide, groove devoid of ridges on the widely convex posterior side of the teeth was previously proposed as autapomorphic for *K. expectatus*. The posterior groove is present in all the preserved teeth of the paratype, but less clear in the first one. Towards the posterior end of the tooth line, the groove is located more medially than in the more anterior preserved teeth.

Despite this, the bone gives no data about the part of the jaw being represented, the morphology of the teeth suggests that it is approximately similar or slightly anterior to the dentary region preserved in the holotype.

4. Discussion

Kawasphenodon peligrensis can be considered as a derived rhynchocephalian, based on the combined presence of acrodont teeth, a secondary bone skirt and a pro-oral jaw motion as inferred by the wear pattern on the teeth and dentary surfaces ([2,15], figure 1). It closely resembles *K. expectatus*, from the Upper Cretaceous Los Alamitos Formation of Patagonia, in the general shape of the additional dentition, as well as in some details of the tooth morphology. This includes the presence of an anterior median ridge and a posterior groove (figure 1), which appears to be unique among rhynchocephalians [9].

The maximum preserved count of five mid to posterior additional teeth in *K. peligrensis* makes this species different from *K. expectatus*, but the total tooth count is unknown in both cases. Furthermore, while in *K. expectatus* all preserved additional teeth are well posterior to the anterior limit of the angular bone, in *K. peligrensis* there are additional teeth at this same limit and perhaps even anterior to this level.

In addition to the striking difference in size (figure 2; see the electronic supplementary material), *K. peligrensis* differs

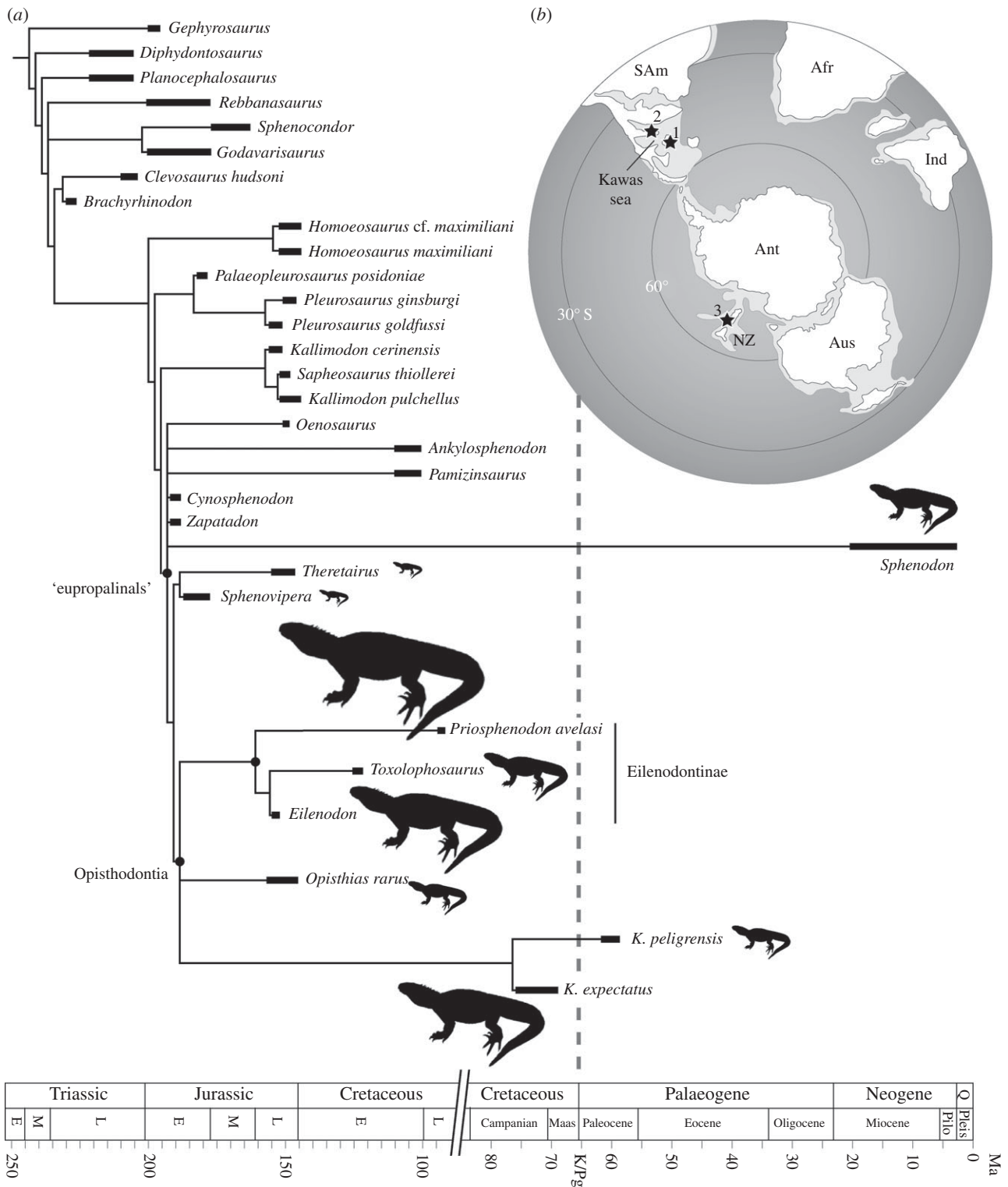


Figure 2. (a) Time-tree of rhynchocephalians based on the strict consensus of 22 most parsimonious trees obtained in the phylogenetic analysis, in which the K/Pg boundary is indicated by a dotted line and black silhouettes indicate the relative size of opisthodontian species and a few other eupropalinal rhynchocephalians (see the electronic supplementary material). (b) Palaeogeographic map of the Late Cretaceous (70 Ma; modified from [16]) showing the record of *Kawasphenodon* (1, *K. peligrensis*; 2, *K. expectatus*) and the other certain post-Cretaceous fossil rhynchocephalians (3, *Sphenodon* or *Sphenodon*-like records from the Miocene and Quaternary of New Zealand [15]). Afr, Africa; Ant, Antarctica; Aus, Australia; Ind, India; NZ, New Zealand; SAm, South America; E, Early; L, Lower; M, Middle; Maas, Maastrichtian; Plio, Pliocene; Pleis, Pleistocene; Q, Quaternary.

from *K. expectatus* in the following features, justifying the recognition of a new taxon: (i) a straighter jaw, (ii) the degree of ornamentation of the dentary surface, (iii) a deep region ventral to the Meckelian groove throughout the preserved length, and (iv) a higher count of additionals. Furthermore, although the angular facet is not preserved in the paratype, it is inferred that the tooth row extended anteriorly beyond the anterior tip of the angular facet.

In rhynchocephalians, the number of additionals increases with age and are added to the tooth row from the rear of the dentary [17]; hence, the higher count of additionals in *K. peligrensis*, which is about one-third the size of *K. expectatus*, is clear evidence that the former constitutes a distinct species and is not a juvenile form of the latter.

In order to assess the evolutionary relationships of *K. peligrensis*, we performed a cladistic analysis in TNT v. 1.1

[18] using a modified version of a recently published data matrix of rhynchocephalians ([19]; see the electronic supplementary material). The analysis yielded 22 most parsimonious trees of 218 steps, in all of which *K. peligrensis* is placed as the sister taxon of *K. expectatus* (as shown in the strict consensus depicted in figure 2) mainly based on the shared presence of a posterior fossa on the additional teeth, which has been previously considered 'one of the most conspicuous autapomorphic traits of *Kawasphenodon*' [9]. In agreement with previous hypotheses [4,19], *Kawasphenodon* as a whole is related to opisthodontians, recovered in a polytomy with *Opisthias* and eilenodontines (figure 2).

Opisthodontians, including *Kawasphenodon*, share the presence of additional teeth that are square to transversely rectangular in cross section and moderately to tightly packed in the jaw, moving in a pro-oral fashion. This kind of dentition has been associated with a grinding and shredding mode of food reduction in rhynchocephalians [20] and, coupled with a large body size, to an herbivorous diet in eilenodontines [1,21]. Although *Opisthias* has been regarded as a generalized form [21], its tooth morphology indicates some capability of plant material processing (S. Apesteguía 2008, unpublished PhD thesis (<http://sedici.unlp.edu.ar/handle/10915/4405>)) [20], as might also be the case in *Kawasphenodon*. In this regard, a deep dentary, as seen in *Kawasphenodon*, has also been linked with herbivory in eilenodontines [21]. As species of *Kawasphenodon* lack the specialized dentition seen in eilenodontines, their dietary habits were more likely omnivorous.

It is noteworthy that *K. peligrensis* is markedly smaller than many of their close relatives. In order to test whether *K. peligrensis* constitutes a case of dwarfism within Opisthodontia, as was also proposed for the eilenodontine *Priosphenodon minimus* [6], the estimated body size (see the electronic supplementary material) was optimized as a continuous character in the Rhynchocephalian phylogeny in MESQUITE [22]. Results indicate that both the small size of *K. peligrensis* and the gigantism of *K. expectatus* are apomorphic with respect to a plesiomorphic mid-size condition in opisthodontians. However, the size reached by *K. peligrensis* is not markedly smaller than that optimized for the opisthodontian ancestor. Therefore, the reduction in size in the lineage of *K. peligrensis* does not require further explanation.

The discovery of *K. peligrensis* reinforces the idea that opisthodontians, whose global record dates back to the Late Jurassic, constituted a successful lineage that survived in Patagonia (e.g. [1,9]) when most other rhynchocephalian lineages apparently became extinct in other parts of the world (e.g. [23]). Augé & Rage [24] reported a possible

rhynchocephalian for the Palaeocene of Morocco, but the specimen is too fragmentary to make a confident identification. The discovery of rhynchocephalians in the Palaeocene of Patagonia adds them to a list of taxa probably well adapted to warm climates, such as large 'madtsoiid' snakes and terrestrial sebecid crocodyliforms, which endured in Patagonia until the global cooling event at the Eocene–Oligocene boundary [25]. South American rhynchocephalians would finally become extinct with other vertebrates at the 'Patagonian Hinge' [26]. The presence of *Kawasphenodon* above the K/Pg boundary indicates that at least two separate lineages of euprobalinal rhynchocephalians survived the end-Cretaceous mass extinction event in southern continents; one represented by the lineage leading to the present-day *Sphenodon*, the other including opisthodontians. *Kawasphenodon* adds to the wide array of ectotherm tetrapod lineages crossing the K/Pg boundary in Patagonia. They include calyptrocephalellid and pipid frogs [27,28], 'madtsoiid' snakes [29] and meiolaniform and chelid turtles [30,31].

It is remarkable that most of the mentioned ectotherm tetrapods of the BNI at Punta Peligro, survived the K/Pg extinction event in Patagonia relatively unscathed and, in some cases, made up conspicuous components of the Peligran fauna [11], as also did some endotherms like gondwanathere, meridiolestoid and monotreme mammals [13,32–34] (N. Páez Arango 2008, unpublished Ms thesis). This agrees with the global pattern previously noticed for ectotherms by Macleod *et al.* ([35]; but see [36] for a different pattern in North American squamates). This scenario markedly contrasts with the dramatic extinction at the K/Pg boundary exhibited by most Mesozoic lineages of endotherms (many mammals and dinosaurs) worldwide [35,37,38]. In this context, the presence of opisthodontian rhynchocephalians along with other typical Mesozoic taxa across the K/Pg boundary suggests [39,40] that Patagonia was affected less severely than Laurasian landmasses by the end-Cretaceous extinction [41].

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Data accessibility. All datasets are deposited in <http://datadryad.org/> and <http://morphobank.org/>.

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